

## Preferences and Food Quality of Fruit-Feeding Butterflies in Kibale Forest, Uganda<sup>1</sup>

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### ABSTRACT

Many butterflies in tropical forests feed on fruits that have fallen to the forest floor. This substrate differs in many ways from floral nectar, and therefore fruit-feeding butterflies are expected to possess adaptations for efficient foraging, choice, and ingestion of their food. Differences in food quality and in spatial and temporal availability are also likely to have led to life history evolution. Here we describe the sugar and nitrogen content of fruits that butterflies feed on in a tropical forest in Uganda, and measure the attractiveness of these fruits to the local butterfly fauna together with the role that decay plays in the attraction. These data are supplemented with feeding observations at fruit falls in the forest. Our results show that (1) fruits contain significant and variable concentrations of sugar and nitrogen, and constitute a nutritious food source for butterflies in tropical forests; (2) fruit-feeding butterflies use cues from the fruits and fermentation products to locate their food; (3) different classes of fruit-feeding butterflies may vary in their preferences for certain fruits, and differ in their ability to find preferred food; and (4) fruit choice is not strongly correlated with attractiveness or nutrient content. The results are discussed in the light of the evolution of food searching and life history strategies.

*Key words:* Charaxinae; foraging; nitrogen; Nymphalinae; Satyrinae; sugar; tropical forest; tropical fruits.

LIFE HISTORY THEORY IS BASED ON THE DISTRIBUTION OF RESOURCES over multiple tasks. Therefore, studies on nutritional ecology—the acquisition of resources and how they are allocated to different tasks—are essential to understand life histories. Lepidoptera form an excellent model system, because significant interspecific variation in feeding behavior and life history has been documented and is available for both descriptive and empirical analysis.

Adult butterflies feed primarily on nectar from flowers and a number of other substrates that contain sugar and/or mineral substances such as fruits, honeydew, tree sap, mud, carrion, and dung. In addition, a few Nymphalid species can feed on pollen (Gilbert 1972). Some species use only one of these substrates, others a combination. Most butterflies in tropical forests can be classified into one of two feeding guilds: the nectar-feeding and the fruit-feeding guilds (DeVries 1988). The fruit-feeding guild is defined as those species attracted to fruit bait, but this does not mean that fruits are the main food source for all the species in this guild. Potential alternative sources are honeydew, tree sap, and rotting plant material. Only a small proportion of butterflies in tropical forests regularly feed on both nectar and fruit.

A diet shift is likely to be accompanied by adaptations that optimize foraging and feeding behavior on novel food. These adaptations can occur at different levels including location of searching behavior, cues used during searching, selection of fruit, uptake of food, and digestion. In the case of butterflies, changing between nectar feeding and fruit feeding requires major changes in key variables of foraging behavior. Butterflies can be expected to have adaptations to four main parameters of the new food source.

First, temporal and spatial distribution patterns of fruits are different from flowers because mainly trees and occasionally large vines typically produce fruits that butterflies feed on, and these fruits

are therefore found at high densities under widely spaced fruiting trees. In addition, phenological patterns of trees can differ between flowering and fruiting, even within the same species (Chapman *et al.* 1999).

Second, flowers attract pollinators by using color and scent signals (Weiss 1997, Weiss & Lamont 1997, Omura *et al.* 1999, Corbet 2000, Omura *et al.* 2000, Bernardello *et al.* 2001, Andersson *et al.* 2002, Andersson & Dobson 2003, Landolt & Smithhisler 2003). Fruits also employ such signals, but these are adapted to attract seed dispersers (Willson & Whelan 1990, Cipollini & Levey 1991, Kalko & Condon 1998, Mollon & Regan 1999, Sumner & Mollon 2000, Altshuler 2001, Alves-Costa & Lopes 2001, Urbani 2002). Moreover, the fruits fed on by butterflies are usually those that have fallen to the forest floor, are overripe or decaying, and their odor may be associated with decay, rather than producing aromatic volatiles typical of the unripe and ripe fruits in the canopy.

Third, the uptake of fluids from fruits can be hampered by a thick or rough skin and fibrous fruit flesh. Two main proboscis morphologies for fruit feeding are distinguished (Norris 1936, Krenn *et al.* 2001) and some ecological consequences are discussed by Molleman *et al.* (in press). Other animals may play an important role in making fruits accessible by damaging skins that are normally impenetrable to butterflies.

Fourth, nutrient quality of fruit juice differs from flower nectar (Baker *et al.* 1998). Fruits contain a wider variety of components, including nutrients (Conklin-Brittain *et al.* 1998), secondary components (Cipollini & Stiles 1993, Wrangham *et al.* 1998), and fiber. Many fruit-feeding butterflies are attracted to and feed on fermenting fruits. Overripe and decaying fruits also contain microbes and microbial products such as organic acids and alcohols (Phaff & Starmer 1987, Morais *et al.* 1995), and these may be toxic. Concentrations of important nutrients such as sugar and amino acids can change during fermentation (Kinzey & Norconk 1993, Genard *et al.* 2003), with potentially profound effects on the diet quality of fruit-feeding butterflies.

<sup>1</sup> Received 24 July 2003; revision accepted 7 January 2005.

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In this paper, we investigate some behavioral patterns associated with fruit feeding in butterflies. We experimentally measured the attractiveness of different fruits to different groups of butterflies, and recorded food choice in a tropical forest in East Africa. These data are discussed in the light of the measured sugar and nitrogen content, possible toxicity, and accessibility of the fruit juice. We tested the hypothesis that odors associated with decay are major attractants. Special attention was paid to the behavior of Charaxinae because they use a feeding technique that is distinct from other butterfly groups (Molleman *et al.* in press).

