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THE ECOLOGY OF THE FLOWERS OF THE SAVANNA TREE *MARANTHES POLYANDRA* AND THEIR VISITORS, WITH PARTICULAR REFERENCE TO BATS

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SUMMARY

(1) Nocturnal observations were made on *Maranthes polyandra* (Chrysobalanaceae), a common tree in the Guinea Savanna zone of West Africa, which shows many adaptations for pollination by bats.

(2) The flowers are borne on stiff pedicels in large white inflorescences, and each flower lasts for only one night. The anthers release pollen from about 19.30 hours, and the stigma matures at about 01.00 hours; nectar production is copious. The flowers are produced in the wet season when few other plants are flowering.

(3) The small bat *Nanonycteris veldkampi* (Pteropinae: Megachiroptera) visited the trees frequently for nectar. Feeding visits were sporadic soon after dusk, but became increasingly frequent until about 21.30 hours, after which very frequent visits were observed until dawn.

(4) Analysis of the pollen loads of twenty-nine bats showed that *Protea elliottii* is visited frequently in addition to *Maranthes polyandra*. The bats probably travel several kilometres during the night. No evidence was obtained for the bats feeding on anything except nectar.

(5) Various other visitors such as small insects, hawkmoths, genets and several bird species feed on the nectar or pollen.

INTRODUCTION

In this paper, the reproductive biology of the savanna tree *Maranthes polyandra* (Benth.) Prance (Chrysobalanaceae) (formerly *Parinari polyandra* Benth., Rosaceae) is examined in relation to the biology of its flower visitors, in particular the small Megachiroptera.

Bats are well-known as pollinators of various plant species in the Old and New Worlds, e.g. the Phyllostomatidae (Microchiroptera) in Central and South America (Vogel 1968–1969; Baker 1970, 1973; Heithaus, Opler & Baker 1974; Heithaus, Fleming & Opler 1975) and the Macroglossinae (Pteropidae: Megachiroptera) in South-east Asia (van der Pijl 1956; Start 1974; Start & Marshall 1976). Most African flower-visiting bats belong to the Pteropinae, which are primarily frugivores. Baker & Harris (1957, 1959) and Harris & Baker (1958, 1959) demonstrated that several species of Pteropinae visit flowers, but the biology of these bats, particularly the small solitary species, is very little known (Rosevear 1965). Ayensu (1974) provides a summary of some aspects of the biology of the West African fruit bats.

The present study was designed along similar lines to the study on *Bauhinia pauletia* Pers. (Caesalpiniaceae) by Heithaus, Opler & Baker (1974).

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MATERIALS AND METHODS

The study was undertaken during July and August 1976 in Mole National Park, Ghana (latitude 9° 20′ N, longitude 1° 50′ W), in the centre of the Guinea Savanna zone of West Africa. *Maranthes polyandra,* a tree up to 10 m tall, grows quite commonly in the park. For convenience and safety trees growing in the compound of the motel *c.* 2 km inside the southern boundary of the park (survivors from natural Guinea Savanna woodland) were studied most intensively, but for comparison, brief observations of pollinator-activity were made on a tree in typical woodland *c.* 400 m outside the compound.

Systematic observations on the visitors to the trees in the motel compound were made at 19.30–05.30 hours on 22–23 July, at 19.15–04.15 hours on 27–28 July, at 19.30–07.00 hours on 7–8 August, and at 19.15–01.15 hours on 15–16 August, with additional incidental observations between 17.30 and 19.30 hours and at dawn on several dates. The tree in typical woodland was observed from 02.00 to 03.00 hours on 7 August and from 21.30 to 22.30 hours on 16 August. All visitors to the flowers were recorded, and the activity of each visitor was noted, including its probable importance as a pollen vector. Observations at night were made by moonlight whenever possible, or using torches. Start (1974) found that bright or moving artificial light may frighten bats, so a steady wide beam was used, although a brighter torch was used occasionally.

