NYHAGEN, D.F. 2004. A study of the bat-fruit syndrome on Mauritius, Indian Ocean. *Phelsuma* **12**: 118—125

A study of the bat-fruit syndrome on Mauritius, Indian Ocean

DORTE FRIIS NYHAGEN

Department of Ecology & Genetics
Aarhus University, Ny Munkegade Block 540,
DK-8000 Aarhus C, DENMARK

Abstract.— This study was conducted over a seven month period on Mauritius, Indian Ocean, and concerns the relationship between the endemic fruit bat *Pteropus niger* and 19 food plants upon which it feeds in regard to the bat-fruit syndrome. This is a set of fruit characteristics which suggest an adaptation to fruit bat dispersal noted throughout the world where fruit bats occur. This study has found some evidence of an adherence to the bat-fruit syndrome. Twenty-one percent of the food plants had five of seven characteristics in accordance with the syndrome, 32% had four, 21% had three, 21% had two and 5% of the species had one of the seven bat fruit characteristics. Although the concept of the bat-fruit syndrome is difficult to prove, some of these species may be classified as bat-fruit trees; a species of particular interest was *Labourdonniasia glauca.* Other food plants had only few traits in accordance with the bat-fruit syndrome, some of which appeared to be adapted to bird dispersal, suggesting a more diffuse relationship between these plants and their seed dispersers and a generalist or opportunistic feeding strategy of *P. niger*.

Keywords.— flying foxes, fruit syndrome, Megachiroptera, *Labourdonnaisia glauca*, *Pteropus niger*,

INTRODUCTION

Following the concept of fruit dispersal syndromes, fruits can be classified according to a set or a syndrome of fruit and seed characteristics (VAN DER PIJL 1982). The fruit of individual plant species may, however, not necessarily possess all characteristics of a particular syndrome (VAN DER PIJL 1982). Previous studies have shown relationships between fruit dispersal syndromes and the attraction of different frugivore taxa in the Old World (KNIGHT 1983, DEBUSSCHE & ISENMANN 1989, KORINE *et al*. 1998) and the New World (JANSON 1983, GORCHOV *et al*. 1995, KALKO *et al*. 1996).

A set of fruit attributes is characteristic to plants being bat-dispersed (VAN DER PIJL 1957, MARSHALL 1983, KORINE *et al.* 1998). These are an easily available, often pendant or cauliflorous position, large fruit size, and large or small seeds (i.e. not of intermediate size), drab or green colours of ripe fruit, strong odours of pulp (e.g. rancid, sour or stale), and juicy pulp (VAN DER PIJL 1957, MARSHALL 1983, KORINE *et al*. 1998). The bat-fruit syndrome appears to be globally valid (VAN DER PIJL 1957). In both the Neo- and the Palaeotropics observations on plants introduced from one continent to the other show that fruit serving as food for bats at one site also attracts bats elsewhere (VAN DER PIJL 1957).

Pteropus niger (KERR, 1792) is the only extant fruit bat species of two, perhaps three species that once inhabited Mauritius (*P. niger*, *P. subniger* and possibly *P. rodricensis*) (CHEKE & DAHL 1981). With an average forearm-length of 152mm it is a species of intermediate size within its genus according to KOOPMAN (1994) (CHEKE & DAHL 1981, NYHAGEN *et al.* 2004). *Pteropus niger* is mainly nocturnal, but occasionally indi-

viduals are seen foraging from early afternoon or even shortly after dawn (NYHAGEN *et al.* 2004). At least 14 major roosts are found in the montane forests of the southeast and southwest of Mauritius and many of these roost sites are found within national park areas (T. BODEY and S. EWING *pers.comm.*, *pers. obs*). The current status of *P. niger* is unknown, however, the population appears to be healthy due to the protection of the species and absence of any major cyclones in recent years. *Pteropus niger* may play an very important role in regeneration of the Mauritian forest as it disperses seeds and carries pollen of many plant species (NYHAGEN *et al.* 2004).