## METHODS

**FIELD SITE.**—This study was conducted in 2000, 2001, and 2002 at Makerere University Biological Field Station in Kibale Forest National Park, Western Uganda (0°35'N, 30°20'E). The field station borders selectively logged moist evergreen forest at an altitude of around 1500 m and is therefore classified as a transition toward montane forest. The mean maximum temperature is 23.3°C and the mean annual rainfall is 167 cm (Chapman *et al.* 1999). In Kibale forest, the phenology of most tree species does not follow a clear seasonal pattern and the availability of different fruit species varies from year to year (Chapman *et al.* 1999). As a consequence, the different experiments discussed below were not performed on one set of fruits, but on those that were available during the particular experiments and surveys.

**FRUIT QUALITY.**—We collected samples of fruits from the forest floor from *Ficus brachylepis* (Hien), *Ficus exasperata* (Vahl), *Ficus natalensis* (Hochst) (Moraceae), *Mimusops bagshawei* (Moore) (Sapotaceae), and *Uvariopsis congolensis* (De Wild) (Annonaceae). When possible, samples were collected from ripe and overripe fruits (stage index) over a 5-mo period to minimize the possible bias caused by seasonal variation in fruit quality. All fruits were weighed before being preserved in 95 percent ethanol.

At Leiden University, fruit samples preserved in ethanol were dried for 2 d and their dry mass measured, and the dried material was then dissolved in 1.5 ml of water. The percentage of sucrose in solution was measured with a hand refractometer assuming that sucrose was the only major factor influencing the refractive index of the sample (Lucas *et al.* 2001), even though the mineral component can affect the refractory index of nectar (Hiebert & Calder 1983). The measured concentration was then used to calculate the sugar concentration in the fresh fruit. After drying and weighing the same samples, the amounts of carbon, hydrogen, nitrogen, and sulphur were measured at the Gorlaeus Laboratory of Leiden University, using a Perkin-Elmer CHNS analyzer 2400 series.

**TRAPPING BUTTERFLIES WITH FOREST FRUITS AS BAIT.**—We used a system of four livetraps for butterflies (height 125 cm, diameter 35 cm; DeVries *et al.* 1997) placed in the understory of continuous forest and widely spaced from any fruiting trees. The platform with the bait was at 40 cm from the ground and the mesh cylinder was

5 cm above the platform, providing butterflies a limited view of the bait. The traps were configured in a square with an intertrap distance of 10 m. For each trial, we collected ripe fruits from the forest and baited two traps with one species of fruit, and two with one tablespoon of fermented banana that had been prepared by mashing banana in a bucket 3 d prior to baiting. Fermented banana is always available, commonly used, and a strong attractant for fruit-feeding butterflies. Both fruits from the forest and fermented banana subsequently decayed in the traps. The traps were scored on 4 consecutive d, and most butterflies were released after scoring but never returned immediately to the trap and mark recapture studies indicated that they do not typically return to the same trap on subsequent days. After scoring a set of traps, to reduce any possible location effect, the fruit and fermented banana baits were exchanged between them.

In each trial on every trapping day, the number of butterflies in traps with similar baits was summed. The attractiveness of a certain fruit to a butterfly species was calculated as the proportion of butterflies trapped in the fruit-baited trap on a particular day and location. The bait that attracted the highest number of butterflies of a particular species or species group in a trial is regarded here as the preferred bait for this particular taxon and coded as 0 for more than 50 percent on fermented banana and 1 for a particular fruit. We used the percentage of butterflies trapped on the least preferred bait of a pair as a measure of ability to find preferred bait. Overall strength of preference for particular baits on a particular day and location (trial) was measured as the percentage caught on that bait of all butterflies caught in the trial (including those on fermenting banana). We then categorized the different trapping occasions with respect to this strength of overall preference. Within these categorized trials, we examined the four most abundant genera separately, calculating the proportion of butterflies attracted to the preferred bait and using its arcsine for statistical tests. The temporarily low abundance of certain butterflies prevented the inclusion of *F. exasperata*, *F. natalensis*, and *Ficus congolensis* in our analysis of the effect of fruit age.

**TRAPPING BUTTERFLIES WITH INDIVIDUAL COMPONENTS.**—To elucidate which components of (fermenting) fruits are responsible for the attraction, we tested the following components: plain water, amino acid solution, yeast solution (2.5 g of dry yeast in 750 ml water), the yeast solution with 50 g of sugar, ripe banana, and fermented banana, and in different combinations. In June and July 2001, we used a similar set-up as with trapping butterflies with fruits from the forest, now with four trial locations with four traps each. However, in this case we did not compare different baits against a standard (such as fermented banana), but they were tested against each other. Liquids were presented in a transparent plastic cup, and banana and fermented banana on a plate. On occasions when the bait of one trap was presented in a cup, the other trap was also supplied with such a cup, filled with only water. When combinations were offered in one trap, the components were not mixed but presented in separate containers inside the trap. Differences between the total number of butterflies collected on two baits at one trap location

were analyzed per trap location per day, using a *t*-test for paired observations.

**FEEDING OBSERVATIONS ON FRUITS IN THE FIELD.**—We observed butterflies feeding on eight species of fruits in the field for a total of 5 h divided into 5–10 min observation blocks in the early afternoon on sunny days. To reduce disturbance effects, observations started at least 5 min after arrival at the observation site. We recorded the fruit species, stage index (unripe, ripe, overripe, and decaying), and the density of the fruits, the diameter of the fruit fall as well as the local temperature.