Mist nets were set for the bats near flowering trees of *Maranthes polyandra* at 20.30–21.20 hours on 15 July, 02.00–03.00 hours on 7 August, 21.00–23.00 hours on 9 August, 19.30–21.15 hours on 15 August, 03.30–05.00 hours on 24 August, and 01.00–02.30 hours on 25 August. On all dates except 15 July, pollen was scraped from the fur on the front of the bats using a scalpel, and transferred to slides using a jelly preparation described by Beattie (1971). Three bats were killed for identification, and their stomach contents were examined.

The time of flower-opening and anthesis, and the numbers of flowers open each night, were determined for two inflorescences. The length of the style in three flowers was measured at hourly intervals during the night of 22–23 August, and notes made on the position of the anthers. The rate of nectar secretion was measured on the night of 10–11 August and 22–23 August: inflorescences were covered with polythene bags, and nectar was removed from five flowers each hour from 19.30 to 03.30 hours and soon after dawn, using a graduated syringe. The flowers were rebagged after each extraction. Further samples of nectar were extracted in the same way from covered flowers at daybreak on 22 July and 25 July.

RESULTS

Flower development

Flattened corymbs each bearing about 200 flowers are borne at the ends of stout branches, thus appearing on the outer surface of the tree (Plates 1 and 2, see also Lock & Marshall 1976). The inflorescences flower over about 2 weeks, with up to forty flowers open on any one night in the middle of that period. Each flower lasts only one night. The flowers start to open and nectar secretion begins at around 17.30 hours; they are completely open by 19.30–19.45 hours, about half an hour after dark, and anthesis then occurs. At this stage the anthers are positioned near the centre of the flower, and the style is 14–15 mm long, soft, and probably not receptive. During the night the anthers gradually move away from

