Preliminary Report

The contribution of fruit bats to forest regeneration in Madagascar – do bat-processed seeds do better?

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Abstract

1. The first study to test germination success of bat-processed seeds on different substrates indicates that the seeds sown on filter paper germinate faster and at higher rate than unprocessed ones.
2. Seeds sown under different shade intensity germinate best in semi-shaded environment and bat-processed seeds have the potential to produce stronger and healthier seedlings
3. Bats are important dispersers of *Ficus polita* which was very abundant in the study area
4. Artificial feeding sites had no success in attracting *Pteropus rufus* although a variety of other animals visited the sites
5. The first GPS-tracking study on *P. Rufus* indicates that the remaining forest fragments within agricultural landscape are important for bats and are visited regularly
6. Bats are likely to be crucial in maintenance of small forest fragments through seed dispersal

Background

Frugivory and seed dispersal by animals (zoochory) have been highlighted as being of major ecological and evolutionary importance (Traveset, 1998). The efficiency of an animal as a successful dispersal agent depends on many aspects of its behaviour, physiology or morphology.

Old World fruit bats (Family Pteropodidae, Order Chiroptera) are phytophagous and feed almost exclusively on fruits, leaves, nectar and pollen (Muscarella and Flemin, 2007). Usually they have broad diets and eat a wide range of native and introduced/cultivated species of plants (Jenkins et al., 2007; Long and Racey, 2007; Andriafidison, 2006; Raheriaisena, 2005; Bollen and Van Elsacker, 2002). Old World fruit bats are also able to consume relatively large quantities of fruits (50- 250% of their body mass) (Izhaki et al., 1995).

Fruit bats are highly mobile, and their wing morphology allows them to track resources over large areas (5-40km) and among scattered forest fragments (Richter and Cumming, 2008; Jenkins et al., 2007; McConkey and Drake, 2007; Thomson et al., 2002). Therefore, they appear to be of fundamental importance in the maintenance and regeneration of tropical forests because they promote the large-scale dispersal of fruit seeds in tropical environments (Muscarella and Fleming, 2007). Indeed, at least 300 plant species are known to rely on Old World fruit bats for their seed dispersal as well as pollination (Sato et al, 2008; Muscarella and Fleming, 2007; Lobova et al., 2003; Shilton et al., 1999). However, there are some controversies remaining about the effectiveness of seed germination after the passage through the bats' guts (Sato et al., 2008).

Introduction

The study was conducted to clarify the role of Madagascar's largest fruit bat *Pteropus rufus* in the regeneration of tropical forest. It was the first study to test the germination success of bat processed seeds in a variety of conditions, from a filter paper and different types of soil to the influence of different shade intensities. It was also the first attempt to use GPS tags on *Pteropus rufus* and map their movements across highly fragmented landscape.

So far 110 plant species have been identified in the diet of *P. rufus* in Madagascar, including 59 (i.e. 55%) endemic species (Long and Racey, 2007; Bollen and Van Elsacker, 2002). This suggests that *P. rufus* has a very diverse diet, which has enabled it to adapt to areas with vastly differing vegetation types, e.g. dry deciduous forest in the south (Long and Racey, 2007), littoral forest on the coast (Bollen and Donati, 2006; Bollen and Van Elsacker, 2002) and lowland rain forest in the north-east (MacKinnon et al., 2003).

The capacity of an animal to ingest different seed sizes is limited by the dimensions of its alimentary tract, particularly the diameter of its oesophagus. Bollen and Van Elsacker (2002) reported a maximum seed size of 10 mm in *P. rufus* diets. Relatively little is known about these endemic Malagasy mammals. Although some previous studies aimed to determine the feeding behaviour and seed dispersal ability of Malagasy bats, not much is known about the effectiveness of this behaviour (e.g. Jenkins et al., 2007; Long and Racey, 2007; Andriafidisonn et al., 2006; Goodman et al., 2005).

Aims and Objectives

- To germinate bat processed seeds (faecal and spat-out seeds) in a variety of progressively more natural conditions.
- To investigate the ability of bats to disperse seeds.
- To attract bats to places they are not likely to visit by constructing artificial feeding sites.
- To conduct a GPS-tagging study to map movements of foraging bats across fragmented landscapes.