## RESULTS

**FRUIT QUALITY.**—The mean sucrose level of all the fruits was 6.1 percent per unit of dry matter and 3.5 percent per unit of fresh weight. Sucrose levels differed significantly among fruit species (Kruskal–Wallis test:  $df = 7$ ,  $P < 0.001$ ), and the range in sugar concentration was relatively wide in overripe *Ficus* fruits (Fig. 1). A general linear modeling (GLM) approach with sucrose percentage per unit of fresh weight as the dependent value ( $R^2 = 30\%$ ) showed no significant effect of stage index ( $F = 0.17$ ,  $df = 1$ ,  $P = 0.89$ ), and no significant interaction between fruit species and stage index ( $F = 0.58$ ,  $P = 0.72$ ).

The average nitrogen content per gram dry weight was 109.09 mg/g, and nitrogen content differed significantly among species (GLM:  $R^2 = 67$ ,  $F = 21.29$ ,  $P < 0.0001$ ; Fig. 2). The stage index (ripe–overripe) showed a weak trend toward higher nitrogen concentrations in overripe fruits ( $F = 2.62$ ,  $P = 0.12$ ), without significant interaction between fruit species and stage index ( $F = 1.55$ ,  $P = 0.22$ ). No significant quantitative differences were detected among the elements carbon, hydrogen, and sulphur.

**ATTRACTIVENESS OF FRUITS.**—We caught 1387 individual butterflies of 53 species in fruit-baited traps. Including the fermented banana treatment, 3635 individuals of 70 species were recorded

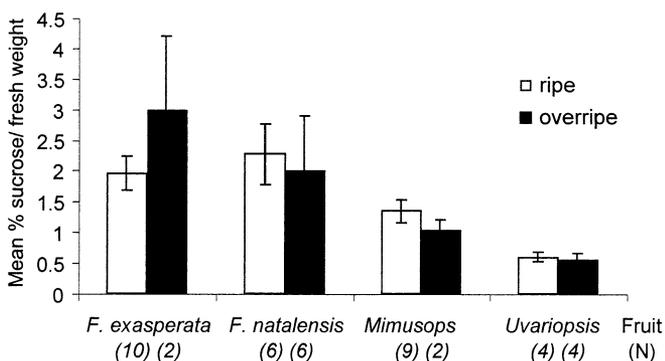


FIGURE 1. Mean percentage of sucrose in ripe and overripe fruits collected from Kibale Forest per unit of fresh weight ( $N$  for each sample is given below the species name and standard error bars are  $\pm 1$  SE).

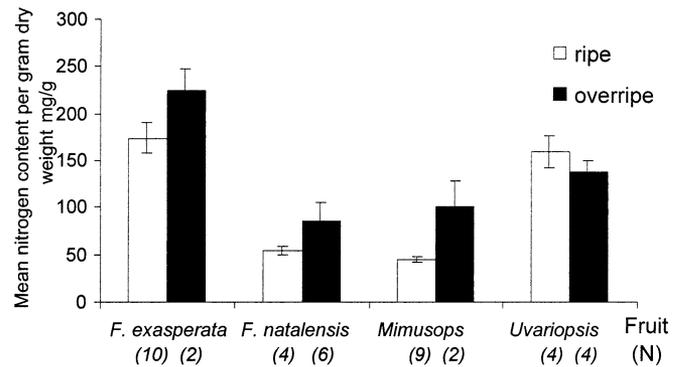


FIGURE 2. Nitrogen contents of ripe and overripe fruits collected from Kibale Forest per unit of dry weight ( $N$  for each sample is given below the species name and standard error bars are  $\pm 1$  SE).

over all trials in this experiment. There were significant differences between the fruits in their attractiveness to butterflies. Attractiveness was influenced by the age of the fruit, and there was a significant interaction between fruit species and age (Table 1).

The fruits of *Diospyros abyssinica*, *F. congestis*, *F. exasperata*, and *M. bagshawei* showed a clear decline in attractiveness with age (Fig. 3). *Strychnose mitis* was more attractive on the second day than on the first day, and *F. natalensis* was the least attractive. In contrast to the other butterfly genera, *Charaxes* tended to prefer *Balanitis wilsoniana* over fermented banana, and *Bicyclus* was the only genus preferring *D. abyssinica* over fermented banana (Fig. 4). Such differences in odor preference among the four most abundant butterfly genera resulted in a nearly significant interaction between the fruit species and butterfly genus (GLM:  $R^2 = 0.17$ ,  $F = 1.67$ ,  $df = 15$ ,  $P = 0.06$ ). Fruit species and butterfly genus were nonsignificant factors in this analysis ( $F = 0.9$ ,  $df = 5$ ,  $P = 0.47$  and  $F = 0.45$ ,  $df = 3$ ,  $P = 0.71$ , respectively).

The relative attractiveness (for a genus) of the least preferred bait (for all butterflies together) differed among the four genera (Fig. 5; GLM:  $R^2 = 0.40$ ; preference,  $F = 53.3$ ,  $P < 0.0001$ ; genus,  $F = 15.1$ ,  $P < 0.0001$ ; interaction,  $F = 4.85$ ,  $P = 0.0027$ ). When the overall strength of preference had values between 0 and 30 percent (clear preference), there were significant differences among the genera (ANOVA  $F = 8.0$ ,  $P < 0.0001$ ), while there were no such differences among these four genera when overall preferences were weak (30–50%;  $F = 2.1$ ,  $P = 0.10$ ).

Following our definitions, the *Charaxes* showed no significant difference in order of odor preference from the other fruit-feeding

TABLE 1. GLM model for natural logarithm of percentage caught on forest fruit analyzed for all butterflies pooled ( $R^2 = 0.43$ ).

