

BIOTROPICA 25(3): 365-368 1993

Varietal Taste Preference for Cacao *Theobroma cacao* L. by the Neotropical Red Squirrel *Sciurus granatensis* (Humboldt)

Key words: cacao; feeding deterrent; taste preference; *Theobroma cacao*; *Sciurus granatensis*; squirrel.

IN TROPICAL FORESTS HERBIVORE DAMAGE of unripe fruit is widespread and can greatly diminish a plant's reproductive success (Fenner 1985, Peres 1991). Unripe fruit tend to be cryptic green in color and may contain compounds to deter herbivore damage before the seeds are mature (Bell 1984). Changes associated with fruit ripening are considered a primary mechanism for the attraction of animal vectors which disperse seeds (Rhodes 1980). The foraging behavior of the animal vectors involved will also influence the reproductive success of the plant whose seeds they disperse. Arboreal frugivores such as squirrels can exploit most of the fruit crop, and because they have first food choice they tend to be more selective than terrestrial ones (Kinzey and Norconk 1990). Optimal foraging models have had much success in predicting how long animals spend in a patch of food (Charnov 1976, Stevens & Krebs 1986). Factors influencing food preference within a patch are less well understood.

The neotropical red squirrel *Sciurus granatensis* (Humboldt) is common throughout much of Central and northern South America. It feeds on a variety of fruits and seeds (Eisenberg 1989). The natural distribution of *S. granatensis* is similar to that of cacao, *Theobroma cacao* L. (Cheesman 1944). In addition to monkeys and rats, squirrels are considered to be among the natural seed dispersal agents of *T. cacao* (Toxopeus 1985). In commercial plantations, however, squirrels may be a serious pest of cacao (Lawrence 1991).

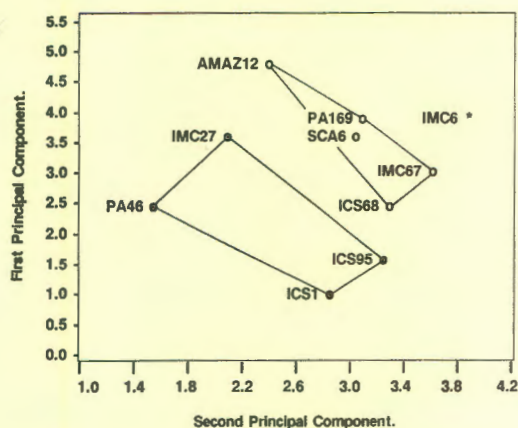


FIGURE 1. A principal component plot of human taste preference. Open circles represent squirrel preferred cacao varieties while closed circles represent the cacao varieties less preferred by squirrels. The variety IMC6 (indicated by a star) was observed never to be attacked by squirrels.

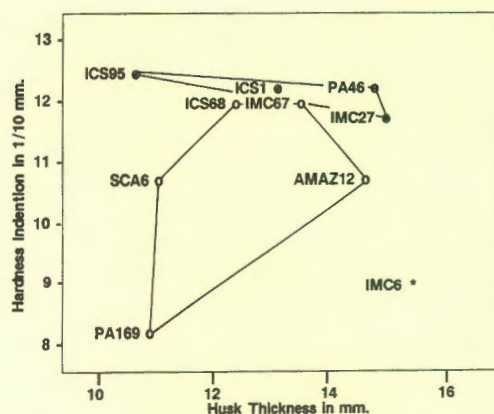


FIGURE 2. A scatter plot of cacao pod husk thickness against hardness. Open circles represent squirrel preferred cacao varieties while closed circles represent the cacao varieties less preferred by squirrels. The variety IMC6 (indicated by a star) was observed never to be attacked by squirrels.

Warren and Emamdie (1993) observed that the neotropical red squirrel consumes the mucilage surrounding the seeds in ripe pods in preference to that in unripe pods of cacao. When only unripe cacao pods were available, squirrels were found to attack certain varieties in preference to others. The ranking of taste preference in terms of number of pods eaten was consistent over sites. However, squirrels always removed a similar amount of tissue irrespective of pod type in terms of either ripeness or variety.

Although much is known about the chemical nature of cacao husks (Blakemore *et al.* 1966, Adomako 1972) the properties which determine the degree of squirrel attraction are unknown. In this study we identify some of the physical and chemical properties of ripe and unripe cacao pods that may influence squirrel taste preference.

