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Food Choice From Endemic North Carolina Tree Species by Captive Prosimians (*Lemur fulvus*)

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Seven captive-born lemurs (*Lemur fulvus*) at the Duke University Primate Center were presented with leaves of different maturity from five species of North Carolina trees. The animals demonstrated three distinct behaviors toward the novel plant material. They sniffed, tasted, and/or ingested it. New leaves were sniffed, but little tasting and ingestion was observed. Intermediate pine needles were sniffed and ingested but little tasted. Mature leaves were sniffed equally, but the mature leaves of tulip trees and honeysuckle were tasted significantly more than pine, sweetgum, and red maple. Pine, sweetgum, and red maple were ingested significantly more than tulip trees and honeysuckle. Male lemurs ate significantly more mature pine needles and new sweetgum leaves than did the females. Chemical analysis of these plant materials indicated that the new and mature leaves of tulip tree and honeysuckle contained alkaloids. Captive-born lemurs apparently use their sense of smell and taste in choosing what to eat and seem just as capable as free-ranging animals in finding food when faced with the chemical defenses that protect trees from insect predation.

Key words: food choice, prosimians, plant secondary compounds, feeding trials, primate–plant interactions

INTRODUCTION

Captive prosimians held in outdoor cages at the Duke University Primate Center (DUPC) were observed to ingest plant material that fell into their cages as well as leaves from certain plants near their cages. These occurrences presented the possibility that, since these were naive animals, they may be ingesting harmful material. If the plant material was not harmful then their ingestion suggested to us the possibility that indigenous vegetation might be used to supplement the diet of captive prosimians at DUPC and other facilities. This paper reports the results of feeding trials where captive-born lemurs were offered the leaves of five plant species endemic to North Carolina. The animals demonstrated preferences, and they apparently made their choices based on the odor and taste of the plant material because they sniffed and tasted each leaf before either eating or rejecting it.

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TABLE I. Age and Sex of the Test Animals*

Animal	Sex	Age at time of trial (months)
Eury	F	39
Tina	F	62
Dido	F	112
Loki	M	14
Lucca	M	39
Priam	M	51
Lucifer	M	74

*All were *Lemur fulvus fulvus* × *Lemur fulvus rufus* hybrids.

MATERIALS AND METHODS

Animals

Seven captive-born animals (*Lemur fulvus fulvus* × *Lemur fulvus rufus* hybrids) were used in the feeding trials (Table 1).

Tree Species

The five plant species tested were: tulip tree, *Liriodendron tulipifera*; sweetgum; *Liquidambar styraciflua*; red maple, *Acer rubrum*; loblolly pine, *Pinus taeda*; and Japanese honeysuckle, *Lonicera japonica*. Both mature and new leaves were collected from each of the five plant species. Age distinction was based on leaf size, color (new leaves are light green or reddish), and texture. Leaves used in the feeding trials were collected immediately prior to the trial. Leaves used for the chemical analysis were collected, air dried, and stored at room temperature in tightly sealed plastic bags until analyzed.

Feeding Trials

Feeding trials were conducted from April 11 to May 1, May 22 to June 18, and July 1 to July 13, 1978. Two types of feeding trials were used. In the initial trials for all animals, one leaf of each of the five plant species was placed on the platform in the test animal's home cage. Each animal was then observed for 15 minutes after which the trial was terminated and all plant material was removed from the cage. Only one trial a day was conducted for each test animal. The animals were tested separately for all leaves except intermediate pine needles. Because of necessary caging changes, intermediate pine needles were tested on groups of three animals (Eury, Loki, Lucifer in one cage and Dido, Lucca, Priam in another). Tina was not presented with intermediate pine needles. Intermediate pine needles were used in the tests because new needles were not available. These single leaf choice trials were run on 5 consecutive days for each animal or group of animals tested.

After the single leaf choice trials, 25 intermediate leaves of pine and 25 new leaves of honeysuckle and sweetgum were presented to the animals. For mature leaves only the two most preferred species, pine and red maple, were presented in the quantity trials. All leaves were placed on the platform of the home cages and the animals were not observed for the 15-minute test duration. At the end of 15 minutes, all remaining leaf material was removed from the home cages. The animals were housed three to a cage for this experiment, except Tina, who was in a cage by herself. She had lost her sight due to glaucoma before the experiment began.