Source	df	Sum of squares	F ratio	P-value
Fruit species	9	15.06	3.86	0.0006
Age bait	1	1.29	2.97	0.090
Age bait $\times$ fruit species	9	7.93	2.03	0.050

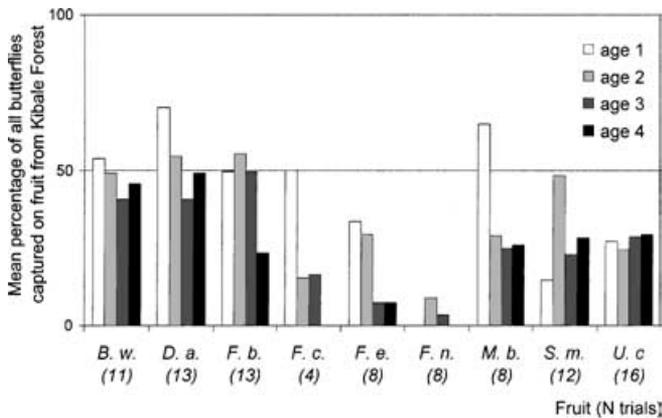


FIGURE 3. Mean percentage of butterflies caught on fruit collected from the forest tested against fermented banana in trials with fruits of different species per day after baiting with ripe fruit at Kibale Forest (*N* for each sample is given below the species name). Note that the fermented banana is aging simultaneously. Abbreviations: *B. w.* = *Balanitis wilsoniana*, *D. a.* = *Diospyros abyssinica*, *F. b.* = *Ficus brachylepis*, *F. c.* = *F. congensis*, *F. e.* = *F. exasperata*, *F. n.* = *F. natalensis*, *M. b.* = *Mimusops bagshawei*, *S. m.* = *Strychnose mitis*, *U. c.* = *Uvariopsis congolensis*.

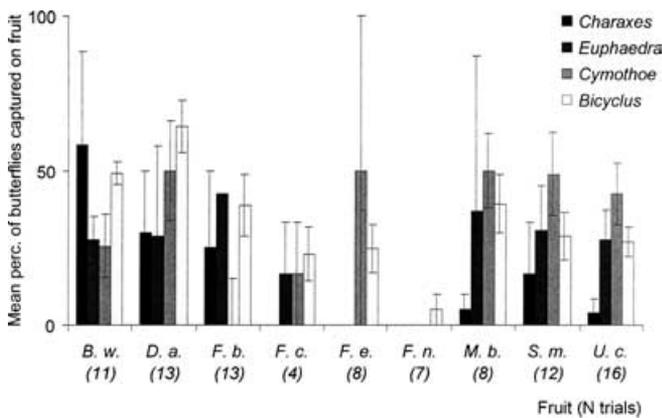


FIGURE 4. Mean percentage of butterflies caught on fruit collected from the forest tested against fermented banana in trials with fruits of different species for the four most abundant fruit-feeding butterfly genera at Kibale Forest (*N* for each sample is given below the species name and standard error bars are  $\pm 1$  SE). Abbreviations: *B. w.* = *Balanitis wilsoniana*, *D. a.* = *Diospyros abyssinica*, *F. b.* = *Ficus brachylepis*, *F. c.* = *F. congensis*, *F. e.* = *F. exasperata*, *F. n.* = *F. natalensis*, *M. b.* = *Mimusops bagshawei*, *S. m.* = *Strychnose mitis*, *U. c.* = *Uvariopsis congolensis*.

butterflies (highest number on the same bait as in other groups), but had a higher ability to find preferred baits (*i.e.*, higher percentage on preferred bait). In this experiment, 2.6 percent of the total catch was *Charaxes*, 80 percent of which were *Charaxes fulvescens*.

ATTRACTIVENESS OF INDIVIDUAL COMPONENTS.—We observed wide variation in attractiveness across the baits tested (Fig. 6). Water alone was not attractive to fruit-feeding butterflies in this study, and amino acids were only slightly attractive (Fig. 6). Yeast solution by

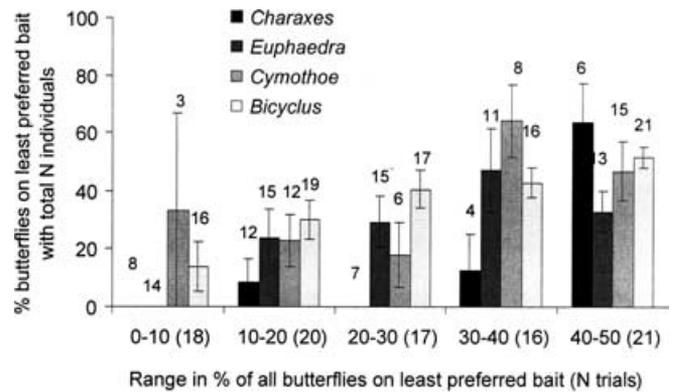


FIGURE 5. Mean percentage of butterflies caught on least preferred bait (based on preference of all butterflies together) in trials with fruits of different species and ages tested against fermented banana, for the four most abundant fruit-feeding butterfly genera at Kibale Forest (*N* for each trial category is given below the species name, and the number of individuals per genus per trial category above the individual bars). The standard error bars are  $\pm 1$  SE. Trials were categorized to overall preference (left strong, right weak) on the x-axis (see text).

itself was slightly attractive, but the addition of yeast to sugar (which subsequently fermented) made this bait more attractive (two-tailed *t*-test for means of paired observations: 7 trials, 66 butterflies,  $P = 0.016$ ). The addition of sugar and yeast to the amino acid solution made it more attractive (Fig. 6; two-tailed *t*-test for means of paired observations: 14 trials, 93 butterflies,  $P = 0.006$ ).

