Colombia, in all predation events described here the possessor tolerated the proximity of conspecifics; this created opportunities for food transfer, either direct and tolerated or, more often, through scrounging. Food transfer in this group was also registered in bird predation events, and scrounging was also the most common type of transfer (Ferreira *et al.*, 2002).

In a review of the genus by Freese and Oppenheimer (1981), vertebrate prey listed included only lizards, birds and rodents in the diet of *C. capucinus*, and frogs in the diet of *C. apella*. While John Oppenheimer was the pioneer in studies of this genus in the wild (*C. capucinus* in particular), this diet list reflected the paucity of information available at the time. As new field studies are conducted, our understanding of the diversity of prey taken by tufted capuchins, and the dynamics of food transfer among them, will continue to improve.

Acknowledgements: We thank the staff of the Tietê Ecological Park for their support, and also Michele Verderane and Guilherme Imura, who helped in the description of the predation on the infant opossum. This work was funded by a grant from the Fundação de Amparo à Pesquisa do Estado de São Paulo – FAPESP (São Paulo State Research Support Foundation) (Process 99/11573-2).

Briseida D. Resende, **Vivian L. G. Greco**, **Eduardo B. Ottoni** and **Patrícia Izar**, Departamento de Psicologia Experimental, Instituto de Psicologia, Universidade de São Paulo, Avenida Prof. Mello Moraes 1721, São Paulo 05508-030, São Paulo, Brazil. E-mail: <briseida@usp.br>.

References

Ferreira, R. G., Resende, B. D., Mannu, M., Ottoni, E. B. and Izar, P. 2002. Bird predation and prey-transfer in brown capuchin monkeys (*Cebus apella*). *Neotrop. Primates* 10(2): 84-89.

Freese, C. H. and Oppenheimer, J. R. 1981. The capuchin monkeys, genus *Cebus*. In: *Ecology and Behavior of Neotropical Primates*, Vol. 1, A. F. Coimbra-Filho and R. A. Mittermeier (eds.), pp.331-390. Academia Brasileira de Ciências, Rio de Janeiro.

Galetti, M. 1990. Predation on the squirrel *Sciurus aestuans* by capuchin monkeys, *Cebus apella*. *Mammalia* 54: 152-154.

Heymann, E. W., Knogge, C. and Herrera, E. R. T. 2000. Vertebrate predation by sympatric tamarins, *Saguinus mystax* and *Saguinus fuscicollis*. *Am. J. Primatol.* 51: 153-158.

Izawa, K. 1978. Frog-eating behavior of wild black-capped capuchin (*Cebus apella*). *Primates* 19: 633-642.

Newcomer, M. W. and De Farcy, D. 1985. White-faced capuchin (*Cebus capucinus*) predation on a nestling coati (*Nasua narica*). *J. Mammal.* 66: 185-186.

Ottoni, E. B. and Mannu, M. 2000. Semifree-ranging tufted capuchins (*Cebus apella*) spontaneously use tools to crack open nuts. *Int. J. Primatol.* 22: 347-358.

Rose, L. 1997. Vertebrate predation and food-sharing in *Cebus* and *Pan*. *Int. J. Primatol.* 18: 727-765.

Terborgh, J. 1983. *Five New World Primates*. Princeton University Press, Princeton, NJ.

Insect-eating by Spider Monkeys

Andres Link

Introduction

Studies on the diet and feeding behavior of spider monkeys (*Ateles* spp.) have revealed they are primarily frugivorous, with fruits representing between 72% and 90% of their diet (Carpenter, 1935; Hladik and Hladik, 1969; Klein and Klein, 1977; Van Roosmalen, 1985; Chapman, 1987; Symington, 1988; Dew, 2001). Flowers and young leaves are also eaten frequently, especially when fruit is scarce (Van Roosmalen and Klein, 1988; Castellanos, 1995; Nunes, 1998; Stevenson *et al.*, 2000). Bark, decaying wood, fungus, seeds, soil from salt-licks and termite nests, insects and other items are seldom consumed and represent only a small part of their diet (see Van Roosmalen and Klein, 1988).

Insect-eating in spider monkeys has been reported in several studies and, except for passive consumption (for example, fig wasps in fig fruits), it represents a minor part of their feeding activities. Wagner (1956) reported that spider monkeys eat insects and insect larvae. Termites are eaten selectively (Klein and Klein, 1977; Van Roosmalen, 1985), but this behavior has been difficult to separate from decaying wood or termite-nest eating (Castellanos, 1995) and has not been observed in several studies (Dew, 2001; Link, pers. obs.). They have been incidentally observed eating meliponid bees in Costa Rica (C. A. Chapman, pers. comm.) and Colombia (P. Stevenson, pers. comm.), and caterpillars are eaten intensively by spider monkeys during short periods of the year in a number of different sites (Van Roosmalen, 1985; Chapman, 1987; Symington, 1988; Cant, 1990).