Estimates of amount ingested were based on counts of whole or partial leaves remaining. Leaf fragments were reassembled.

The single leaf choice tests were used to determine if the lemurs would eat any or all of the five test species and, if they did demonstrate any preference, how the choice was made. The quantity trials were used to determine how much of the preferred plant material they would ingest in addition to their regular diet of monkey chow and fruit.

The animals' behavior in the feeding trials was scored in three ways. Inspection of the leaf without mouthing was scored as a sniff. Tasting or biting into the leaf without ingesting any, i.e., none of the leaf was missing, was scored as a taste. Ingesting part or all of the leaf was scored ingest.

Chemical Analysis

Air dried samples were tested qualitatively for alkaloids and tannins. For the alkaloid determinations, aliquots from 80% ethanol extracts were subjected to an acid–base–organic solvent–acid procedure to remove impurities, and the residue was then tested with Mayer's reagent (Farnsworth, 1966; Fong, Tin-wa, and Farnsworth, unpublished manuscript). A ferric chloride–gelatin–salt block procedure was used to determine absence or presence of phenolics in an aliquot from the 80% ethanol extract (Farnsworth, 1966; Fong, Tin-wa, and Farnsworth, unpublished manuscript). Ferric chloride distinguishes between hydrolyzable and nonhydrolyzable tannins.

Statistical Analysis

One-way analysis of variance tests (ANOVA) were run on the sniffing, tasting, and ingesting results. The Duncan Multiple Range Test was carried out to detect differences between the five plant species if the ANOVA indicated significant differences. The alpha level for significance was 0.05.

RESULTS

The animals' behavior (sniffing, tasting, and ingesting) did not differ significantly between the new leaves of the four plant species (Table 2). Generally, for the new leaves of all four species, they did considerable sniffing and little tasting or ingesting. Nor did any of their behaviors for the intermediate pine needles differ significantly from that for new leaves of the other four plant species. However, their behavior toward mature leaves of the five species was very different. The amount of sniffing was not significantly different between the five species, but the amount of tasting and ingesting between the five species was significantly different (Fig. 1).

TABLE II. Summary of Single Leaf Tests*

	New leaves			Intermediate leaves			Mature leaves		
	S	T	I	S	T	I	S	T	I
Pine	—	—	—	21	4	20	2	0	23
Sweetgum	34	3	11	—	—	—	13	2	22
Red maple	32	6	5	—	—	—	13	1	29
Tulip tree	37	19	3	—	—	—	22	12	4
Honeysuckle	31	5	6	—	—	—	21	11	2

Abbreviations: S, sniff; T, taste; I, ingest; — = not tested.
*Since there were no significant individual differences only the total of each behavior is given for each tree species.
Intermediate pine needles were used because new needles were not available when the tests were performed.

