

An investigation into the role of the Mauritian flying fox, *Pteropus niger*, in forest regeneration

Dorte Friis Nyhagen^{*}, Stephen David Turnbull, Jens Mogens Olesen, Carl G. Jones¹

Department of Ecology and Genetics, Aarhus University, Ny Munkegade Block 540, DK-8000 Aarhus C, Denmark

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Abstract

This study was conducted over a 7-month period in the south-west of Mauritius and investigates the diet of the endemic flying fox *Pteropus niger* and its potential role as pollinator and seed disperser. The identification of food plants and seed dispersal events were made by direct observations of bats or indirectly by the analysis of ejeta found on the ground. *P. niger* was observed to visit 22 plant species for food of which 20 were visited for fruit, two for floral resources, and one for foliage (one species was visited for both fruit and floral resources). Two thousand thirty-two *P. niger* fruit ejeta from 16 species were collected containing 2460 seeds. Ejeta from eight of these species (including five endemic to Mauritius) contained seeds, all of which were mature and intact (with one possible exception) and some were germinating. Forty-seven observations were made of the dispersal of seeds in fruit, ejeta and faeces, including seeds from three endemic and one native plant species. All seeds in dispersed ejeta were found to be mature and undamaged by bats. Pollen smears from the lips of six dead and 12 captured bats showed that these animals carried a minimum of 18 pollen species. Each smear had an average of 2.2 pollen species and a pollen load of 17.7 grains. Our results suggest that *P. niger* plays an important role in maintaining plant diversity in the heavily fragmented landscape of Mauritius.

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1. Introduction

Three species of *Pteropus* flying foxes (Pteropodidae) once inhabited the island of Mauritius (*Pteropus niger*, *P. subniger* and apparently *P. rodricensis*) (Cheke and Dahl, 1981). Today *P. niger* Kerr is the only extant species (Cheke and Dahl, 1981). Whilst *P. niger* is not under immediate threat, very little is known about how it survives on an island greatly changed since the arrival of humans. In a 1974 census, populations were considered to be declining as a result of hunting for sport and food and the severe impact of several cyclones (Cheke and

Dahl, 1981). The IUCN status of this species is Vulnerable, based on its limited distribution (Mickleburgh et al., 1992), and its status has not been revised since. Although *P. niger* has been protected since 1993 (Y. Mungroo, pers. comm.), the bats are still being hunted and their habitat is strongly influenced by deforestation and invasive species. Less than 1.9% of the area of Mauritius supports native vegetation (Page and D'Argent, 1997) and the reproduction of native plant species is poor (Lorence and Sussman, 1986), e.g. some of the most rare dioecious *Diospyros* species survive without reproduction in unisexual stands (unpublished). Throughout their geographical range, *Pteropus* species are regarded as important pollinators and seed dispersers (Crome and Irvine, 1986; Gould, 1978; Izhaki et al., 1995; Kress, 1985; Shilton et al., 1999; Utzurrum and Heideman, 1991; Wolton et al., 1982) and on some

^{*} Corresponding author. Tel.: +45 27147500.

E-mail address: friis_nyhagen@hotmail.com (D.F. Nyhagen).

¹ Present address: Forestry Quarters, The Mauritian Wildlife Foundation, Black River, Mauritius.

Old World oceanic islands flying foxes may be particularly important (Cox et al., 1991). However, little is known of the mutualistic role of many flying foxes and no previous studies have been made on the role of *P. niger* as a pollinator and seed disperser. This study aims to investigate this role and expand on the list of its food plant species.

2. Methods

2.1. Study species

Within its genus, *P. niger* is a medium-sized species (Koopman, 1994). Adult forearm-length averages 152 mm (range = 143–165 mm, $n = 14$), with no significant difference between males and females. Non-reproductive adult females weigh an average of 473 g (range = 380–540 g, $n = 5$); at present no data on weight of adult males are available (Cheke and Dahl, 1981; Nyhagen, 2001). *P. niger* is mainly nocturnal/crepuscular, but occasionally individuals were seen foraging during the day. Many bats were actively foraging at 1700 h, and most had left their roost by sunset. Flight speed of *P. niger* whilst leaving or returning to roosts averaged 18.5 km h⁻¹ (range = 11.5–24.0 km h⁻¹, SD = 3.5 km h⁻¹, $n = 14$). Roosts of *P. niger* were found near ridge tops with slopes of 30–45° in primary forest or in areas containing a mixture of native and introduced trees (Nyhagen, 2001).