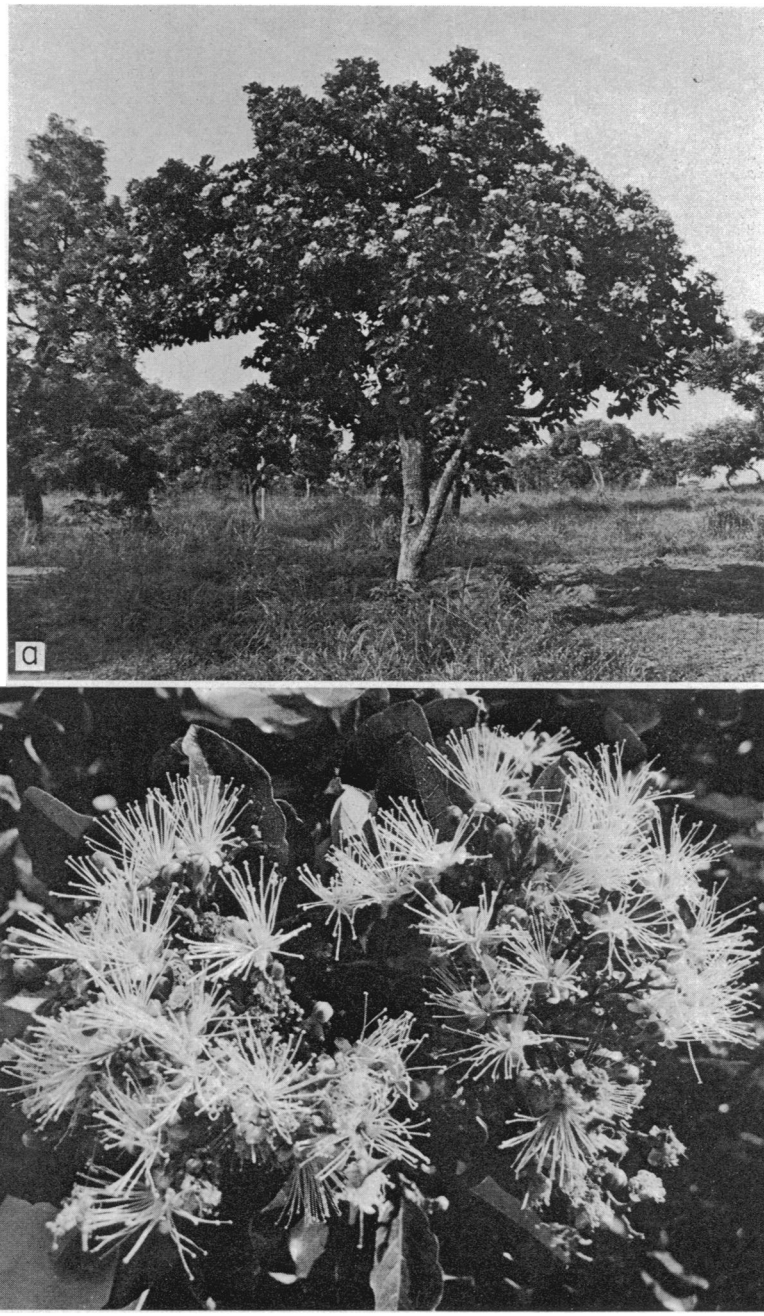


PLATE 1. (a) A well-grown tree of *Maranthes polyandra*, one of the trees used for observations. (b) Inflorescence of *Maranthes polyandra* at the peak of its flowering period; photograph taken in the morning, showing previous night's flowers, with anthers widely spaced and prominent style in the centre of each flower. Also visible are withered flowers from preceding nights, and buds (the most swollen buds will open on the following night). (Photographs by J. A. H. Benzie.)

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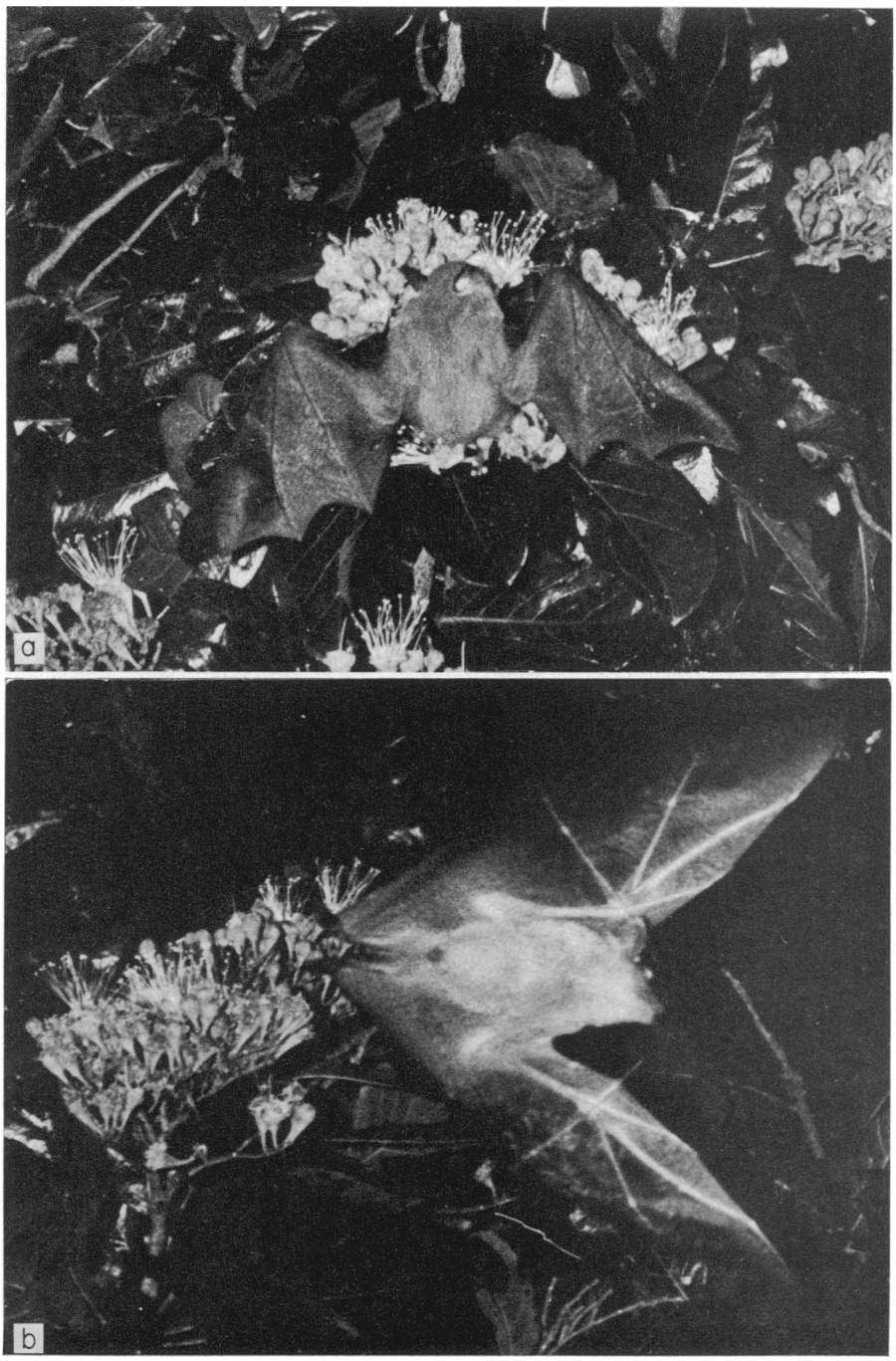


