

# An exotic plantation crop as a keystone resource for an endemic megachiropteran, *Pteropus rufus*, in Madagascar

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**Abstract:** The single most important food source for *Pteropus rufus* at Berenty, in south-east Madagascar, is the pollen of *Agave sisalana*, a commercial species introduced to the area 60 y ago, which was widely available and constantly eaten by the bats during this 28-mo study. The diet of the bats at this site is unique in this respect when compared with *P. rufus* elsewhere in Madagascar and with other *Pteropus* species. The dietary breadth of *P. rufus* at Berenty is narrow, consisting of only 14 plant species, identified through microscopic faecal analysis and direct field observations, and three unidentified ones. The bats also eat locally cultivated and introduced fruits (*Mangifera indica*, *Psidium* cf. *cattleianum*, *Sclerocarya caffra*, *Cordia sinensis* and *Hylocereus* species) and native and endemic forest species (*Tamarindus indica*, *Celtis philippensis*, *Ficus megapoda*, *F. grevei*, *F. pachyclada* and *Grewia* species). The majority of the plant species used by *P. rufus* for food are located within the gallery forests of the Mandrare valley. No evidence of adjacent endemic spiny forest species was identified in their diet. Thus, conservation of the remaining gallery forest as well as retention of the sisal plantations is important to maintain the food sources of *P. rufus* at this site.

**Key Words:** *Agave sisalana*, bats, diet, folivory, frugivory, pollen, Pteropodidae

## INTRODUCTION

Old World fruit bats (Suborder Megachiroptera) are phytophagous, feeding almost exclusively on fruits, leaves, nectar and pollen (Marshall 1985). The majority of species roost in trees, the leaves of which are often eaten (Mickleburgh *et al.* 1992). They are highly mobile and are capable of long migrations when exploiting a seasonal food resource (Eby 1995, McWilliam 1985–86), although a typical foraging range for a large megachiropteran (450–900 g) is within about 20 km of their roost site (Banack & Grant 2002, Eby 1995, Palmer & Woinarski 1999). Their wing morphology allows fast direct flight, rather than the slower more manoeuvrable flight required for the cluttered environment of the subcanopy (Fleming 1993, Kalko 1997). They do not echolocate, but rely on well-developed night-vision and an acute sense of smell to locate food (Acharya *et al.* 1998, Luft *et al.* 2003, Richards 1990). Thus, many of the fruits they eat are presented prominently at the end of branches, have a strong scent and are often pale in colour (Marshall 1983, Richards

1990). The bats generally land in a fruiting tree and crawl about in the canopy using their thumbs and hind legs to reach ripe fruits (Fleming 1993, Richards 1995).

When feeding, fruit bats chew food thoroughly before pressing it against their hard palate and swallowing the juice and soft pulp, voiding the remaining fibre in a pellet (Lowry 1989, Morrison 1980). These distinctive ejecta pellets are often found under feeding trees and temporary feeding perches along with partially eaten fruit and/or leaves and can be used to identify the bats' food sources (Thomas 1984, 1988).

*Pteropus rufus* (Geoffroy) is the largest of Madagascar's three endemic fruit bats and weighs about 620 g (Peterson *et al.* 1995). It has a widespread distribution particularly in lowland and coastal areas although it is uncommon in the central high plateau and is at risk from over-hunting throughout the island (MacKinnon *et al.* 2003). Only a few roost sites have been located in the drier southern region of the island, including those at the Berenty Reserve (project study site), the Mahafaly plateau and near the town of Ampanihy, with further sites along the humid east coast in fragments of littoral forest at Ste. Luce and 'Enato Anandrano' near the village of Mandena (Bollen & Van Elsacker 2002, MacKinnon *et al.* 2003). Surveys have

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revealed that roosts typically contain several hundred individuals (MacKinnon *et al.* 2003).