2.2. Study site

Mauritius is situated at 20°20'S 57°30'E, and covers 1865 km². Its climate is subtropical–tropical with a warm, wet season from December to April and a dry, cooler period from June to October (Strahm, 1996). The Black River Gorges National Park in the south and south-west of Mauritius covers 65.7 km². The park includes two important lower montane forest areas, Combo and Lower Bel Ombre (150–704 m a.s.l.) (Fig. 1) (Safford, 1997) with several roosts of *P. niger*.

This study was conducted from October 1999 to April 2000, mainly in the lower Bel Ombre forest (here referred to as Bel Ombre), but includes observations from Combo forest and Black River Village, situated on the south-western coastline. At the time of study, two large roost areas existed in Bel Ombre, each comprising at least 400 individuals; both roosts varied seasonally in size. One of the roosts extended over several thousand square meter and consisted of three sub-roosts, between which the bats flew regularly. One roost was located in Combo forest, whereas no roosts were found in the village although bats came here to forage on crop plants (Nyhagen, 2001).

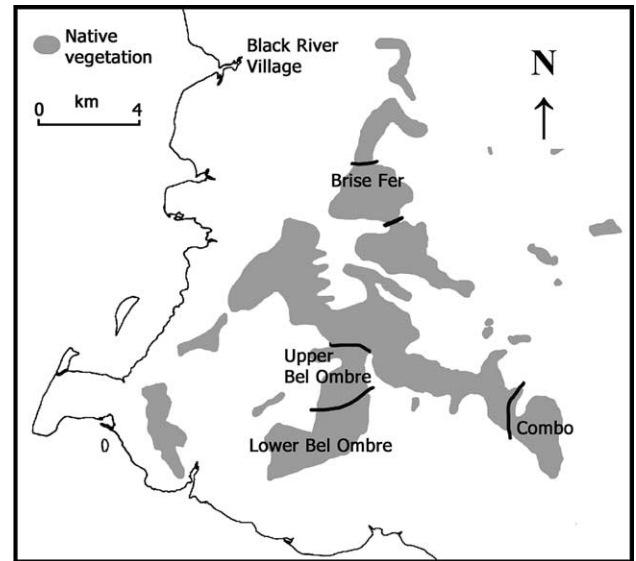


Fig. 1. Map of south-west Mauritius, showing areas of native vegetation and boundaries of forest sections, including study sites (modified from Safford (1997)).

2.3. Ejecta seed loads

Food plants were identified through direct observations of bats feeding on fruits and floral resources using binoculars (10 × 30), and indirectly through ejecta, which were searched out and collected during regular walks throughout the study sites. Ejecta are pellets of fruit pulp squeezed dry of juice between the bat's tongue and palate and are easily identifiable since no other Mauritian animal processes fruit in this manner. Ejecta from different plant species were distinguished from each other on the basis of pulp colour and texture and seed morphology.

All ejecta found were collected and analysed for their seed content. Seeds were counted, identified, and categorised as either mature with testa undamaged by bats, mature with broken testa ('damaged'), or immature. Seed maturity was evaluated on the basis of testa colour and hardness and by comparison with seeds that had just sprouted. Seeds were also categorised as either small (<5 mm), medium (5–25 mm), or large (>25 mm) (length of longest side). The categorisation was based on the fact that large Australian pteropodids have an oesophageal lumen distendable to 4–5 mm, through which passage of smaller seeds is possible (Richards, 1995). Preliminary surveys suggested that seeds longer than 25 mm were too large to be included in ejecta.