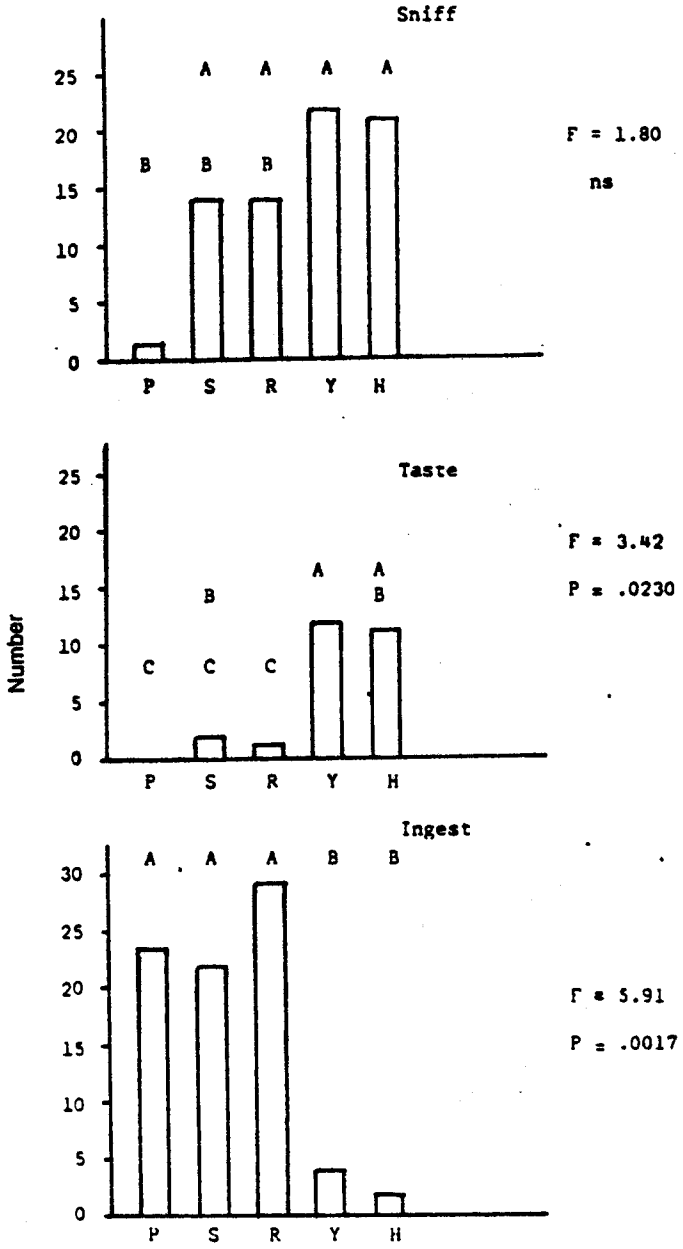

Fig. 1. Duncan multiple range test on the animal's behavior toward mature leaves. P, pine; S, sweetgum; R, red maple; Y, tulip tree; H, honeysuckle. Tree species with the same letter indicate that there is no significant difference in the behavior directed toward those species. For example, pine, sweetgum, and red maple were ingested equally as were tulip tree and honeysuckle, but the lemurs ingested significantly more of pine, sweetgum, and red maple than they did of tulip tree and honeysuckle.

TABLE III. Statistical Results*

Species	Behavior	N	Mature leaves[a]	N	New leaves[a]	F	P < F
	Sniff	6	0.33 ± 0.82	4	5.3 ± 2.5	21.02	0.0018
Pinus taeda[b]	Taste	6	00	4	1.0 ± 0.82	9.60	0.0147
	Ingest	6	0.38 ± 2.4	4	5.0 ± 4.3	0.31	0.5941
	Sniff	6	2.2 ± 1.6	4	8.5 ± 4.0	12.45	0.0077
Liquidambar styraciflua	Taste	6	0.33 ± 0.81	4	0.75 ± 0.96	0.55	0.48
	Ingest	6	3.7 ± 2.4	4	2.8 ± 3.6	0.24	0.64
	Sniff	6	2.2 ± 2.0	4	8.0 ± 2.8	14.57	0.0051
Acer rubrum	Taste	6	0.17 ± 0.41	4	1.5 ± 1.9	2.88	0.1279
	Ingest	6	4.8 ± 2.4	4	1.3 ± 0.96	7.81	0.0234
	Sniff	6	3.7 ± 2.7	4	9.3 ± 2.4	11.07	0.0104
Liriodendron tulipifera	Taste	6	2.0 ± 1.3	4	4.8 ± 6.4	1.11	0.32
	Ingest	6	0.67 ± 1.0	4	0.75 ± 0.96	0.02	0.90
	Sniff	6	3.5 ± 3.9	4	7.8 ± 2.8	3.53	0.0971
Lonicera japonica	Taste	6	1.8 ± 2.4	4	1.3 ± 1.5	0.22	0.65
	Ingest	6	0.33 ± 0.82	4	1.5 ± 2.4	1.29	0.29
			Mature leaves				
			Males		**Females**		
Pinus taeda	Ingest	4	5.3 ± 1.3	2	1.0 ± 00	20.28	0.0108
			New leaves				
			Males		**Females**		
Liquidambar styraciflua	Ingest	1	8.0 ± 00	3	1.0 ± 1.0	36.75	0.0206
Liriodendron tulipifera	Taste	1	1.0 ± 00	3	0.67 ± 1.2	26.33	0.0359

*The behavioral responses in Table 2 were analyzed for differences between leaf maturity and for sexual differences.
[a]Values are means ± standard deviation.
[b]Intermediate instead of new pine needles.

