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Abstract: *Research was conducted at the El Zota biological field station to determine the amount and type of food processing exhibited by mantled howling monkeys (Alouatta palliata) prior to consumption. Mantled howling monkeys have been labeled as behavioral folivores with limited morphological adaptations for foliage digestion. The purpose of this study was to determine if A. palliata displayed any food manipulations and how food was selected by the species. Breakdown of the data was done to evaluate differences based on sex for these feeding and foraging behaviors. Results showed no behaviors that could be classified as manipulating food items and limited inspection or sampling. Low reported manual dexterity for the species and foraging through learned behaviors is reasoned for the lack of these behaviors. A.. palliata was shown to select food items smaller than the size of their hand which were most likely immature leaves. Female selectivity may be greater with regards to food inspection; however further studies would be necessary to test this finding. A focal sampling methodology was used to show these findings and 434 full feeding bouts were observed over 32.5 observation hours.*

Introduction

Mantled howling monkeys (*Alouatta palliata*) are New World monkeys and one of three species of primates that inhabit the El Zota biological field station located near the town of Tortuguero and the Barro del Colorado reserve in Costa Rica. The station is reported to be one of the largest of this non-tourist type of protected land and contains undisturbed forests as well as swamp and reforested areas.

Howlers are generally described as large, prehensile-tailed monkeys with an especially large larynx and cupped hyoid bone that allows them to be heard from over a kilometer away (Strier 2003). Howler monkeys' diet includes leaves (immature and mature), flowers, fruits, leaf buds, and leaf petiole and pulvinus (stem parts). Howlers

are considered to be specialists for leaves and are considered the most folivorous (leaf-consuming) of New World primates (Milton 1998).

Some aspects of the howlers' morphology suggests that folivory is a long-term adaptation of the species. Scheoninger *et al.* note that "Howlers have the tooth morphology of a folivore, the digestive tract morphology of a folivorous frugivore, and their food passage time is the slowest" of four studied New World monkeys (1997: 72). In fact, howlers, on average, digest food items for around 23 hours and with a range of 16 to up to 72 hours of passage time (Milton 1998).

Milton (1998) noted that howler's have simple acidic stomachs and not the complex acidic and alkaline chambers seen in colobines. The intestine is considered short for their diet of leaves and their cecum's surface area is large, typical in herbivores; however it is comparable to the spider monkey's surface area and they are a highly frugivorous (fruit-eating) species. In addition the colon surface area does not differ greatly from other species. All of these factors resulted in Milton concluding that the howler's gut does not morphologically resemble that of a typical folivore. However, she also speculates that the long digestion time may be connected to the ability of howling monkeys to break down cell wall material for energy, showing different physiological adaptations.

Howlers' movement in tropical forests is slow, at most 90 meters per hour on average (Bramblett 1976). The slow movements and directed travel are thought to conserve energy and that body posturing while resting is used to control body temperatures (Milton 1998). Most of their diurnal activity is spent resting which consists of 74% of *A. palliata* activity (Smith 1977). The time required for digestion with this selection of leaves is also longer than other New World primates that are less folivorous, making for long resting times to use energy for digestion (Milton 1998).

Howler monkeys are known to prefer immature leaves that are usually free of such compounds and materials that cause gastrointestinal stress and reduced digestibility. Strier states that "folivorous primates are selective about which leaves they eat, generally preferring those with the lowest tannins and highest protein contents, and with the fewest secondary compounds" (Strier 2003: 187). However, Milton (1980) shows that other than the maturity of the leaves, thorns on leaves, hair-coating on leaves, thorny petioles and stems seem not to deter the howlers from including these plants in their diet. Leaves are somewhat problematic for folivores as they contain generally low nutritional value, only three to four percent dry weight is usable (Milton 1998).

Leaves are an important source of protein for all folivorous primates (Milton 1980). Although forests are seemingly filled with leaves, howling monkeys must be selective to meet this nutritional demand. The niche that they occupy does not allow them to eat every leaf because of fiber content and poor digestibility of some compounds. Therefore, Glander (1981) states that "the tropical forest should not be viewed as a well-stocked larder waiting to be exploited, but rather as a spatially and temporally changing mosaic of items of varying value and availability."