2.4. Seed dispersal

Direct observations of bats carrying fruit and dropping ejecta or fruit in flight were recorded before dark using binoculars (10 × 30). Indirect observations of

dispersal were made by collecting ejecta and bat faeces from the forest floor followed by a search for the nearest possible source tree. Such observations were made only of ejecta and faeces that were found beyond the canopy of the source tree. When the actual dispersal distance could not be determined, the minimum possible dispersal distance was recorded for both direct and indirect observations. All observations were made in areas frequently visited by bats close to roost sites.

2.5. Fur pollen loads

Indirect evidence of bats visiting flowers was obtained by analysing pollen loads of six dead and 12 captured bats. The dead bats were found on overhanging electric wires; all but one had died shortly before the samples were taken. The live bats were caught in Bel Ombre in mist-nets ('Ecotone' denier: 110/2 N, mesh: 30 mm, 4 shelves, 3.2 × 12 m in size). Suitable sites for mist-netting were found to be areas close to trees in which bats were feeding, and where trees made up a background behind the net disguising its outline. Nets were set up at dusk between two trees at a height of approximately 8 m and were constantly watched when open. One scanning electron microscopy (SEM) stub with double-sided sticky tape was applied to the lip region of each dead and captured bat. Pollen from flowering plants in the area was also applied to SEM stubs for future reference. Stubs were kept in airtight plastic containers and later

coated with gold in an Edwards Sputter coater 5150B and analysed for pollen.

3. Results

3.1. Diet of *P. niger*

Floral resources were observed to be consumed from two species (but see Section 3.4), leaves from one species, and fruit from 20 species (one species was visited for both fruit and flowers) (Table 1). In total, 22 food plant species belonging to 19 genera and 13 families were recorded. Thirty-two per cent of these species are endemic to Mauritius, 18% are native and 50% are introduced. Of the native and endemic plant species, 36% are either vulnerable or rare (Walter and Gillett, 1998).

From November to February immature fruits of five species were consumed by *P. niger* (*Diospyros tessellaria*, *Grangeria borbonica*, *Labourdonnaisia glauca*, *Sideroxylon cinereum* and *Terminalia catappa*). Furthermore, ejecta from *G. borbonica* and *S. cinereum* contained a larger proportion of immature than mature seeds (59%, $n = 39$; 94%, $n = 64$, respectively).

The total number of direct observations of bats feeding on fruits and floral resources was 132 and 55, respectively. Fifty-four of the latter observations were of young bats feeding in a single tree of the introduced

Table 1
Food plants species of *Pteropus niger*

| Family | Species | Status | Food type |
|------------------|--|-------------|------------------|
| Anacardiaceae | <i>Mangifera indica</i> | Introduced | Fruit |
| Arecaceae | <i>Dypsis lutescens</i> | Introduced | Fruit |
| Burseraceae | <i>Protium obtusifolium</i> | Endemic | Fruit |
| Celastraceae | <i>Cassine orientalis</i> ^a | Native | Fruit |
| Chrysobalanaceae | <i>Grangeria borbonica</i> | Native | Fruit |
| Combretaceae | <i>Terminalia catappa</i> | Introduced | Fruit |
| Ebenaceae | <i>Diospyros tessellaria</i> | Endemic (V) | Flower and fruit |
| Flacourtiaceae | <i>Aphloia theiformis</i> ^a | Native | Fruit |
| Melastomataceae | <i>Warneckia trinervis</i> | Endemic | Fruit |
| Moraceae | <i>Artocarpus heterophyllus</i> | Introduced | Fruit |
| Moraceae | <i>Ficus reflexa</i> | Native | Fruit |
| Myrtaceae | <i>Callistemon citrinus</i> | Introduced | Flower |
| Myrtaceae | <i>Psidium cattleianum</i> ^a | Introduced | Fruit |
| Myrtaceae | <i>Psidium guajava</i> ^a | Introduced | Fruit |
| Myrtaceae | <i>Syzygium jambos</i> | Introduced | Fruit |
| Pandanaceae | <i>Pandanus eydouxia</i> | Endemic (R) | Fruit |
| Pandanaceae | <i>Pandanus utilis</i> ^a | Introduced | Fruit |
| Sapotaceae | <i>Labourdonnaisia glauca</i> | Endemic (V) | Fruit |
| Sapotaceae | <i>Madhuca latifolia</i> | Introduced | Foliage |
| Sapotaceae | <i>Mimusops coriacea</i> ^a | Introduced | Fruit |
| Sapotaceae | <i>Mimusops petiolaris</i> | Endemic (V) | Fruit |
| Sapotaceae | <i>Sideroxylon cinereum</i> ^a | Endemic | Fruit |