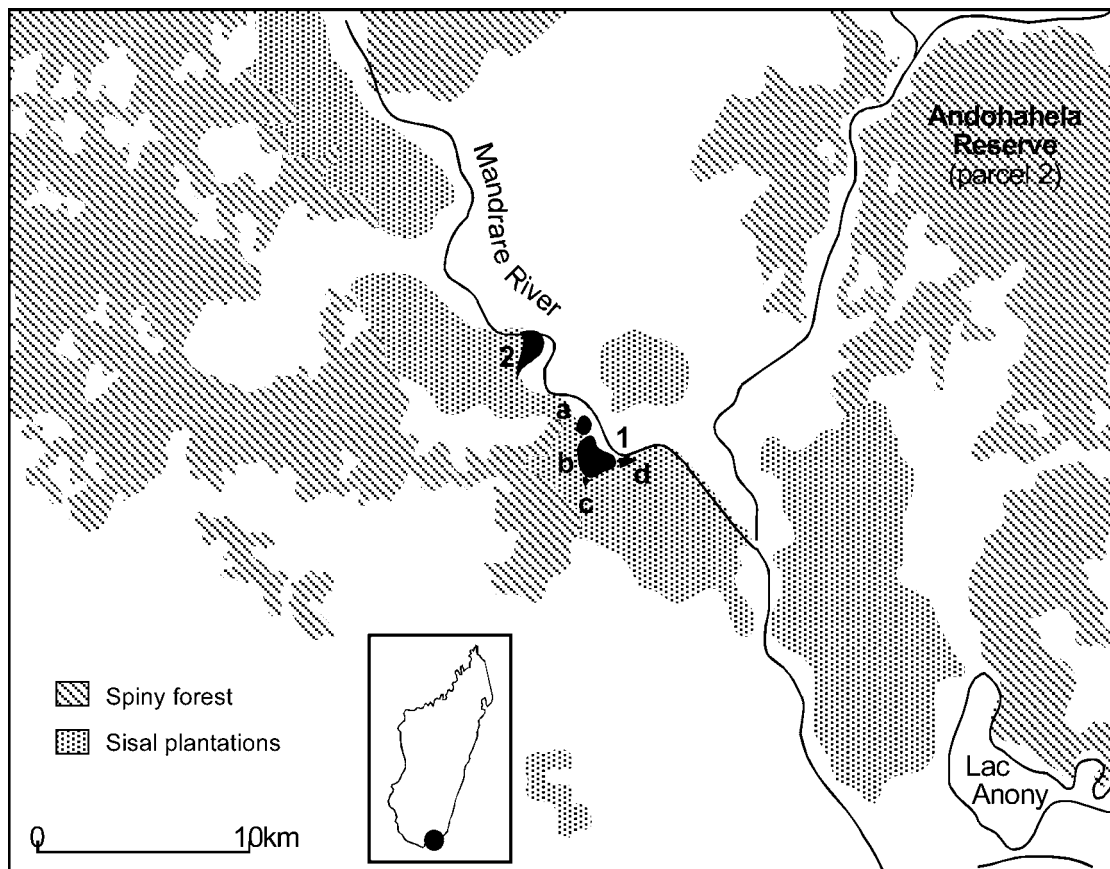
This study concentrates on the colony of *P. rufus* at Berenty Reserve and is the first study to investigate the diet of *Pteropus rufus* in the arid south-east of Madagascar. Both native gallery and endemic spiny forest are present within the reserve, which is surrounded by extensive sisal plantations. The aim of this project was to examine the diet of *P. rufus* at this site where a variety of endemic, native and commercial species co-exist.

## STUDY SITE

The gallery forest of Malaza (25°00'S, 46°18'E) is part of the 200-ha Berenty Reserve contained within the de Heaulme family's 6000-ha estate in the lower Mandrara River Valley, and has been a protected area since 1936 (Figure 1). It lies at 50 m asl, about 85 km west of the coastal town of Fort Dauphin and 25 km north of the Indian Ocean. The climate is sub-arid with low annual rainfall (400–600 mm) and a mean temperature of 25–

35 °C (O'Connor 1987). Most rain falls during the wet season (October–March) and temperatures are lowest during the cool dry season (April–September).

Berenty Reserve contains natural gallery forest (classed as > 50% 'closed canopy'), transitional 'scrub' (classed as > 50% 'open canopy') and endemic spiny forest (Jolly *et al.* 2002). Malaza forest (111 ha) is the largest fragment and contains both gallery and scrub vegetation. This is directly linked to 'Parcel 4', a small (~12-ha) patch of spiny forest to the south and 'Ankoba', a 16-ha patch of secondary forest to the north, which is dominated by the introduced *Pithecellobium dulce* (Roxb.) Benth. Scrub vegetation becomes more dominant with increasing distance from the Mandrara River, which borders the reserve along its eastern boundary. A previous study of the vegetation ecology of Malaza forest (O'Connor 1987) identified 112 plant species, but only 52 tree species, many of which are rare (known only from single individuals). The main tree species include *Tamarindus indica* L., *Rinorea greveana* Baill., *Neotina isoneura* (Radlk.) Capuron, *Crataeva excelsa* Boj. and *Acacia roovumae* Oliv. The gallery forest of southern and south-western Madagascar is rare



**Figure 1.** Map of study area showing two remaining fragments of gallery forest adjacent to sisal plantations and surrounded by spiny forest. Madagascar is inset, and the location of Berenty shown (●). Gallery forest: 1 = Berenty: a = Ankoba (plantation from 1930s); b = Malaza (gallery forest); c = Parcel 4 (spiny forest); d = Anaramalangy (degraded gallery). 2 = Bealoka.

