

The Foraging Itinerary of Spider Monkeys: When to Eat Leaves?

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Introduction

The study of foraging behaviour has focussed on decisions made by animals with respect to patch selection and diet choice [1, 2]. Primate studies have contributed a great deal to the development of this theoretical focus, as the feeding behaviour of many primate species is easily quantified by direct observation [3-7]. However, there have been few investigations which have documented the temporal patterning of diet choice.

In this report, we describe the foraging itinerary of spider monkeys (*Ateles geoffroyi*), focussing on the pattern of leaf consumption over the day relative to other activities. We also provide a comparison with data on other species in order to examine the generality of temporal patterns. We suggest that detailed studies of foraging itineraries can

increase our understanding of potential selective pressures favouring animals to eat specific types of foods.

Methods

A spider monkey community living in Santa Rosa National Park, Costa Rica, has been studied for 36 months over the last 5 years (July to August 1983, January to August 1984, January to July 1985, February to August 1986, April 1987 to April 1988). The forest of Santa Rosa is primarily successional tropical dry forest, and during the dry season (December to May), the majority of the non-riparian trees lose their leaves. This, coupled with the fact that the canopy is rarely higher than 30 m, produces very favourable conditions for the observation of arboreal primates.

To obtain information on foraging patterns and range use, subgroups containing specific recognizable individuals were located in the morning or early afternoon and followed. Behavioural data were collected

using a focal animal sampling regime with 10-min sessions. Whenever possible, the subject chosen for observation was selected according to a fixed rotation between individuals and/or age-sex classes. When the focal animal was feeding, the food item and the plant species were recorded.

To evaluate the degree of feeding effort devoted to eating leaves relative to other food items (i.e. fruits, flowers), the percentage of feeding time spent eating each type of food item was calculated for each hour of the day. For more information on the study site, the community or the sampling methods, see Chapman [6, 8] and Chapman et al. [9].

Results

The spider monkeys of Santa Rosa fed primarily on fruit, which accounted for 71.4% of their feeding time. Leaves, flowers and insects accounted for 12.5, 14.0 and 2.1% of their feeding time, respectively.

Spider monkeys exhibited considerable diurnal variation in the amount of feeding time devoted to eating leaves (range 0–38.5%, fig. 1). On average, leaf eating was highest in the late morning, just prior to the time of the day when spider monkeys typically rest, and late in the day just before they entered their sleeping trees. Based on hourly averages, the proportion of feeding time devoted to eating leaves was related to the amount of time that the spider monkeys spent resting in the subsequent hour ($r = 0.72$, $p = 0.013$, $n = 11$).

It was not uncommon to follow a subgroup into the vicinity of one of their regularly-used sleeping trees at dusk and to watch the members feeding heavily on leaves [10]. Based on this observation, one would predict that leaf eating occurs preferentially in close proximity of the sleeping site. We observed a negative relationship between the length of the leaf-feeding bout and the distance that

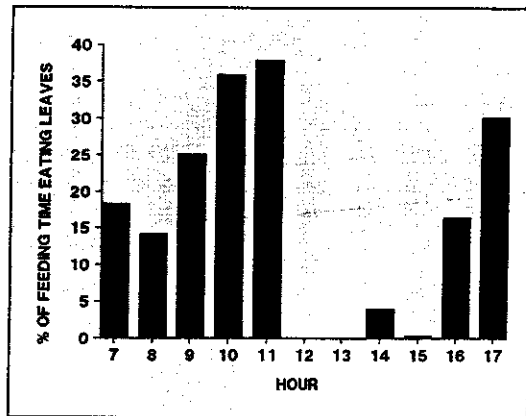


Fig. 1. The proportion of their feeding time that the spider monkeys (*A. Geoffroyi*) of Santa Rosa National Park, Costa Rica, spent eating leaves in each hour of the day.

the animal was from the sleeping site used that night ($r = -0.20$, $p = 0.048$, $n = 73$ leaf-eating bouts).