The diet of *P. niger* is mainly composed of fruit, flower parts and nectar and occasionally leaves. *Pteropus niger* visits at least 22 plant species for food belonging to 19 genera and 13 families (NYHAGEN *et al.* 2004). 32% of these species are endemic to Mauritius, 18% are native and 50% are introduced (SLEUMER & BOSSER 1980, FRIEDMANN 1981, RICHARDSON 1981, MOORE & GUÉHO 1984, BERG & VAN HEUSDEN 1985, SCOTT 1990, WICKENS 1990a, WICKENS 1990b FRIEDMANN 1997a, FRIEDMANN 1997b, MARAIS 1997). Of the native and endemic plant species, 36% are either vulnerable or rare (WALTER & GILLETT 1998).

This study investigates the characteristics of fruit eaten by *Pteropus niger* and addresses the question of whether or not these fruits conform to the bat-fruit syndrome.

MATERIAL AND METHODS

Study area

This study was conducted from October 1999 to April 2000, in The Black River Gorges National Park in the south and south-west of Mauritius. The park covers 65.7km^2 and includes two lower montane forest areas, Combo and Lower Bel Ombre (150-704m a.s.l.) (SAFFORD 1997) and includes several roosts of *P. niger*. The study was mainly carried out in the lower Bel Ombre forest, but includes observations from Combo forest and Black River Village, situated on the south-western coastline.

Description of fruits

Fruit consumed by *P. niger* was characterised according to its accessibility, size, seed size, colour, odour, flavour and water content. For each characteristic its particular state was scored as either "in accordance" or "not in accordance" with the bat fruit syndrome.

By observing bats landing in and crawling around in trees and noting how easily fruits were retrieved, plant species were grouped in accordance to the accessibility of their fruits. Trees, in which no bats were observed, were categorised on the basis of the position of their fruit.

Size of fruit were classified as small (<10mm), medium (30≥10mm) or large (>30mm) and seeds were categorised as either small (<5mm), medium (5-25mm), or large (>25mm) (length of longest side). Unfortunately, no size categories have been specified in previous studies of the bat-fruit syndrome. In this study, the selection of fruit categories was agreed upon by three fieldworkers and the author as to which fruit sizes were regarded as small, medium and large. The categorisation of seed sizes was based upon the fact that large Australian pteropodids have an oesophageal lumen distendable to 4-5mm, through which passage of smaller seeds is possible (RICHARDS 1990). Previous surveys suggested that seeds longer than 25mm were too large to be included in ejecta of *P. niger*

(pellets of fruit pulp squeezed dry of juice between the bat's tongue and palate).

Often, a fruit possessed more than one state of each character, e.g. a fruit could taste both sweet and bitter, and in this study, for the sake of analytical simplicity, only the most pronounced state was included. Some fruits eaten by bats had multicoloured epicarp when ripe or partially ripe. Here, both colours were included in the data set. Bat-consumed immature fruit was also included and fruit which was consumed as both immature and mature was described as mature.

RESULTS

Bat-consumed fruit from 19 different species (of which 12 were native or endemic) was analysed. The most common fruit characteristics were as follows; easily accessible fruit (95%), medium size fruit (47%), medium size seed (68%), vivid colours (53%), sweet smell (58%), sweet odour (74%), and not juicy, i.e. low water content (58%) (Table 1).

Table 1 Presence of characteristics in accordance or not in accordance with the bat-fruit syndrome in 19 food plants of *Pteropus niger*.

	"In accordance"		**"Not in accordance"**	
Position of fruit	Easily accessible	95%	Not easily accessible	5%
Size of fruit	Large	42%	Medium (47%) or small (11%)	58%
Size of seed	Large (21%) or small (11%)	32%	Medium	68%
Colour of epicarp	Drab	47%	Vivid	53%
Odour	Musty, sour or rancid	11%	Other	89%
Flavour	Sweet or sour	79%	Other	21%
Consistency of pulp	Juicy	42%	Not juicy	58%

