FOOD AND FEEDING HABITS OF THE FRUIT-EATING BAT *CAROLLIA PERSPICILLATA*

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Introduction

On 16 July 1992 I realised that a small group of bats, perhaps three or four, had been hanging up in a corner of my bedroom to feed. They did not roost there during the day but used the spot as a temporary roost for feeding only. Getting rid of them I thought might be difficult so I decided to study their feeding behaviour instead. To do that I simply put a sheet of newspaper below the roost to collect the discarded food and faeces and examined the collection later. At first I did this the next day; later the collections accumulated over several days. My interest at the start of the project was simply the food they ate, but when casual obserations suggested that feeding activity was much greater after mid-night than before, I changed the paper at mid-night so I could separate the collections into one before mid-night and one after. At first I could not identify all the fruit or eliminated seeds I found, but by comparing them with fruit I could pick on nearby trees and by growing plants from the seeds, I eventually identified almost all of the species involved.

All the observations were made at this one site at Haven Hill Farm, Talparo. On 16 May 1993 the bat was identified as *Carrollia perspicillata* by April Allgaier.

The food

Most of the food consists of fruit, and Table 1 records the species, and their monthly distribution throughout the study. The droppings consisted of whole green fruit, portions of uneaten fruit, fruit skins that were more or less complete, bits of skin, calyces, seeds, pulp, and faeces containing seeds and pulp. Some fruit were comparatively easy to recognise, some were not.

There were two species of *Vismia* and two of *Piper*. *Vismia cayennensis* has slightly larger fruit than *Vismia falcata* . However, I could not absolutely identify the two species by the sizes of the discarded fruit skins, so I decided on the species collected by looking at the species in fruit at the time. The two species of *Piper* were identified from plants grown from the seeds of discarded fruit and faeces, as well as from recognisable portions of discarded fruits. I could not reliably identify the species from the appearance of the seeds alone so in Table 1 the two species were not separated. *Pothomorphe* seeds also could not be reliably distinguished from *Piper* so I relied on the examination of full- grown plants for ripe fruit when deciding presence or absence. A single spat, dark blue in colour, contained seeds resembling those in the family Melastomataceae and this is entered in Table 1 with a question mark.

The "white pulp" referred to in Table 1 sometimes contained seeds, sometimes not. Four plants were grown from the seeds and later identified as *Philodendron acutatum.* It is probable that this pulp at different times contains the fruit of other monocot species such as *Monstera spp* and *Musa spp*; I have seen the bats eat ripe plantains. I have also seen the bats collect the fruit of *Passiflora tuberosa* and *Pothomorphe peltata* which aided the identification of some of the droppings.

Not all the food is fruit. Partly-eaten leaves of *Cassia bacillaris* turned up so frequently that it is hard not to think of them as deliberately sought rather than accidently gathered. *C. bacillaris* flowers, though not so frequent as the leaves, also seem to be deliberately sought. There were at times other leaves, which remain unidentified. During May and June when beetles are usually common, wings, elytra and legs of a fairly large reddish brown beetle were frequently found and again it is hard to think of these beetles as not deliberately sought.

The condition of the uneaten parts of the fruit sometimes gave

Table I. Foods eaten by *Carollia perspicillata* from 1992 to 1994

Year	92						93												94					
Species	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
Vismia falcata **b**	●	●	●									●	●	●	●									
Piper spp **c**				●		●		●	●	●	●	●	●			●	●	●		●	●	●	●	●
Banara guianensis **b**		●	●												●									
Pothomorphe peltata **c**																		●			●			
Cecropia peltata **c**			●	●	●				●	●	●				●	●	●				●	●	●	
Rollinia exsucca **c**			●	●	●	●	●	●	●						●	●	●	●	●	●	●			
Vismia cayennensis **b**				●	●	●	●	●	●	●	●	●				●	●	●	●	●	●		●	●
Cassia bacillaris **l**							●	●	●	●	●								●	●	●	●	●	
"White pulp" P. acutatum **c**							●	●	●	●						●	●	●	●	●		●	●	
Castilla elastica **p**										●	●	●										●	●	
Passiflora tuberosa **b**																	●	●	●					
Melastome ? **b**																●			●					
Ficus trigonata **f**											●													
Psidium guajava **b**				●																				
Acnistus arborescens **b**												●											●	
Cassia bacillaris leaf, **fl**		●	●	●	●		●			●	●		●	●	●	●	●	●	●	●	●	●		
Insect parts											●	●						●					●	●

b = berry, **c** = composite fruit, **f** = fig, **l** = legume, **p** = fruit of partially fused carpels, **fl** = flower

information about the bats' manner of feeding. The uneaten parts of the *Vismia* fruits consisted of the skins with perhaps the calyx and stalk attached; the bats evidently squeeze the fruits, suck out the contents and spit out the skins. The fruits of *Banara guianenesis* were treated in the same way but because the fruit skin is not so tough as that of *Vismia* the skin was often torn into several pieces. On the other hand, the berry of *Acnistus arborescens* seems as a rule to be swallowed whole because I have never found discarded skins. The fruits of *Rollinia exsucca* were bitten open, the soft central parts with the seeds consumed and the harder material discarded. Although the entire fruit of *Cecropia peltata* seemed to be eaten sometimes, at other times the central columns (rhachides) were discarded. The difference in treatment may be due to the difference in size of the bats in the group for it seemed to consist of a mother and juveniles. The rhachides of *Piper* and *Pothomorphe* were regularly discarded. The seeds of *Cassia bacillaris* with adhering pulp were swallowed but the seeds of *Castilla elastica*, being somewhat larger, were sucked clean of pulp and discarded.