PLATE 2. (a) Small fruit bat feeding on the flowers of *Maranthes polyandra*. (b) Bat leaving an inflorescence of *Maranthes polyandra*. (Photographs by J. A. H. Benzie.)

the centre of the flower, and the style grows to its full length of 16–19 mm (mean of sixteen flowers, 17·3 mm); this process is completed by 01.00 hours. By about 10.00 hours only withered and unopened flowers can be seen. In some inflorescences the styles, though varying in length from 10 to 17 mm (mean of eleven flowers, 13·4 mm) never fully matured; the flowers all dropped off very soon after the night of opening. The difference in style lengths between these and normal flowers is significant ($t = 6{\cdot}17$, d.f. $= 25$, $P < 0{\cdot}001$), and those flowers with short styles are almost certainly functionally staminate.

Visitors to the flowers

Table 1 summarizes the floral cycle and flower visitors. The small insects which visited the flowers towards dusk left as darkness fell. Shortly after dark, visits by bats were sporadic and often very brief, but they became increasingly frequent until about 21.30

TABLE 1. Floral cycle of *Maranthes polyandra* in Ghana, based on observations in July–August 1976

Time (hours)	Flowers	Visitors
17.30	Flowers start to open and nectar secretion begins	Very many small insects including honeybees, feeding on nectar
18.30		
19.30	Flowers fully open and anthesis occurs	First bats visit the tree
20.30	Anthers near centre of flower; style immature	
21.30	Nectar copious	Vigorous bat activity (also a few hawkmoths and genets)
22.30		
23.30		
00.30	Anthers widely spaced; style mature, central	
01.30		
02.30		
03.30		
04.30		
05.30		Bat visits cease; very numerous honeybees (collecting pollen only)
06.30	All pollen gone	
07.30		Birds of several species feeding on remaining nectar
11.30	Flowers withered	

hours, after which very frequent visits occurred until about 05.20 hours, when they declined rapidly. Dawn broke at about 05.30 hours. On 7–8 August, when observations were perhaps most accurate owing to bright moonlight, two to four bats were feeding simultaneously on the observation tree on many occasions, though there was apparently no tendency to feed in flocks. Figure 1 shows the number of 'bat-minutes' spent by bats feeding from the flowers and flying around the tree between 19.30 and 23.30 hours (recorded by one observer) on 7 August. The pattern of visits was similar on the other observation nights, although, in general, slightly smaller numbers were recorded. These visits were all by small fruit bats, of which *Nanonycteris veldkampi* (Jentink) (Pteropinae: Pteropidae) was the only species collected and certainly identified. This species and *Micropteropus pusillus* (Peters) are indistinguishable in the field, and insufficient measurements were made on handled individuals for certain identification. Both species occur in the study area (Dr A.G. Marshall, personal communication). When visiting the flowers,

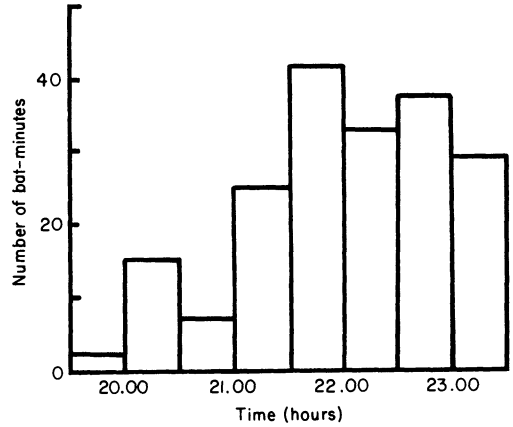


FIG. 1. Numbers of 'bat-minutes' spent by bats feeding and flying around the observation tree during successive 0·5-h periods on the night of 7 August.