Only two the seven categories (flavour and accessibility) had more species with characteristics in accordance with the bat-fruit syndrome. Five percent of the species had only one of seven characteristics in accordance with the bat fruit syndrome. 21% had two, 21% had three, 32% had four, 21% had five and none had six or all of the seven bat fruit characteristics. The species with five characteristics in accordance with the bat fruit syndrome were *Artocarpus heterophyllus* (Moraceae), *Diospyros tessellaria* (Ebenaceae), *Mangifera indica* (Anarcardiaceae) and *Mimusops petiolaris* (Sapotaceae) (Table 2). The fruits of *M. indica* and *A. heterophyllus* are pendant and cauliflorous, respectively. *Diospyros tessellaria* and *M. petiolaris* are endemic to Mauritius, whereas *A. heterophyllus* and *M. indica* are introduced cultivated plants and all four species were popular food plants of *P. niger*.

Table 2 Four of *P. niger's* food plants with five of seven characteristics in accordance with the bat-fruit syndrome

Artocarpus heterophyllus	Green/brown (drab) colour, musty smell, sweet flavour, cauliflorous position, large fruit
Diospyros tessellaria	Green (drab) colour, sweet flavour, juicy, easily accessible position, large fruit size
Mangifera indica	Sweet flavour, juicy, pendant position, large fruit size, large seed size
Mimusops petiolaris	Green (drab) colour, sweet flavour, easily accessible position, large fruit size, large seed

Labourdonniasia glauca (Sapotaceae), another popular food tree of *P. niger*, possessed four of the seven characteristics typical of bat-fruits. This species has a medium-sized fruit which is dull-green, smells vaguely sour and contains a single medium sized seed. Fruits are placed in the outer canopy on fairly thick twigs, making fruits visible from above and easily accessible. Bats appeared to land and forage in these trees with ease, due to the thick and open branch structure of the tree. The fruiting season of the study population of *L. glauca* started in November, and mature fruits were found until the end of April, providing a source of food for the bats for much of the year. Besides *P. niger* the only other vertebrate foraging on these fruits was the introduced monkey (*Macaca fascicularis*).

Fruit of the species *Protium obtusifolium* (Burseraceae) also had four traits in accordance with the bat-fruit syndrome, although other characteristics contradict this classification. The thick epicarp contained a bitter juice (the taste resembled turpentine) and opened asymmetrically along a crevice. This shell was unattached to the sweet, pink pulp, which was well-fastened to the seed. Bats were not capable of breaking up this fruit and they chewed on the bitter epicarp without being able to separate it from the pulp. Parrots, however, neatly handled these fruits using their beak, first to open the fruit and discard the epicarp and subsequently the pulp was scraped off the seed and ingested. These observations were made on introduced ring-necked (*Psittacula krameri*) and captive echo-parakeets (*P. eques*), the later being endemic to Mauritius and once inhabited the areas where *P. obtusifolium* is found.

Several other food plants of *P. niger* also seemed to be more adapted to bird dispersal according to the "bird syndrome". This syndrome includes fruits that are small (JANSON 1983, GAUTIER-HION *et al*. 1985, GORCHOV *et al*. 1995, KALKO *et al*. 1996, KORINE *et al*. 1998), taste sweet (GAUTIER-HION *et al*. 1985), are green when immature (VAN DER PIJL 1982) and have signalling colours such as black, purple or red when ripe (VAN DER PIJL 1982, JANSON 1983, GAUTIER-HION *et al*. 1985, GORCHOV *et al*. 1995, KALKO *et al*. 1996). Fruits of the three species; *Sideroxylon cinereum* (Sapotaceae), *Grangeria borbonica* (Chrysobalanaceae) and *Warneckea trinervis* (Melastomataceae) are small, have green immature fruits, which turn red, purple or black when ripening and therefore possess several characteristics typical of bird-fruits.

DISCUSSION

The bat-fruit syndrome is based around seven plant characteristics which on their own seem quite vague, e.g. juicy or easily accessible fruits are common traits amongst fruits in general. The most common combination of fruit characteristics amongst the 19 fruit species was sweet flavour, high water content and an exposed position. However, these characteristics are also found among fruits eaten by other animal taxa such as other mammals and birds (VAN DER PIJL 1982, GAUTIER-HION *et al*. 1985, KALKO *et al*. 1996).