FEEDING IN THE FIELD.—During previous work, no butterflies were observed feeding on *B. wilsoniana* fruits even when the fruits were piled in a large heap or when starved butterflies were provided them in captivity. Therefore, we made no further observations on this fruit.

A total of 381 individuals of 32 species were observed feeding at natural fruit falls during short scan observations. Two individual Charaxinae were observed at fruit in the field: *Charaxes pleione* and a male from the *Charaxes etheocles*-group. *Charaxes* represented only 0.4 percent of the individuals observed feeding on natural fruit falls, a small fraction of their relative abundance in the trapping experiment.

Abundance of butterflies at a fruit fall is dependent on their phenology. Since we could not control for this factor the following numbers should be treated with caution. However, most fruit species were tested at different times during the field study.

The abundance of fruits in a fruit fall was correlated with fruit species (Fig. 7;  $R^2 = 37\%$ ,  $F = 3.9$ ,  $P = 0.0137$ ). The number of butterflies that gathered at a fruit fall depended on fruit species (ANOVA:  $F = 6.0$ ,  $P = 0.0014$ ) and was not affected by the number of fruits nor varied with the narrow weather and temperature range (GLM:  $R^2 = 0.51$ ; total number of fruits,  $F = 0.48$ ,  $P = 0.49$ ; interaction between fruit species and total number of fruits,  $F = 0.33$ ,  $P = 0.8$ ; weather,  $F = 0.64$ ,  $P = 0.69$ ; temperature,  $F = 0.67$ ,  $P = 0.42$ ).

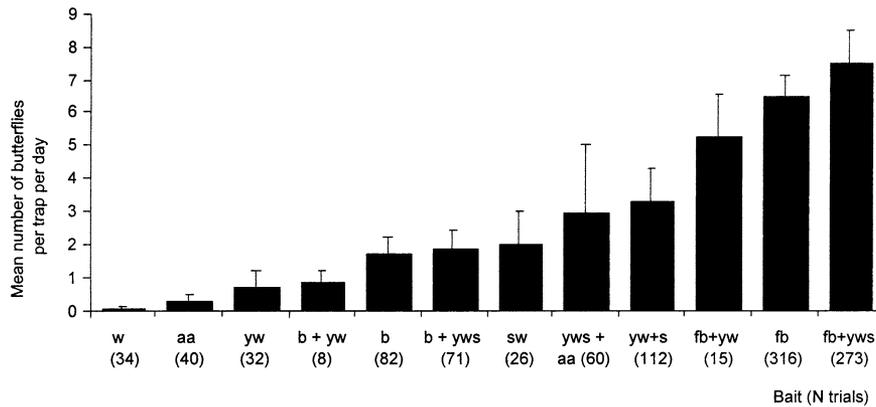


FIGURE 6. The mean number of butterflies trapped per trap per day for all baits with a set of more than seven trials at Kibale Forest ( $N$  for each sample is given below the bait name and standard error bars are  $\pm 1$  SE). Abbreviations: w = water, yw = yeast water, yws = yeast water with sugar, s = sugar, aa = amino acid solution, b = banana, fb = fermented banana.

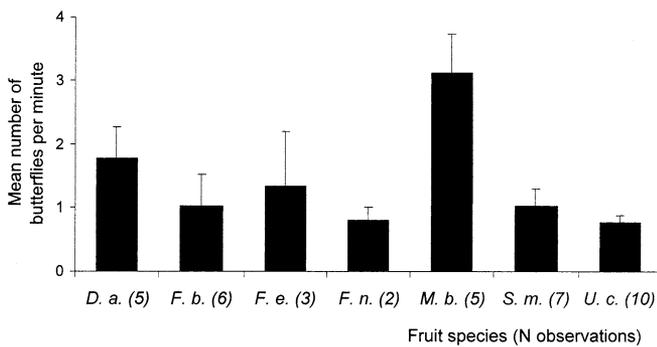


FIGURE 7. The average number of butterflies observed per minute at a fruit fall for different fruit species at Kibale Forest ( $N$  for each sample is given below the bait name and standard error bars are  $\pm 1$  SE). Comparisons among fruits have to be taken with caution because butterfly abundance is not constant over time. Abbreviations: *D. a.* = *Diospyros abyssinica*, *F. b.* = *Ficus brachylepis*, *F. e.* = *F. exasperata*, *F. n.* = *F. natalensis*, *M. b.* = *Mimusops bagshawei*, *S. m.* = *Strychnose mitis*, *U. c.* = *Uvariopsis congolensis*.

## DISCUSSION

All fruits had significant concentrations of sucrose that tended to fall within the range found in floral nectar (Baker & Baker 1990; Hainsworth & Hamill 1993; Brown & Hopkins 1995; Baker *et al.* 1998; Bernardello *et al.* 1999, 2000). The sucrose variation within fruits may be explained by variation among trees (Chapman *et al.* 2003), position in the tree, ripeness, or stage of decay. As ripening proceeds, sugar concentrations can rise but subsequently decrease rapidly as fermentation occurs. The nitrogen content of fruits varied (Fig. 2) but was generally higher than floral nectar.