the bats would normally fly up towards the tree and settle on an inflorescence for 1–3 s with the wings outstretched; they would then throw themselves backwards off the inflorescence before righting themselves and flying off (Plate 2). Occasionally longer visits of up to 10 s were seen. A few apparently larger bats were observed visiting the flowers between 19.30 and 21.00 hours on 22 July and 27 July; none was caught or identified. The tree in typical woodland had many fewer inflorescences than the tree in the compound, and received a much smaller number of visits.

In addition to bats, hawkmoths (Sphingidae) visited the trees in small numbers on each night of observation (ten visits observed on 27–28 July), and a few other moths were seen. Genets (*Genetta tigrina* Schreber), visited the trees regularly for nectar on 7–8 August and thereafter. At the first trace of dawn, honeybees appeared in large numbers and collected the remaining pollen, most of which had gone by 06.30 hours, when very few honeybees remained. For the first few hours of the day various bird species visited the flowers for nectar, e.g. the bulbul *Pycnonotus barbatus* (Desfontaines), the finch *Serinus mozambicus* (Müller), the sunbirds *Chalcomitra senegalensis* (L.) and *Cyanomitra verticalis* (Latham), the weavers *Ploceus cucullatus* (Müller) and *Plocepasser superciliosus* (Cretzchmar), and the warbler *Eremomela pusilla* Hartlaub. The activity of these birds on the flowers gradually declined until 10.00 hours, after which there were only a few sporadic visits. A few ants (Formicidae) and thrips (Thysanoptera) also fed on the nectar during the early morning.

Altogether, twenty-nine bats were caught in the mist nets. Microscopic analysis of the pollen loads (Table 2) showed that in addition to *Maranthes polyandra* pollen (which

TABLE 2. The numbers of captured bats bearing different types of pollen load

Total number of bats examined	*Maranthes polyandra* only	*M. polyandra* + *Protea elliottii*	*M. polyandra* + *P. elliottii* + *Adansonia digitata*
29	3	25	1

occurred on every slide), pollen from *Protea elliottii* (identified from a reference collection of pollen) occurred on most of the slides, although on some in very small amounts.

The three bat stomachs examined contained very little solid material. A small amount of *M. polyandra* pollen was present in two of the stomachs, one of which also contained the cuticles of a few thrips.

Nectar secretion

The rate of nectar secretion recorded on 10 August was constant from 19.30 to 23.30 hours (Fig 2(a): *c.* 0·07 ml h^{-1} per flower), after which production gradually declined until dawn. The average amount of nectar secreted per flower during the night was 0·47 ml (estimated from a bulked sample from five flowers). Other samples collected in the early morning from individual flowers (covered overnight) contained slightly less, *c.* 0·35–0·40 ml. Near the end of the flowering season on 22 August the average rate of secretion, estimated from bulked samples of five flowers, was 0·20 ml per flower per night (Fig 2(b)).