Although tulip tree and honeysuckle were tasted significantly more than pine, sweetgum, and red maple, they were ingested significantly less (Fig. 1).

Table 3 contains the statistical results for the comparison of the animals' behavior toward new and mature leaves of the same plant species (or between intermediate and mature needles in the case of pine). The animals sniffed and tasted intermediate pine needles significantly more than they did the mature needles. There was no difference in the amount they ingested. For sweetgum, they sniffed new leaves significantly more with no difference in tasting or ingesting between the stages of maturity. Red maple new leaves were sniffed and ingested significantly more than mature leaves with no difference in the amount of tasting. Tulip tree new leaves were sniffed significantly more than mature leaves but the animals demonstrated no differences in tasting or ingesting the differently aged tulip tree leaves. There were no significant differences in sniffing, tasting, or ingesting for new and mature honeysuckle leaves.

A significant sex difference was demonstrated for ingestion of mature pine needles, ingestion of new sweetgum leaves, and the tasting of new tulip tree leaves (Table 3). The males ingested significantly more mature pine needles than the females. Males also ingested more new sweetgum leaves and tasted more tulip tree leaves, but only one male was tested for new leaves.

New and mature leaves of tulip tree and honeysuckle contained alkaloids while the new leaves of sweetgum and red maple contained hydrolyzable tannins (Table 4). Phenolics other than tannins were present in all but the new leaves of sweetgum and red maple.

The quantity trial results are similar to the results from the individual multiple choice tests. The animals ingested very few new leaves (less than 12% in all cases)

TABLE IV. Chemical Results

	Leaves					
	Alkaloids		Tannin		Other phenolics	
Tree species	New	Mature	New	Mature	New	Mature
Pinus taeda	–	–	–	–	+	+
Liquidambar styraciflua	–	–	H	–	–	+
Acer rubrum	–	–	H	–	–	+
Liriodendron tulipifera	+	+	–	–	+	+
Lonicera japonica	+	+	–	–	+	+

Abbreviations: H, hydrolyzable tannin.

TABLE V. Results of the Quantity Tests*

Species	No. leaves	No. ingested	Percentage ingested
		New leaves	
Pinus taeda	75	8.5	11.3
Lonicera japonica	75	4.5	6.0
Liquidambar styraciflua	75	8.0	10.7
		Mature leaves	
Pinus taeda	250	88.0	35.2
Acer rubrum	250	126.5	50.6

*Intermediate pine needles were used because new needles were not available.

of the three species offered to them, but consumed 35% of mature pine needles and 50% of red maple leaves (Table 5).

DISCUSSION

Naive lemurs faced with novel plant food made discriminations which appeared to be based on the odor and taste of the plant material. Prosimians depend a great deal on smell first and then taste to make choices. Vision probably plays only a minor role in food selection. One of the animals (Tina) was blind from glaucoma, but she made the same choices as the sighted animals and in the same fashion.

When presented with a novel item, the animals spent considerable time sniffing the leaves of all species regardless of either leaf maturity or plant species. Careful sniffing apparently provides the necessary information to make a choice, at least for the five plant species tested here. The lemurs did spend more time sniffing the new leaves than they did mature leaves of each plant species except for honeysuckle, where new and mature leaves were treated similarly (Table 3).

