Feeding ecology, habitat use and reproduction of *Rousettus madagascariensis* Grandidier, 1928 (Chiroptera: Pteropodidae) in eastern Madagascar

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Abstract

We studied the diet, habitat use and biology of *Rousettus madagascariensis*, a relatively small (∼55–77 g) fruit bat endemic to Madagascar, between July 2004 and May 2005. Faecal analysis revealed few seeds in the diet, suggesting that the bats either feed extensively on nectar, flowers and leaves or on fruits with seeds too large to ingest. However, bats were captured near fruiting *Ficus* sp. inside relatively intact forest and *Ficus* sp. seeds were found in the faeces during March and April. Defecated *Ficus rubra* seeds germinated significantly faster than seeds from ripe fruits under controlled conditions, but germination rates were similar. Radio tracking and observations of light-tagged individuals revealed that *R. madagascariensis* travelled a straight line distance of at least 8 km between the roost and feeding locations, with round trip foraging routes of up to 27 km. Most juveniles were trapped between March and July and we infer that weaning of young started before 8 weeks of age. The features used to distinguish juveniles from adults were no longer evident in December and it appears therefore that *R. madagascariensis* reaches somatic maturity within a single year. Pregnancy, lactation and weaning in this species coincide with the austral summer when food availability is higher.

Keywords: diet; Madagascar; radio tracking; reproduction; *Rousettus*.

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Introduction

In tropical forests, the old world fruit eating bats exhibit high species diversity and play an active role in ecosystem function and forest regeneration (Heithaus 1982). Flight enables them to cover large distances in short periods of time, crossing different vegetation types and landscapes that could constitute physical barriers for other mammal species (Norberg and Rayner 1987). Differences in morphology and ecology (e.g., echolocation used by *Rousettus*) can also make some species more suited to foraging in specific habitats, such as the spatially complex forest interior or open areas (Norberg and Rayner 1987, Bernard 2001). In spite of their important role in tropical habitats, little is known about how fruit bats are affected by habitat fragmentation (Fenton et al. 1992). Such information can contribute to a better understanding of the impact of such fragmentation on seed dispersers and pollinators and can be used in establishing conservation and management programmes. The native forest of Madagascar continues to be converted into agricultural land (Harper et al. 2007), and in the fragments that remain, bats and birds play important roles in seed dispersal and pollination, facilitating forest recovery (Howe and Smallwood 1982, Guevara and Laborde 1993).

The fruit bats of Madagascar (Pteropodidae) consist of three endemic species that differ in body mass, pelage and roosting ecology (MacKinnon et al. 2003). Advances have been made recently in describing the diet of the Madagascar flying fox *Pteropus rufus* E. Geoffroy, 1803 (Bollen and Van Elsacker 2002, Raheriarisena 2005, Long and Racey 2007) and its role in seed dispersal (Bollen et al. 2004, Racey et al. 2010). The diet of *Eidolon dupreanum* Schlegel, 1866 has also been studied at a few sites (Picot et al. 2007, Ratrimomanarivo 2007) and is believed to be one of the main pollinators of endemic baobabs *Adansonia grandidieri* and *Adansonia suarezensis* of Madagascar (Baum 1995). By contrast, the feeding ecology of the smallest fruit bat, *Rousettus madagascariensis* G. Grandidier, 1928, of Madagascar has yet to be studied, although it has been observed feeding on the fruits of *Litchis chinensis* and *Musa paradisiaca* (Sapindaceae and Musaceae, respectively; Goodman 1999) and *Dimocarpus longan* (Sapindaceae) (Andrianaivoarivelo et al. 2007).

Rousettus madagascariensis dwells in caves during the day (MacKinnon et al. 2003) and uses a variety of different habitat types at night, where it is easily trapped in mist nets (Andrianaivoarivelo et al. 2007). It is widely distributed in Madagascar and is classified as Near Threatened mainly because of hunting pressure (Andriafidison et al. 2008),

although relatively few roost sites have been located (MacKinnon et al. 2003, Goodman et al. 2005, Cardiff et al. 2009). MacKinnon et al. (2003) noted that this species is associated with native forest, and although Goodman et al. (2005) considered that it is not dependent on intact forest, the extent to which this reflects feeding or roosting requirements has been insufficiently explored. *R. madagascariensis* has been netted inside *Eucalyptus* plantations and deciduous dry forest, where it flies along relatively open linear features such as trails and edges (Randrianandriananina et al. 2006, Kofoky et al. 2007).

Given its wide distribution, dietary requirements and small size, it is potentially an important seed disperser and pollinator in forests because the two other fruit bat species of Madagascar are relatively large and are unable to fly within dense foliage. A better understanding of the foraging ecology of *Rousettus madagascariensis* is therefore required to describe its role as a seed disperser and pollinator in different types of vegetation.

We studied a colony of *Rousettus madagascariensis* in eastern Madagascar. Our objectives were (i) to describe the diet of *R. madagascariensis*, (ii) to assess its role in seed dispersal and germination, (iii) to describe aspects of its breeding biology, and (iv) to determine foraging habitats and movement patterns.