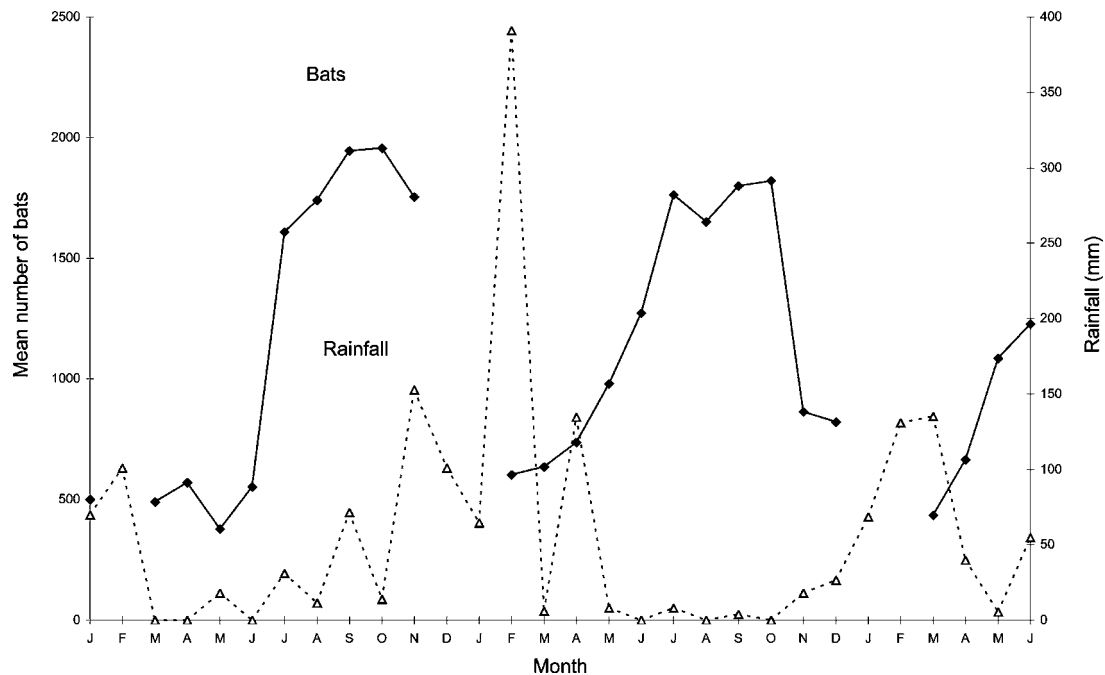


Figure 2. Variation in the numbers of *Pteropus rufus* counted in the roost at Berenty (■-■) and rainfall (Δ-Δ) recorded during the study.

(Sussman & Rakotozafy 1994). Only Malaza and its sister forest Bealoka (92 ha), 7 km north of Berenty, remain as viable patches of forest on the banks of the lower Mandrare River (O'Connor 1987). The remaining gallery forest outside these reserves is highly fragmented due to clearance for commercial sisal plantations, and is badly degraded from over-grazing by cattle (zebu) and wood extraction by local Tandroy villagers.

Berenty Reserve is a major tourist attraction in south-east Madagascar. The hotel complex and connecting roads have been planted with many non-native, ornamental plants such as *Azadirachta indica* L., *Cordia sinensis* Lam., *Cassia siamea* Lam., *Flacourtia indica* (Burm.f.) Merr., *Sclerocarya caffra* Sond. and a small stand of *Eucalyptus* (~60 trees).

GIS data show that the major vegetation types surrounding Berenty are commercial sisal plantations, xerophytic scrub, dense dry Didiereaceae (spiny) forest and savanna-like vegetation (*P. Andriamanambina*, *pers. comm.*). The 30 000 ha of sisal plantations that surround Berenty were established between the late 1930s and early 1940s and lie mainly to the north and south-east of the reserve. These plantations are interspersed with small pockets of endemic spiny forest, which were either left to act as windbreaks or to preserve traditional sacred sites for the local Tandroy people. The most common spiny forest species found at Berenty and in surrounding areas, which are arborescent in form, include *Alluaudia humbertii* Choux, *A. procera* (Drake) Drake, *Azima tetracantha* Lam., *Decarya madagascariensis* Choux, *Maerua filiformis* Drake,

*Operculicarya decaryi* Perrier and *Terminalia mantaly* H. Perrier. Approximately 80% of the spiny forest has been degraded by anthropogenic processes resulting in the formation of large areas of scrub and grassland (Du Puy & Moat 1996). The largest remaining areas of spiny forest occur approximately 25 km north-west near Ifotaka and 30 km east within Parcel 2 of the Andohahela Reserve (Figure 1).

The colony of *Pteropus rufus* at Berenty roosts at the centre of Malaza forest in mature *Tamarindus indica* and *Acacia royumae* trees. It ranges in size from 500–600 individuals during the middle of the wet season (January–February) and 1800–2000 individuals at the end of the dry season (August–September) and is relatively large compared with others elsewhere in Madagascar (Bollen & Van Elsacker 2002, Long 2002, MacKinnon *et al.* 2003) (Figure 2). Fieldwork was carried out between November 1996 and June 1999, including three wet seasons (October–March) and three dry seasons (April–September). Data were collected continuously except for December 1997 to February 1998 and January to mid-February 1999.