Information about distribution, conservation status and nomenclature of plant species is from Flore des Mascareignes (Berg and Van Heusden, 1985; Friedmann, 1981, 1997a,b; Marais, 1997; Moore and Guého, 1984; Richardson, 1981; Scott, 1990; Sleumer and Bossler, 1980; Wickens, 1990a,b) and Walter and Gillett (1998), respectively. V, vulnerable, R, rare.

^a Only indirect observations (ejecta) recorded. The status of the Mauritian flora is currently in the process of being revised by the Mauritian Wildlife Foundation and the National Parks Office, Mauritius (Dulloo, E. Dulloo, pers. commun.).

Callistemon citrinus. No bats were observed to eat whole *C. citrinus* flowers, and no ejecta of flower material were found beneath the tree. The duration of feeding at each *C. citrinus* inflorescence was 15 s ($n = 24$, $SD = 12$ s). In addition, one observation was made of an adult bat ingesting whole flowers of *D. tessellaria* and two ejecta, both containing parts from several flowers, were discarded after feeding.

3.2. Ejecta seed loads

A total of 2032 ejecta, containing 2460 seeds and fruit remains from 16 species, was analysed (the ejecta of *Psidium cattleianum* and *P. guava* were not distinguished) (Table 2). Seeds and pulp from different species were never found within the same ejectum. The largest seeds found in ejecta were those of *L. glauca* and no seeds longer than 22 mm and wider than 13 mm were found. Average number of seeds per ejectum decreased significantly with increasing seed size (Table 2; Spearman correlation analysis: $n = 18$, $r = -0.66$, $p = 0.01$). One seed of *D. tessellaria* and 15 of *L. glauca* were found germinating in the ejecta.

The pulp of *L. glauca* fruits had a high concentration of latex. Compared to fresh latex in fruit, latex in ejecta was firmer and stickier (quite like chewing gum), causing the seed and pulp to stick together. Feeding observations of bats in the wild showed that the duration of processing one fruit into ejecta was 222 s for *L. glauca*

($n = 17$, $SD = 119$ s) compared with 106 s for *D. tessellaria* ($n = 7$, $SD = 46$ s), which has fruits of similar size to *L. glauca*. The difference was highly significant (Mann–Whitney U test: $U = 20.0$, $p = 0.001$).

3.3. Seed dispersal

A total of 47 direct and indirect observations of the dispersal of fruit, ejecta or faeces containing seeds were recorded. Dispersal distances ranged 2–250 m beyond the canopy of the parent tree.

Dispersal range of fruit was 2–200 m ($n = 33$) and included four, possibly more, species; two endemic (*D. tessellaria*, $n = 21$ and *L. glauca*, $n = 5$), two introduced (*Mangifera indica*, $n = 1$ and *Syzygium jambos*, $n = 1$) and five unidentified fruit.

Dispersal range of ejecta containing seeds was 2–40 m ($n = 9$) and included three species; two endemic (*L. glauca*, $n = 6$ and *Protium obtusifolium*, $n = 1$) and one native (*Ficus reflexa*, $n = 2$). Seeds within dispersed ejecta were mature and undamaged by bats.

Five faeces, each containing 5–20 *Ficus* seeds were found at a distance of 250 m from the nearest fig tree (*F. reflexa*).