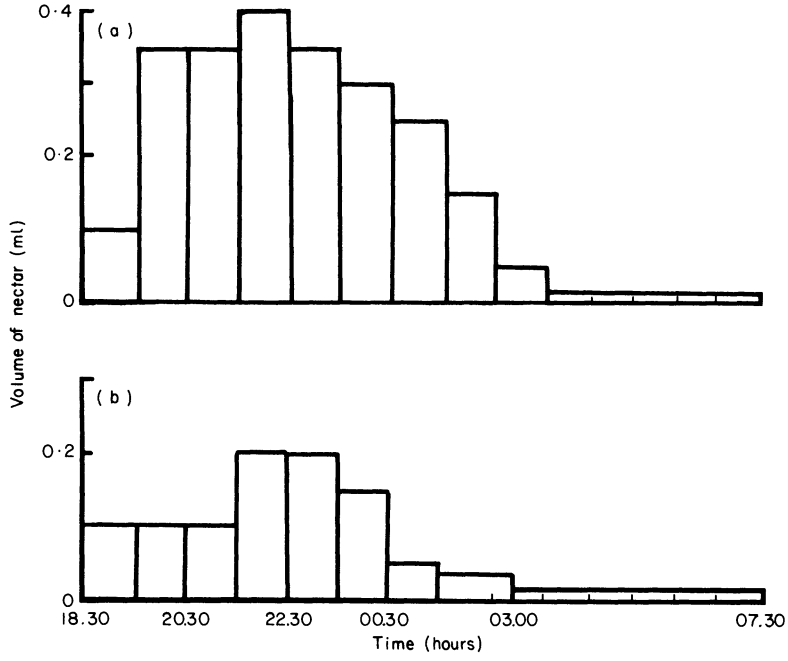


FIG. 2. Volumes of nectar (ml) secreted by five flowers of *Maranthes polyandra* over hourly periods on (a) 10 August, and (b) 22 August.

DISCUSSION

Pollination of Maranthes polyandra

Maranthes polyandra shows many adaptations to bat-pollination. The smell and taste of the nectar is strong and sweet, but unpleasant, and this aspect of bat-pollinated flowers needs further study (Start 1974). Nectar production is copious, and the data suggest that it may be stimulated by constant removal. The smaller quantity of nectar per flower secreted on the second study night may be explained by the fact that, although the flowers were similarly situated on the same tree, the second sample was taken towards the end of the

flowering season, an important consideration when assessing nectar production (Percival 1965). This difference may have affected the frequency of bat visits towards the end of the flowering season.

Andromonoecism (the occurrence of functionally staminate and hermaphrodite flowers on the same plant) has been recorded in several plants in Jamaica (Percival 1974), and I have recorded it in other savanna tree species. The condition may be widespread in tropical plants; Heithaus, Opler & Baker (1974) have discussed it in relation to the bat-pollinated *Bauhinia pauletia*.

The many small insects which visit the flowers for nectar at dusk are not involved in pollination, since anthesis occurs after dark when the style is immature. The honeybees in the morning fed only on the pollen and in general did not contact the stigma, hence they also are irrelevant to pollination. The birds foraging very early may occasionally pollinate the tree, but it is doubtful if they could pick up much pollen, and quite shortly after dawn all the pollen had been taken by the honeybees. Although the diurnal visitors are incidental to the pollination of the tree, the flowers may be an important food source for some of them; in particular, the activity of the honeybees on the anthers is very vigorous, as it is also on the pollen of *Detarium microcarpum* Guill. & Perr. (Caesalpiniaceae), another savanna tree which flowers around the same period, suggesting that this is an important food source. July and August, the middle of the wet season, may be a period of shortage of nectar and pollen since few species flower and all the dominant savanna trees are in leaf. Baker, Cruden & Baker (1971) have described a parallel example in the neotropical bat-pollinated *Ceiba acuminata* (S. Wats.) Rose (Bombacaceae), which also flowers when few other trees are in flower.

All the nocturnal visitors are potential pollinators. The hawkmoths and other moths are infrequent visitors, but may be effective in pollination since they may contact the anthers and stigma. Moths have been recorded visiting many bat-pollinated flowers (Harris & Baker 1958; Baker 1961; Heithaus, Opler & Baker 1974), but in the present case their importance as pollinators is probably minor. Interesting regular nocturnal visitors were the genets which apparently do not damage the flowers, and may act as occasional pollinators, although their importance must be negligible (Lack 1977). The most abundant nocturnal visitors are the bats, which presumably are the main pollinators of these trees.

The activity patterns of neotropical bats have been described by Brown (1968) and Laval (1970), who showed that most of the visitors to fruits and flowers have a peak of feeding activity towards the middle of the night, but extending towards dawn. Baker (1973) has emphasized the differences between Old World and New World nectarivores in their methods of orientation (visual and olfactory in the Megachiroptera, primarily by sonar but also olfactorily in the Microchiroptera), and stated that the Megachiroptera feed most actively shortly after dusk. Start & Marshall (1976) confirmed this conclusion for most of the South-east Asian Macroglossinae. The pattern shown here, however, for the bat visitors to *Maranthes polyandra* is similar to that described for the New World nectarivores (the same on moonlit and dark nights).

