The feeding ecology of *Eidolon dupreanum* (Pteropodidae) in eastern Madagascar

Monica Picot[1,2], Richard K. B. Jenkins[3,4]*, Olga Ramilijaona[1], Paul A. Racey[3] and Stephanie M. Carrière[2]

[1]*Département de Biologie Animale, Faculté des Sciences, Université d'Antananarivo, B.P. 906, Antananarivo (101), Madagascar,* [2]*Programme GEREM-Fianarantsoa, IRD/CNRE, B.P. 434, Tsiadana, Route d'Ambohipo, Antananarivo (101), Madagascar,* [3]*School of Biological Sciences, University of Aberdeen, Aberdeen, AB24 2TZ, U.K. and* [4]*Madagasikara Voakajy, B.P. 5181, Antananarivo (101), Madagascar*

Abstract

We investigated the diet of the endemic fruit bat *Eidolon dupreanum* (Chiroptera: Pteropodidae) in eastern Madagascar. We collected faecal and ejecta samples under day roosts and at nocturnal feeding trees. *Eidolon dupreanum* ate mainly fruit, although *Eucalyptus* spp. flowers were also consumed. In total, 30 plant species (fourteen identified and sixteen unidentified) were recorded in the diet, including six introduced taxa. *Polyscias* spp. trees, which occurred in humid forest at least 5 km from the roost, were the most frequently recorded plant in the diet. Fruits of *Psidium* spp. were abundant near to the roost but relatively uncommon in the faeces. Passage through the alimentary canal was limited to seeds $\leqslant 7$ mm and there was some evidence for a positive effect on germination after passage through bats' stomachs. The role of fruit bats as seed dispersers in forest ecosystems in Madagascar should be used as an additional leverage for their conservation.

Key words: diet, *Eidolon*, frugivory, Madagascar, seed dispersal

Résumé

Nous avons étudié le régime alimentaire de la roussette endémique*Eidolon dupreanum* (Chiroptères: Pteropodidae) dans l'est de Madagascar. Nous avons récolté des échantillons de crottes et d'éjections sous les perchoirs diurnes et les arbres qui les nourrissent pendant la nuit. *Eidolon dupreanum* mange principalement des fruits même s'il consomme aussi des fleurs d'*Eucalyptus* spp. Au total, on a relevé 30 espèces végétales (14 identifiées et 16 non identifiées), y compris six taxons introduits, dans les matières consommées. Les arbres de *Polyscias* spp. qui poussent dans la forêt humide située à cinq kilomètres, au moins, des abris diurnes étaient l'espèce la plus souvent rapportée dans le régime alimentaire. Les fruits de *Psidium* spp. étaient abondants près de l'abri mais relativement peu communs dans les excréments. Le passage dans le tube digestif était limité à des semences de moins de 7 mm, et il semblait y avoir des preuves d'un effet positif de leur passage par l'estomac des chauves-souris sur leur germination. On pourrait invoquer le rôle des roussettes dans la dispersion des semences dans les écosystèmes forestiers de Madagascar pour justifier davantage leur conservation.

Introduction

Old World fruit bats are prodigious consumers of fruit and nectar (Marshall, 1983) and contribute important ecological services through pollination and seed dispersal (Cox *et al.*, 1991; Mickleburgh, Hutson & Racey, 1992; Rainey *et al.*, 1995; Law & Lean, 1999; Shilton *et al.*, 1999). Deforestation of Madagascar's natural forests is a major threat to the island's biodiversity and the remaining expanses of intact vegetation are becoming increasingly fragmented (Ganzhorn, Goodman & Dehgan, 2003; McConnell, Sweeney & Mulley, 2004). Fruit bats, because of their mobility and diet, are important seed dispersers in fragmented landscapes because they transfer seeds and pollen between isolated sites (Bollen, Van Elsacker & Ganzhorn, 2004).

Madagascar's frugivore community is relatively depauperate (Goodman & Ganzhorn, 1997) and its primates are largely restricted to ranges within the remaining areas of intact forest (Ganzhorn *et al.*, 1999, 2003). In contrast, the

Correspondence: E-mail: jenkins@wanadoo.mg and r.jenkins@abdn.ac.uk

large size and long-range flight of pteropids create large seed shadows for the plant species that provide their fruit diet. Recent research on the diet of *Pteropus rufus* and *Eidolon dupreanum* has highlighted the role of the Madagascar's fruit bats in seed dispersal and pollination from lowland sites (Baum, 1995; Bollen & Van Elsacker, 2002; Long, 2002), but little information is available from the higher elevation dense, humid forests in the east of the island.