The concept of fruit syndromes is questioned by several authors (HOWE 1980, HEITHAUS 1982, HOWE and SMALLWOOD 1982, HERRERA 1985, HERRERA 1987, WILLSON *et al*. 1989). WILLSON (1989) suggests that fruit colour may attract fruit or seed destroyers as well as dispersers and colours may serve alternative functions such as affecting the thermal regime of developing fruits. Phylogenetic and historical constraints on the evolution of fruit colours may also be an important factor (HERRERA 1985, WILLSON *et al*. 1989).

Adjustments between plants and their dispersers may be coarse or diffuse, rather than finely tuned (HOWE 1980, HERRERA & JORDANO 1981, HEITHAUS 1982, HOWE & SMALLWOOD 1982). HERRERA (1985) discusses the co-evolution of plants with fleshy fruits and their vertebrate dispersers and some of the ecological and evolutionary constraints, which may be important to any occurrence of plant-animal evolution. He states that traits in plants and their dispersers resulting in successful seed dispersal are a necessary, but not a sufficient condition to infer co-evolution (HERRERA 1985). For example, introduced plants or birds may interact with native counterparts and result in successful seed dispersal (HERRERA 1985).

The evolution of species-specific systems may be affected several factors. First, it is harmful to plants to restrict access to their fruits beyond a certain threshold (JANSON 1983, HERRERA 1985), as plants thereby become vulnerable to loss of dispersers. This may explain the presence of coarse or diffusely evolved plant-animal dispersal systems ("guild-syndromes"), where plants have evolved fruit traits which attract a wide variety of animal taxa, which may again consume a wide variety of fruit types. Secondly, high environmental variance (as opposed to genetic variance) and selective pressures by non-dispersers may combine to produce a low uniform selection from dispersers on plants (HERRERA 1985). Such factors may have played a part in the evolution of Mauritian plants and their plant-disperser species. Thus, most plants analysed in this study may have fruit characteristics suitable for attracting a variety of dispersers including fruit bats and confirm more to a kind of "guild syndrome".

Four species had five of seven characteristics consistent with the bat-fruit syndrome (*Artocarpus heterophyllus, Diospyros tessellaria, Mangifera indica* and *Mimusops petiolaris*). These species may be classified as "bat-fruit trees", and were certainly popular food plants of the bats.

In the description of the syndrome, no measurements of fruit or seed sizes were specified and the classification into size groups was made subjectively. Had fruit and seed sizes been set differently, a different picture would have emerged, i.e. had seeds larger than 25mm in length been included as "large fruit", three species would have had another trait in accordance with the syndrome.

One of these species is *Labourdonniasia glauca,* an endemic tree to Mauritius with four of the seven bat-fruit characteristics. A curious trait of *L. glauca* is a very high concentration of latex in the fruit pulp (NYHAGEN *et al.* 2004). 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 *L. glauca* fruit into ejecta was significantly higher compared with e.g. *Diospyros tessellaria*, which has fruits of similar size to *L. glauca*. Four times as many *L. glauca* ejecta contained seeds than those of *D. tessellaria*. 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. Seeds of *L. glauca* have been observed to be dispersed by *P. niger*, and seeds in ejecta from this species have been found germinating (NYHAGEN *et al.* 2004).

Pteropus niger is the only native vertebrate to feed on *L. glauca* fruits, but it is likely that the extinct fruit bat *P. subniger* or other extinct animals of Mauritius fed on these fruits as well. Based upon fruit characteristics in accordance with the bat-fruit syn-

drome, the high latex contents of the pulp, its popularity and general foraging behaviour of the bats on this species, and the fact that no other native vertebrate feeds on its fruit, *L. glauca* appears to be closely associated with bats for seed dispersal and may be an example of a bat tree described by VAN DER PIJL (1957), MARSHALL (1983) and KORINE *et al.* (1998).