The ten cacao varieties used were those for which we had previously established squirrel taste preference, in terms of numbers of pods eaten (Warren and Emamdie 1993): ICS1, ICS68, ICS95, IMC6, IMC27, IMC67, PA46, PA169, SCA6, AMAZ12. These ten varieties were originally collected from natural forests in the upper Amazon region of Peru and from Trinidad. Two fully expanded unripe pods were collected from each of these ten varieties from The International Cocoa Germplasm Collection Trinidad (I.C.G.T.). The pods were washed, dried, and the pod husks cut into 2 cm square pieces. Fifteen human tasters were requested to sample the husks from all ten varieties and give each a score on a scale from 1 to 5 for the following criteria: hardness, mucilage content, and unpleasantness of taste. A principal component analysis was then performed for the ten varieties on the three mean values over the fifteen tasters (Fig. 1).

Ten pods from each of the same ten varieties were collected from the I.C.G.T. Each pod was transversely sectioned and the thickness of the pod wall measured. An additional two ripe and two fully expanded unripe pods of the same varieties were collected to measure hardness using a Seta penetrometer. Hardness was recorded as the depth of penetration in tenths of millimeters, caused by a 32 g cone plus 50 g weight applied to the pod wall for 5 seconds. Five hardness readings were taken from each of the 40 pods. The mean values for both ripe and unripe pods were calculated for each variety over the ten observations. A paired sample *t*-test was performed on the mean hardness values for ripe versus unripe pods over all ten varieties.

During June 1992 twenty unripe pods of the most favored SCA6 variety were collected from the I.C.G.T. using gloved hands. The pods were divided into two groups of ten. The pods were weighed and labeled. String was tied to their cut peduncles for attachment to cacao trees.

The twenty pods were taken to an abandoned cacao estate on Mount St. Benedict, in Trinidad's Northern Range, where large numbers of squirrels had previously been observed. Very few intact cacao

pods were apparent at the site as the majority had been consumed. Since cacao is the most abundant tree species in the area, cacao pods are presumed to form an important part of the squirrels' normal diet. The two samples of ten pods were attached to adjacent trees. The first group of ten pods were coated with 50 ml of SCA6 extract. The second group of ten pods were coated with 50 ml of IMC6 extract. The extracts were prepared from either four unripe pods of the favored SCA6 or four unripe pods of the uneaten IMC6. The pods were washed, dried, and the outer epidermal layer of pod wall was scraped off. For both varieties 50 g of epidermal tissue was ground with sand in 50 ml of ethanol and left to stand for 16 hours. The samples were filtered before being applied to the pods in the field. After 48 hours the number of eaten pods were recorded, and a chi-squared analysis performed.

During June 1992 ten unripe IMC6 pods from which the epidermis had been removed and ten intact unripe IMC6 pods were weighed, labeled, and string attached to their peduncles. The two groups of pods were fastened throughout adjacent cacao trees in the abandoned Mount St. Benedict estate. Epidermal extract from the favored SCA6 was applied to the ten peeled IMC6 pods. After 48 hours the number of eaten pods was recorded.

Human tasters were able to discriminate between squirrel preferred and unpreferred cacao varieties (Fig. 1). The first principle component contains 61 percent of the total variation and is comprised equally of the three taste criteria, while the second contains 29 percent of the total variation and is composed of hardness and taste data alone. Preferred types tend to be hard, low in mucilage, and contain no unpleasant taste. Interestingly, the uneaten variety IMC6 was described as being hard, low in mucilage, and containing no unpleasant taste. Since squirrels were never observed even to "sample" this variety, it is clear that they are not discriminating against it on the same taste criteria used by humans.

Squirrel taste preference for the nine eaten varieties can be explained by just two physical properties: the thickness and hardness of the husk (Fig. 2). Preferred types tend to have hard, thin husks. Both variables are required to discriminate fully between the preferred and unpreferred classes. The observation that hardness is important in food preference is consistent with Kinzey and Norconk (1990) who found that hardness played a significant role in food choice in mammalian arboreal frugivores.

The uneaten IMC6 type was observed to have thick, hard husks. The hardness should tend to make it attractive to squirrels, while the thickness might be expected to deter them. However, the physical properties of IMC6 cannot relate to its unattractive nature, as it was never "sampled" by squirrels. Furthermore, IMC6 is not grown in Trinidad, so the squirrels could have no prior knowledge of it.

Ripe pods were significantly harder than unripe pods ($t = 25.18$, $df = 9$, $P < 0.01$). The mean indentation measure from ripe pods was 0.875 mm compared with 1.127 mm for unripe pods. If the changes associated with ripening are adaptive and result in the fruit becoming more attractive to animal vectors, then this suggests that squirrels prefer hard rather than soft pods. This is consistent with the observed variation in unripe pods among varieties. Squirrels tended to prefer hard rather than soft unripe pods. This is unusual as most fruits become more attractive to animal vectors during ripening by softening (Rhodes 1980).