The two species of *Eidolon* are both African, with *Eidolon helvum* found on the mainland and some offshore islets (Mickleburgh *et al.*, 1992) and *E. dupreanum* endemic to Madagascar (MacKinnon, Hawkins & Racey, 2003). *Eidolon helvum* is a migratory species (Fayenuwo & Halstead, 1974; Baranga & Kiregyera, 1982; Thomas, 1983; Richter & Cumming, 2006) that aggregates in large colonies (e.g. Sorensen & Halberg, 2001). Although its potential role as a seed disperser has been recognized for sometime (Par & Huggel-Wholf, 1965; Ayensu, 1974; Funmilayo, 1976) quantitative data on its ecological role are still lacking.

Eidolon dupreanum differs from *E. helvum* in that it usually roosts in rock cavities as opposed to trees and large aggregations are rare (MacKinnon *et al.*, 2003). Despite its abundance in many areas of Madagascar, there have been few attempts to determine the ecological role of *E. dupreanum*. Observations in western and northern Madagascar indicate that this species pollinates two endangered baobab trees (Baum, 2003; Andriafidison *et al.*, 2006) and a study of faeces collected from a number of roosts in the central highlands revealed a diet consisting of both native and introduced plants (Ratrimomanarivo, 2003). In this study, we assessed the diet of *E. dupreanum* from a site with extensive agricultural land and mid-elevation dense, humid forest. We investigated the relative contribution of forest plants to the diet and comment on the role of *E. dupreanum* as a seed disperser.

Study area

The corridor of rainforest between Ranomafana and Andringitra National Parks in south-eastern Madagascar is an area of considerable conservation importance because it maintains the belt of humid forest along the eastern escarpment (Carrière *et al.*, 2005). The corridor varies in width between 5 and 20 km and underwent deforestation between 1974 and 1993 because of timber exploitation and agricultural expansion (Rabetaliana, 2001).

This study was conducted from April 19 to May 25 2004 at a site 35 km north-east of Fianarantsoa, near the village of Ambendrana (21°22,748′S, 47°18,513′E; 1128 m a.s.l.). This period was chosen because ripe fruits from native forest and cultivated trees were simultaneously available in the study site. The intact vegetation is mid-elevation, humid forest and *Weinmannia* spp. (Cunoniaceae) and *Tambourrissa* spp. (Monimiaceae) are the common canopy-forming gender trees (Koechlin, Guillaumer & Morat, 1974). Land use outside of the mid-altitude humid forest is mainly various stages of regenerating secondary forest called '*kapoka*', pseudo-steppes grassland, *Eucalyptus, Pinus, Acacia* plantations, orchards and rice fields (Fig. 1) resulting in a heterogeneous landscape (Carrière *et al.*, 2005). The humid forest corridor is approximately 5 km from the rock outcrop where three *E. dupreanum* roosts were located. Each roost was 0.6–2 km apart and 0.8–1.3 km from the nearest human settlements. We were unable to count directly the animals because of the inaccessibility of the roost sites and cannot rule out that we collected repeated samples from the same individuals.

Materials and methods

Our data on the diet of *E. dupreanum* were obtained by collecting and analysing faecal and ejecta pellets samples on plastic sheeting (3 m × 1.50 m) placed underneath three day roosts of *E. dupreanum*. Fruit bats produce ejecta pellets when feeding on ripe fruits by squeezing juices into their mouth and discarding the remains. Additional ejecta pellets were collected opportunistically under feeding trees.

Each seed was identified using a reference collection of fruiting plants collected during the study. Botanists at the Parc Botanique et Zoologique de Tsimbazaza (Antananarivo) and at the Missouri Botanical Garden verified our identifications. We measured the length of a sample of all identified seeds. We recorded the presence or absence of pollen in each faecal pellet and identified the presence of flower parts, such as stamens.