Trees and leaves also show inconsistency (polymorphisms) in the amount of secondary compounds and nutritional content between seasons and between trees in any given season (Glander 1981). Howling monkeys must be highly selective if they are going to forage on the highest nutritionally valued items in a forest. Some parts of plants are free of such problematic compounds or contain beneficial nutrients so they will be selected over the actual leaf or fruit (Glander 1978).

The nutritional strategy of howling monkeys is to get an optimal mix of nutrients while avoiding secondary compounds (Smith 1977; Glander 1981; Milton 1998). New leaves present an easy way to accomplish this as they contain more of certain amino acids, more water content, and less tannins and fiber that bind protein in digestion. Mature leaves that are selected tend to resemble immature leaves in nutritional content, but have more protein and less water. Therefore, nutritional content is more important than simply maturity of the leaves, but more often immature leaves serve this purpose (Glander 1981).

For extracting food items, howling monkeys have poor manual dexterity resulting from the opposition of the thumb and first finger to the other three digits. Most other new world primates show higher degrees of dexterity than howling monkeys. The common method that howlers employ for extraction is to grab a branch around 30 cm from a food item and remove it with their teeth and lips. Any manipulation expected traditionally from howling monkeys occurs in the mouth, without the aid of the hands, and typically results in either swallowing or spitting (Smith 1977). In this study, the frequency of manual extraction versus extraction by this method with the mouth will be examined.

With the array of foods items and the need for howlers to be selective foragers due to the co-evolutionary race with the plants, how do howlers go about inspecting and selecting food items? Howlers are very selective as Glander (1981) found that they foraged from 62 of 96 available tree species but spent 81.2% in 15 species. Previous work of

his showed that nearly all the time these species were not the most abundant in the forests he studied either. Selectivity is not only exhibited on parts of the tree, but also between different trees of the same species, and between different species and families of trees. In fact, Glander observed the monkeys passing through trees of a certain species to reach a tree of the same species to feed in (1978).

Milton (1998) shows that fermentation occurs past the small intestine in howlers and that easily digestible protein would be the underlying reason for howler selectivity. She concludes that leaves are chosen on the fiber-digestible protein ratio more so than secondary compounds. Secondary compounds are sometimes not a deterrent in foraging as golden bamboo lemurs are able to consume twelve times the assumed lethal amount of cyanide in their diet each day (Glander *et al.* 1989 in Milton 1998). Physiological adaptations can overcome the secondary compounds, but it seems for howlers they still avoid them. However, since tannins and fiber bind the protein, these are stronger selecting agents (Glander 1981; Milton 1998).

In order to know which leaves are to be selected for, sampling of foods must occur by one or more members of a group in order to track the changes in a tree's leaf quality. Color and size may relate information as well as previous knowledge of foraging on the item, but presumably some sampling must take place occasionally to update this database of edibles. Hypothetically, this would occur by one member tasting or examining while others observe to obtain information about the food source (Glander 1981; Whitehead 1986). Such examination was seen in caged howlers that would glance and sniff *Ficus insipida* leaves and either consume or reject immediately (Milton 1998).

Learned foraging behaviors have to exist in addition to sampling as sampling every tree and leaf would be inefficient and often redundant for the small home range of howling monkeys. Two types of learning were purposed to occur in howling monkey foraging: observational learning in the social setting and trial and error (sampling) learning by individuals. These two types are employed throughout the life of the monkeys and are important in developing foraging skills as an infant (Whitehead 1986).

More often than not, infants are near their mothers and feed upon leaves that their mother or another group member has consumed. The infants follow the mother to obtain this information and can be seen even grabbing the same branches with the mother to forage. These trends are true for leaves, but not for fruits or items similar to fruits. About half of the time, infants would try to consume a fruit item before the mother tried it. Selectivity for leaves must be higher than in fruits which contain much more digestible constituents (Whitehead

1986). Similarly, young captive howling monkeys would only eat spinach leaves after the mother masticated some and the infant sniffed the mouth of the mother first (Milton 1998).

Through these learned behaviors howling monkeys are able to create paths through the forest to the highest quality food items in the least amount of time. Complete optimal foraging is not assumed by the traditional model because howlers have to balance the digestibility of the item and optimal foraging models assume complete digestion (Glander 1981). However, it is assumed that the learned behaviors and sampling when necessary produce the optimal selective behaviors of an optimal mix of nutrients in a changing environment (Whitehead 1986).