After 48 hours, eight out of the ten SCA6 pods coated with SCA6 extract had been eaten, while the SCA6 pods treated with IMC6 extract were untouched. The epidermal extract of the uneaten IMC6 variety was observed to significantly deter squirrels ($\chi^2 = 13.33$, $df = 1$, $P < 0.01$). When the reverse procedure was tried, the SCA6 extract was unable to mask the unattractive nature of the IMC6 pods. After 48 hours neither the IMC6 pods treated with SCA6 extract or the untreated IMC6 pods had been eaten. This demonstrates that a purely chemical plant defense is able to deter squirrels from attacking an otherwise preferred food type.

Although thick husked, the uneaten IMC6 variety was described by the human tasters as similar to the preferred types in that it was hard, low in mucilage, and contained no unpleasant taste. Its unattractiveness was demonstrated without the squirrels tasting the pod husk. This, and the epidermal extract evidence, suggests that IMC6 derives its defense against herbivores from an odorous compound, rather than by an unpleasant taste or physical property. Pods of cacao are known to contain methylmethionine sulphonium compounds which act as precursors to many unpleasant smelling organo-sulphur compounds (Lopez 1969). It seems likely that one of these may be acting as a feeding deterrent in IMC6. For the varieties other than IMC6, however, squirrel preference in terms of number of pods consumed seems to be related both to the taste and physical properties of the husk.

The squirrel food choice did not appear to be related to familiarity as the local Trinidadian ICS

varieties fell into both preferred and unpreferred classes. Similarly, the upper Amazon IMC and PA types also fell into both preferred and unpreferred groups.

The observation of varietal taste preference is perhaps not surprising since food was probably not in short supply in the field site, so squirrels could afford to be highly selective in their diet. What is surprising, however, is the observation of an odorous chemical deterrent in the IMC6 variety, since noxious smells are not usually considered to be important in food preference (Rhoades 1979).

We would like to thank K. Sankar and A. R. Maxwell for their assistance, and J. S. Kenny for commenting on the manuscript.

- ADOMAKO, D. 1972. Cocoa pod husk pectin. *Phytochemistry* 11: 1145-1148.
- BELL, E. A. 1984. Toxic compounds in seeds. In D. R. Murray (Ed.). *Seed physiology*. Vol. 1 Development, pp. 245-262. Academic Press, Sydney, Australia.
- BLAKEMORE, W. R., E. T. DEWAR, AND R. A. HODGE. 1966. Polysaccharides of the cocal pod husk. *J. Sci. Food Agric.* 17: 558-560.
- CHARNOV, E. L. 1976. Optimal foraging: the marginal value theory. *Theor. Popul. Biol.* 9: 122-136.
- CHEESMAN, E. E. 1944. Notes on the nomenclature, classification and possible relationships of cacao populations. *Trop. Agric. (Trinidad)* 21: 144-159.
- EISENBERG, J. F. 1989. *Mammals of the neotropics*. Vol. 1. University of Chicago Press, Chicago, Illinois.
- FENNER, M. 1985. *Seed ecology*. Chapman and Hall, Ltd., London, England.
- KINZEY, W. G., AND M. A. NORCONK. 1990. Hardness as a basis of fruit choice in two sympatric primates. *Am. J. Phys. Anthropol.* 18: 5-15.
- LAWRENCE, G. A. 1991. The non-insect pests of cocoa. *J. Agric. Soc. Trinidad & Tobago* 1: 16-19.
- LOPEZ, A. 1969. Methylmethionine sulphonium salt in cocoa. *Ann. Rep. Cacao Res. C.R.U. U.W.I. (Trinidad)*.
- PERES, C. A. 1991. Seed predation of *Cariniana micrantha* (Lecythidaceae) by Brown Capuchin Monkeys in central Amazonia. *Biotropica* 23(3): 262-270.
- RHOADES, D. F. 1979. Evolution of plant chemical defence against herbivores. In G. A. Rosenthal and D. H. Janzen (Eds.). *Herbivores*. Academic Press, New York, New York.
- RHODES, M. J. C. 1980. The maturation and ripening of fruit. In K. V. Thimann (Ed.). *Senescence in plants*. CRC Press, Inc., Boca Raton, Florida.
- STEVENS, D. W., AND J. R. KREBS. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey.
- TOXOPEUS, H. 1985. Botany, types and populations. In G. A. R. Wood and R. A. Lass (Eds.). *Cocoa*, pp. 11-37. Fourth edition. Longman Group UK Ltd., Harlow, Essex, England.
- WARREN, J. M., AND D. Z. EMAMDIE. 1993. Rodent resistance in cacao. *Theobroma cacao* L. *Trop. Agric. (Trinidad)* 70(3): 285-287.

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