The seed viability after passage through the digestive tract of *E. dupreanum* was tested by germinating seeds from faeces, ejecta and ripe fruits after removal of the pulp. The seeds were sown simultaneously in Petri-dishes containing disks of filter paper soaked with water and were placed in a drying oven (EBT 260, Médisciences®, Paris, France) at temperatures of 20°–25°C. A total of 208 seeds were sown from eight plant species. We used χ^2 analyses to compare the number of germinated seeds among the three different treatments.

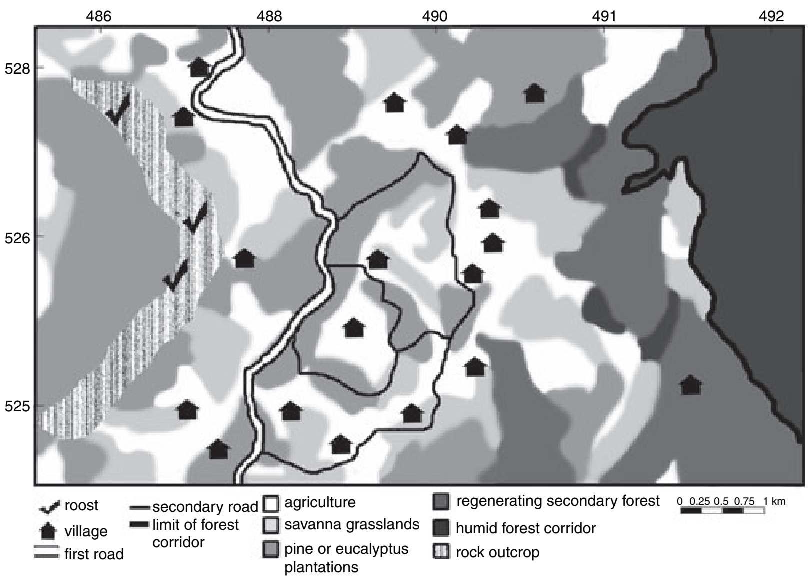

Fig 1 Map showing the location of *E. dupreanum* roosts, human settlements and major habitat types

Results

Dietary composition

We analysed the contents of 453 faecal pellets and 63 ejecta pellets. *Eidolon dupreanum* consumed mainly fruits; 65% of faecal pellets contained only seeds and 26% contained seeds with other plant parts. Faeces with seeds and leaf fragments were found in 5% of the samples. Six per cent of the samples were composed entirely of pollen and 3% consisted of only fruit debris (e.g. pulp/fibres).

We identified fourteen plant taxa from ten families in the diet of *E. dupreanum* during our study (Table 1). Seeds from a further sixteen plant species remained unidentified but made a small contribution to the overall diet in terms of percentage frequency (faeces = 4.5%, ejecta = 1.5%). None of these seeds matched our extensive reference collection made from plants in agricultural areas and we therefore concluded that the seeds were from forest plants.

Faecal analysis

Seeds of *Polyscias* trees were the most common in the faeces and the two *Polyscias* spp. were present in over 70% of the faecal samples (Table 1). *Psidium guajava* was the most frequently recorded introduced species in the diet of *E. dupreanum* and although *Psidium cattleianum* was also found in faecal samples, it only made a small contribution to the diet (Table 1). Pollen and flower parts of *Eucalyptus* spp. were also found in the faeces, indicating that *E. dupreanum* uses nonfruit resources.

Ejecta analysis

Five of the seven species found as ejecta pellets under feeding trees were also present in faeces collected at the roosts (Table 1). Three species (*P. guajava, Ficus pyrifolia* and *P. subpeltata*) were collected as seeds from both faecal and ejecta pellets at the roost site, which suggested that these fruits are orally transported by the bats, either as seeds or fruit, from feeding to roosting sites. There appeared to be differences between the two *Psidium* species and although *P. cattleianum* was more abundant during the study, *P. guajava* was more frequently found in faecal and ejecta samples (Table 1). The percentage contribution of both species to ejecta samples collected under feeding trees was similar; however, *P. guajava* was more frequently collected in ejecta and faecal samples under the roost and no *P. cattleianum* ejecta pellets were found under the roost and it was present in only 0.2% of the faeces (Table 1).