Life history can be expected to evolve in response to the nutrient content and temporal and spatial distribution of fruits, involving changes in the level of stored nutrients, or in phenology, dispersal, and longevity. In particular, fruits are thought to be more protein-rich than nectar, and adult fruit-feeding butterflies could use these

proteins for reproduction (Brakefield & Kesbeke 1995), making the reproductive output less dependent on stored nutrients from the larval stage (Boggs 1987). Such a change from capital to income breeding can affect the evolution of traits such as longevity (Dunlap-Pianka *et al.* 1977) and may ultimately affect the population dynamics of a species (Tammaru & Haukioja 1996). However, data on such effects in fruit-feeding butterflies are rare and a study on the fruit-feeding *B. anynana* showed no effect of protein on longevity and female reproduction (Molleman 2004).

Since fruits and other odorous baits in traps are successfully located, fruit-feeding butterflies likely use odor cues to find food. Learning may affect butterfly behavior in trapping experiments, but mark recapture data indicate no large role for it (F. Molleman, pers. obs.; Hughes *et al.* 1998; Ferman *et al.* 2003), and location effects were avoided by exchanging baits between traps in a trial. Attractiveness of fruit odors differed among fruits and between the indices for ripeness. The change in attractiveness with the age of the fruit differed among fruits and may be due to differences in chemical composition or fruit size. The dynamics of this process probably depends on size of the fruit, amount of sugar that can be fermented, weather conditions, and chemical defense against fungi (Cipollini & Stiles 1993).

The extra attraction of fermented banana compared to fermenting sugar may be due to additional volatiles in fermented banana. Yeast alone was only slightly attractive to the butterflies. Likely candidates responsible for this attraction are quinones that are attractive to saprophagous Scarabaeidae (Krell *et al.* 1999), many of which were regularly found in butterfly traps. Other candidate substances include the organic acids. Fruit-specific volatiles probably also play a role since unfermented banana also attracted significant numbers of butterflies, although fewer than fermenting sugar or fermented banana. The important role of odors in foraging behavior is shared between fruit- and nectar-feeding butterflies, although, the nature of the scents used differs greatly (Andersson *et al.* 2002, Andersson & Dobson 2003).

Since butterflies can be intoxicated by alcohol, the attractiveness of fermentation products may not mean that fermenting fruits

are the most preferred for ingestion. However, the strong odor of fermenting fruits can likely be detected at long distances, and in a forest environment it probably forms a reliable cue for locating a fruit fall.

Attractiveness of fruits (as shown in trapping experiments) was not strongly correlated with acceptance (feeding observations and fruit falls; Figs. 3 and 7). This may, in part, be due to changes in population density of butterflies and fruiting trees that reflect observations on fruit falls. The discrepancy between attractiveness and acceptability was marked in *B. wilsoniana*; these sweet odorous fruits were very attractive to butterflies but were never accepted as food in captivity, and natural fruit falls were not associated with significant numbers of butterflies. *Balanitis wilsoniana* fruits are eaten by only a few vertebrate species and their seed dispersal relies mostly on elephants (*Loxodonta africana*). Moreover, they are used locally as fish poison and in shampoos to remove hair lice (Chapman *et al.* 1992). They are, therefore, probably poisonous for butterflies as well. In contrast, *F. natalensis* attracted few butterflies to the traps even though the fruits are juicy, sweet, have a soft skin, and are also readily accepted (Molleman *et al.* in press.).

The accessibility of juice seems important for fruit acceptance by butterflies. *Ficus exasperata* fruits have a rough skin, are not rich in juice, and are fed on by few butterflies because the fruits on the ground are hard. A rough or thick skin can, however, be circumvented when other animals damage it. For example, occasionally *F. exasperata* fruit falls were well visited (Fig. 7), and this coincided with the presence of ripe fruits partly eaten by other animals. *Strychnose mitis* fruits both attracted, and were accepted by butterflies after monkeys had removed the skin of the fruit, but without this interaction the fruits would be inaccessible to butterflies.

Our results suggest that there may be differences in odor preferences among butterfly genera (Fig. 4). Butterfly genera differed in their ability to find preferred food. When a clear preference was detected in all butterflies together (more than 70% on one of the baits), *Charaxes* often showed the highest ability to find the preferred fruit and *Bicyclus* the lowest. The set up with traps in groups of four provided the butterflies with a choice. The distance between the traps together with the sensitivity, size, and mobility of particular butterfly species probably determined the amount of opportunity to make a choice. For example, the small size and weak flight of *Bicyclus* contrasted with the large size and strong flight in *Charaxes*, and this can make the area that is sampled by a trap larger for *Charaxes* than *Bicyclus* species.

Charaxinae were rarely observed feeding on fruits in the forest (0.4% of all observed butterflies), even though they were attracted to fermented banana bait (2.1% of all trapped butterflies on fermented banana). Charaxinae may be able to accurately locate high-quality foods, including alternative resources such as bleeding trees that were not included in the surveyed fruit falls. Additionally, there is evidence that Charaxinae are able to feed more efficiently on certain fruits than are other butterflies (Molleman *et al.*, in press), and may thus spend less time at a fruit fall and overall be less likely to be observed feeding on fruit.

Our results show that (1) fruits contain significant and variable concentrations of sugar and nitrogen and constitute a nutritious

food source for butterflies in tropical forests; (2) fruit-feeding butterflies use odor cues from both fruits and fermentation products to locate their food; (3) different classes of fruit-feeding butterflies may vary in their preferences for certain fruits, and differ in their ability to find preferred food; and (4) fruit choice is not strongly correlated with attractiveness or nutrient content. This study provides background information for trapping studies on fruit-feeding butterflies and a basis for elucidating behavioral and life history evolution associated with differences in diet and among different classes of fruit-feeding butterflies.