Apparently sniffing provides enough information to make a decision, but tasting provides additional information if sniffing does not produce satisfactory or contradictory evidence. The significant increase in tasting of mature tulip tree and honeysuckle is mirrored by a significant decrease in the ingestion of these two plant species (Fig. 1). Tasting apparently was not needed to make a decision about ingesting mature pine, sweetgum, and red maple leaves, but was needed to avoid mature tulip tree and honeysuckle. In fact, the avoided tulip tree and honeysuckle were the only mature leaves which contained alkaloids. The new leaves of these species also contained alkaloids, and the animals avoided the new leaves of these two species. However, since they generally avoided all new leaves of the five species tested, their reduced use of tulip tree and honeysuckle does not appear statistically significant. It is possible that the new foliage of these species contains other chemicals that make them unpalatable. Ikeda et al. (1977) and Edmunds and Alstad (1978) suggested that resin acids may serve as deterrents to insect predation of jack pine (*Pinus banksiana*) and ponderosa (*P. ponderosa*) pine.

The fact that the lemurs found the new leaves of the four species unattractive and preferred mature leaves of some of the same tree species should not be surprising. Glander (1981) documented that there are only a few differences between all mature and all new leaves in a forest (mature leaves have less water, methionine, lysine, and proline and more fiber than new leaves). The major chemical differences between mature and new leaves occur only in terms of whether or not primates select or reject particular leaves and not simply because a leaf is mature or new (Glander, 1981). Leaves are chosen because they contain a certain chemical or mix of chemicals (or because certain chemicals are absent) and not because they are of a certain maturity. Some trees use the strategy of investing their new leaves with deterrent chemicals while others protect their mature leaves (McKey, 1974). Thus, the a priori assumption that new leaves are more nutritious than mature leaves simply because they are less mature is not valid.

The experiments reported here and data from other work (Oates et al., 1977; McKey et al., 1978; Glander 1981, 1982) suggest that both captive and free-ranging primates can discriminate between plant material that does and does not contain potentially toxic or digestibility-reducing compounds. If captive animals are allowed to choose, they can indicate which if any local vegetation they will consume. And, similar to free-ranging animals which are assumed to maximize the quality of their diet (Milton, 1980; Glander, 1981), captive animals also may be able to help their caretakers supplement captive diets with local vegetation that may provide vital ingredients.

The effects of tannin on lemur food choice remain questionable since none of the tested species had condensed tannin present. Hydrolyzable tannin has been shown to have little impact on primate food choice (Glander, 1981), while condensed tannin has been shown to affect leaf selection (McKey et al., 1978; Glander, 1981; Wrangham and Waterman, 1981).

The lemurs' preference for maple leaves (*Acer rubrum*) seems to be in contrast to those reports that maple leaves (*A. saccharum*) are high in condensed tannins which reduce digestibility. These and similar reports simply reinforce the fact that primates can and do discriminate between leaves with different chemical properties. Glander (1981) demonstrated that leaves of different species, leaves of adjacent trees of the same species, and leaves of the same tree had different secondary compounds and different nutrients. Each tree (and possibly each leaf) has to be dealt with individually. The reported chemical nature of one tree or leaf is not necessarily valid for any other.

The animals' stereotyped tasting procedure of puncturing the leaf surface with their canines or premolars and then momentarily pausing or dropping the leaf appears to be designed to bring the taste buds and vomeronasal organ into play. After this brief delay, the leaf can then be picked up and processed or, if held in the mouth, chewed and swallowed.

These results should not be interpreted to mean that only secondary compounds of plants affect primate food choice. Nutrient content is obviously important (Milton, 1980; Glander, 1981), and the nutrient content of preferred and avoided leaves needs to be determined in a similar test situation. Plans are underway to carry out these tests at the DUPC. However, plant secondary compounds can and do interfere with the availability of nutrients and therefore are an important component in plant–primate interactions (Glander, 1982).

These feeding trials demonstrate that completely naive animals can be selective when exposed to novel foods, either under captive conditions or when captive-born animals are introduced into natural areas. In fact, based on the above feeding trials, two groups of captive-born lemurs (*Lemur catta* and *L. fulvus*) were placed in a 1.2-acre natural habitat enclosure at the DUPC. During the past 2 years they have shown the same plant preferences described in this study, have not poisoned themselves, and are in robust health.

CONCLUSIONS

1. Captive-born lemurs demonstrated a clear preference for leaves of particular tree species and maturity.
2. Naive lemurs discriminated between harmful and nonharmful food items.
3. Local vegetation can be used to supplement the diet of captive primates.

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