3.4. Fur pollen load

Eighteen pollen samples taken from the fur of the lip region of individual bats carried a minimum of 18 pollen

Table 2

Variation between species in average number of seeds per ejecta, proportion of ejecta containing >1 seed and proportion of ejecta with >1 undamaged seed (mature with intact testa)

| Species | Seed size | Number of ejecta | Average number of seeds per ejectum | Proportion of ejecta with seeds (%) | Proportion of ejecta with undamaged seeds (%) |
|-----------------------------------|-----------|------------------|-------------------------------------|-------------------------------------|---|
| <i>Mangifera indica</i> | L | 117 | – | – | – |
| <i>Dyopsis lutescens</i> | M | 16 | – | – | – |
| <i>Protium obtusifolium</i> | M | 92 | 1.0 | 100 | 100 |
| <i>Grangeria borbonica</i> | | | | | |
| Immature seeds | M | 23 | 2.0 | 100 | ? |
| Mature seeds | M | 16 | 1.9 | 100 | 100 |
| <i>Terminalia catappa</i> | L | 159 | – | – | – |
| <i>Diospyros tessellaria</i> | M | 97 | 0.1 | 9.3 | 4.1 |
| <i>Aphloia theiformis</i> | M | 73 | – | – | – |
| <i>Warneckia trinervis</i> | M | 56 | 3.9 | 100 | 91.1 |
| <i>Artocarpus heterophyllus</i> | M | 85 | – | – | – |
| <i>Ficus reflexa</i> ^a | S | 3 | 428.0 | 100 | 100 |
| <i>Psidium</i> spp. | S | 20 | 6.1 | 90.0 | 90.0 |
| <i>Syzygium jambos</i> | M | 29 | – | – | – |
| <i>Labourdonnaisia glauca</i> | M | 956 | 0.4 | 43.7 | 42.3 |
| <i>Mimusops coriacea</i> | M | 8 | – | – | – |
| <i>Mimusops petiolaris</i> | L | 218 | – | – | – |
| <i>Sideroxylon cinereum</i> | | | | | |
| Immature seeds | M | 60 | 3.8 | 100 | ? |
| Mature seeds | M | 4 | 3.0 | 100 | 100 |
| Total number of ejecta | | 2032 | | | |

Seed sizes: Large, L: >25 mm; medium, M: 5–25 mm and small, S: <5 mm.

^a Seeds found in faeces. Presence of fig wasp holes was not noted.

species; a total of 319 pollen grains were found, only some of which could be identified to genus or species. Each sample had an average of 17.7 pollen grains (SD = 28.9, range = 1–110 grains, $n = 18$) belonging to 2.2 pollen species (SD = 1.5, range = 1–5, $n = 18$). Eight samples only had one pollen species, but one sample carried five species of pollen, viz. one *Sideroxylon* species, two other Sapotaceae species, *Diospyros* cf. *tessellaria* and one *Pandanus* species. Pollen of Myrtaceae was most common, being present on half of the samples. Pollen of an unknown species was found on 39% of the samples, and 22% carried pollen of *T. catappa*.

4. Discussion

4.1. Diet of *P. niger*

Our list of food plants is not exhaustive because data were obtained only during the 7-month study period and observations covered a small part of the range of *P. niger*. The methods employed were designed to identify food plants of *P. niger* but cannot quantify the extent to which their diet is composed of those species.

In this study, the diet of *P. niger* was composed mainly of fruit. Whether floral resources or leaves are important dietary components in areas and/or seasons not studied here remains to be seen.

This study documented 22 species of food plants of *P. niger*, however, 36% of the native or endemic food plants are vulnerable or rare and their availability to the bats may decrease even further in the future. The fact that half of the food plant species were introduced suggests that *P. niger* is an opportunistic feeder, strongly influenced by habitat alteration resulting from human activity.

Visitation by bats to the small flowers of *D. tessellaria* is detrimental to the reproductive potential of the tree. Bats may forage on these flowers for the same reason that they consume leaves containing important nutrients, e.g. to obtain protein, which is in low quantity in fruit (Entwistle and Corp, 1997; Funakoshi et al., 1993; Kunz and Diaz, 1995; Tan et al., 1998), or they visit flowers in periods of fruit shortage. *C. citrinus* is introduced from Australia where flying foxes are also found, but there are no records of Australian bats visiting these flowers.