Materials and methods

Site

Maromizaha Forest (930–1040 m a.s.l.) is found to the southeast of the Réserve Spéciale d'Analamazaotra, approximately 30 km from Moramanga in the Alaotra Mangoro Region, eastern Madagascar (48°27′11.5″E, 18°57′40.5″S). It is a classified forest (∼20,000 ha) in the public domain and at the time of study was managed jointly by Stiftung Natur und Artenschutz in den Tropen and the Direction des Eaux et Forêts, Madagascar. The forest contains at least 177 tree species some of which have high commercial value, e.g., *Canarium* spp., *Diospyros* spp., *Stephanostegia* spp. and *Uapaca* spp. (Abraham et al. 1996), and more than 200 species of orchids. Also present are exotic plants such as *Clidenia hirta*, *Psiadia altissima*, and *Lantana camara* (Koechlin et al. 1974, Ford 1996), as well as pioneer native tree species such as *Trema orientalis* and *Harungana madagascariensis* (Hladik et al. 2000). Annual rainfall is approximately 2000 mm and heaviest precipitation occurs in January and February (Service de la Météorologie d'Ampandrianomby, Antananarivo). The dry and cold season extends from June to October and is characterised by drizzle and fog. The monthly average temperature varies between 14°C and 24°C. We obtained information on precipitation and temperature from the recording station at Analamazaotra, 3 km west of Maromizaha.

We studied a colony of *R. madagascariensis* in a cave located above an abandoned quarry, in the northwestern edge of the Maromizaha forest. The main landscape and habitat features in the study area were a road (Route Nationale 2),

mid-altitude humid forest, *Eucalyptus* plantations, open grassland and villages with associated small-scale agriculture (Figure 1). Two entrances of the Maromizaha cave were accessible by people and also used by bats, and the height from the floor to the ceiling was approximately 15 m. The cave interior was 17.6 m long (east to west), and the eastern entrance (1.4 m high and 0.9 m wide) was larger than the western entrance (0.6 m high and 0.8 m wide). Bats also emerged from two other narrow entrances in the western side of the cave, which are inaccessible to people. *Mormopterus jugularis* (Peters, 1865), a molossid bat, also occupied the cave and two individuals were trapped in March 2005.

Mist netting

Mist nets (2×6 m and 1×12 m) were erected on sloping grass banks outside the western entrances of the cave during the afternoon before each trapping session. We were unable to install mist nets at the other entrances because of the presence of vegetation or the risk of personal injury. Mist nets were opened the following morning before dawn from 03:00 to 04:30 h and bats were trapped as they returned to the roost so that we were able to sample bats that had recently fed. Between July 2004 and May 2005 we trapped bats during six occasions (16 and 17 July 2004, 9–19 October 2004, 13 December 2004, 11–22 January 2005, 22–30 March 2005, 23–29 May 2005).

We also placed mist nets along trails in the relatively intact forest situated on the edge of the quarry and on one occasion erected nets next to a fruiting *Ficus soroceoides* tree. We calculated the bat capture rate and expressed it throughout as number of bats caught per 6 m of mist net deployed for 1 h. We also placed mist nets in sites (small banana plantations *Musa paradisiaca*) identified during the radio tracking component of this study (see below) at increasing distances (3.8 km, 5.6 km, 7.0 km, 8.1 km and 11.4 km) from the roost to determine the distances travelled by the bats from the cave. Nets were open for 3 h at these localities, starting 1 h after sunset. The maximum lower and upper heights of the net were 1 and 5 m, respectively. Bats were fitted with chemiluminescent light tags (Buchler 1976) weighing <0.5 g by gluing them (with Silastic medical adhesive) to the dorsal surface of the bat. The light tag remained bright for 20 h and allowed us to see if the bats captured in the banana plantations bats roosted in the Maromizaha cave. We were unable to reliably assess the colony size during the day because the bats roosted high up in crevices in the cave that were not clearly visible. However, the number of individuals was estimated at 400.