The bat-consumed fruit species included in this study showed much variation and may be adapted to dispersal by bats and/or other frugivores. This may indicate that *P. niger* is a fruit generalist or opportunist. Alternatively, this pattern may be explained by convergent evolution of "guild syndromes" among these food plants of *P. niger.*

ACKNOWLEDGEMENTS

I am grateful to volunteers from MWF who helped and assisted on this project. D. FLORENS, J. C. SEVATHIAN, M. VIRAHSAWNY and G. D'ARGENT of the Sugar Research Institute of Mauritius helped with the identification of plant species. Sincere thanks to N. BUNBURY, D. HANSEN, J. TAYLEUR, D. HALL and especially S. TURNBULL for useful discussions and critical comments. This project was supported by Aarhus University, The Mauritian Wildlife Foundation, Bat Conservation International, The Percy Sladen Memorial Fund, The Midtbank Fund, The Kjebi Fund, and the Danish Science Research Council.

REFERENCES

BERG, C.C. & VAN HEUSDEN, E.C.H., 1985. 164. Moracées. Pp 1-21 in Bosser, J., Cadet, T., Guého, J. & Marais, W. (eds.). *Flore des Mascareignes*. The Sugar Industry Research Institute, Réduit.

CHEKE, A.S. & DAHL, J.F., 1981. The status of bats in the Western Oceanic Islands with special reference to *Pteropus*. *Mammalia* **45**: 205-238.

DEBUSSCHE, M. & ISENMANN, P. 1989. Fleshy fruit characters and the choices of bird and mammal seed dispersers in a Mediterranean region. *Oikos* **56**: 327-338.

FRIEDMANN, F.1981. 116. Sapotacées. Pp. 1-27 in Bosser, J., Cadet, T., Guého, J. & Marais, W. (eds.). *Flore des Mascareignes*. The Sugar Industry Research Institute, Réduit.

FRIEDMANN, F.1997a. 77. Anacardiaceae. Pp. 1-11 in BOSSER, J., CADET, T., GUÉHO, J. & MARAIS, W. (eds.). *Flore des Mascareignes*. The Sugar Industry Research Institute, Réduit.

FRIEDMANN, F. 1997b. 82. Chrysobalanacées. Pp. 1-4 in BOSSER, J., CADET, T., GUÉHO, J. & MARAIS, W. (eds.). *Flore des Mascareignes*. The Sugar Industry Research Institute, Réduit..

GAUTIER-HION, A., DUPLANTIER, J.M., QURIS, R., FEER, F., SOURD, C., DECOUX, J.P., DUBOST, G., EMMONS, L., ERARD, C., HECKETSWEILER, P., MOUNGAZI, A., ROUSSILHON, C. & THIOLLAY, J.M. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia (Berlin)* **65**: 324-337.

GORCHOV, D.L., CORNEJO, F., ASCORRA C.F., & JARAMILLO, M. 1995. Dietary overlap between birds and bats in the Peruvian Amazon. *Oikos* **74**: 235-250.

HEITHAUS, E.R. 1982. Coevolution between bats and plants. In *Ecology of bats*, vol. 9 (ed. T. H. KUNZ), p. 327-367. New York: Plenum press.

HERRERA, C.M. 1985. Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. *Oikos* **44**: 132-141.

HERRERA, C.M. 1987. Vertebrate-dispersed plants of the Iberian Peninsula: A study of fruit characteristics. *Ecol. Monogr.* **57**: 305-331.

HERRERA, C.M. & Jordano, P. 1981. *Prunus mahaleb* and birds: The high-efficience seed dispersal system of a temperate fruiting tree. *Ecol. Monogr.* **51**: 203-218.

HOWE, H. F. 1980. Monkey dispersal and waste of neotropical fruit. *Ecol.* **61**: 944-959.

HOWE, H.F. & SMALLWOOD, J. 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* **13**: 201-228.

JANSON, C.H. 1983. Adaption of Fruit Morphology to Dispersal in a Neotropical Forest. *Science* **219**: 187-189.

KALKO, E.V., EDWARD, A.H. & HANDLEY, C.O.J. 1996. Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. *J. Biogeog.* **23**: 565-576.

KNIGHT, R.S. 1983. Inter-Relationships between type, size and colour of fruits and dipsersal in southern African trees. *Oecologia* (Berlin) **56**: 405-412.

