The Relationship Between Frugivory and Insectivory in Primates

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ABSTRACT. Fruit and insects are two of the major components of primate diets. Previous investigators have often assumed that the consumption of fruit by primates was unassociated with the consumption of insects. We contend that much of what has been termed fruit-eating by primates involves a significant and deliberate ingestion of insects. The implications of this are discussed.

INTRODUCTION

Fruit and invertebrates are two of the most important constituents of primate diets. Many studies on primate feeding have attempted to quantify the relative importance of these two dietary components (HLADIK & HLADIK, 1972; ROBINSON, in press). Biologists observing primate feeding have usually defined fruit eating as the time spent consuming fruit and invertebrate eating as the time spent engaged in performing behaviors which either do, or look as if they should, result in the capture of invertebrates (RUDRAN, 1978; WASER, 1977b).

It is our contention that a significant percentage of the observed behaviors called fruit eating result in a significant and deliberate ingestion of invertebrates, usually insects. Two of us (TEL and GAF) have been involved in a number of studies on the ecology and behavior of free-ranging marmosets in central Brazil (FONSECA, 1981; FONSECA et al., 1980; FONSECA & LACHER, 1984; LACHER et al., 1981, 1984). As a part of this research, we fed captive marmosets a variety of natural foods and experimentally modified diets. One such diet involved presenting three adult pairs of captive marmosets (*Callithrix jacchus penicillata*) two bananas each test period: one plain and one with *Tenebrio* larvae placed in the banana.

Regardless of the stage of ripeness of the bananas, the marmosets actively searched out the *Tenebrio*, and in the process consistently consumed more of the "*Tenebrio*-infested" bananas (Table 1). The six *Tenebrio* were almost always consumed (Table 2). The fruit was never rejected because of the presence of insects. This was an interesting observation to us, for frequently fruit is conceived of as the supermarket variety (i.e., free of infestation), while in the wild, a very high percentage of fruits can be infested by insects (see RUDRAN, 1978). These observations provoked us to examine the generality of this phenomenon.

Observers of monkeys eating fruit have commented on their messiness (OPPENHEIMER, 1977; HLADIK & HLADIK, 1969; BONACCORSO, GLANZ & SANDFORD, 1980). For example, in a study of *Callimico*, HELTNE, WOJCIK and POOK (1981) reported that a monkey would choose a fruit, take a few bites and drop the remainder. We would like to suggest that in many cases such as this the monkey might not be feeding wastefully but is in fact feeding selectively: feeding on insects infesting the fruit. The fruit is dropped because it is not the primary object

Table 1. Consumption of banana (average grams consumed plus or minus one standard deviation) by marmosets (N = 3 males and 3 females) according to stage of ripeness and presence or absence of *Tenebrio* larvae.

Stage of ripeness	Treatment	Mean gr eaten (S.D.)
Green	with *Tenebrio*	2.50±(1.20) b, c
	without *Tenebrio*	0.67±(0.97) c
Ripe	with *Tenebrio*	13.17±(6.98) a
	without *Tenebrio*	4.25±(4.60) b, c
Rotten	with *Tenebrio*	11.83±(5.63) a
	without *Tenebrio*	7.72±(7.19) b

Groups were compared with a Kruskal-Wallis One-Way Analysis of Variance by ranks ($H = 61.65$, $df = 5$, $p < 0.001$). Individual group rank sums were compared in a pairwise fashion, with the experiment-wise error rate set at 0.05 (HOLLANDER & WOLFE, 1973). Groups followed by the same letter were statistically indistinguishable.

Table 2. Numbers of *Tenebrio* consumed by marmosets (N = 2 males and 3 females) during the three experimental periods.

	Green	Ripe	Rotten	Total
Eaten	107	137	81	325
Not eaten	1	7	9	17
Total	108	144	90	342
Percent eaten	99.1	95.1	90.0	95.0

Consumption of *Tenebrio* was contingent on the stage of ripeness of the bananas ($G = 9.33$, $df = 2$, $p < 0.01$).

of the feeding monkey. In some cases the only thing consumed by the monkey may be the insect while in other cases both insect and fruit may be eaten.

The purpose of this paper is two-fold: first, to document other cases in which primates deliberately ingest insects while apparently feeding on plant material; and second, to explain some of the observed patterns between frugivory and insectivory.