Diet: faecal collection

Plastic sheeting was placed on the cave floor directly under roosting bats and faecal samples were collected every 2 weeks between July 2004 and May 2005. Faecal matter was removed, sun-dried and stored for later identification. Collections of fruits were made every month throughout the study to create a seed reference collection. Faeces were sorted under a low-power microscope and seeds were extracted
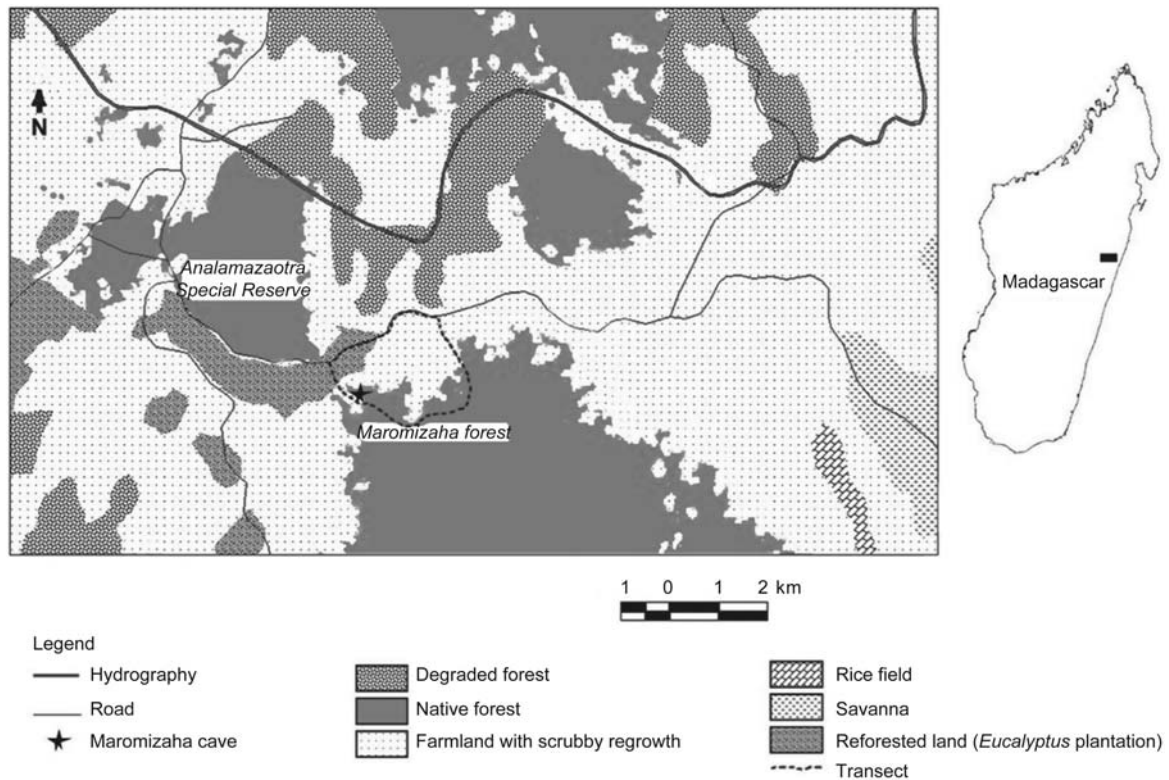
Figure 1 Vegetation and transect map of Maromizaha study site, eastern Madagascar.

and identified using the reference collection made in the field and those held at an herbarium at the Parc Botanique et Zoologique de Tsimbazaza in Antananarivo. We observed seeds from sample fruits and/or those from faeces. The seed samples were identified by two of the authors (A.A.R. and N.R.) by comparing them with reference collections held at the Tsimbazaza herbarium in Antananarivo. We followed the taxonomy used by Berg and van Heusden (1985), Turk (1995) and the online Missouri Botanical Gardens (Tropico database). The length and width of seeds were measured using an eyepiece reticule.

Diet: fruit transects

A 8.2-km transect crossing three habitats (Figure 1), native forest (3.4 km), reforested *Eucalyptus* plantation (0.5 km) and farmland with scrubby regrowth (4.3 km) in the study area was surveyed for the presence or absence of fruit and flowers each month from October 2004 to April 2005. Fruits were collected and their seeds dried, measured and glued on the slide or put in an envelope and stored in the office in Antananarivo for reference and later identification. A short questionnaire survey was carried out in villages near the transect to investigate the level of awareness of local people about fruit bats feeding in their banana plantations.

Diet: germination trials

Germination of *Ficus rubra* seeds extracted from bat faeces was compared to those taken from ripe fruits (Fleming and

Sosa 1994, Naranjo et al. 2003). Seeds taken from intact fruits were washed, dried and stored before processing. Seeds taken from faeces were either collected 2 weeks (trial 1) or 4 weeks (trial 2) before the experiment started. Seeds were washed with fungicide and arranged on moistened filter paper and placed in a 8×8-cm covered box for germination (Lieberman et al. 1979). Ten seeds were sown in each box and six boxes were used for each treatment, giving 60 seeds for each of the two treatments (seeds collected from faeces and seeds collected from fruits). All trials were conducted in Antananarivo in partial shade and at room temperature and natural day length (i.e., 15–28°C and ∼12 h of daylight). Boxes were inspected every 2 days for signs of germination using a hand lens, until several successive inspections revealed no further germination (∼1 month). The filter paper was watered regularly. A seed was considered to have germinated upon the first appearance of the radicle (Janzen 1978, Utzurrum and Heideman 1991). The effect of the passage of the seeds through the digestive system of *R. madagascariensis* was assessed using two analysis of variance (ANOVA) comparisons. The first used the number of germinated seeds as the dependent variable and the second used mean number of days to germination. The factor was treatment in all cases.

Habitat use: radio tracking and mapping movements

Six adult bats, three male and three female, were fitted with collars incorporating PD-2 radio transmitters (Holohill Systems Ltd., Carp, Canada). Collars consisted of plastic sheaths

with thin wire inside joined by a biodegradable link. Complete units weighed no more than 3 g ($\sim$4.5% of the body mass) and had an expected life of 12 weeks. Bats with radio tags were released within 1 h of capture but were not followed until the subsequent night. Bats were followed from when they emerged from the cave until they returned the following morning. Signals from the radio transmitters were monitored using Yagi directional antennae connected to Regal 2000 receivers (Titley Electronics, Ballina, Australia). Two teams consisting of two or three people tracked the bats on foot or from a vehicle during January, March and April 2005 for a total of 22 nights.