## METHODS

### Identifying food sources of *Pteropus rufus*

The foods eaten by *P. rufus* were identified from three sources: faecal samples, feeding remains (ejecta pellets)

and direct feeding observations. Ten 1 × 1-m pieces of semi-permeable/plastic sheeting were placed under five 'core' roost trees, i.e. trees that were always used as roosting perches by bats regardless of the number of bats present at the roost site. After initial trial placements, the sheets were placed at the same location for the remainder of the study, which maximized the level of sample deposition. A representative subsample of between 20–35 faecal samples was collected twice weekly for microscopic analysis, including as many different samples based on colour and seed content as possible. The bats also ate the leaves of their roost trees (*Tamarindus indica*) so the sheets were also checked daily for leaf ejecta pellets. The deposition of ejecta pellets at the roost site was monitored to establish monthly differences in the daily pattern of tamarind leaf consumption between February and December 1998. The number of ejecta pellets was corrected for the number of bats present by dividing the total number of pellets deposited per month by the average colony size for the month (and to give average daily deposition, by dividing this figure by the number of days in the month). This was to compensate for the change in colony size between the wet and dry seasons (Long 2002).

Ejecta pellets and faecal samples were also opportunistically collected from under the bats' feeding trees. Berenty forest contains a well-developed trail system, which totals 15.8 km (G. Williams, *pers. comm.*) and is swept daily to prevent the accumulation of leaf litter and reduce the risk of fire. As part of daily fieldwork a minimum of 3 km of forest trails were walked and evidence of bats feeding in trees lining the trails (i.e. ejecta pellets, partially eaten fruit or faeces) was easily detected. These samples were examined to identify what tree species the bats were feeding on and the proximity of these trees to the roost.

A total of 4318 faecal samples were examined, but due to the ease of collection at the roost site the majority of samples ( $n = 3632$ ) were collected from this source. The remaining 686 faecal samples were collected from under temporary feeding perches or feeding trees along trails and access roads. Wet preparations of faecal samples were examined using a light microscope to determine the content based on the presence of pollen, fruit pulp, seeds, leaf material and insect remains.

Opportunistic feeding observations were made during 189 dispersal counts as the bats left the roost to forage after dusk (October 1997–April 1999) and 25 fly-in counts as bats returned to roost in the hour before sunrise (October 1998–May 1999). These allowed identification of food trees within Malaza and confirmed the use of plant species by the bats. Feeding observations were also made at fruiting figs and the bats' use of sisal and minimum foraging range was confirmed by a brief radio-tracking study between May and June 1999, which was part of a study on seed dispersal (Long 2002).

The number of different foods eaten by the bats on a monthly basis was estimated from the foods identified in

faecal samples collected from under the roost and feeding trees/perches and from ejecta pellets of fruits and leaves under feeding trees. For many of these plant species direct feeding observations also confirmed use by the bats.

### Food availability

Monthly fruit patrols (adapted from Thomas 1984) were carried out within the forests of the Berenty reserve to assess the availability of fruit species eaten by *P. rufus*. From faecal analysis and direct feeding observations, three *Ficus* species were identified as food sources for *P. rufus*. Figs are an important keystone food source (Terborgh 1986) so monitoring efforts concentrated on these trees. The whole reserve was surveyed to locate all mature ( $\geq 10$  cm dbh) fig trees. These were identified and mapped, the absolute density calculated for each species and their fruiting status checked each month. The monthly fruit availability index (FAI) was calculated based on the number of trees bearing ripe fruit vs. the total number of fig trees surveyed during the study period (March 1998–June 1999).

Approximately 6 km of trails were walked during the monthly fruit patrol of figs and at the same time the other plants identified as bat food sources, all of which fruited synchronously, were inspected and their fruit/leaf availability was recorded on a presence/absence basis (Tan *et al.* 1998, Thomas 1988). Only trees that could be viewed from the trails walked as part of the fruit patrol had their status recorded. Samples of fig trees and other bat food plants were collected for identification by staff of the herbarium of Parc Tsimbazaza in Antananarivo.

The availability of sisal flowers was initially assessed on a presence/absence basis within the de Heaulme estate by monthly drives along two main access roads (totalling  $\sim 21$  km), which bisect the plantations. However, because access to other concession owners' plantations in the region was prohibited it was difficult to monitor availability accurately, and thus availability was retrospectively inferred from the presence of sisal pollen in the bat faeces. The annual abundance of sisal flowers was estimated based on: a minimum planting density of  $\sim 4000$  plants  $\text{ha}^{-1}$  and a minimum plantation size of 125 ha (Lock 1969), and the rotational planting system of 8–9 y used on the de Heaulme estate. This figure was extrapolated for the total 30 000 ha of sisal plantations in the Mandrare River valley.