DISCUSSION

CASES OF DELIBERATE INSECT INGESTION

A few primatologists have recognized that animals feeding on plant material may be ingesting significant quantities of insect material (Table 3). Of particular importance are WASER's (1977a, b) and FREELAND's (1979) study of *Cercocebus albigena* and OPPENHEIMER's (1977, 1982) and ROBINSON's (in press) study of *Cebus* spp. The *Cercocebus* observed by WASER would choose unripe, latex-filled figs in which a weevil was developing, remove the insect and discard the fig. They also consumed other fruits and a type of mushroom that were found to be heavily infested by insects. FREELAND (1979) states that most "fig-eating" by mangabeys consisted of opening the fig, removing the contained insects and some of the pulp and discarding most of the fruit. The mangabeys were also seen commonly to open seed pods (*Pterygota mildbraedii* or *Newtonia buchanani*) and remove large lepidopteran larvae. As WASER (1977a) pointed out "fruit eating by mangabeys may be viewed as a form of insectivory."

In a study of *Cebus capucinus* OPPENHEIMER (1977, 1982) found that monkeys spent 35% of their feeding time during March removing bruchid beetle larvae (*Amblycerus centralis*) from *Apeiba membranacea* fruits. Fruits were sniffed, the infested ones pulled off the tree, opened,

Table 3. Invertebrates obtained from fruits and other plant material.

Species	Plant material	Invertebrate material	References
Hylobates spp.	figs	fig wasps and their predators	GITTINS & RAEMAEKERS, 1980
Colobus guereza	figs and other fruit	arthropods	STRUHSAKER, 1978
Cercocebus albigena	*Ficus brachylepis* fruits (unripe)	weevil larvae	WASER, 1977a
	Pancovia turbinata fruits	beetle, wasp, moth, fly larvae	WASER, 1977b
	mushroom	insects	WASER, 1977b
	Pterygota mildbraedii seed pods	large lepidopteran larvae	FREELAND, 1979
	Piptadeniastrum africanum seed pods	arthropods	FREELAND, 1979
	Newtonia buchanani seed pods	arthropods	FREELAMD, 1979
	Ficus spp.	insects	FREELAND, 1979
Cebus capucinus	*Apeiba membranacea* fruit	*Amblycerus centralis* (weevil) larvae	OPPENHEIMER, 1977
	palm nuts	maybe larvae	STRUHSAKER & LELAND, 1977; DEFLER, 1979
C. olivaceus	palm nuts, galls		ROBINSON, in press
	figs (unripe, overripe), *Cordia* sp. fruits	arthropods	
Pan paniscus	figs	*Blastophaga* (wasp)	NISHIDA & HIRAIWA, 1982
	leaves	*Macromiscoides aculeatus* (ant) nests	HLADIK, 1973
	leaves	*Chlorophora excelsor* (gall fly) galls	GOODALL, 1963
Pongo pygmaeus	leaf galls, epiphyte stems	insects	RIJKSEN, 1978
	rolled leaves	crickets	RIJKSEN, 1978
	fig	fig wasp	RIJKSEN, 1978
Homo sapiens	corn	corn ear worms	CURRAN, 1937 in BODENHEIMER, 1951
	palm nuts	"grub"	CHAGNON, 1977

and the larvae removed. After a group of monkeys had been feeding, the ground under an *Apeiba* tree was "littered with pods and seed disks or fragments of both" (OPPENHEIMER, 1977). The fruit had been dropped, opened but uneaten, with the insects removed.

ROBINSON (in press) reported another case of *Cebus* consuming insects from plant material. On 115 occasions *C. olivaceus* were observed to uncover old *Copernicia* palm seeds, open them, and remove large grubs. Seeds were often checked for the presence of insects before an attempt was made to open them.

WHY SELECT INSECTS FROM INSECT-INFESTED FRUITS?

Several factors might affect a monkey's decision in choosing between an "average" fruit and an "average" insect infesting the same fruit. In favor of fruit is its high carbohydrate content, high water content and availability (HERRERA, 1982) while factors which might mitigate against it are low protein content, fairly low fat content and possible toxicity (HERRERA, 1982; MILTON, 1980). Insects, particularly larvae, have in their favor high fat and protein contents (REDFORD & DOREA, in press), and the fact that their protein is generally more available or more useful than plant protein because of its amino acid spectra (VELLAYAN, 1981; ROBBINS, 1983). Insects directly, or indirectly through molds and yeasts, often "sour" the fruit on which they feed (JANZEN, 1977; STEPHENSON, 1981). JANZEN (1977) and HERRERA (1982) have pointed out that this would be expected to make the fruit unattractive to its dispersal agent and therefore "protect" the insect in the fruit. However, this assumes that dispersal agents are interested in consumption of only the fruit, whereas, as has been shown for primates, the insect is often eaten as well. Both the external signs of insect infestation on fruits and nuts (JOHANSEN, 1971; BOETHEL & EIKENBARY, 1979) and the frequent sniffing, feeling and biting of fruit performed by monkeys (HELTNE, WOJCIK & POOK, 1981; FREESE & OPPENHEIMER, 1981) suggest that primates may be able to distinguish infested from uninfested fruits without opening them.