## ACKNOWLEDGMENTS

We would like to thank the late Patrick Kagoro, and Boniface Balyeganira, Dennis Sebugwawo, and Moses Musana for their great assistance with the fieldwork. We are grateful to Easter Mugwusi for accurate data entry. Helene de Vos and Jos van Brussel greatly assisted with the chemical analyses. The manuscript benefited substantially from comments from Phil DeVries, Richard Vane-Wright, and two anonymous reviewers. This study was conducted with kind permission of the Uganda Wildlife Authority (UWA) and the Ugandan National Council for Science and Technology (UNCST). The funding for this project was provided by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO) (W80-82-238 to PMB) and NWO (811-34.005 to BJZ).

## LITERATURE CITED

- ALTSHULER, D. L. 2001. Ultraviolet reflectance in fruits, ambient light composition and fruit removal in a tropical forest. *Evol. Ecol. Res.* 3: 767–778.
- ALVES-COSTA, C. P., AND A. V. LOPES. 2001. Using artificial fruits to evaluate fruit selection by birds in the field. *Biotropica* 33: 713–717.
- ANDERSSON, S., AND H. E. M. DOBSON. 2003. Behavioral foraging responses by the butterfly *Heliconius melpomene* to *Lantana camara* floral scent. *J. Chem. Ecol.* 29: 2303–2318.
- , L. A. NILSSON, I. GROTH, AND G. BERGSTROM. 2002. Floral scents in butterfly-pollinated plants: Possible convergence in chemical composition. *Bot. J. Linn. Soc.* 140: 129–153.
- BAKER, H. G., AND I. BAKER. 1990. The predictive value of nectar chemistry to the recognition of pollinator types. *Isr. J. Bot.* 39: 157–166.
- , ———, AND S. A. HODGES. 1998. Sugar composition of nectars and fruits consumed by birds and bats in the tropics and subtropics. *Biotropica* 30: 559–586.
- BERNARDELLO, G., G. J. ANDERSON, T. F. STUESSY, AND D. J. CRAWFORD. 2001. A survey of floral traits, breeding systems, floral visitors, and pollination systems of the angiosperms of the Juan Fernandez Islands (Chile). *Bot. Rev.* 67: 255–308.
- , L. GALETTO, AND G. J. ANDERSON. 2000. Floral nectary structure and nectar chemical composition of some species from Robinson Crusoe Island (Chile). *Can. J. Bot.* 78: 862–872.
- , ———, AND A. FORCONE. 1999. Floral nectar chemical composition of some species from Patagonia. II. *Biochem. Syst. Ecol.* 27: 779–790.
- BOGGS, C. L. 1987. Ecology of nectar and pollen feeding in Lepidoptera. In F. J. R. Slansky and J. G. RODRIGUEZ (Eds.). *Nutritional ecology*