Fixed reference points were made at a number of locations within the study site and logged on a GPS unit. Bearings were taken on a handheld compass and were read to the nearest degree. Positions of stationary bats were determined by triangulation from either the fixed points or from mobile tracking teams in radio contact with handheld radios (Motorola Talkabout, Raleigh, NC, USA). Bearings, time, signal strength and gain were recorded every 5 min. Owing to the hilly terrain we regularly lost radio contact with focal animals. We tracked feeding or stationary bats to actual foraging sites. Fixes, determined from triangulation or direct observation, were transferred onto a large-scale (1/100,000) topographic map using MapSource.exe and ArcView GIS 3.3 (Applegate 1991–1995). We measured the straight-line distance between roost and capture sites using fixes obtained in the field with a GPS in ArcView GIS 3.3. We also calculated minimum convex polygons from the triangulated points to represent the minimum possible area that contains all the points and can be imagined as the surface area used by the bats.

Breeding biology

Bats were measured (forearm length in mm and body mass in g), sexed by observing the conspicuous penis or a single anterior pair of nipples (Racey 1988). Juvenile bats were distinguished from adults by the presence of cartilaginous epiphyseal plates in finger bones (Anthony 1988). Females were classified as lactating, pregnant, parous or nulliparous (Racey 1988). Juvenile bats were those weighing less than 50 g and with unfused phalangeal epiphyses. Bats were released at the capture site within 15 min of capture and always before sunrise. Individual bats were fur clipped so that recaptures during the same field trip could be identified. However, they were not individually marked and it is possible that we recaptured the same individual on successive field trips. ANOVA was used to test for differences in body mass between sexes and seasons.

Results

A total of 175 *Rousettus madagascariensis* were captured (116 adults and 59 juveniles, 96 females and 79 males). The variation in the number of captured bats returning to the roost appeared to be unrelated to trapping effort, and captures were lowest during May (Table 1). Most captures (n=153) occurred at the cave entrance (423 net h), but six bats were trapped in relatively intact humid forest (240 net h) and 16 in banana plantations (270 net h).

Diet: species consumed, fruit availability and seed germination

Most of the faeces appeared as green or brown-green dense matter that was composed of leaves or unripe fruit. Seeds of six plant species were also found in the faeces but they were only common in the diet during March and April (Table 2). The species of Solanaceae and Rosaceae recorded in the faeces were not found during the fruit transects but the four *Ficus* species were observed fruiting in relatively intact humid forest. *Rousettus madagascariensis* voided seeds with a mean length of 2.5 mm (Table 2). Ripe fruit of *F. rubra* was observed in native forest and its seeds were present in bat faeces in February 2005. A single *Dypsis* sp. seed (11×14 mm) was collected beneath roosting bats in the cave. We found no evidence of banana fruits being eaten by bats and the farmers did not report damage to their fruits except by rats.

A total of 47 plant species from 26 families fruited during the transect survey. Out of these 17 of the species identified were collected in the degraded habitat and farmland, and 29 in the native forest (Table 3). Even though the invasive and introduced species *Psidium cattleianum* (Myrtaceae) and *Clidemia hirta* (Melastomataceae) fruited during March at the study site they were not evident in the faeces.

Table 1 The numbers of *Rousettus madagascariensis* of different reproductive status caught returning to a cave roost in Maromizaha, eastern Madagascar (2004–2005).

	Adult male	Adult Parous female	Nulliparous female	Lactating female	Pregnant female	With pup female	Juvenile female	Juvenile male	Total female	Total male	Total caught
July (3)	3	10	3	0	0	0	2	0	15	3	18
October (3)	25	4	3	0	1	0	3	0	11	25	36
December (1)	3	0	0	0	3	7	0	0	10	3	13
January (3)	19	9	1	0	0	5	15	3	30	22	52
March (6)	6	8	0	0	0	0	8	5	16	11	27
May (3)	0	2	0	0	0	0	4	1	6	1	7

The duration (days) of each trapping session is given in parentheses. Females were classified as lactating, pregnant, parous or nulliparous (Racey 1988). Pregnant females were netted in October and December, and no juvenile bats were captured in December.

Table 2　The timing and frequency of occurrence of seeds of plant species recovered in the faeces of *Rousettus madagascariensis* in Maromizaha, eastern Madagascar (2004–2005).

Month	Number of samples	Moraceae			Rosaceae *Rubus mollucanus*	Solanaceae sp. a
		F. soroceoides	*F. botryoïdes*	*F. rubra*		
October 2004	24	0	0	0	1	1
February 2005	186	0	0	3	0	0
March 2005	107	1	3	17	0	1
April 2005	207	0	0	44	0	0
Seed length 2005	(mm)	1.0±0.02 (n=13)	1.4±0.02 (n=3)	1.3±0.03 (n=13)	1.43±0.02 (n=4)	2.5±0.04 (n=4)

Ficus rubra was the most commonly occurring seed in bat faeces.

Ficus rubra seeds that passed through the gut of *Rousettus madagascariensis* germinated significantly faster than those extracted from the fruits (ANOVA $F_{2,6}=308$, $p\leq0001$). Seeds which had passed through the gut germinated 2.7 days±0.21 days (trial 1) and 2.0 days±0.00 SE (trial 2) after sowing, whereas those collected from ripe fruit germinated after 9.0 days±0.26 SE. Percentage germination, however, was similar across the three treatments (ANOVA $F_{2,6}=0.4$, NS).