The time of feeding

Quite early in the study I realised that feeding after midnight seemed to be much more common than feeding before midnight. By changing the sheet of paper below the roost at midnight I collected two samples per night for 23 nights during the period from 24 July to 24 August 1992. At this time the bats were feeding almost exclusively on *Vismia falcata* fruit and by counting the discarded skins from which the contents had ben sucked out I could get a quantitative measure of feeding before and after midnight. Nights where there was something additional on the sheets were simply excluded from the count as were nights when I forgot to record the results.

There were 145 skins before midnight and 516 skins after midnight so the bats consumed significantly more food ($\chi^2 = 208$, $P<0.001$; all statistical treatments are as given in Moroney 1956) after midnight than before, 3.56 times more. Dividing these figures by 23 (the number of nights) the average number of fruits eaten per night was 6.3 before midnight and 22.4 after midnight. However, it was clear from examination of all the figures that counts on individual nights might differ greatly from the mean. Furthermore, it seemed that the higher figures occurred on nights when there was moonlight and lower ones when there was no moon. This suggested that moonlight helped the bats to find their food. Unfortunately, in July 1993 I was not collecting the droppings in two lots per night so I cannot check these results with results from the 1993 observations.

The influence of moonlight

For the examination of this topic a slightly different set of results was used i.e. the counts for the period 30 July (new moon) - 24 August (three days before new noon), Table II. The counts for 5, 8 and 12 August, which had been omitted from the analysis in the previous section because of tiny amounts of *Cecropia* fruit in the droppings, were now included. This allowed me to have eleven days of records before the full moon of 13 August and eleven days from 13 August to 24 August. In the first set of 11 days 348 fruits were eaten and in the second set 310, a non-significant difference when tested by χ^2 .

However, when the 11 days around full moon (7-19 August, Table II) were compared with the 11 days near new moon (30 July - 5 August plus 20 August-24 August, Table II) there was a great difference, with

Table II Numbers and distribution of *V. falcata* fruit eaten by *C. perspicillata* in the period 30 July-24 Aug. 1992 NM 30 July, FQ 5 August, FM 13 August, LQ 21 August

Period	Before midnight	After midnight
30 July - 6 August*	26	111
7 August - 12 August+	48	163
13 August - 19 August#	57	161
20 August - 24 August	13	79

*Excluding 1 Aug., 2 Aug.; +Excluding 10 Aug.; #Excluding 16 Aug.

429 fruits consumed in the first period and 229 in the second. Tested by χ^2 ($\chi^2 = 60.8$) they were significatly different at $P<0.001$.The bats consumed about twice as much food per night around full moon as around new moon.

Using the same figures in Table II, I did a further test of the influence of moonlight on the bats' behaviour. The ratio of fruits consumed before midnight to after midnight for the period 30 July-12 August is 74:274 or 1:3.70. The ratio for the period 13 August-24 August is 70:240 or 1:3.43. By the χ^2 test the difference between these two ratios was not significant. However, the same ratio for the eleven days around full moon (7 August-19 August) is 105:324 or 1:3.09 and for the eleven days near new moon (30 July-6 August plus 20 August-24 August) is 39:190 or 1:4.87. Tested by χ^2 this difference is significant ($\chi^2 = 4.42$, $P<0.05$). During the period of bright moonlight the bats increased their early feeding proportionally more (2.69 times) than they did their late feeding (1.71 times) and this difference is caused by the moonlight.

Discussion

Looking at the foods listed in Table 1 we can see that some of the foods were eaten for very long periods (*Vismia, Cecropia, Piper* and *Rollinia*) whereas others were eaten for short periods only. This is a reflection of their availability. In fact *Vismia* can be regarded as a staple food since it was eaten for all but one of the months in the two year period. The two species have virtually identical seeds, and although the fruits of *V.cayennensis* are slightly larger, determining which is which after the bats have discarded them is difficult. I determined which was present in the food at any one time by examining the trees around the farm for ripe fruit rather than by trying to distinguish the fruit in the droppings. *V. falcata* flowers for only about two months between May and July and the fruits are available from July to September. *V. cayennensis* fruits virtually throughout the year. It may be noted in passing that the various fruit consumed are almost all berries or compound fruit, since figs and the fruit of *Castilla* are also compound fruit though slightly different from the others. The odd one is the legume of *Cassia bacillaris*.