Study site

The study took place between 27th July and 27th October 2011 in the Mandena conservation zone, situated near Taolagnaro (Fort Dauphin), Anosy Region, Madagascar, (24° 57' 0" S, 46° 59' 0" E). Mandena is now part of Madagascar's national network of protected areas (SAPM) and is managed by QIT Madagascar Minerals (QMM) which established a long-lasting project on forest restoration in the mining area.

Materials and methods

- *Seed collection*

Between 2nd and 23rd August 2011 seeds (faecal, spat-out and from ripe fruits) were collected from the roost site in Amborabao (24º 49′ 086′′ S; 47º 01′ 87′′ E) as well as surrounding feeding trees. Three semi-permeable plastic sheets (3x5m; 3x5m and 3x10m) were placed in the roost forest under the trees which were most often occupied by bats. The seeds were collected daily, dried in a dark place and kept in paper envelops to prevent any initial germination. Additionally, a roost in Ivolo (24º 55′ 47′′ S; 46º 55′ 22′′ E) was visited where local people agreed to collect seeds throughout August. The seeds were taken from locals at the beginning of September. Seeds were also collected from at least five feeding trees around Mandena along with fresh fruits.

All the collected seeds were identified as *Ficus polita* (order Rosales, family Moraceae) (Fig.1.)

Fig.1. *Ficus polita*. Left: the aerial roots of *F. polita* growing on the host tree. Top right: ripe fruit with seeds. Bottom right: fruits attached to branches.

Ficus polita is a common species found in lowland rainforest and gallery forest of Africa and Madagascar, up to 1200m altitude. It is a strangler tree and it usually starts germination between brunches of other trees. In Madagascar it is pollinated by the fig wasp *Courtella bekiliensis* (Order: Hymenoptera; Family: Agaonida). *Ficus* species are thought to be the key stone species in many rainforest habitats as they provide fruits asynchronously, throughout the year (Corlett and Primack, 2011).

- *Germination experiments*

Between 10th September and 26th October 2011 two experiments were conducted to investigate germination success of bat-processed seeds in comparison to unprocessed seeds.

1. Different substrate experiment

The seeds (faecal, spat-out and unprocessed) were divided into two groups (sterilized in 10% ethanol solution and unsterilized) and sown on filter paper (100mm) moistened with 3 ml of water in Petri dishes (91mm) and on 15g of sterilized and unsterilized soil (littoral, clay and ferralitic) which was also moistened (Fig.2.). Each Petri dish was sealed with clear Vaseline and contained 20 seeds. Each treatment was replicated 15 times. In total 630 Petri dishes were placed on an outside table in the Mandena tree nursery (W150cm, H100cm, L400cm) with a roof made from plastic mesh to protect seeds from direct sun and overheating (Fig.2.). The seeds were randomly chosen randomly from the collected pool of seeds. Seeds were rejected only when they were obviously damaged. The seeds were checked first after 5 days and then they were checked continuously every second day.

Fig.2. Different substrate experiment. Left: Petri dishes placed on the outside table in Mandena nursery. Right: three types of soil used: from top left- ferralitic, littoral and clay.

The seeds were coded as follow: F- seeds from faecal samples, P- seeds from spat-out pellets, N- natural seeds; and Fs, Ps and Ns denotes that similar samples were sterilized in 10% ethanol solution. The treatments were coded using following numbers: 1- filter paper, 2- sterilized littoral soil, 3- sterilized ferralitic soil, 4- sterilized clay soil, 5- unsterilized littoral soil, 6- unsterilized ferralitic soil, 7- unsterilized clay soil. Thus e.g. Fs1 represents sterilized seeds from bat faecal samples sown on filter paper.

2. Shade experiment

Unsterilized seeds (faecal, spat-out and unprocessed) were sown in unsterilized littoral soil in plastic bags (10x15cm; 20 seeds in each) (Fig.3.) and placed in direct sun, semi-shade on the edge of the forest and shade inside a thick forest. Each treatment was replicated 15 times. The seeds were watered twice a day: in the morning and in the evening and checked first after 5 days and then every second day.

Treatments were coded as follow: s- sun, ss- semi-shade and sh- shade. Thus, e.g. ssFaecal refers to seeds taken from bat faeces and sown in semi-shade conditions.

Fig.3. Seeds from faecal samples sown in plastic bags in shaded conditions.