From November to February immature fruits of five species were consumed by *P. niger* and ejecta from two species contained a larger proportion of immature than mature seeds. These results suggest a scarcity of ripe fruit and that during such periods bats may have a detrimental effect on the reproduction of their food plants. Banack (1998) and Marshall (1985) emphasise that pteropodids prefer ripe over unripe fruit and Funakoshi et al. (1993) state that fruit

bats only consume immature fruit when ripe fruit resource levels are low. The nutritional composition of unripe fruit consumed by Samoan pteropodids following severe hurricanes showed no difference from ripe fruit in mean levels of organic and mineral components (Nelson et al., 2000). However, bats may prefer ripe to immature fruit as it is more palatable, i.e. it has softer pulp and pericarp, and lower levels of secondary plant compounds.

4.2. *Pteropus niger* as seed disperser

Bats may provide several advantages to the plants on which they feed. Separation of pulp from seeds by frugivores may increase survival by reducing seed predation and microbial attack (Willson and Traveset, 2000). Insects and fungi attacked 6% and 31% of the fallen, mature fruits sampled beneath *D. tessellaria* and *L. glauca* trees, respectively, damaging approximately 85% of the seeds (Nyhagen, 2001).

Potentially, fruit of any plant species eaten by *P. niger* may have its seeds dispersed by bats in flight – even those with the size of a mango (M. Burgess, pers. commun.). Dispersal by ejecta is limited to species with medium-sized or small seeds, and dispersal by faeces is limited to very small seeds such as those of *Ficus* and perhaps of *Psidium*.

This study demonstrated that *P. niger* disperses intact seeds in ejecta and therefore, the size of the ejecta seed loads is important in terms of seed dispersal. Some species have fruits smaller than ejecta, and several seeds of single-seeded species such as *G. borbonica*, *Warneckia trinervis* and *S. cinereum* were observed to be dispersed in a single ejecta, although this may not be an advantage. Such seeds will be dropped in clumps and perhaps suffer from increased competition. However, multi-seeded dispersal may be advantageous in dioecious species (e.g. *S. cinereum*), as female plants are dependent on male individuals in their vicinity for pollination.

Labourdonnaisia glauca and *D. tessellaria* were frequently visited food species of *P. niger* in the study area. The duration of processing fruit into ejecta was significantly longer for *L. glauca* than e.g. *D. tessellaria*, and bats appeared to have difficulties in discarding the seeds of *L. glauca*. The average number of seeds in whole fruits of *D. tessellaria* and *L. glauca* was five and one, respectively; however, four times as many *L. glauca* ejecta contained seeds than those of *D. tessellaria*. Almost half of all *L. glauca* ejecta contained a seed and most of these were classified as undamaged and mature. The high content of latex in *L. glauca* fruits may prolong the feeding duration and length of time which seeds are attached to the pulp, explaining the high seed load of ejecta which may enhance the dispersal of *L. glauca* seeds.

4.3. *Pteropus niger* as pollinator

The pollen analysis revealed that at least 18 flower species are visited by *P. niger*, although *P. niger* was observed to visit flowers of only two species. Pollen of Myrtaceae was most abundant, both in number of bats carrying this pollen type, and in the total amount of pollen found on bats. This is most likely explained by the fact that several bats were captured flying from a flowering *C. citrinus* tree. As pollen grains within this plant family are very similar in appearance, the sampled pollen could not be determined to species or genus. However, the Myrtaceae is well represented in the Bel Ombre forest, e.g. by *S. jambos*, which was flowering during the study and may be visited by bats.

Individuals of both *T. catappa* and *L. glauca* were flowering and fruiting simultaneously (pers. obs.), thus, fruit-harvesting bats might also pollinate.

Pollen samples were limited to only on one SEM stub per animal and yet pollen from at least 18 species was found. These bats may carry pollen on chest, shoulder and facial fur (unpublished for *P. subniger*), and therefore the pollen load size and composition found in this study is likely to be an underestimate of the actual load of pollen carried by the bats.

The impact of *P. niger* as pollinator cannot be quantified without further investigation. However, its influence on seed fitness may be large, because it flies long distances in a short time, mediating out-crossing among small, scattered populations in a heavily fragmented landscape.

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