Discussion

The results suggest that spider monkeys may structure their foraging itinerary to eat leaves prior to resting, either at midday or in the evening. There are a number of factors that may explain the functional significance of such a strategy. Leaves are often fibrous, difficult to digest and contain a number of secondary compounds [3, 11]. Thus, animals relying on leaves must eat large volumes to meet their energetic and nutritional requirements. Although the spider monkeys preferentially fed on young leaves, it has been shown that, in some plant species, young leaves can be difficult to digest and are bulky because of high water content [11]. If the

Table 1. The diurnal dietary variation documented for a number of primate species (the time period state represents the peak period of feeding on that item)

Species	Food item and feeding peak	Reference No
<i>Galago demidovii</i>	fruit: early in the night insects: late in the night	16
<i>Galago elegantulus</i>	fruit: no consistent trend insects: no consistent trend	16
<i>Callicebus torquatus</i>	fruit: beginning and end of the day insects: midday leaves: all day	17
<i>Saimiri sciureus</i>	fruit: early morning peak	18
<i>Cebus olivaceus</i>	fruit: early morning insects: morning low	15
<i>Ateles geoffroyi</i>	fruit: morning high leaves: midday and dusk high	this study
<i>Colobus guereza</i>	fruit: more in the afternoon than morning leaf buds: more in the afternoon than morning flowers: midday peak	19 *
<i>Cercocebus albigena</i>	fruit: no consistent trend leaves: no consistent trend	20
<i>Hylobates klossi</i>	fruit: early morning; late afternoon figs: early morning decreasing during the day leaves: only after 11.00 h	21
<i>Hylobates syndactylus</i>	fruit: 70% dawn; 20% midday; high just before dusk young leaves: 30% dawn; 70% afternoon mature leaves: no diurnal variation	22
<i>Hylobates lar</i>	fruit: morning high; afternoon low; dusk high leaves: morning low; afternoon high; dusk low	13
<i>Hylobates syndactylus</i>	fruit: morning high leaves: afternoon high	13
<i>Hylobates agilis</i>	fruit: morning high figs: early morning high; dusk high leaves: midday high; dusk high flowers: midday high	14
<i>Pongo pygmaeus</i>	fruit: morning high; afternoon high leaves/bark: midday high	23
<i>Pan troglodytes</i>	fruit: eaten earlier than leaves	24

leaves eaten by the spider monkeys are difficult to digest, by choosing to feed on leaves just prior to resting at midday or at night close to the sleeping site, a spider monkey may reduce the distance travelled with a stomach full of leaves. In addition, if a spider monkey fed on leaves and subsequently encountered a more profitable food source, it might not be able to consume the profitable items due to the volume of leaves in its stomach. By patterning leaf consumption prior to resting, a spider monkey may minimize the potential of encountering a more profitable food resource which it is, for the moment, unable to consume.

To determine to what extent the temporal patterning of feeding itineraries is general among primates, we conducted a literature survey for studies providing information on diurnal variation in diet (table 1). From this compilation, it was evident that many species exhibited some form of diurnal variation in food types consumed. One of the most common temporal patterns observed was a peak in fruit consumption early in the morning. The animals may be choosing to eat easily digestible, high-energy fruit at this time to restore the energy deficiency that has accumulated over the night [12-15].

A second pattern which emerges from the data set is a temporal peak in fruit eating late in the day, often just prior to entering a sleeping site. It is conceivable that these animals are attempting to obtain high caloric foods prior to an overnight fast [13]. Two additional patterns are apparent in table 1: a midday and a late afternoon peak in leaf eating. As suggested for the spider monkeys, these strategies may minimize travel costs associated with load size and minimize the potential of encountering higher-quality food patches which cannot be exploited. It is

premature to discuss why different species exhibit contrasting forms of temporal patterning of dietary selection; however, it is apparent that a variety of species do exhibit some form of diurnal patterning in the types of plant parts eaten. Increased documentation and analysis of such patterning may provide insights into the adaptive significance of primate foraging strategies.

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