- of insects, mites and spiders, pp. 369–391. John Wiley and sons, New York.
- BRAKEFIELD, P. M., AND F. KESBEKE. 1995. Raised adult lifespan and female fecundity in tropical fruit-feeding *Bicyclus* butterflies. *Proc. Exp. Appl. Entomol.* 6: 93–98.
- BROWN, E. D., AND M. J. G. HOPKINS. 1995. A test of pollinator specificity and morphological convergence between nectarivorous birds and rain-forest tree flowers in New-Guinea. *Oecologia* 103: 89–100.
- CHAPMAN, C. A., L. J. CHAPMAN, K. D. RODE, E. M. HAUCK, AND L. R. MCDOWELL. 2003. Variation in the nutritional value of primate foods: Among trees, time periods, and areas. *Int. J. Primatol.* 24: 317–333.
- , R. W. WRANGHAM, L. J. CHAPMAN, D. K. KENNARD, AND A. E. ZANNE. 1999. Fruit and flower phenology at two sites in Kibale National Park, Uganda. *J. Trop. Ecol.* 15: 189–211.
- CHAPMAN, L. J., C. A. CHAPMAN AND R. W. WRANGHAM. 1992. *Balanites wilsoniana*: Elephant dependent dispersal? *J. Trop. Ecol.* 8: 275–283.
- CIPOLLINI, M. L., AND D. J. LEVEY. 1991. Why some fruits are green when they are ripe: Carbon balance in fleshy fruits. *Oecologia* 88: 371–377.
- , AND E. W. STILES. 1993. Fruit rot, antifungal defense, and palatability of fleshy fruits for frugivorous birds. *Ecology* 74: 751–762.
- CONKLIN-BRITTAIN, N. L., R. W. WRANGHAM, AND K. D. HUNT. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *Int. J. Primatol.* 20: 971–998.
- CORBET, S. A. 2000. Butterfly nectaring flowers: Butterfly morphology and flower form. *Entomol. Exp. Appl.* 96: 289–298.
- DEVRIES, P. J. 1988. Stratification of fruit-feeding Nymphalid butterflies in a Costa Rican rainforest. *J. Res. Lepid.* 26: 98–108.
- , D. MURRAY, AND R. LANDE. 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biol. J. Linn. Soc.* 62: 343–364.
- DUNLAP-PIANKA, H. L., C. L. BOGGS, AND L. E. GILBERT. 1977. Ovarian dynamics in Heliconiine butterflies: Programmed senescence versus eternal youth. *Science* 197: 487–490.
- FERMON, H., M. WALTERT, AND M. MUHLENBERG. 2003. Movement and vertical stratification of fruit-feeding butterflies in a managed West African rainforest. *J. Insect Conserv.* 7: 7–19.
- GENARD, M., F. LESCOURET, L. GOMEZ, AND R. HABIB. 2003. Changes in fruit sugar concentrations in response to assimilate supply, metabolism and dilution: A modeling approach applied to peach fruit (*Prunus persica*). *Tree Physiol.* 23: 373–385.
- GILBERT, L. E. 1972. Pollen feeding and reproductive biology of *Heliconius* butterflies. *Proc. Natl Acad. Sci. USA* 69: 1403–1407.
- HAINSWORTH, F. R., AND T. HAMILL. 1993. Foraging rules for nectar: Food choices by painted ladies. *Am. Nat.* 142: 857–867.
- HIEBERT, S. M., AND W. A. CALDER. 1983. Sodium, potassium and chloride in floral nectars: Energy-free contributions to refractive index and salt balance. *Ecology* 64: 399–402.
- HUGHES, J. B., G. C. DAILY, AND P. R. EHRLICH. 1998. Use of fruit bait traps for monitoring of butterflies (Lepidoptera: Nymphalidae). *Rev. Biol. Trop.* 46: 697–704.
- KALKO, E. K. V., AND M. A. CONDON. 1998. Echolocation, olfaction and fruit display: How bats find fruit of *Flagellichorou cucurbitis*. *Funct. Ecol.* 12: 364–372.
- KINZEY, W. G., AND M. A. NORCONK. 1993. Physical and chemical-properties of fruits and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. *Int. J. Primatol.* 14: 207–227.
- KRELL, F. T., T. SCHMITT, AND K. E. LINSENMAIR. 1999. The rhinoceros beetle *Cyphonistes tuberculifrons* Quedenfeldt 1884 attracted by quinones (Coleoptera Scarabaeidae Dynastinae): Primary olfactory attraction of a saprophagous beetle by its source of food? *Trop. Zool.* 12: 297–307.
- KRENN, H. W., K. P. ZULKA, AND T. GATSCHNEGG. 2001. Proboscis morphology and food preferences in nymphalid butterflies (Lepidoptera: Nymphalidae). *J. Zool.* 254: 17–26.
- LANDOLT, P. J., AND C. L. SMITHHISLER. 2003. Characterization of the floral odor of Oregon grape: Possible feeding attractants for moths. *Northwest Sci.* 77: 81–86.
- LUCAS, P. W., T. BETA, B. W. DARVELL, N. J. DOMINY, H. C. ESSACKJEE, P. K. D. LEE, D. OSORIO, L. RAMSDEN, N. YAMASHITA, AND T. D. B. YUEN. 2001. Field kit to characterize physical, chemical and spatial aspects of potential primate foods. *Folia Primatol.* 72: 11–25.
- MOLLEMAN, F. 2004. Patterns of biodiversity and life history in fruit-feeding butterflies. PhD Thesis, Leiden University, Leiden.
- MOLLEMAN, F., H. KRENN, M. E. VAN ALPHEN, P. M. BRAKEFIELD, P. J. DEVRIES, AND B. J. ZWAAN In press. Food intake of fruit-feeding butterflies: Evidence for adaptive variation in proboscis morphology. *Biol. J. Linn. Soc.*
- MOLLON, J. D., AND B. C. REGAN. 1999. The spectral distribution of primate cones and of the macular pigment: Matched to properties of the world? *J. Optical Technol.* 66: 847–852.
- MORAIS, P. B., M. B. MARTINS, L. B. KLACZKO, L. C. MENDONCAHAGLER, AND A. N. HAGLER. 1995. Yeast succession in the amazon fruit *Parahancornia amapa* as resource partitioning among *Drosophila* spp. *Appl. Environ. Microbiol.* 61: 4251–4257.
- NORRIS, M. J. 1936. The feeding-habits of the adult Lepidoptera Heteroneura. *Trans. Roy. Entomol. Soc. London* 85: 61–90.
- OMURA, H., K. HONDA, AND N. HAYASHI. 2000. Floral scent of *Osmanthus fragrans* discourages foraging behavior of cabbage butterfly, *Pieris rapae*. *J. Chem. Ecol.* 26: 655–666.
- , ———, A. NAKAGAWA, AND N. HAYASHI. 1999. The role of floral scent of the cherry tree, *Prunus yedoensis*, in the foraging behavior of *Leuhdorfia japonica* (Lepidoptera: Papilionidae). *Appl. Entomol. Zool.* 34: 309–313.
- PHAFF, H. J., AND W. T. STARMER. 1987. Yeast associated with plants, insects and soil. In A. T. Rose and J. S. Harrison (Eds.). *Biology of yeasts*, pp. 123–180. Academic Press, London.
- SUMNER, P., AND J. D. MOLLON. 2000. Chromaticity as a signal of ripeness in fruits taken by primates. *J. Exp. Biol.* 203: 1987–2000.
- TAMMARU, T., AND E. HAUKIOJA. 1996. Capital breeders and income breeders among Lepidoptera: Consequences to population dynamics. *Oikos* 77: 561–564.
- URBANI, B. 2002. A field observation on color selection by new world sympatric primates, *Pithecia pithecia* and *Alouatta seniculus*. *Primates* 43: 95–101.
- WEISS, M. R. 1997. Innate colour preferences and flexible colour learning in the pipevine swallowtail. *Anim. Behav.* 53: 1043–1052.
- , AND B. B. LAMONT. 1997. Floral color change and insect pollination: A dynamic relationship. *Isr. J. Plant Sci.* 45: 185–199.
- WILLSON, M. E., AND C. J. WHELAN. 1990. The evolution of fruit color in fleshy-fruited plants. *Am. Nat.* 136: 790–809.
- WRANGHAM, R. W., N. L. CONKLIN-BRITTAIN, AND K. D. HUNT. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *Int. J. Primatol.* 19: 949–970.