White-bellied spider monkeys (*Ateles belzebuth*) have been studied in the Tinigua National Natural Park in Colombia for several years and, until this study, no insect-eating behavior had been observed except by Pablo Stevenson (pers. comm.), who reported it as a minor part of the diet of one of his study groups (MB-1); no individuals in his other groups had ever been seen actively consuming insects. During the study reported here, I observed white-bellied spider monkeys eating insects on a number of occasions and, although it represents a small part of their total diet in the study year, it was an important food item at certain times.

Study Site

This research was carried out at the Centro de Investigaciones Ecológicas de La Macarena (CIEM), part of Tinigua National Natural Park in the northwestern Amazon, located

between the eastern Andes and the Serranía de La Macarena, Departamento de Meta, Colombia (2°40'N, 74°10'W; 350-400 m a.s.l.). Annual temperature is relatively constant at approximately 26°C and rainfall is highly seasonal, with a dry season between December and March and the rainy season between April and November. Peak rainfall is in June and July, and the region averages 2700 mm annually (Kimura *et al*., 1994; Stevenson, 2002).

Field Methods

Observations of insect-eating by white-bellied spider monkeys were recorded during 13 months of fieldwork, from January 2001 to January 2002. Focal animal sampling (Altmann, 1974) was used to study their basic ecology and diet. Instantaneous sampling (every five minutes) was used to quantify activity budgets and habitat use. Continuous sampling was used every time the focal animal began to feed. Total feeding time per bout, the species and item eaten, and DBH (diameter at breast height) in trees and lianas were recorded, in addition to the number of individuals feeding on the same item and, when possible, consumption rates (measured in number of ingested items per minute).

Results

Sixteen insect-eating bouts were observed during the study, during which the spider monkeys ate orthopterans (n = 2), meliponid bees (n = 8) and lepidopteran larvae (n = 6). Fifteen of these bouts were observed directly, while one event was inferred by insect exoskeletons found in fecal samples. Grasshoppers (Orthoptera) were probably eaten opportunistically. Caterpillars and bees were eaten intensively, and active foraging to obtain these food items was observed in all of these feeding bouts.

Insect-eating constituted 1.5% of the total feeding time during the study year. All age/sex classes were seen eating insects and, although no aggression was seen on these occasions, there were some displacements at the meliponid bee nests. Spider monkeys were observed eating grasshoppers twice: in February, I collected two fecal samples next to each other, each of which contained one-half of the exoskeleton of an orthopteran (*c.* 40 mm long); and in April, one small grasshopper was caught from the top of a leaf and eaten by a female with an infant (J. Cajiao, pers. obs.).

Meliponid bees (*Scaptotrigona* sp.) were also part of the diet of this spider monkey group. Bee-eating was seen repeatedly throughout the year, and although it is an infrequent activity (compared to eating fruits or leaves), large quantities of bees were eaten on each occasion. Six out of eight observations were at the same two bee nests located on the trunk of an emergent *Bombacopsis quinata* (Jacq.) Dugang (Bombacaceae) tree, another nest was in another *B. quinata* tree, and one in an unidentified tree. All were in the canopy, about 20-25 m above the ground. One to three monkeys were seen eating bees simultaneously at the same nest (excluding dependant infants). They usually hung from their tails in front of the bee nest, or sat on the trunk and branches nearby waiting for their turn to gain access. When bees attacked and flew into the monkey's fur, they were easily captured and eaten. Mothers ate simultaneously with their juveniles and infants, capturing bees on their own or another individual's fur. When the bees stopped attacking, the spider monkeys would disturb the nest with their hands, and the bees would start attacking again. The feeding bouts lasted 2, 4, 5, 6, 6, 7, 11 and 13 minutes, and average feeding rates were 18.0 ± 6.2 bees/min (SD), range 12-30 (n = 9). These few observations reveal that spider monkeys could be eating a large quantity of bees per feeding bout, and although data were only collected from focal animals, several spider monkeys fed on these nests after and before the focal animal started its feeding bout.