## RESULTS

### The diet of *Pteropus rufus*

Fourteen plant species were identified in the diet of *P. rufus* (Table 1), with a further three species tentatively ascribed to family level. The majority of food plants were

**Table 1.** The food plants of *Pteropus rufus* at Berenty Reserve, indicating methods of detection; ejecta pellets (E), faecal samples (F) and direct feeding observations (O) and the occurrence of food items in faecal samples collected from the roost site and other opportunistic sampling sites (e.g. temporary feeding roosts).

| Family          | Species                    | Plant parts eaten | Evidence | % Faeces (roost)  | % Faeces (other)  |
|-----------------|----------------------------|-------------------|----------|-------------------|-------------------|
| Agavaceae       | <i>Agave sisalana</i>      | pollen/nectar     | F, O     | 79.6              | 56.5              |
| Anacardiaceae   | <i>Mangifera indica</i>    | fruit             | F        | 7.0               | –                 |
|                 | <i>Sclerocarya caffra</i>  | fruit             | E, F     | 0.3               | –                 |
| cf. Bombacaceae | unidentified sp.           | pollen/nectar     | F        | 0.1               | –                 |
| Boraginaceae    | <i>Cordia sinensis</i>     | fruit             | F, O     | –                 | 5.5               |
| Cactaceae       | <i>Hylocereus</i> sp.      | fruit             | F        | 0.1               | –                 |
| cf. Cactaceae   | unidentified sp.           | pollen/nectar     | F        | 0.2               | –                 |
| Fabaceae        | <i>Tamarindus indica</i>   | fruit             | E, F, O  | 16.3 <sup>a</sup> | 36.8 <sup>a</sup> |
|                 |                            | leaves            | E, F, O  | 34.9 <sup>b</sup> | 8.3 <sup>b</sup>  |
| Moraceae        | cf. <i>Albizia</i>         | pollen/nectar     | F        | 0.1               | –                 |
|                 | <i>Ficus grevei</i>        | fruit             | E, F, O  | 1.3               | 1.3               |
|                 | <i>Ficus polita</i>        | fruit             | E, F, O  | 0.5               | 0.7               |
|                 | <i>Ficus pachyclada</i>    | fruit             | E, F, O  | 0.1               | –                 |
|                 | <i>Ficus</i> sp.           | fruit             | F        | 0.3               | –                 |
| Myrtaceae       | <i>Eucalyptus</i> sp.      | flowers           | F, O     | 3.4               | 8.8               |
|                 | <i>Psidium cattleianum</i> | fruit             | F        | 0.3               | 0.3               |
| Tiliaceae       | <i>Grewia</i> sp.          | fruit             | E        | –                 | –                 |
| Ulmaceae        | <i>Celtis philippensis</i> | fruit             | E, F, O  | 1.0               | 0.9               |
|                 |                            | leaves            | E, F, O  | 1.3               | –                 |

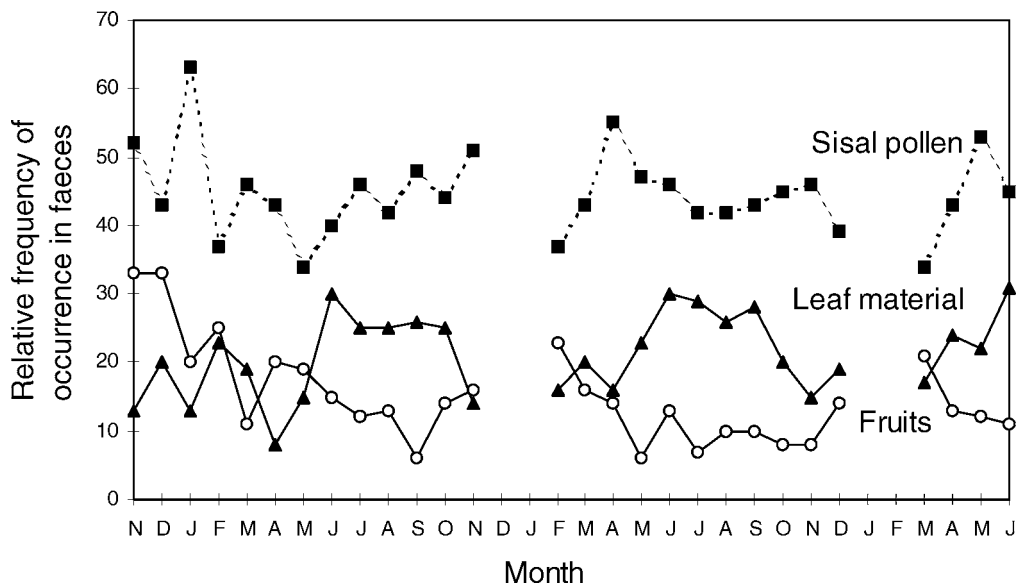
<sup>a</sup> = May contain other fruits that oxidize and turn brown after gut passage or mask colour of pale-coloured fruits.

<sup>b</sup> = May contain some *Celtis philippensis* as samples were difficult to differentiate if mixed with pollen.

identified from faecal samples collected at the roost site, with the exception of *Cordia sinensis*, which was detected in faecal samples collected at a temporary feeding perch, and *Grewia* fruits found in an ejecta pellet under a *Sclerocarya caffra* tree.