Food origins

Eight of the tree species in the diet are associated with native forests and six with cultivated land or other human-impacted landscapes (Table 1). *Eidolon dupreanum* transported more faeces with forest plants than introduced species during our study. The six introduced fruits were

Table 1 Percentage frequency of dietary components collected at the feeding and roosting sites of the fruit bat *Eidolon dupreanum* in eastern Madagascar

					Faeces		Ejecta	
		Origin	Habitat	Seed size, mm Mean (SE)	Foraging site (n = 2)	Under roost (n = 451)	Foraging site (n = 24)	Under roost (n = 41)
Araliaceae	*Polyscias* sp.1	N	FOR	6.9 ± 0.7 (10)	50.00	66.23	17.07	0.00
Myrtaceae	*Eucalyptus* spp. Smith	I	AGR	–	0.00	17.88	0.00	0.00
Araliaceae	*Polyscias ornifolia* (Baker) Harms	N	FOR	3.4 ± 0.5 (10)	50.00	15.23	4.88	0.00
Myrtaceae	*Psidium guajava* L.	I	AGR	3.2 ± 0.4 (10)	0.00	10.60	17.07	60.87
Aquilifoliaceae	*Ilex mitis* (L.) Radlk.	N	FOR	3.0 ± 0.6 (10)	0.00	10.60	26.83	0.00
Moracaeae	*Ficus pyrifolia* Lamk.	N	FOR	0.9 ± 0.1 (7)	0.00	6.62	0.00	26.09
Passifloraceae	*Passiflora subpeltata* Ortega	I	AGR	5.0 (1)	0.00	3.75	0.00	8.70
Gentianacaeae	*Anthocleista* sp. 1	N	FOR	2.9 ± 0.6 (17)	0.00	2.87	0.00	0.00
Moracaeae	*Ficus brachyclada* Baker	E	FOR	1.0 ± 0.0 (10)	0.00	1.32	0.00	0.00
Myrtaceae	*Psidium cattleianum* Sabi.	I	AGR	4.1 ± 0.4 (10)	0.00	0.23	14.63	0.00
Icacinaceae	*Cassinopsis madagascariensis* Baill.	E	FOR	5.0 (1)	0.00	0.22	0.00	0.00
Sapindaceae	*Allophylus cobbe* Leenhouts	N	FOR	6.5 ± 0.6 (4)	0.00	0.00	9.75	0.00
Rosaceae	*Rubus rosaefolius* Sm.	I	AGR	2.5 ± 0.5 (10)	0.00	0.00	0.00	4.35
Solanaceae	*Solanum auriculatum* Aiton	I	AGR	1.4 ± 0.5 (10)	0.00	0.00	9.75	0.00

FOR, plants found in the humid forest; AGR, plants found in the agricultural area between the roost and the humid forest; I, introduced; N, native; E, endemic

found in 17.8% of faecal and 53.9% of ejecta samples (Table 1). The two endemic species encountered in the diet were relatively infrequent and were only found in faeces collected from under roosting bats (Table 1).

Seed size

Seeds found in the diet of *E. dupreanum* ranged from a mean of 0.9 to 6.9 mm (Table 1). The high frequency of *Polyscias* sp. 1 seeds in faeces collected at the roost is strong evidence that *E. dupreanum* can easily ingest and defaecate seeds up to 7 mm long and that differences in the percentage frequency of other seeds, similar or smaller in size, in the diet are unlikely to be related to the size of the seeds or the dimensions of the bats' alimentary passage.

Germination

We pooled intrageneric germination results for *Polyscias*, *Psidium* and *Ficus* species owing to small ($\leqslant 5$) sample sizes for some categories to allow χ^2 analysis. There were significant differences in germination success between *Ficus* spp. seeds obtained from faeces and ripe fruits ($\chi^2 = 20.1$, d.f. = 1, $P \ll 0.001$); 20% of *F. brachyclada* and 40% of *F. pyrifolia* seeds from faeces germinated whilst no germination was recorded from seeds taken from ripe fruits. *Polyscias ornifolia* seeds germinated from ripe fruit (30%) and faeces (40%) but not from ejecta. In contrast, *Polyscias* sp. 1 only germinated from ripe fruit (10%). There was no significant association with seed origin and germination for *Polyscias* spp. ($\chi^2 = 1.45$, d.f. = 2, $P = 0.48$). *Psidium* spp. germination was generally high across all treatments (90–100%), with the exception of seeds from ripe fruit of *P. cattleianum* (10%). Germination success was significantly associated with seed origin in *Psidium* ($\chi^2 = 11.13$, d.f. = 2, $P \ll 0.005$) and increased after passage through bats.