KOOPMAN, K.F. 1994. *Chiroptera: Systematics. Handbook of Zoology, A Natural History of the Phyla of the Animal Kingdom*. Berlin: WALTER DE GRUYTER, p. 1-191

KORINE, C., IZHAKI, I. & ARAD, Z. 1998. Comparison of fruit syndromes between the Egyptian Fruit Bat (*Rousettus aegypticus*) and birds in East Mediterranean habitats. *Acta Oecol.* **19**: 147-153.

MARAIS, W. 1997. 72. Célastracées. Pp. 1-11 in BOSSER, J., CADET, T., GUÉHO, J. & MARAIS, W. (eds.). *Flore des Mascareignes*. The Sugar Industry Research Institute, Réduit.

MARSHALL, A. G. 1983 Bats, flowers and fruit: evolutionary relationships in the Old World. *Biological Journal of the Linnean Society* **20**: 115-135.

MOORE, H.E. & GUÉHO, L. J., 1984. 189. Palmiers. Pp. 1-34 in BOSSER, J., CADET, T., GUÉHO, J. & MARAIS, W. (eds.). *Flore des Mascareignes*. The Sugar Industry Research Institute, Réduit.

NYHAGEN, D.F., TURNBULL, S.D., OLESEN, J.M. & JONES, C. G. 2004. An investigation into the role of the Mauritian flying fox, *Pteropus niger*, in forest regeneration. *Biol. Conserv.* (in press).

RICHARDS, G.C. 1990 The Spectacled Flying Fox, *Pteropus conspicillatus* (Chiroptera: Pteropodidae), in North Queensland 2. Diet, Seed Dispersal and Feeding Ecology. *Australian Mammalogy* **13**: 25-32.

RICHARDSON, I.B.K., 1981. 117. Ebenacées. Pp. 1-19 in BOSSER, J., CADET, T., GUÉHO, J. & MARAIS, W. (eds.). *Flore des Mascareignes*. The Sugar Industry Research Institute, Réduit.

SAFFORD, R.J., 1997. A survey of the occurrence of native vegetation remnants on Mauritius in 1993. *Biol. Conserv.* **80**: 181-188.

SCOTT, A.J., 1990. 92. Myrtacées. Pp. 1-70 in BOSSER, J., CADET, T., GUÉHO, J. & MARAIS, W. (eds.). *Flore des Mascareignes*. The Sugar Industry Research Institute, Réduit.

SLEUMER, H. & BOSSER, J., 1980. 42. Flacourtiacées. Pp. 1-26 in BOSSER, J., CADET, T., JULIEN, H. R. & MARAIS, W. (eds.). *Flore des Mascareignes*. The Sugar Industry Research Institute, Réduit.

VAN DER PIJL, L. 1957. The Dispersal of Plants by Bats (Chiropterochory). *Acta Bot.*

Nederland. **6**: 291-315.

VAN DER PIJL, L. 1982. *Principles of dispersal in higher plants*. Berlin heidelberg, New York: Springer-verlag, p. 215

WALTER, K.S. & GILLETT, H.J. (eds.), 1998. *1997 red list of threatened plants*. Compiled by the World Conservation Monitoring Centre, IUCN – The World Conservation Union, Gland, Switzerland and Cambridge, U.K.

WICKENS, G.E., 1990a. 91. Combretacées. Pp. 1-13 in BOSSER, J., CADET, T., GUÉHO, J. & MARAIS, W. (eds.). *Flore des Mascareignes*. The Sugar Industry Research Institute, Réduit.

WICKENS, G.E., 1990b. 94. Mélastomatacées. Pp. 1-20 in BOSSER, J., CADET, T., GUÉHO, J. & MARAIS, W. (eds.). *Flore des Mascareignes*. The Sugar Industry Research Institute, Réduit.

WILLSON, M.F., IRVINE, A. K. AND WALSH, N. G. 1989. Vertebrate Dispersal Syndromes in Some Australian and New Zealand Plant Communities, with Geographic Comparisons. *Biotropica* **21**: 133-147.