The most frequently occurring food item found in the bats' faeces was *Agave sisalana* pollen (c. 80% of roost faeces and 57% of faeces from other collection sites), which was eaten throughout the 28-mo study (Figure 3). The majority of the faecal samples collected beneath the

roost contained sisal pollen, most of the grains of which were empty indicating the nitrogen-rich protoplast had been extracted by the bats. *Eucalyptus* blossom was also eaten (and digested) when available, but was less evident in the faecal samples examined (c. 3% of roost samples and 9% of samples from other sites). Leaves, particularly *Tamarindus indica*, were eaten on a daily basis as confirmed from ejecta pellets deposited at the roost and analysis of faecal samples (35% of roost faeces and 8% of faeces collected from other sites) (Figure 3). The bats also ate



**Figure 3.** Variation in the relative frequency of occurrence of sisal pollen (■-■), leaf material (▲-▲) and fruits (○-○) in the faeces of *Pteropus rufus* at Berenty.

tamarind fruits, both unripe and ripe. The pulp of these fruits oxidized from bright green to brown for unripe fruit and was more common in faecal samples collected at other localities (16% of roost versus 37% from other sites). The bats' use of *Celtis philippensis* leaves and fruit was more easily identified from ejecta pellets deposited under feeding trees. The small fruits of *C. philippensis* (10 mm long) have relatively large seeds (c. 6 mm long), which were not swallowed by the bats, and were often found alongside leaf ejecta pellets.

Other fruits were more difficult to detect since only seeds from *Ficus grevei*, *F. megapoda* and *F. pachyclada* (seeds  $\leq 1.5$  mm long), *Psidium cattleianum* (seeds  $\leq 3.5$  mm long) and the *Hylocereus* species (seeds  $\leq 2$  mm long) were found in the bats' faeces. Identification based purely on fruit pulp characteristics was complicated, particularly when faecal samples contained mixtures of fruits, leaves and pollen. Certain fruits could be identified by the colour, texture and smell of the faeces (e.g. *Cordia caffra* and *Mangifera indica*). Distinctive ejecta pellets and direct feeding observations helped to confirm the timing and use of plant species that were less well represented in the faecal samples, such as *Eucalyptus* sp., *C. philippensis*, *Grewia* sp. and *Sclerocarya caffra*. Despite this, the plant origins of approximately a quarter of all faecal samples examined could not be identified due to a lack of clearly identifiable features.

Microscopic analysis of faecal samples also revealed that insect remains were present in faeces. Wing scales were found in 7% of the samples whilst pieces of exoskeleton (e.g. antennae, hairs and thorax) and whole insects (Thysanoptera, 'thrips') were found in 4%. When combined, these insect remains were found in a total of 10% of the samples examined. Ninety-five per cent of all insect remains were found in faecal samples containing sisal pollen, indicating accidental ingestion due to surface contamination of these flowers by insect visitors.

*Pteropus rufus* fed mainly on the leaves of their roost trees, but ejecta pellets of tamarind leaf material were also occasionally found under trees along trails within 350 m of the roost. Feeding remains of *C. philippensis* leaves and fruit were found under trees either lining the trails adjacent to or within 200-m of the roost site. Trees of the three *Ficus* species eaten by *P. rufus* were found within a 600-m radius of the roost. The *Eucalyptus* trees were located approximately 530 m from the roost site, whilst the *S. caffra* trees visited by the bats border an access road about 1 km from the roost. A short-term radio-tracking study revealed that the bats flew 5–17 km from the roost when feeding on sisal flowers between May and June 1999, which included the north-western and south-eastern margins of the sisal plantations in the Mandrare River valley. Typically the bats flew straight to a flowering patch of sisal and commenced feeding

immediately. One collared individual tracked to a feeding location in sisal one night was found feeding with other bats at the same location early the following morning indicating that they spend a large proportion of the night feeding in the plantations.

From analysis of faecal samples, ejecta pellets and direct feeding observations, the number of plants eaten by *P. rufus* varied each month between 3 to 13 species. Most were eaten at the end of the wet season (February–March, 8–13 species) when the colony contained 500–600 bats and fewest during early–middle dry season (May–June, 3–4 species) when 1000–1250 bats were present. Thirteen of the 17 plants eaten by *P. rufus* occur within the de Heaulme estate, but none grow in the spiny forest. Thus, it was concluded that *P. rufus* frequently ate gallery forest and introduced commercial crop species such as sisal, mango and guava (when available), but that the use of spiny forest species was unlikely due to lack of feeding evidence or feeding remains in the bats' faeces.

#### Food availability and use by *Pteropus rufus*

The monthly availability and use of food resources by *P. rufus* are recorded in Table 2, with the exception of pollen from three unconfirmed species and the unidentified *Ficus*, *Grewia* and *Hylocereus* fruits as well as the crop species (mango and guava), as no phenological data were recorded for these species, only the timing of use by the bats. *Pteropus rufus* ate *Agave sisalana* pollen throughout this study. Based on observations in the de Heaulme plantations it was estimated that approximately 3000-ha (10% of total cultivated area) flowered within the Mandrare Valley each year. Sisal plants each flowered for about 1-mo and flowering was staggered so that not all plants within a plantation flowered at the same time, allowing flowers to be produced over a period of several months within each plantation. Similarly, not all the sisal estates in the Mandrare produced flowers at the same time, due to differences in the timing of annual planting regimes. Consequently, sisal flowers were available to the bats throughout the 28-mo study.