Discussion

The persistence of *E. dupreanum* in modified landscapes with little forest cover, but large human populations, has led to the notion that the species is relatively resistant to the effects of deforestation, hunting pressure and is not dependent on food plants that are associated with intact forest formations (Goodman *et al.* 2005; MacKinnon *et al.*, 2003). Many of the large colonies of *E. helvum* on the African mainland are also located considerable distances away from natural forests and these bats survive on a mixed diet of native and cultivated fruits (e.g. Ayensu, 1974; Okon, 1974; Funmilayo, 1976). Furthermore, some *Pteropus* species survive in anthropogenic landscapes because of their plastic diet and ability to switch roosts during unfavourable conditions (Brooke, 2001). Our results show that *E. dupreanum* eats fruit and flowers and both native and introduced plants feature in its diet. A longer study duration would allow a more complete assessment of the relative contribution of different food types.

Ratrimomanarivo (2003), in a study of *E. dupreanum* diet from four roost sites on the central Malagasy highlands, found the seeds of thirteen plant species during 3 months (February, July and December). Maximum monthly taxon richness was seven (Ratrimomanarivo, 2003) and the species richness was therefore lower during a 3-month period from the central highlands than from our 1 month study. The greater fruit diversity in the diet of *E. dupreanum* in our study may be due to the close proximity of humid forest.

Eidolon dupreanum fed on fruits from the rainforest corridor and introduced species, e.g. *Psidium*, were relatively rare in the diet despite an abundance of ripe fruit within close proximity to the roosts. In Nigeria, *E. helvum* was reported to fly at least 24 km each night and often stopped at a number of locations between leaving the roost and arriving at the foraging site (Okon, 1974). Richter & Cumming (2006) reported flights of over 15 km for *E. helvum* in Kasanka National Park. Other evidence for its flight capabilities comes from reported cases of long-distance migration (Thomas, 1983). Our preliminary results therefore indicate the importance of forest plants for *E. dupreanum* and suggest that, in flying over 5 km to the forest, they are exerting a selection for native plants over the abundant, but rarely eaten, *Psidium* that are found within close proximity to the roosts.

The dimensions of the alimentary tract is one intrinsic factor that influences seed dispersal; there are few obligate avian frugivores in Madagascar and lemurs are the main forest frugivores and are capable of dispersing large, viable seeds up to 15 mm in length (e.g. Bollen *et al.*, 2004). Bollen & Van Elsacker (2002) reported a maximum seed size of 10 mm and mean size of 4.4 mm for *P. rufus* in the littoral forests of south-east Madagascar. We found a maximum seed size of 7 mm and mean size of 3.2 mm for *E. dupreanum* and the ecological services provided by this species appear to be limited by the dimensions of its intestinal tract. However, further data collection and nocturnal observations are needed because larger seeds may be transported in the mouth and dropped before reaching the roost. *Eidolon helvum* in Ghana was thought to be responsible for the dispersal of *Azadirachta indica* (Meliaceae) seeds between its roosts and forests feeding sites (Ayensu, 1974); seeds were carried in the mouth of flying bats and were often ejected during flight (Ayensu, 1974).We provide further evidence that fruit bats make a positive contribution to seed germination and call for such ecosystem services to be used as leverage for fruit bat conservation in Madagascar and in particular for day roosts to receive protection.

Acknowledgements

This work was supported by the IRD-CNRE project Gestion des Espaces Ruraux et Environnement Madagascar (GEREM-Fianarantsoa). Additional support was provided by a grant from the UK government's Darwin Initiative programme (162/10/024). Permission to undertake the work was kindly provided by the Ministère de l'Environnement, Eaux et Forêt, through protocols of collaboration (1) between the School of Biological Sciences, University of Aberdeen, Département de Biologie Animale, l'Université d'Antananarivo and Association Nationale de Gestion des Aires Protégées and (2) Ministère de la Recherche et de l'Enseignement Supérieur Malgache, le Centre National de la Recherche sur l'Environnement and the french government institution called Institut de Recherche pour le Développement supprimé français. We would like to thank Radosoa Andrianaivoarivelo, Fanja Ratrimomanarivo, Guillaume Rembert and our local guides (Dieu Donné and Rakotomaro) for their valuable assistance in the field and Modeste Rakotondramanana, Noly Razanajaonarijery and Daniel Razafimamonjy for logistic assistance. Richard Razakamalala assisted us in our plant identification. Comments by An Bollen and Steven Goodman helped us to improve an earlier version of the manuscript.