Habitat use

Of the six bats fitted with radio collars, only one male and one female were subsequently located often enough to allow an assessment of movements and range. The maximum straight-line distance covered by individual radio tagged bats was 14.2 km (females) and 14.8 km (males) in a single night. On two occasions for each bat we maintained contact throughout the foraging period, from dusk until approximately 03:30 h, when bats flew back to the roost. On 24 and 30 March 2005, the female made round-trip foraging flights of 24.0 km and 27.2 km, respectively (Figure 2), whereas on 26 March and 1 April 2005, the male made round-trip foraging flights of 17.0 km and 16.0 km, respectively (Figure 2). Minimum convex polygons, based on data collected throughout the study, were 30.9 km² for the female and 16.7 km² for the male (Figure 3).

A total of 16 bats were netted and fitted with light tags whilst feeding on the nectar of banana flowers at five sites. Three of these bats were later observed in the roost, between 4.0 km and 8.1 km from the site of capture. The longest straight line travelled between roost and foraging sites from radio tracking and light tags were 7 km and 8.1 km, respectively. Four other bats were trapped, but not fitted with light tags, in relatively intact forest whilst flying along trails in October and one in March. Trails were 1–2 m wide and the bats were netted in areas between forest trees.

Breeding biology

Captures of males outnumbered those of females during two of the six trapping sessions (Table 1). The body mass of adult females differed significantly between trapping sessions (Figure 4) and was heavier in December and January (wet season) when pregnancy and lactation occurred, and lowest in May and July (ANOVA $F_{1,47}=11.61$, $p<0.02$). Pregnant females weighed more than non-pregnant adult females (ANOVA $F_{3,93}=72.66$, $p<0.0001$). Male body mass did not vary significantly between season (ANOVA, $F_{1,58}=0.07$, $p=0.42$) but was lowest in May (Figure 4).

Pregnancy was observed during October and December. All lactating bats trapped in December and January were carrying young. Juvenile bats were netted during all months of capture with the exception of December. The features used to distinguish adults and juveniles were no longer evident in December and thus *Rousettus madagascariensis* reached somatic maturity within a single year.

Discussion

This is the first extended study of the diet, habitat use and breeding biology of *Rousettus madagascariensis* and reveals that it rarely ingests seeds but feeds on both native and introduced plants within and can travel at least 8 km straight-line distance in search of food.

Diet and feeding

Seeds were relatively rare in the diet of *R. madagascariensis* compared to the two larger Malagasy fruit bats (Bollen and Van Elsacker 2002, Long and Racey 2007, Picot et al. 2007). The largest seeds in the faeces of *R. madagascariensis* during this study were notably smaller than the largest recorded for the other Malagasy fruit bats, *Pteropus rufus* (10 mm; Bollen and Van Elsacker 2002) and *Eidolon dupreanum* (7 mm; Picot et al. 2007). However, observations in eastern Madagascar show that *R. madagascariensis* frequently carries fruit in its mouth from feeding trees and that the size of consumed fruits can therefore be underestimated if based entirely on the occurrence of seeds in faeces (Andrianaivoarivelo et al. 2007). The bats were observed feeding on banana nectar and this mixed diet of nectar and seeds has been observed in other small pteropodids, such as *Rousettus leschenaultii* (Singaravelan and Marimuthu 2004) and *Rousettus obliviosus* (Reason et al. 1994, Sewall et al. 2003).

There was strong seasonality in the occurrence of seeds in the faeces, which was restricted to the warm, wet season (February–April). However, we also trapped a bat at a fruiting *Ficus* tree in October. In South Africa, observations of

Table 3   Fruiting plant species observed in a given month on a transect and in bat faeces (in bold font) in Maromizaha, eastern Madagascar (2004–2005).