The monthly fruit patrols of the reserve revealed the seasonality of the bats' food sources. *Tamarindus indica* and *C. philippensis* leaf material were available to *P. rufus* throughout the 28-mo study. Tamarind trees are the second most numerous trees in the forest (26.3 trees ha<sup>-1</sup>) and dominate the upper canopy above 15 m. *Celtis philippensis* is less numerous with only 7.2 trees ha<sup>-1</sup>, but is an important canopy tree both in Malaza (Berenty) and Bealoka forest.

Although the tamarind trees annually shed their leaves at the end of the dry season (September) leaf fall is staggered throughout the forest. Buds and new leaves reappear by late October as the trees regain their canopy



eaten by the bats. For example, although *Ficus pachyclada* fruited between March and June 1998 (three trees with ripe fruit) and March to May 1999 (two trees with ripe fruit) no ejecta pellets were found under these trees or along forest trails nearby, indicating that the bats had not fed there. Thus it was concluded that other smaller patches of forest were used by the bats as feeding sites.

## DISCUSSION

### Diet and habitat use by *Pteropus rufus*

The low diversity in the diet of *Pteropus rufus* at Berenty is unique when compared with other sites in Madagascar and with other *Pteropus* species. Only 17 plant species occurred in the diet of *P. rufus* at this site, two of them in every month: *Agave sisalana*, the pollen of which was consumed and probably also the nectar and *Tamarindus indica* the leaves of which were eaten. Only nine of these species were used for their fruit. In contrast, Bollen & Van Elsacker (2002) showed that in the littoral forest of Ste. Luce c. 100 km east of Berenty, *P. rufus* ate the fruits of 40 endemic species. Similarly two studies in the Mahafaly region found that *P. rufus* ate 38 species, including five eaten by the bats at Berenty and a further ten that occur in the Mandrare Valley (Racey *et al.* in press). Currently 110 plant species have been identified in the diet of *P. rufus* in Madagascar (Bollen & Van Elsacker 2002, Long 2002, Racey *et al.* in press), of which 59 (55%) are endemic. This suggests that *P. rufus* has a very diverse diet, which has enabled it to adapt to areas with vastly differing vegetation types, e.g. dry deciduous forest in the south, littoral forest on the coast, and lowland rain forest in the north-east.

Elsewhere, other *Pteropus* species also have the typically broad 'generalist' diets associated with this genus. For example, in Australia, fruit and blossom bats eat over 152 plant species including 133 native species of which 90 are fruits, 43 are blossom and 3 are leaves or bark (Eby 1998, Law 2001, Palmer *et al.* 2000, Parry-Jones & Augee 2001, Richards 1990). *Pteropus marianus* in the Mariannas archipelago feeds on fruits of 54 plant species (Wiles *et al.* 1997), *P. vampyrus* in Sarawak feeds on 24 species (Gumal 2001) and *P. seychellensis* eats 27 species, including 17 fruits (Racey & Nicoll 1984). In Mauritius, *P. niger* ate 22 plant species, 20 of which were visited for fruit, two for floral resources and one for leaves (Nyhagen *et al.* 2005). Thus, compared with other *Pteropus* species, the diet of *P. rufus* at Berenty contains a surprisingly low number of fruit species. Instead, *P. rufus* relies on a diet based on sisal pollen and leaves (*T. indica* and *C. philippensis*), which is supplemented by wild and cultivated fruits when available. In this respect its diet closely resembles that of *P. poliocephalus* where a large proportion of the bats' diet is made up of Myrtaceae pollen (Parry-Jones & Augee 2001),

or the common blossom bat *Syconycteris australis*, which feeds mainly on pollen, particularly *Syzygium* species (Law 2001). What distinguishes the diet of *P. rufus* at Berenty is its reliance on an introduced, cultivated species rather than a native or endemic species, and the fact that 80% of 3632 faecal samples collected beneath the roost contained sisal pollen which suggests that this is a keystone resource for the bats (Terborgh 1986).