References

Andriafidison, D., Andrianaivoarivelo, R.A., Jenkins, R.K.B., Ramilijaona, O., Razanahoera, M., MacKinnon, J. & Racey, P.A. (2006) Nectarivory by endemic Malagasy fruit bats in the dry season. *Biotropica* **38**, 85–90.

Ayensu, E.S. (1974) Plant and bat interactions in West Africa. *An. Miss. Bot. Gar.* **61**, 702–727.

BARANGA, J. & KIREGYERA, B. (1982) Estimation of the fruit bat population in the Kampala Valley, Uganda. *Afr. J. Ecol.* **20,** 223–229.

BAUM, D.A. (1995) The comparative pollination and floral biology of Baobabs (Adansonia - Bombacacae). *An. Miss. Bot. Gar.* **82,** 323–348.

BAUM, D.A. (2003) Bombacaceae, Adansonia, Baobab, Bozy, Fony, Renala, Ringy, Za. In: *The Natural History of Madagascar* (Eds S. M. GOODMAN and J. P. BENSTEAD). University of Chicago Press, Chicago.

BOLLEN, A. & VAN ELSACKER, L. (2002) Feeding ecology of *Pteropus rufus* (Pteropodidae) in the littoral forest of Sainte Luce, SE Madagascar. *Acta Chiropt.* **4,** 33–47.

BOLLEN, A., VAN ELSACKER, L. & GANZHORN, J.U. (2004) Relations between fruits and disperser assemblages in a Malagasy littoral forest: a community-level approach. *J. Trop. Ecol.* **20,** 599–612.

BROOKE, A.P. (2001) Population status and behaviour of the Samoan flying fox (*Pteropus samoensis*) on Tutuila Islan, American Samoa. *J. Zool.* **254,** 309–319.

CARRIÈRE, S.M., ANDRIANOTAHIANANAHARY, H., RANAIVOARIVELO, N. & RANDRIAMALALA, J. (2005) Savoirs et usages des recrus post-agricoles du pays Betsileo: valorisation d'une biodiversité oubliée à Madagascar. *Vertigo* **6,** 1–14.

COX, P.A., ELMQVIST, T., PIERSON, E.D. & RAINEY, W.A. (1991) Flying foxes as strong interactors in South Pacific island ecosystems: a conservation hypothesis. *Conserv. Biol.* **5,** 448–554.

FAYENUWO, J.O. & HALSTEAD, L.B. (1974) Breeding cycle of the straw-colored fruit bat *Eidolon helvum* at Ife-Ife, Nigeria. *J. Mammal.* **55,** 453–454.

FUNMILAYO, O. (1976) Diet and roosting damage and environmental pollution by the straw-colored fruit bat in south-western Nigeria. *Nigerian Field* **41,** 136–142.

GANZHORN, J.U., FIETZ, J., RAKOTOVAO, E., SCHWAB, D. & ZINNER, D. (1999) Lemurs and the regeneration of dry deciduous forest in Madagascar. *Conserv. Biol.* **13,** 794–804.

GANZHORN, J.U., GOODMAN, S.M. & DEHGAN, A. (2003) Effects of forest fragmentation on small mammals and lemurs. In: *The Natural History of Madagascar* (Eds S. M. GOODMAN and J. BENSTEAD). University of Chicago Press, Chicago.

GOODMAN, S.M. & GANZHORN, J.U. (1997) Rarity of figs (*Ficus*) on Madagascar and its relationship to a depauperate frugivore community. *Rev. Eco. (Terre Vie)* **52,** 321–329.

GOODMAN, S.M., ANDRIAFIDISON, D., ANDRIANAIVOARIVELO, A.R., CARDIFF, S.G., IFTICENE, E., JENKINS, R.K.B., KOFOKY, A., MBOHOAHY, T., RAKOTONDRAVONY, D., RANIVO, J., RATRIMOMANARIVO, F.H., RAZAFIMANAHAKA, H.J., RAZAKARIVONY, V. & RACEY, P.A. (2005) The distribution and conservation of bats in the dry regions of Madagascar. *Anim. Cons.* **8,** 53–165.