- ***Seed dispersal***

To observe bats' ability to disperse seeds, semi- permeable plastic sheeting (3x5m) was placed under a feeding tree of bats in Ananadrano village (24° 56′ 075′′ S; 46° 59′ 33′′ E) and monitored daily between 24th August and 30th August 2011 from 19.00h until 23.00h which coincides with peak activity of *P.rufus* (Andriafidison et al., 2006). The following morning the site was visited to count number of faecal droppings and spat-out pellets on the plastic sheeting.

- ***Artificial feeding sites***

The feeding sites were constructed from 4m long *Corymbia citriodora* trunks (order Myrtales, family Myrtaceae) which were bought from a local plantation. Two trunks were placed 3m apart with a black polyester material (3m x 60cm) stretched between. The fruits were put onto the material and also rubbed all over it to intensify the scent. Semi-permeable sheeting (3x3m) was placed on the ground to see dispersed seeds (Fig.4.). Five sites were constructed around the Mandena forest, in openings which seemed to be unattractive to bats due to a lack of any fruiting trees in the vicinity. Between 26th September and 26th October, the sites were monitored every evening from 19.00h until 23.00h. Fresh fruits were added every second evening. Because the study was conducted in the dry season the only available fruits were bananas, dried tamarind (*Tamarindus indica*), custard apple (*Annona cherimola*) and sugar apple (*Annona squamosal*). Some fresh fruits of *F. polita* where used as well.

Fig.4. Artificial feeding site.

- *GPS tagging study*

Between 20th September and 14th October 2011, four bats were caught in a handmade fishing net (6mx4m) in the roosting forest at Amborabao. Each bat was weighed and measured and a collar with GPS and RF tag (MicroTraX TSTX GPS Tag, Code: 070602) was attached (Fig.5.). The attachment weight 30g which account for around 4% of the body mass of a bat. The GPS tag recorded fixes every 30 minutes from 18.00h to 06.00h with three fixes during a day. Every morning attempts were made to locate the bat using a RF receiver and GPS data were downloaded remotely using a Bluetooth system. The collar was designed to drop off eventually, due to bat's movements and grooming behaviour.

Fig.5. Left: GPS and RF tag on a collar. Right: collar attached to *P. rufus*.

Analysis

The data were analysed using Microsoft Excel 2011 and MiniTab 15. To check if the data were normally distributed, the Anderson- Darling test for normality was used. The Mann-Whitney test was used to establish if there were any significant differences between the medians.

The median number of germinated seeds was calculated for each treatment and converted into the percentage germination among all treatments. Also, the median time for the first seed to germinate was calculated for each treatment.

These are preliminary analysis and all the data will be analysed in more details in the final report.

Results

Germination experiments:

- *Different substrate experiment*

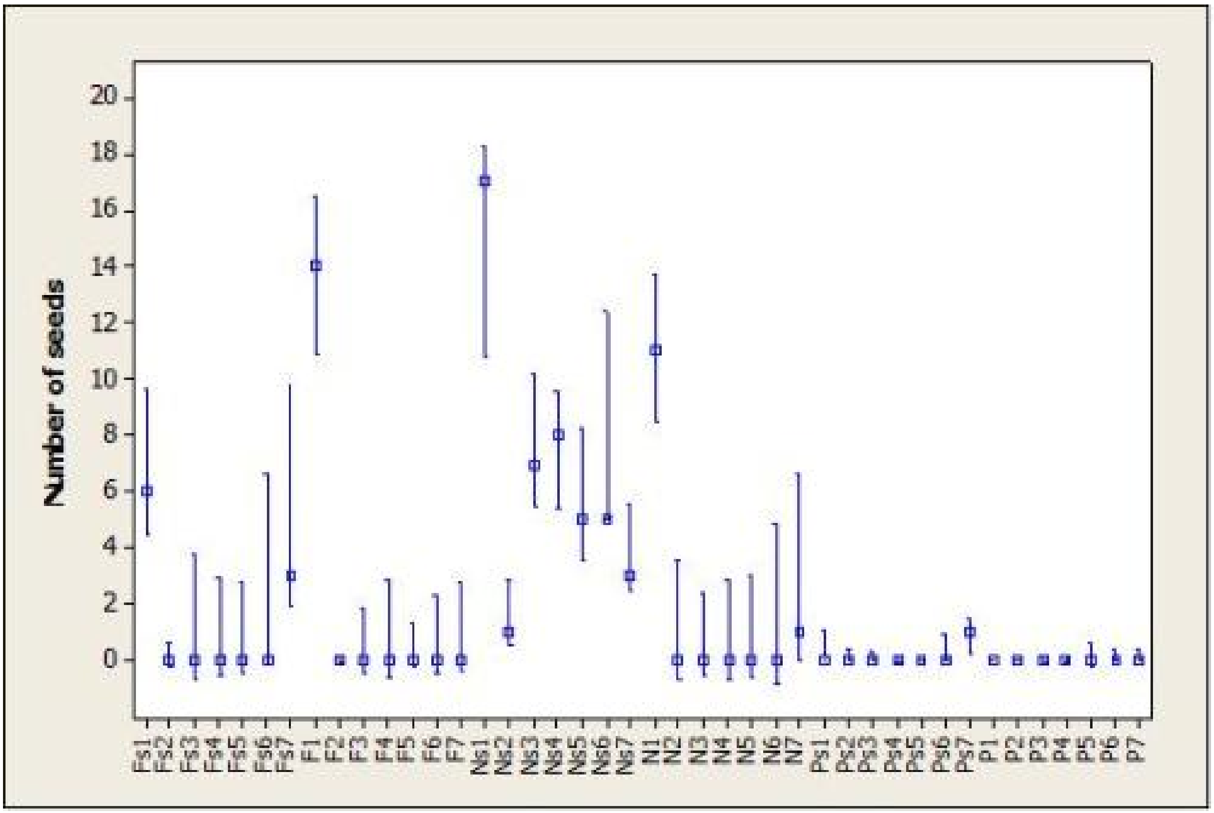

Fig.6. Median number of germinated seeds between treatments. The bars represent 95% CI for the mean. Seed codes: Fs- bat-processed sterilized seeds; F- bat-processed unsterilized seeds; Ns- unprocessed sterilized seeds; N- unprocessed unsterilized seeds; Ps- spat-out sterilized seeds; P- spat-out unsterilized seeds. Substrate codes: 1- filter paper; 2- sterilized littoral soil; 3- sterilized ferralitic soil; 4-

sterilized clay soil; 5- unsterilized littoral soil; 6- unsterilized ferralitic soil; 7- unsterilized clay soil.

Median number of germinated seeds (Fig.6.) varies between treatments. The highest number of germinated seeds was recorded in Ns1 treatment (17), followed by F1 (14) and N1 (11). The remaining treatments had germination rates lower than 50% (Tab.1.). Those treatments which scored median germination number of 0 were rejected from further analysis.

Table.1. Germination rate (%) taken from the median number of germinated seeds in each treatment.

Treatment	Ns1	F1	N1	Ns4	Ns3	Fs1	Ns5	Ns6	Fs7	Ns7	N7	Ns2	Ps7
Germination Rate (%)	85	70	55	40	35	30	25	25	15	15	5	5	5

Time for start of germination was also different among each group (Fig.7.). The quickest seeds to germinate were F1, Ns1 and N1 (7th day after sowing) with N7- 'natural seeds sown on clay soil' and Ps7- 'sterilized spat-out seeds sown on clay soil' being the latest (27th and 29th day respectively).