Family	Genus/species	Habitat	Seed (mm)		Months						
			Width	Length	Jan	Feb	Mar	Apr	Oct	Nov	Dec
Anacardiaceae	*Protorhus*[n]	F	12.00	20.00				x			
Flacourtiaceae	*Aphloia theiformis*[n]	F	3.18	3.83	x	x					
Arecaceae	*Dypsis* sp. 1[e]	F	3.33	9.83		x		x			
	***Dypsis* sp. 2**[e]	F	**12.30**	**9.60**							
Buddleiaceae	*Buddleia* sp.[n]	D	0.70	0.20					x		x
Burceraceae	*Canarium boivini*[e]	F	11.00	29.00			x				
Clusiaceae	*Symphonia fasciculata*[e]	D	8.68	15.75					x		
Euphorbiaceae	*Macaranga* sp.[e]	D	2.78	7.13						x	x
Flacourtiaceae	*Homalium* sp.[n]	F	1.65	3.55			x				
Melastomataceae	*Dichaetantera oblongifolia*[e]	F	0.17	0.30	x						
	Clidemia hirta[i]	F	0.31	0.45			x				
	Memecylon sp.[n]	D	7.55	9.10						x	x
Monimiaceae	Tambourissa sp.[e]	F	0.65	0.84			x				
Moraceae	*Bleekrodea madagascariensis*[e]	F	0.64	1.10						x	x
	F. soroceoides[e,a]	**F, C**	**0.67**	**1.05**	x		x	x			
	F. botryoïdes[e,b]	F	**0.65**	**0.81**	x	x	x				
	F. rubra[e,c]	F	**0.88**	**1.40**		x	x	x			
	F. lutea[n,b]	F	0.78	1.00			x	x			
	Ficus sp. 1	F	0.75	1.22							x
Myrsinaceae	*Oncostemum* sp.	F	4.45	5.30					x		
	Maesa lanceolata	F	2.10	2.33	x	x	x				
	Memecylon sp.[e]	F	7.55	9.10					x		
Myrtaceae	*Psidium cattleianum*[i]	D	3.51	4.00			x	x			
	Syzigium emirnensis[e]	F	8.45	9.65	x	x					
Olacaceae	*Olax* sp.[n]	F	8.30	15.20							x
Passifloraceae	*Passiflora* sp.[i]	F	4.43	7.13						x	x
Phytolacaceae	*Phytolaca dodecandra*[i]	D	2.08	2.65	x	x	x				
Piperaceae	*Piper* sp.[n]	F	2.33	2.15			x		x		
	P. borbonense[e]	F	2.77	3.15					x		
Rosaceae	***Rubus mollucanus***[i]	**D**	**0.76**	**1.43**		x			x		x
	R. roridus[i]	D	2.61	3.87					x	x	
Rubiaceae	*Sabicea diversifolia*[e]	D	0.24	0.29	x	x					
	Mapouria parkeri[e]	D	4.31	4.28		x					
	Sabicea sp.[e]	D	0.18	0.39			x				
	Enterospermum sp.[e]	F	5.30	4.83				x			
	Tricalysia cryptocalyx[e]	F	2.40	5.00				x			
	Craterispermum sp.[n]	D	0.48	0.61					x		
	Mapouria sp.	F	4.25	15.90					x	x	
Salicaceae	*Scolopia* sp.[n]	D	7.85	9.18					x	x	
Sapindaceae	*Allophylus cobbe*[i]	F	8.20	7.55			x				
Sapotaceae	*Faucherea* sp.[e]	F	3.90	5.48					x	x	x
Smilacaceae	*Smilax kraussiana*[i]	D	3.98	5.10				x			
Solanaceae	*Physalis* sp.[i]	D	1.52	2.00			x	x	x	x	x
	Solanum auriculatum[i]	D	1.34	2.00	x				x	x	x
	Unknown sp.		**2.25**	**2.47**							
Sterculiaceae	*Dombeya* sp.	F	1.32	1.85					x	x	x
Verbenaceae	*Lantana camara*	D	3.04	3.75	x		x	x			x

Source: [a]Berg and van Heusden (1985); [b]MBG (Tropico database); [c]Turk (1995).
F: native forest, D: degraded habitats and farmlands, C: cave, x: the fruit species were found along a transect. Faecal samples contained *Ficus* seeds during the rainy season, but those collected in the dry season were lacking seeds. Bats ingested small seeds but can transport large seeds to the cave. The plants are noted if endemic ([e]) native ([n]) or introduced ([i]).

fruiting trees revealed that *Rousettus aegyptiacus* fed mainly on *Ficus* spp., although other fruits, such as litchis *Litchis chinensis* and jamba *Syzygium* spp. were also consumed during other seasons (Jacobsen and Du Plessis 1976).

Seed dispersal and germination

Our results show that *Rousettus madagascariensis* ingests small seeds when consuming *Ficus rubra* fruits, and that
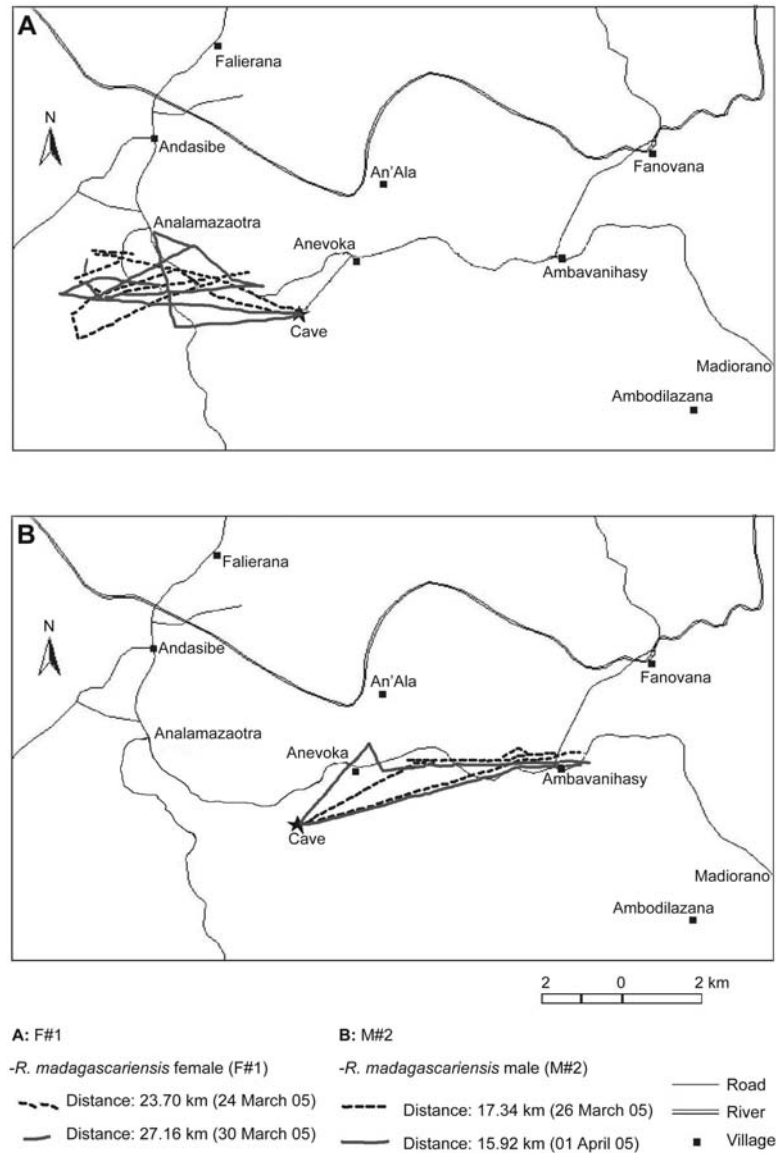
Figure 2 Movements of two *Rousettus madagascariensis* determined by radio tracking from the time the bats emerged to feed until they returned to the roost.