KOECHLIN, J., GUILLAUMER, J.L. & MORAT, P. (1974) *Flore et végétation de Madagascar*. J. Kramer, Vaduz.

LAW, B.S. & LEAN, M. (1999) Common blossom bats (*Syconycteris australis*) as pollinators in fragmented Australian tropical rainforest. *Biol. Cons.* **91,** 201–212.

LONG, E. (2002) The feeding ecology of *Pteropus rufus* in a remnant gallery forest surrounded by sisal plantations in South-east Madagascar. PhD Thesis, University of Aberdeen, Aberdeen.

MACKINNON, J.L., HAWKINS, C.E. & RACEY, P.A. (2003) Pteropodidae, Fruit Bats, *Fanihy, Angavo*. In: *The Natural History of Madagascar* (Eds S. M. GOODMAN and J. P. BENSTEAD). University of Chicago Press, Chicago.

MARSHALL, A.G. (1983) Bats, flowers and fruit: evolutionary relationships in the Old World. *Biol. J. Linn. Soc.* **20,** 115–135.

MCCONNELL, W.J., SWEENEY, S.P. & MULLEY, B. (2004) Physical and social access to land: spatio-temporal patterns of agricultural expansion in Madagascar. *Agric. Ecosyst. Environ.* **101,** 171–184.

MICKLEBURGH, S.P., HUTSON, A.M. & RACEY, P.A. (1992) *Old World fruit bats. an action plan for their conservation*. IUCN/SSC Chiroptera Specialist Group. IUCN, Gland, Switzerland.

OKON, E.E. (1974) Fruit bats at Ife: their roosting and food preferences. *Nigerian Field* **39,** 33–40.

PAR, H. & HUGGEL-WHOLF, M.L. (1965) La biologie d'*Eidolon helvum* (Kerr) (Megachiroptera). *Acta. Trop.* **22,** 1–10.

RABETALIANA, H. (2001) *Le tavy dans la région de Fianarantsoa: L'expérience de la préservation du corridor forestier entre Ranomafana et Andringitra.* Actes de l'Atelier: Cultures sur brûlis: vers l'application des résultats de recherche. Projet BEMA/FOFIFA, Antananarivo.

RAINEY, W.E., PIERSON, E.D., ELMQVIST, T. & COX, P.A. (1995) The role of flying foxes (Pteropodidae) in oceanic island ecosystems of the Pacific. In: *Ecology, Evolution and Behaviour of Bats* (Eds P. A. RACEY and S. M. SWIFT). Symposium of the Zoological Society of London, **67,** 47–62.

RATRIMOMANARIVO H.F. (2003) *Etude du régime alimentaire d'un Mégachiroptère Eidolon dupreanum (Pollen, 1866) dans les Hautes - Terres centrales malgaches et son rôle potentiel sur la dispersion des graines de plantes dans l'écosystème modifié par l'homme.* DEA en Sciences Biologiques Appliquées, option Ecologie - Environnement. Département de Biologie Animale, Faculté des Sciences, Université d'Antananarivo, Antananarivo, Madagascar.

RICHTER, H.V. & CUMMING, G.S. (2006) Food availability and annual migration of the straw-colored fruit bat (*Eidolon helvum*). *J. Zool.* **268,** 35–44.

SHILTON, L.A., ALTRINGHAM, J.D., COMPTON, S.G. & WITTAKER, R.J. (1999) Old World fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut. *Proc. Roy. Soc. Lond. B* **266,** 219–223.

SORENSEN, U.G. & HALBERG, K. (2001) Mammoth roost of non-breeding straw-coloured fruit bat *Eidolon helvum* (Kerr, 1792) in Zambia. *Afr. J. Ecol.* **39,** 213–215.

THOMAS, D.W. (1983) The annual migrations of three species of West African fruit bats (Chiroptera: Pteropodidae). *Can. J. Zool.* **61,** 2266–2272.

(Manuscript accepted 28 March 2007)

doi: 10.1111/j.1365-2028.2007.00788.x