Caterpillars were eaten intensively during a short period of the year in October, as well as on one occasion in February, when a medium size (*c.* 30-40 mm long) caterpillar was eaten by a female with twins. The other five caterpillar-eating bouts were observed during focal animal sampling; in each case the spider monkeys ate caterpillars of a single species, which were heavily clumped in the leaves of a few individual trees. During October almost 9% of the feeding time of spider monkeys was invested in this item, which was the fourth most commonly eaten item during that month. One to three monkeys were seen eating caterpillars in the same tree. Each individual actively foraged for and captured the caterpillars by directly licking or biting the fresh or dry leaves. These five feeding bouts lasted 1, 17, 27, 11 and 53 min. No feeding rates were obtained due to the difficulty in recording when a single caterpillar had been ingested, but large quantities of caterpillars were consumed at each feeding bout.

Discussion

Insect-eating by spider monkeys is uncommon, but may reveal some important aspects of their feeding ecology and adaptations. The few species of insects eaten are the only animal matter in their otherwise plant-supported diets. In several studies carried out on different species of spider monkeys, caterpillars were the only group of insects observed in the diet of this genus. In all of these studies, this activity occurred in specific short periods (*c.* 15 days) of the year (Van Roosmalen, 1985; Chapman, 1987; Symington, 1988; this study), probably when the caterpillars of some lepidopteran species hatch and aggregate on the leaves of particular trees. These caterpillars were eaten only in a short period of the year, which is similar to the availability of other food items such as some fruits, flowers and leaves of particular plant species (in contrast with meliponid bees, which were available throughout the year). Taxonomic identification of these caterpillars, and those eaten at other sites, would be useful to determine if they are phylogenetically related, and whether they might have been part of the diet of an ancestral spider monkey, or if the exploitation of this food resource has evolved separately in isolated populations.

Meliponid bees were eaten at different times of the year, and this is the first report on such repeated feeding bouts at bee nests. In these cases, the spatial and temporal availability of bees is predictable and somewhat constant throughout the year. Nevertheless, the spider monkeys ate them on only a few occasions, and this feeding source was totally ignored at other times, even though they rested or passed very close to the nests, and bees were seen flying around them. It would seem that fruit availability is not an important determinant of this behavior, as bees were eaten during periods of fruit abundance and scarcity alike (Link, unpubl. data).

Insect-eating by spider monkeys, and its selectivity and possible consequences, are still not well understood. There are few data available, and practically no information on the taxonomic groups eaten or on their nutritional components. Most studies of primate diets focus on quantitative and qualitative analysis of the major food items. Considerable information of this sort is now available for several species of spider monkeys at different localities (Carpenter, 1935; Hladik and Hladik, 1969; Klein and Klein, 1977; Van Roosmalen, 1985; Chapman, 1987; Symington, 1987; Van Roosmalen and Klein, 1988; Cant, 1990; Castellanos, 1995; Nunes, 1998; Wallace, 1998; Dew, 2001). It is possible that food items such as insects, which are only a small part of their diet, contribute essential or complementary nutrients, besides the soil eaten by both howler and spider monkeys at salt-licks (see Izawa, 1993).

One important aspect of the feeding ecology of spider monkeys that has not been studied in detail is the set of physical constraints they experience while capturing, manipulating and exploring objects with their hands. Their thumbless hands make them less agile at such foraging when compared with other genera such as *Saimiri, Cebus* or *Lagothrix*. This is supported by the fact that other primate groups which have vestigial or absent thumbs (i.e., *Colobus* spp.) rarely include insects in their diets (see Davies and Oates, 1994). Thumbless hands and long fingers are adaptations that are probably associated with their locomotive patterns and a diet based on fruits and leaves, which certainly constrains their ability to capture fast-moving animal prey.

Given the "precision-grip" constraints on the spider monkey hand, the caterpillars and meliponid bees which were eaten in Tinigua Park might represent a food resource which does not require high energetic costs in foraging and capturing. Meliponid bees are found in their nests and easily captured when they entangle in a monkey's fur. The caterpillars are densely clumped in individual trees, and move slowly enough that they may be captured with the hands or directly with the mouth. The abundance and predictable location of these food resources, as well as the ease with which the spider monkeys capture them, may explain why they are among the few insects eaten by this primate species.

Many studies have assessed differences in the ecological strategies of the atelines, especially comparing spider monkeys and woolly monkeys (*Lagothrix* spp.); these genera overlap widely in their geographic distribution, and are sympatric at several northwestern Amazonian sites in Ecuador and Colombia (see Strier, 1992; Stevenson *et al.*, 2000; Dew, 2001). Differences in their diets include the higher proportion of lipid-rich fruits eaten by spider monkeys, and the more frequent foraging and insect-eating by woolly monkeys.