these seeds germinated significantly faster after they had passed through the digestive tract of bats. More research is required to investigate the ability of such seeds to germinate under natural conditions. Other mammals in Madagascar have similar positive effects on seed germination and there is evidence that both lemurs and bats increase either the rate of germination or its success (Dew and Wright 1998, Picot et al. 2007). The rapid germination of seeds recovered from faeces indicates that zoochory by *R. madagascariensis* is a viable life history tactic for plants such as *F. rubra*, but similar studies with other *Rousettus* species have found no significant impact on germination after passage through the bats (Izahaki et al. 1995, Tang et al. 2007).

The full extent of the role of *Rousettus madagascariensis* as a seed disperser and pollinator in eastern Madagascar remains to be described. It has a clear potential as a seed

disperser because it defecates and transports viable seeds (Andrianaivoarivelo et al. 2007). Importantly, *R. madagascariensis* can regularly traverse areas of open grassland, up to 8.1 km in our study, and therefore has the potential to link isolated forest fragments, in much the same way that *Pteropus rufus* does in southeastern Madagascar (Bollen and Van Elsacker 2002, Bollen et al. 2004, Long and Racey 2007). More information is now required on the distribution and fate of seeds dispersed by *R. madagascariensis*.

Habitat use and movement

The longest straight-line distance between the *Rousettus madagascariensis* roost and foraging sites from radio tracking and chemiluminescent light tags were 7.0 km and 8.1 km, respectively, a limit that might have reflected the end point
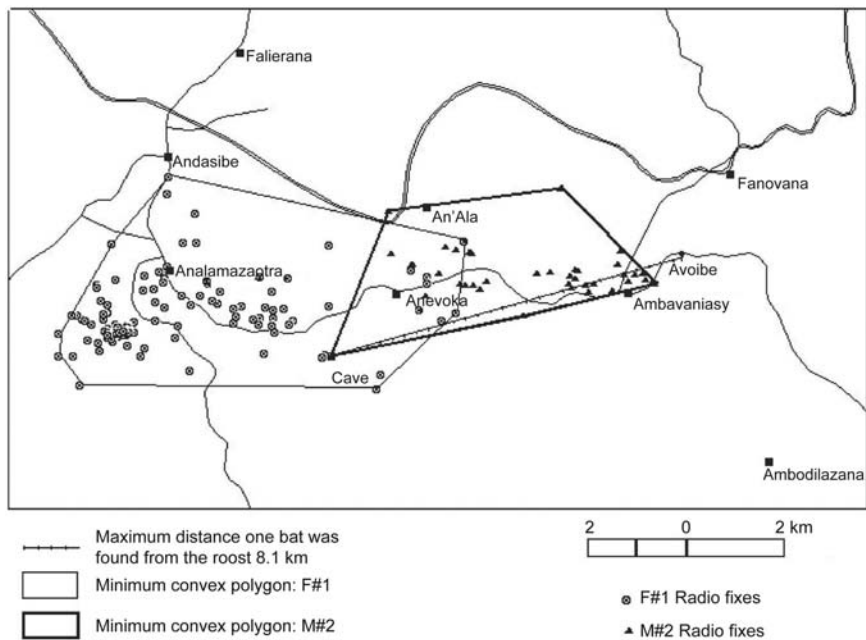
Figure 3   Minimum convex polygons of radio fixes for an adult female (grey line) and male (black line) *Rousettus madagascariensis* determined by radio telemetry. The female bat had a larger home range that overlapped with the male.