Sisal flowers are adapted to encourage bat visitation. They produce large quantities of protein-rich pollen and nectar at night, are pale in colour and have a strong musty smell. The commercial sisal plantations are clearly an important source of food for *P. rufus* at this site. If sisal production were to cease, the bats would lose the single most important component of their diet, sisal pollen which consists of 36% protein (Long 2002), and a large proportion of their foraging habitat. Fortunately there has been a recent revival in the use of sisal fibre, which has become a popular form of natural biodegradable insulation, and continued production at Berenty seems assured for the foreseeable future (B. Simmen, *pers. comm.*). It was difficult to establish by direct observation whether the bats actively consumed sisal nectar or pollen. However, it is likely that the main floral resource that the bats were targeting was nectar as *Agave* flowers have been shown to provide nectar as a reward for their native pollinators, which include nectarivorous bats (Arizaga *et al.* 2000). Other studies of bat-flower interactions have shown that pteropodid bats tend to land on flowers or inflorescence to probe for nectar, with bats only occasionally licking pollen directly from the stamens (Start & Marshall 1976). In addition studies of pteropodid bats in Australia has shown that the majority of pollen has been ingested during grooming after bats have visited flowers, as during feeding they become covered with sticky pollen (Law 1992). Individuals of *P. rufus* were observed crawling around in the sisal inflorescences during feeding and are likely to have accumulated heavy pollen loads on their fur, which would suggest that the majority of pollen was ingested as a by-product of feeding on *Agave* nectar.

Leaves are eaten by *P. rufus* throughout the year although *T. indica*, the dominant tree species of the gallery forest, sheds its leaves at the end of the dry season (September) resulting in lower availability at this time. Elsewhere, fruit bats eat the leaves of many trees including other nitrogen-rich legume species such as *Albizia*, *Erythrina* and *Cassia*, which provide them with an additional source of protein (Kunz & Diaz 1995, Lowry 1989, Tan *et al.* 1998). It has also been suggested that leaves may provide bats with important minerals (e.g. calcium), steroidal sapogenins and alkaloids, which may play a role in regulating hormone levels, or other secondary compounds that could have an antihelminthic effect (Kunz & Ingalls 1994). Steroidal sapogenins have not been identified in *T. indica*, but their leaves are a source of protein,

which improves the amino acid profile and protein quality of human diets during periods of famine in Southern Mali (Nordeide *et al.* 1996). Thus, it is more likely that protein and possible mineral content are the main reasons for the consumption of these leaves by *P. rufus*.

Wild fruiting trees such as figs were present at much lower densities (0.2 trees ha<sup>-1</sup>) with a patchy distribution. The *Ficus* species eaten by *P. rufus* are asynchronous in their fruiting, with only a handful of trees producing two or more fruit crops a year. Despite occurring in an area of high endemism (Phillipson 1994), the diversity of trees in Berenty's gallery forest is low compared with that of tropical rain forest, e.g. 52 species versus 820 tree species in 50 ha of primary lowland rain forest in Malaysia (Saw *et al.* 1991) or 239 species from a line transect within a 1-ha plot in the Amazon (Korning *et al.* 1991), but similar to the dry deciduous forests of western Madagascar which have between 22 to 53 species recorded from forest patches ranging in size from 3 to 30 000 ha (Ganzhorn *et al.* 1999). Interestingly, the density of fig trees in Malaza forest is similar to that found in tropical forests elsewhere (Gautier-Hion & Michaloud 1989), suggesting that although not abundant, this resource is not restricted at Berenty. Other plant species had very specific and highly seasonal fruiting seasons, and as such only contributed a small percentage of the bats diet on an annual basis.

It was assumed that due to the lack of remaining gallery forest that the bats would rely heavily on Berenty's gallery forest for food, since it is the largest and most pristine fragment remaining within the Mandrare region. Half of the identified plant species eaten by *P. rufus* are native and endemic gallery forest species. Faecal analysis has shown that other patches of forest are incorporated into the bats' foraging range, allowing them to feed on foods when these are not available at Berenty, e.g. *Eucalyptus* blossom, unidentified *Ficus* fruits. This implies that all remaining gallery forest in the lower Mandrare River Valley, regardless of fragment size and species diversity, is an important constituent of the bats' foraging area. Prior to the large-scale sisal cultivation in the Mandrare Valley, the roost at Berenty contained 'many more bats' and a second bat roost was present in Ambinany forest, which is located on the opposite bank of the Mandrare River and is now heavily degraded (M. de Heulme, *pers comm.*). This reduction in bat numbers is most likely to be linked to the loss of pristine gallery forest, which provides both suitable roost sites and food resources for the bats.

No evidence was found to show that *P. rufus* uses the endemic plants of the spiny forest in the Mandrare region. MacKinnon *et al.* (2003), when mapping the distribution of Madagascar's three fruit bats, *P. rufus*, *Eidolon dupreanum* Pollen and *Rousettus madagascariensis* Grandidier, failed to locate any roost sites within the

endemic spiny forests of south-west Madagascar, and it seems unlikely that fruit bats have formed a close association with this vegetation type.

In conclusion, the diet of *P. rufus* in the Mandrare region is not typical of fruit bats elsewhere, due to its reliance on the introduced species *Agave sisalana*. The bats' natural environment has been heavily modified during the last 60–70 y of sisal cultivation, resulting in the loss of large areas of gallery and endemic spiny forests, and those that remain are often heavily degraded. This has restricted the availability of fruiting gallery forest species such as figs, but provided the bats with a predictable and abundant food source: *Agave sisalana*.

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