WHY SELECT INSECT-INFESTED FRUIT?

Fruits are physiological sinks for the plant that bears them and nutrients move into them preferentially (BOLLARD, 1970). Galls too are characterized by an abundance of proteins, fats, starches or sugars (MANI, 1964; SHANNON & BREWER, 1980) resulting from an alteration of the plant's sap flow by the gall-forming organism. In both cases feeding on these plant tissues enables some animals to get from the plant previously unavailable nutrition. In an analogous fashion larvae which feed on toxic fruits (or seeds) may not themselves be toxic (see ROSENTHAL, 1983).

A primate can consume both the insect infesting a fruit and the fruit it infests. As we observed in marmosets, a banana was not rejected because of the presence of insects: both the *Tenebrio* and the banana were eaten. The amount of a banana consumed varied with the stage of ripeness: on average for bananas without *Tenebrio* rotten bananas were preferred over ripe which were preferred over green ones. This can be explained by comparing green with ripe bananas: green bananas are astringent and starchy while ripe ones are sugary and lack astringency (PALMER, 1970). At all three stages of ripeness, more banana was consumed if *Tenebrio* were present than if they were absent. The banana eaten was generally from the vicinity of the holes made to contain the larvae. A possible explanation for this is that the banana in the vicinity of the larvae may have tasted of *Tenebrio*, but this is unlikely to explain the consumption of more than a trivial amount. An alternative explanation may lie in the "protein-sparing" function of carbohydrates. Proteins eaten without carbohydrates are metabolized for energy while the inclusion of carbohydrates in a meal allows the proteins to be used for other vital functions (WILSON, FISHER & FUGUA, 1975). The *Tenebrio* represent the protein (REDFORD & DOREA, in press) and the bananas, which are very low in protein (0.5 to 1.6%, PALMER, 1970), represent a rich source of carbohydrates (WILSON, FISHER & FUGUA, 1975).

Damage to a fruit, such as attack by an insect, can cause localized or overall premature ripening of the fruit (MCGLASSON, 1970). This fact further complicates interpreting the observation of a primate eating only a portion of a fruit and discarding the rest. The primate may be eating the insect because of its nutritional value or ingestion of the insect may be incidental while consuming the ripe portion of the fruit containing the insect.

Fruits or other plant tissues may also be consumed because they are a good place for a primate to find insects (Table 3). For example, JANZEN (1979) reports that at some time of the year Coleoptera and Diptera larvae become so numerous you can open a fig and find it "filled to capacity with larvae." The obligate association between figs and their insect pollinators and predators makes figs an excellent source of animal protein (VELLAYAN, 1981). The low fat and low nitrogen content of many figs (VELLAYAN, 1981) is offset by the high fat and nitrogen content of many larval insects (REDFORD & DOREA, in press). Despite the small size of the fig wasps, they can occur in very large numbers in a single fig (JANZEN, 1979) and can be ingested in large amounts by primates (RIJKSEN, 1978). Figs are important food for primates throughout the world, a fact perhaps linked to this association with insects.

The association between fruits and insects does not necessarily lead to the ingestion of fruit by animals in pursuit of insects. In a study of *Tarsius bancanus* FOGDEN (1974) reported that animals would go to a fruiting tree with fruit lying on the ground and prey on the insects attracted to the fallen fruit. Similarly, EMMONS (1975) reports squirrels (*Funisciurus lemninatus*) eating ants attracted to a sticky fruit and HOWELL (1980) reports that bats (*Antrozous pallidus*) may feed on moths attracted to the fruit of organ pipe cactus.

The association between frugivory and insectivory applies to animals other than primates and for plant tissues other than fruits. House mice (*Mus musculus*) remove weevils from peas (LINDUSKY, 1942), rodents eat brucid beetles out of *Scheelea* palm nuts (JANZEN, 1971), peccaries (*Tayassu tajacu*) may remove larvae from *Astrocaryum* palm seeds (KILTIE, 1980), and white-tailed black cockatoos (*Calyptorhynchuys funereus*) eat weevil larvae from *Banksia* fruits (SCOTT & BLACK, 1981). Parrots and macaws in particular would be expected to confront many of the same situations mentioned in this paper for primates (see MCINNES & CARNE, 1978). Insects may be obtained from other plant tissues as well. For example, orangutans remove insects from rolled leaves and from bromeliad stems (RIJKSEN, 1978) while ROBINSON (in press) reported *Cebus olivaceus* licking leaves to obtain scale insects.

More careful observation and experimentation should clarify the complicated relationship between fruit eating and insect eating by primates. Future research on primate frugivory should test this idea and previous analyses of primate diet should be re-examined.

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