Differences in the diets of the atelines are apparent in the proportions of food items they consume, which probably evolved to avoid direct competition. Although all are frugivorous, each species complements its diet with different items. Howler monkeys (*Alouatta* spp.) eat a great variety of mature and young leaves, as well as other vegetative plant parts (Neville *et al.,* 1988; Juliot and Sabatier, 1993) and there is also limited evidence of insect-eating. Woolly monkeys eat young leaves and insects, especially in periods of fruit scarcity (Ramirez, 1988; Defler and Defler, 1996; Stevenson *et al.,* 1994). *Ateles* and muriquis (*Brachyteles* spp.) base their diet on fruits and leaves, but the former relies more on fruits, while the latter feeds more on leaves (Van Roosmalen and Klein, 1988; Nishimura *et al.,* 1988; Strier, 1991; Nunes, 1998). Both spider and howler monkeys include small proportions of selected insects in their diet (Milton, 1980; references above) and more information is needed to understand why they do not rely on other insects, as woolly monkeys do, in order to complement their nutritional requirements, considering the widespread availability of this resource in the forest (Izawa, 1993).

Acknowledgements: I thank G. de Luna and J. Cajiao for their support and data collection in the field. C. Chapman, K. Izawa, P. Stevenson, H. Castellanos and G. de Luna provided useful comments on the manuscript. G. Nates (Universidad Nacional de Colombia) helped with the identification of the insects eaten by *Ateles* in our study site. G. de Luna, N. Silva, A. Sanabria and B. Ramírez helped in collecting the insects. Members of the Unidad Administrativa Especial del Sistema de Parques Naturales Nacionales de Colombia collaborated with this research at Tinigua National Park. Finally, I thank the Colombian-Japan agreement through K. Izawa and C. Mejía, who provided permission for this research at the CIEM.

Andres Link, Doctoral Program in Physical Anthropology at New York University, Rufus D. Smith Hall, 25 Waverly Place, New York, NY 10003, USA. E-mail: <al898@nyu.edu>.

References

Altmann, J. 1974. Observational study of behavior: Sampling methods. *Behavior* 49: 227-267.

Carpenter, C. R. 1935. Behavior of red spider monkeys in Panama. *J. Mammal.* 16: 171-180.

Cant, J. H. 1990. Feeding ecology of spider monkeys (*Ateles geoffroyi*) at Tikal, Guatemala. *Hum. Evol.* 5: 269-281.

Castellanos, H. G. 1995. Feeding behaviour of *Ateles belzebuth* E. Geoffroy, 1806 (Cebidae: Atelinae) in Tawadu

forest, southern Venezuela. Doctoral dissertation, The University of Exeter, Devon, UK.

Chapman, C. A. 1987. Flexibility in diets of three species of Costa Rican primates. *Folia Primatol.* 49: 90-105.

Davies, A. G. and Oates, J. F. (eds.). 1994. *Colobine Monkeys: Their Ecology, Behaviour and Evolution.* Cambridge University Press, Cambridge.

Defler, T. R. and Defler, S. B. 1996. Diet of a group of *Lagothrix lagothricha lagothricha* in southeastern Colombia. *Int. J. Primatol.* 17: 161-189.

Dew, J. L. 2001. Synecology and seed dispersal in woolly monkeys (*Lagothrix lagothricha poeppigii*) and spider monkeys (*Ateles belzebuth belzebuth*) in Parque Nacional Yasuní, Ecuador. Doctoral dissertation, University of California, Davis, CA.

Hladik, A. and Hladik, C. M. 1969. Rapports trophiques entre végétation et primates dans la forêt de Barro Colorado (Panama). *La Terre et la Vie* 23: 25-117.

Izawa, K. 1993. Soil-eating by *Alouatta* and *Ateles*. *Int. J. Primatol.* 14: 229-242.

Julliot, C. and Sabatier, D. 1993. Diet of the red howler monkey (*Alouatta seniculus*) in French Guiana. *Int. J. Primatol.* 14: 527-550.

Kimura, K., Nishimura, A., Izawa, K. and Mejía, C. 1994. Annual changes of rainfall and temperature in a tropical seasonal forest at La Macarena field station, Colombia. *Field Studies of New World Monkeys La Macarena Colombia* 9: 1-3.

Klein, L. L. and Klein, D. J. 1977. Feeding behavior of the Colombian spider monkey. In: *Primate Ecology*, T. H. Clutton-Brock (ed.), pp.153-181. Academic Press, London.