The objective of this research is to determine the types of pre-consumption manipulation, sampling, and general food items that *A. palliata* foraged upon at the El Zota biological field station. The analysis included differentiating oral extraction versus manual extraction of foods, manipulations such as rolling leaves after extraction, olfactory and visual inspections, and the gender differences in these behaviors. Sizes of fruits, leaves, and flowers will also be compared with the amount of manipulation observed.

This project is designed to see if *A. palliata* actively manipulates leaves as some folivorous primates do. For example; gorillas have been shown to prepare protein rich nettles by encompassing the stinging needles in leaf blades for consumption (Bryne & Bryne 1993 *in* Strier 2003). With evidence that howler monkeys do not base their selectivity upon the presence of some deterrents, a significant finding would be to observe similar preparation by howling monkeys (Bramblett 1976).

The best known example of manipulating the natural environment is the use of manipulated twigs and grasses by chimpanzees to extract termites from a mound (Goodall 1971). The manipulation of food prior to consumption shows the capacity of primates to actively alter their environmental conditions rather than be forced to survive only on easily available food resources.

Several hypotheses were tested in order to determine how mantled howling monkeys select and may manually process food items. The initial step of extraction was tested between five variables. The two major actions were grasping a branch or petiole and removing the food item with the mouth or whether howlers would manually remove food items. Among the food items it was predicted that the inspection of leaves would be more frequent due to the greater presence of secondary compounds and protein-binding effects than other food items. Similarly, large leaves were expected to be manipulated more often as physical deterrents (such as sharp ends and needles) is assumed to be

present more often on mature leaves. It was also predicted that small and medium food items would be preferred and therefore consumed in higher frequencies due to the infrequency of secondary compounds present in these leaves, generally assumed to be immature.

Hypotheses were also put forth to test the differences in *A. palliata* feeding behaviors with regards to sex. The nutritional demands on females due to gestation and lactation result in that females being considered the choosier foraging sex (Strier 2003). Because of the high demands of reproduction, females need to be highly selective and consume more to keep an energetic balance. This may show females manipulating and inspecting food more often or less prior to ingestion. Strier notes, "in nearly all species, females have higher quality diets than males, in other words, females are pickier about what they eat and focus their diets as much as possible on foods that contain the highest essential nutrients available" (Strier 2003: 181).

Male mantled howling monkeys are on average twenty percent larger than females (Bramblett 1976). Male howling monkeys actually forage less despite their larger size using 14% of the day versus females at 18% (Smith 1977). Males being larger aren't as able to forage on thin branches containing immature leaves; therefore males may be foraging on lower quality items as a consequence. A similar pattern is seen in white faced capuchins (Strier 2003). With differences seen in general foraging with regards to sex, one can expect differences in the behaviors being analyzed in this study.

Female data were separated from male data to test if they would inspect food items more often to meet the requirements for reproductive activities. Males were predicted to manipulate food items as their diet should include less quality food items than females. Males were thought to consume larger leaves as their body size would not allow them to reach as many immature terminal leaves as females. The questions posed are an attempt to further understand *A. palliata* foraging behaviors. By testing these hypotheses, the intricacies of *A. palliata*'s feeding behaviors as a unique adaptation can be assessed.

Methods

Observations of *A. palliata* were made between July 29 and August 7, 2004 using focal feeding behavioral sampling (data points) with time lapses of at least twenty seconds between subsequent feedings. Data were collected at the El Zota biological field station, Costa Rica (10°57.6' N and 83°75.9' W). The forest setting contains many natural feeding trees and it has been described as a lowland rainforest spanning around 1000 hectares in size (Pruetz & LaDuke

2001). The station included trails that entered secondary disturbed forest and primary natural forests. Data points were taken from various howler groups to eliminate specific group and individual biases.

Choice of focal subjects was made upon contact with a group and was the center-most sex-appropriate *A. palliata* that was feeding. If more than one fit this description, the one lowest on the tree was chosen. Rotations of one hour or twenty-four data points (whichever came first) was used to determine focal sample length. Males and females were given equal observations to ensure proper analysis of behaviors by sex. Although groups were rotated, opportunistic locations (i.e. known feeding trees) were used to begin observations and initially find groups.