of our transects as much as the bats ability to travel greater distances. In South Africa, *Rousettus aegyptiacus* was radio tracked travelling 24 km between its roosts and foraging sites (Jacobsen and Du Plessis 1976). The distance travelled is likely to be a function of food availability or its distribution. The lack of alternative roost sites and nectar available in abundance in banana plantations not far from the cave could be possible explanations of the regular movements recorded in the present study. Mist netting demonstrated that *R. madagascariensis* forages in relatively intact forest and highly modified habitats close to villages. A previous study in close proximity to the Maromizaha cave netted *R. madagascariensis* in a *Eucalyptus* plantation and not a single individual of

this species was netted in relatively intact humid forest despite considerable effort (Randrianandriananina et al. 2006). Nevertheless, the presence of *Ficus* spp. in the diet of *R. madagascariensis* and its capture within the forest indicates that it has a potentially unique role amongst Malagasy fruit bats through its mobility below the canopy. In Africa, *R. aegyptiacus* foraged on *Ficus* spp. inside the forest canopy and dispersed seeds whilst flying and consuming fruit on perches (Mutere 1968, Jacobsen and Du Plessis 1976). *R. obliviosus* is also reported to be highly manoeuvrable, capable of flying inside closed forest (Sewall et al. 2003). In the Bemaraha karst formation, *R. madagascariensis* was significantly more abundant in the forest gaps and edge than in
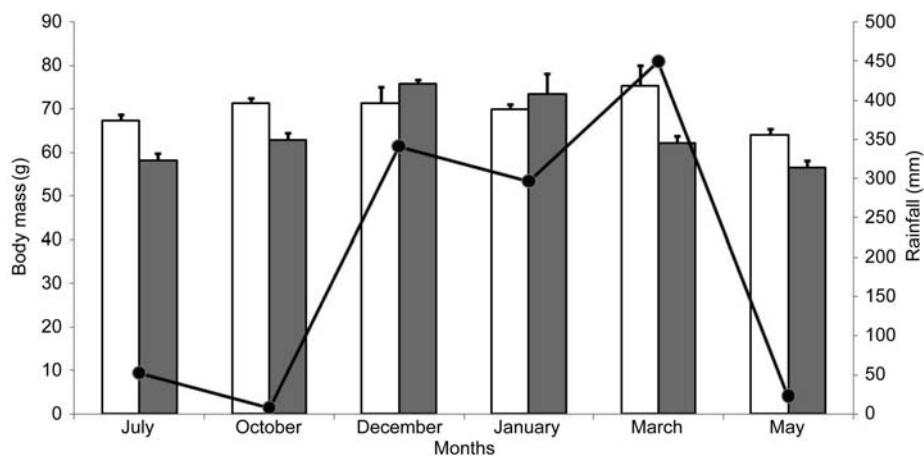

Figure 4   Mean (±SE) body mass of adult male and female *Rousettus madagascariensis* caught returning to a cave roost in Maromizaha, eastern Madagascar. Monthly average rainfall (black line) is given for the period 1984–1994 from a weather station 3 km west of Maromizaha. Adult males (open bar) were heavier than females (shaded bar) except during pregnancy.

the cleared habitat or grazing pasture, indicating that this species appeared to rely on native forest whilst foraging (Kofoky et al. 2007).

Breeding biology

The climatic data collected in Analamazaotra showed a pronounced rainfall peak from February to April and low temperature in June to July. The low body mass of *Rousettus madagascariensis* during May and July could be related to an increase in basal metabolic rate triggered by low temperature and food scarcity (McNab 1969), as also reported for *Rousettus aegyptiacus* (Jacobsen and Du Plessis 1976). Bat body mass and reproduction period can be influenced by fruit availability and phenology. However, overall fruit availability varies seasonally in the eastern forests of Madagascar, with the summer being more productive than the winter (Overdorff and Hemingway 1999). Similarly, the peak of fruit production in a single *Ficus* sp. tree was in the summer in the eastern rainforest (Goodman et al. 1997). The absence of *Ficus* seeds in the faeces of *R. madagascariensis* during the winter could reflect a genuine dietary preference, with the bats feeding on nectar, or the low availability of *Ficus* fruits in the vicinity of the study site. Another possibility is that the bats fed on larger fruits during the winter with seeds too large to ingest. Further research at our study site is necessary to investigate the reason for the seasonal occurrence of *Ficus* seeds in the diet of *R. madagascariensis*.

Cumming and Bernard (1997) found that parturition in African Chiroptera occurs 1–2 months before peak rainfall, and that also seemed to be the case for *Rousettus madagascariensis* in our study site. Lactation or parturition occurred in the early rainy season and females carried young in flight during December and January 1 or 2 months before the peak rainfall in February or March. There was a high proportion of seed in the diet after weaning, towards the end of the wet season (March and April). Therefore, *R. madagascariensis*, like other fruit bats, probably times its breeding to coincide with high temperature and food availability in the austral summer. From the dates that pregnant and lactating bats were observed, we infer that weaning at Maromizaha started before 8 weeks of age. According to Korine and Arad (1999), the offspring of *R. aegyptiacus* are totally dependent on their mothers for the first 6 weeks of life.

Rousettus in Africa have different breeding strategies that are presumably based on local environmental conditions (Mutere 1968, Jacobsen and Du Plessis 1976, Reason et al. 1994). Our results suggest that *R. madagascariensis* in Maromizaha was monoestrus and the absence of juvenile bats in December suggests that they reach somatic maturity in a single year. The single breeding season of *R. madagascariensis* is also the case for other studied tropical fruit bats (Racey and Entwistle 2000), although *R. aegyptiacus* in Uganda exceptionally has a bimodal breeding pattern that can be correlated to two distinct rainfall peaks (Mutere 1968).

Acknowledgements

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