Milton, K. 1980. *The Foraging Strategy of Howler Monkeys: A Study in Primate Economics*. Columbia University Press, New York.

Neville, M. K., Glander, K. E., Braza, F. and Rylands, A. B. 1988. The howling monkeys, genus *Alouatta*. In: *Ecology and Behavior of Neotropical Primates*, Vol. 2, R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho and G. A. B. da Fonseca (eds.), pp.349-453. World Wildlife Fund, Washington, DC.

Nishimura, A., Fonseca, G. A. B. da, Mittermeier, R. A., Young, A. L., Strier, K. B. and Valle, C. M. C. 1988. The muriqui, genus *Brachyteles*. In: *Ecology and Behavior of Neotropical Primates*, Vol. 2, R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho and G. A. B. da Fonseca (eds.), pp.577-610. World Wildlife Fund, Washington, DC.

Nunes, A. 1998. Diet and feeding ecology of *Ateles belzebuth belzebuth* at Maracá Ecological Station, Roraima, Brazil. *Folia Primatol.* 69: 61-76.

Ramírez, M. 1988. The woolly monkeys, genus *Lagothrix*. In: *Ecology and Behavior of Neotropical Primates,* Vol. 2, R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho and G. A. B. da Fonseca (eds.), pp.539-575. World Wildlife Fund, Washington, DC.

Stevenson, P. R. 2002. Frugivory and seed dispersal by woolly monkeys at Tinigua National Park, Colombia. Doctoral dissertation, State University of New York, Stony Brook.

Stevenson, P. R., Quiñones, M. J. and Ahumada, J. 1994. Ecological strategies of woolly monkeys (*Lagothrix lagothricha*) at La Macarena, Colombia. *Am. J. Primatol.* 32: 123-140.

Stevenson, P. R., Quiñones, M. J. and Ahumada, J. 2000. Influence of fruit availability on ecological overlap among four Neotropical primates at Tinigua National Park, Colombia. *Biotropica* 32: 533-544.

Strier, K. B. 1991. Diet in one group of woolly spider monkeys, or muriquis (*Brachyteles arachnoides*). *Am. J. Primatol.* 23: 113-126.

Strier, K. B. 1992. Atelinae adaptations: Behavioral strategies and ecological constraints. *Am. J. Phys. Anthropol.* 88: 515-524.

Symington, M. M. 1988. Demography, ranging patterns and activity budgets of black spider monkeys (*Ateles paniscus chamek*) in the Manu National Park, Peru. *Am. J. Primatol.* 15: 45-67.

Van Roosmalen, M. G. M. 1985. Habitat preference, diet, feeding behavior and social organization of the black spider monkey, *Ateles paniscus paniscus*, in Surinam. *Acta Amazonica* 15: 1-238.

Van Roosmalen, M. G. M. and Klein, L. L. 1988. The spider monkeys, genus *Ateles*. In: *Ecology and Behavior of Neotropical Primates*, Vol. 2, R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho and G. A. B. da Fonseca (eds.), pp.455-537. World Wildlife Fund, Washington, DC.

Wagner, H. O. 1956. Freidlandbeobachtungen an Klammeraffen. *Zeit. für Tierpsychol.* 13: 302-313.

Wallace, R. B. 1998. The behavioral ecology of black spider monkeys in north-eastern Bolivia. Doctoral dissertation, University of Liverpool, Liverpool, UK.

LAGOTHRIX LAGOTHRICHA OR *LAGOTHRIX LAGOTRICHA*: WHICH IS IT?

Thomas R. Defler

When von Humboldt (1812) wrote the holotypic description of Humboldt's woolly monkey, he spelled the species name both *lagotricha* and *lagothricha*. According to some, *lagothricha* (and its variant *lagothrica*) are incorrect Latinizations of the Greek words λάγο(ς) - *lago(s)* (hare) + θρίχο(ς) - *thrico(s)* (hair)[1] because of the preceding vowel, *o*, which would require the form "trichos" rather than "thrichos". The use of the two versions was certainly a *lapsus* on von Humboldt's part. However, when revising the genus, Fooden (1963), under Article 24 (24.2) of the *International Code of Zoological Nomenclature*, chose the variation *lagothricha* as the "correct legal spelling" for *Lagothrix lagothricha*.

"Article 24: Precedence between simultaneously published names, spellings or acts.

24.1. Automatic determination of precedence of names. When homonyms or synonyms are established

[1] No pun intended, as von Humboldt was writing in French, not English.