If a focal went out of sight for more than ten minutes, a new focal was chosen (same criteria) of the same sex until that hour or twenty-four data points concluded. The category of 'other' behavior, which included resting and non-feeding behaviors as well as out of sight, was recorded if necessary. Only adult howling monkeys were observed as the age and sex of the immature are difficult to assess. Feeding strategies are also more defined in adult versus immature primates; the immature are often learning from direct observation or possibly sampling fruit items. A maximum of eight hours was spent in continuous contact with a focal group to ensure that observer fatigue did not occur during data collection.

Data for this analysis were collected during 42.3 field hours with 32.5 contact hours. The total number of feeding observations yielded 434 data points (feedings); 216 female and 218 males. Observations were generally made from three separate groups at El Zota. The total number of observations and frequencies were calculated for extraction methods, types of food, size of food, and recorded ingestions in order to analyze the hypotheses posed. Size of food was determined as smaller than the howler's hand (small), the same size (medium), or larger than the hand (large). The inspections (noticeable visual, olfactory, or tasting) observed were also examined for the type of food item and sex of inspector to test all of the hypotheses.

Results

The most often utilized method of extraction was with the mouth alone as illustrated by Table 1. The behavior was exhibited in 81.6% of total feedings; 86.7% male and 76.4% by female. 'Manual removal' of a food item for was second at 8.3% of all feedings; 7.3% for males and 9.3% for females.

Table 1. *Observations and frequencies of method of extraction.*

	Total (n=434)	Male (n=218)	Female (n=216)
Extraction with mouth	354 (81.6%)	189 (86.7%)	165 (76.4%)
Manual removal	36 (8.3%)	16 (7.3%)	20 (9.3%)
Holding food item	35 (8.1%)	9 (4.1%)	26 (12.0%)
None	4 (0.9%)	1 (0.5%)	3 (1.4%)
Hand Sweep	5 (1.2%)	3 (1.4%)	2 (0.9%)

The method of 'holding the food item and directly biting it while still attached to the tree' was seen 8.1% of the observations; 4.1% in males and 12.0% in females. 'Hand sweeps' were apparent in 1.2% of total observed, 1.4% for males and 0.9% of females. 'No extraction with apparent inspections' was seen 0.9% of the time with 0.5% for males and 1.4% for females.

Data compiled on size of food items are organized in Table 2. Small food items were ingested a total of 53.7% of all observations. For males, small food items were consumed for 52.3% of the feedings and females were observed 55.1% similarly. Medium food items comprised 22.4% of feeding encounters with 21.6% for males and 23.1% for females. Large food items were observed being fed upon 23.9% of time for all howlers, with 26.1% for males and 21.8% for females.

Table 2. *Observations and frequencies of size of food item eaten.*

	Total (n=434)	Male (n=218)	Female (n=216)
Small	233 (53.7%)	114 (52.3%)	118 (55.1%)
Medium	97 (22.4%)	47 (21.6%)	50 (23.1%)
Large	104 (23.9%)	57 (26.1%)	47 (21.8%)

Types of foods consumed are presented in Table 3. Leaves were consumed 58.1% of the time, followed by fruit (29.3%) and leaf

buds (12.7%). Flowers were not observed being consumed during any of the feedings. For males leaves comprised 61.0% of observed feedings. Fruit was encountered by males 29.8% of the time and leaf buds likewise at 9.2%. For females, leaves made up 55.1% of feedings, followed by fruit (28.7%), and leaf buds (16.2%).

Table 3. *Observations and frequencies of types of foods consumed*

	Total (n=434)	Male (n=218)	Female (n=216)
Leaf	252 (58.1%)	133 (61.0%)	119 (55.1%)
Fruit	127 (29.3%)	65 (29.8%)	62 (28.7%)
Leaf Bud	55 (12.7%)	20 (9.2%)	35 (16.2%)
Flower	0 (0.0%)	0 (0.0%)	0 (0.0%)
Other	0 (0.0%)	0 (0.0%)	0 (0.0%)

The amount of observations in which the food item was actually ingested and not ingested (spit out or passed by after inspection) was recorded and a food item was eaten 96.8% of observations for all mantled howlers; 97.7% of the time for males and 95.8% for females. During inspections analysis of the data revealed that nine visual inspections, four olfactory inspections, and three taste inspections were observed. Of all inspections, 75.0% were of leaves and 68.8% were done by females. Fruits were inspected for the remainder (25.0%) of the observations. One incident of manipulation was observed; by definition it was a 'leaf crumple'.