The bats recorded in this study visited each inflorescence for a very short period of time, much shorter than the periods observed by Baker & Harris (1957, 1959) and Harris & Baker (1958, 1959). The reason for these brief and repeated visits is not clear, but it may be connected with avoidance of predators, since the bats are conspicuous and vulnerable on the upright white inflorescences; they are much less so on the dark pendant inflorescences

of, for example, *Parkia clappertoniana* Keay (Mimosaceae). The genet may be a potential predator, since Carpenter (1970) recorded *Genetta rubiginosa* Pucheran (=*G. tigrina* sensu lato) feeding on bats; also the large owl, *Bubo africanus* J.F.Stephens, was seen at night near the trees.

The active flight of the bats and their frequent short visits to the inflorescences will clearly promote outcrossing in the tree, particularly since the bats may cover considerable distances. One bat had *Adansonia digitata* pollen on its fur, and the nearest flowering *A. digitata* to the study area was *c.* 4 km distant. The African bats are probably opportunistic feeders, and are not constant to particular plant species (most of the pollen loads analysed contained some *Protea elliottii* pollen), nor do they follow a regular feeding route (Baker 1973).

Food for the bats must be available throughout the year, and it is likely that several other African savanna tree species are visited regularly by bats. *Protea elliottii* may be an important floral food source during its main flowering season in September, when flowering in *Maranthes polyandra* is largely over. It has many features typical of bat-pollinated flowers, though it has not been described as such (upright white inflorescences 10–15 cm across, anthesis occurring at about 19.00 hours, and a powerful unpleasant odour). Other species which have been documented as bat-pollinated and which occur in this area are *Parkia clappertoniana, Kigelia africana* Benth. (Bignoniaceae) and *Ceiba pentandra* (L.) Gaertn. (Bombacaceae) (Baker & Harris 1957, 1959; Harris & Baker 1958). A further possibility, suggested by Dr J. M. Lock (personal communication), is *Daniellia oliveri* (Rolfe) Hutch. & Dalz. (Caesalpiniaceae), as its floral structure may be suitable for bats (judged from specimens and illustrations), and Rosevear (1965, p. 62) recorded unidentified fruit bats attacking the buds of this species. *Butyrospermum parkii* (G. Don) Kotschy (Sapotaceae) may also have suitable flowers. Fruit may be an important constituent of the diet of bats at certain times of year (Ayensu 1974), though Wilson (1973) suggested that *Nanonycteris veldkampi* was entirely a flower feeder. Heithaus, Fleming & Opler (1975) showed that phyllostomatid nectarivores and frugivores in Costa Rica vary their diet considerably, depending on the availability of flowers and fruit at the different seasons. Pollen is a protein source of the New World nectorivores (Howell 1974), but the stomachs of the bats which were examined contained very little pollen, perhaps ingested accidentally with the nectar. The bats may clean their fur of pollen and consume this in the morning (Start & Marshall 1976).

Pollination in other Maranthes *species*

The genus *Maranthes* contains ten species in Africa, one in South-east Asia and one in South America. Herbarium specimens and illustrations of these species were examined, and all show withered and unopened flowers, indicating that all species produce their flowers nocturnally. Some species of *Maranthes*, e.g. *M. gabunensis* (Engl.) Prance, have a hollow receptacle and protruding anthers, and are almost certainly pollinated by moths (F. White, personal communication), whereas others, e.g. *M. floribunda* (Bak) F. White and *M. glabra* (Oliv.) Prance (White 1976), have a very similar inflorescence structure to *M. polyandra*, and it is likely that these are bat-pollinated. Dr J. M. Lock (personal communication) observed hawkmoths visiting *M. glabra* at dusk, but did not see any bats; his observations were very brief, however, and did not extend beyond 20.30 hours. Baker (1961, 1973) emphasized that hawkmoth-pollination and bat-pollination involve similar adaptations, and *Maranthes* may contain examples of both types, with some species able

to be pollinated by either, but sustained observations on several species are clearly required.

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