The only other similar study with which I am familiar is that of Greenhall (1956, 1957). He studied three species of bat, of which one was *C. perspicillata*, over the years 1954-1956 in various parts of Trinidad. Comparing the two lists of food plants it is immediately obvious that only a few species are common to both lists: *Cecropia peltata, Piper spp* and *Psidium guajava*. There are twenty other species on Greenhall's list so together the two studies record 36 food plants. From the presence of many ornamental and cultivated plants in Greenhall's

list I conclude that at least some of the localities studied were in Port of Spain and Greenhall (pers. comm. 1997) has confirmed this. Yet it is very strange that neither of the two *Vismia* species, nor *Rollinia,* so prominent in my list turns up in his and hogplum (*Spondias mombin*) common around Haven Hill Farm, does not turn up in mine though it appears in his.

There is every indication that the list can be further extended if studies were conducted in new areas. Furthemore, by separating the species lumped together, *Piper spp* for example, the list can again be lengthened. Thus *C. perspicillata* conforms with the expectation of Freeland and Janzen (1974) that as a generalist herbivore it consumes a wide range of plants. However, I am not at all sure that the term generalist herbivore should be appplied to a basically fruit-eating animal rather than a leaf-eating one; fruits have evolved to make themselves attractive to herbivores whereas leaves have evolved mechanisms to discourage herbivory.

The finding that more food was consumed in the six hours after midnight than the six hours before came as a surprise. I draw attention to the fact that I did not actually watch the bats feed. More bats may have come to the roost after midnight than before, and thus account for the difference, but I think this unlikely. Goodwin and Greenhall (1961) state that "*Carollia perspicillata* probably feeds twice during each night." The present results may be regarded as giving some support to this supposition though there is nothing in them to rule out the possibility of more or less continuous feeding. But even so, they don't give any clue as to why they should feed in two bouts, or why there should be more feeding in the second bout than the first. How do the bats spend their "free" time in the period before midnight? In increased searching for food or in some other entirely unrelated behaviour? In a population feeding night after night on the same food as these bats were doing, it would seem that the bats should know where to find their food and should have to spend relatively little time on searching for new sources. So my belief is that they spend most of the "extra" time in searching their surroundings for new roosts, in dominance rivalries and in sexual behaviour.

The increase in the amount of food taken at full moon compared with new moon also came as a surprise. The authors of two popular books (Peterson 1964, Schober 1984) mention that the eyes of the fruit-eating bats of the Old World tropics have special adaptations for seeing in the dark and that these adaptations help the bats to find their food. There is no mention of anything similar in the fruit-eating bats of the New World, but the present results show that they too use their eyesight. By the χ^2 test the increase in feeding near full moon as compard with that near new moon is significant and related to the presence of moonlight. From first quarter to full moon the moon is visible during the whole period of darkness up to midnight and with each passing night becomes visible for an increasingly long time in the period from midnight to dawn until at full moon it is visible all night long. From full moon to last quarter the moon is visble during the whole period from midnight to dawn but is visible in the period from dusk to midnight for decreasing lengths of time. During the whole period from first quarter to last quarter there is much more moonlight than in the period from last quarter to first quarter (Fig. 1) and the bats increase their feeding significantly in this period. The conclusion must be drawn that the moonlight helped the bats to find their food through the use of their eyes.

Figure 1 shows that in the period of moonlight from first quarter to last quarter there is as much light available from midnight to dawn as from dusk to midnight; yet, at this period around full moon as compared with that around new moon the bats increased their feeding in the first bout before midnight more than they increased their feeding in the second bout after midight. The χ^2 test clearly indicates that the difference is real and related to the moonlight. Why should it be so? I suggest that it is a case of striking while the iron is hot, making the best use of existing good conditions rather than waiting for later ones. With appetite at least partly sated in the first bout feeding in the second bout would not increase proportionally.

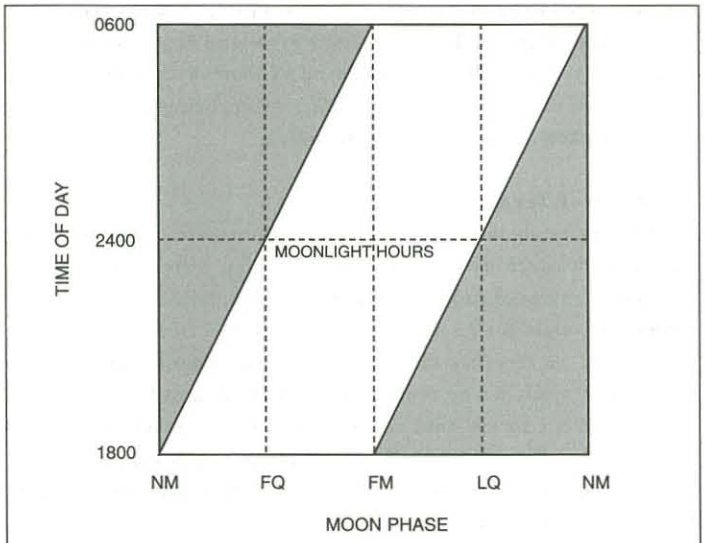

Figure 1: Idealised diagram to show the relationship between moon phase and the number of hours of moonlight between dusk and dawn.
NM - New Moon FQ - First Quarter FM - Full Moon
LQ - Last Quarter

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