Discussion

A. palliata was observed 81.6% of the time biting their food items directly from the tree or liana. This left little evidence that howlers manipulate food items regularly. During the combined 71 observed possibilities where food manipulation could be observed, only one occurrence was recorded. The incident involved a female switched body position on a branch at 3:11:59 PM on August 3rd, 2004. During the hand switch, a leaf was in hand and crumpled when a fist was made and placed on the limb. A hand exchange was made of the leaf and it was ingested; however this example is seen as an accidental occurrence as a result of moving. The lack of evidence, by this study, shows that

A. palliata has not been shown to actively manipulate food items by the parameters set forth in this research and used by others.

Preferences were shown by howlers to grab a branch or petiole and bring the item of food to their mouth rather than remove it prior to consumption (81.6%). This is expected with a lack of dexterity in the hand and using the mouth is most likely more efficient. Inspections were more often seen with leaves (75.0%); however with only 16 total noted inspections of 434 total feedings, learned behaviors overrode the need to inspect food items while foraging. This would be selected for to keep foraging efficient. Females were shown to inspect more than males (68.8%) in the 16 total inspections. This result follows the behavioral ecological model that females are choosier by the nature of their reproductive needs (Strier 2003).

Leaves were most often consumed, as expected, by both sexes with males ingesting slightly more than females on average. Fruits contain more carbohydrates needed in energetic processes and therefore it was assumed females would be shown feeding on them more often. Leaf buds, however, made the difference between types of foods ingested with females eating just under double the amount of leafs buds that males did. During observation, one group had the males and females foraging in different tree crowns; females stayed to feed on the buds of one.

Females were observed to remove large food items nearly as often as males; no difference was seen in preference to size. However, among all of the size categories of food items, small leaves were preferred with 53.7% of leaves ingested being small versus both medium and large leaves. Reasons for this trend can be explained by the fact that immature leaves are smaller on average, and therefore probably higher quality food items. Flowers, although observed to be eaten in other studies at other sites, were not seen to be fed upon during this study.

In testing the comparison to the manipulative behaviors seen in other primates, no noted feeding was made in trees that contained physical deterrents that may contain quality nutrients and have an adaptive foraging behavior associated between the howling monkeys and the species of tree. Howlers minimize energy expenditure by utilizing foliage for their nutritional needs and with directed slow travels. In this regard, they may not need to manipulate food items as fruits still make up around 30% (Table 3.) of their feeding choices. They are not habitual folivores completely; they can rely on a significant amount of fruit and therefore also be choosier about which leaves they ingest. Smaller leaves, presumably immature and easy to ingest, can be consumed as well. The need for selecting leaves with

physical deterrents to obtain nutritional needs has not been selected for or howlers are incapable of manipulating with their hands easily.

It is assumed that since inspections of foods were infrequent, that the amount of information that the mantled howling monkey carries about efficiency of foraging and quality of food items is vast and most of the time sampling of food items is not required. Learned behaviors from infancy (watching mother) most likely play a large role in this behavior. The ability to learn the best foraging would play a large part in selection for this species as being an optimal folivorous forager seems slightly more complex than in most optimal foraging models. Mothers would especially want to display this trait as it would have consequences for the "teaching" of all of her offspring.

Sample sizes would need to be larger to confirm results in regard to type and sizes of food items consumed by *A. palliata* at El Zota. The lack of manipulations confirmed easily within the sample size of this study that howlers definitely were shown to not handle their food items often. Improved methods could lead to understanding of the inspection of food items in further studies as inspections were difficult to observe under the parameters of this research. Analysis on the species of trees where observations took place could lead to nutritional studies to better determine how food items are selected.

Conclusions

Alouatta palliata does not exhibit behaviors that can be classified as active manipulation as is seen in gorillas. Diet was shown to include a majority of leaves; however, with a significant portion of fruits included, this study follows the concept of *A. palliata* as a behavioral folivore with unique adaptations among New World primates. Further research could be conducted to analyze the exact reasons for preferentially choosing small leaves and the nature of food inspection in *A. palliata.*

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