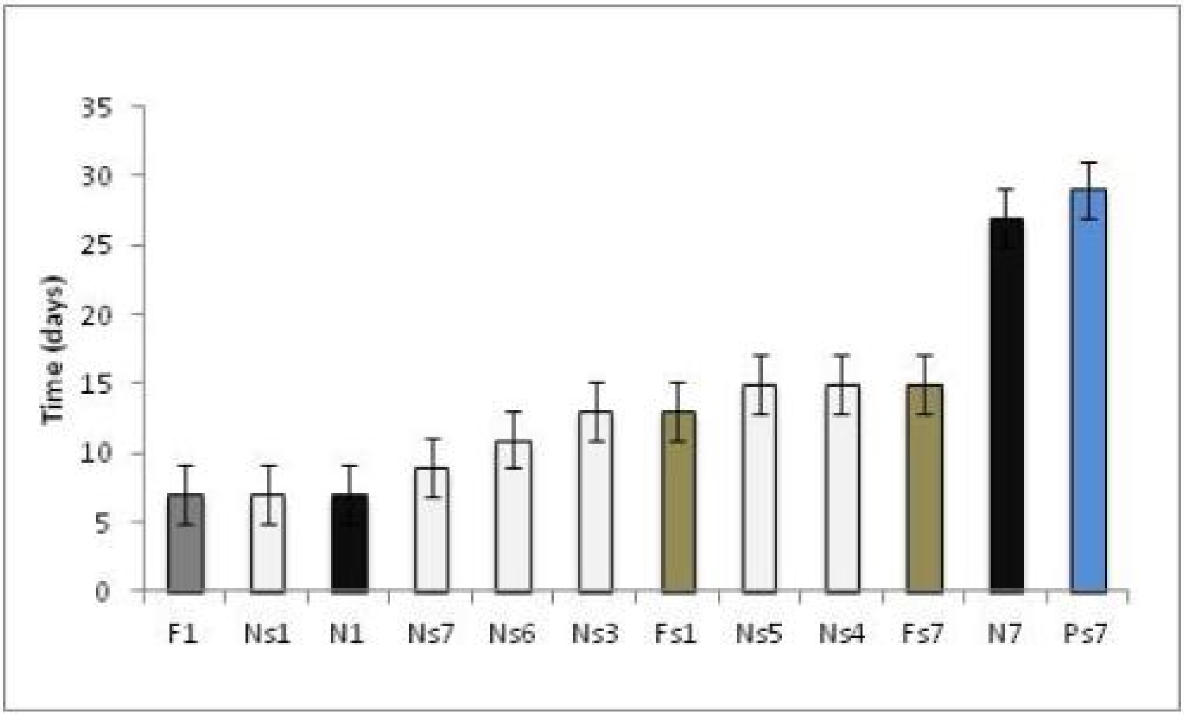

Fig.7. Median start of germination across the treatments. The bars represent standard error.

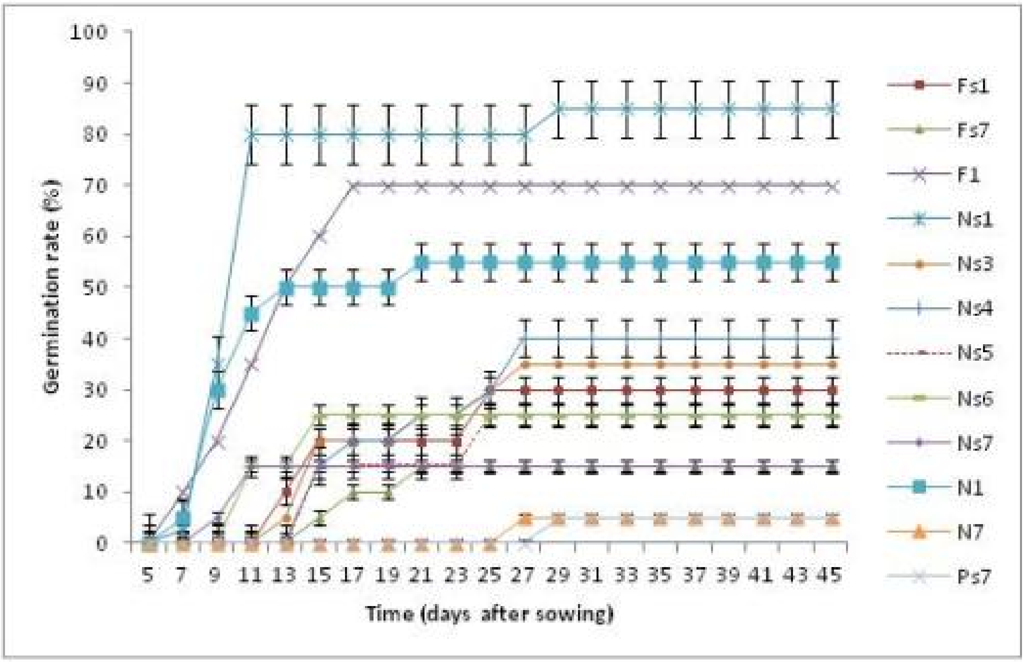

Fig.8. Germination rate (take from the median) of seeds as a proportion of germinated seeds at given day after sowing. The bars represent standard error.

Median germination rate (Fig.8.) of seeds in Ns1 was significantly different from F1 (Mann-Whitney test, $p=0.0054$; $W=264$) and N1 ($p=0.0058$; $W= 263.5$). No statistically significant difference was found between F1 and N1 ($p=0.0596$; $W=244.5$). However, in terms of median number of germinated seeds (Fig.6.), F1 was significantly different from N1 ($p=0.0012$; $W= 580.5$).

- *Shade control*

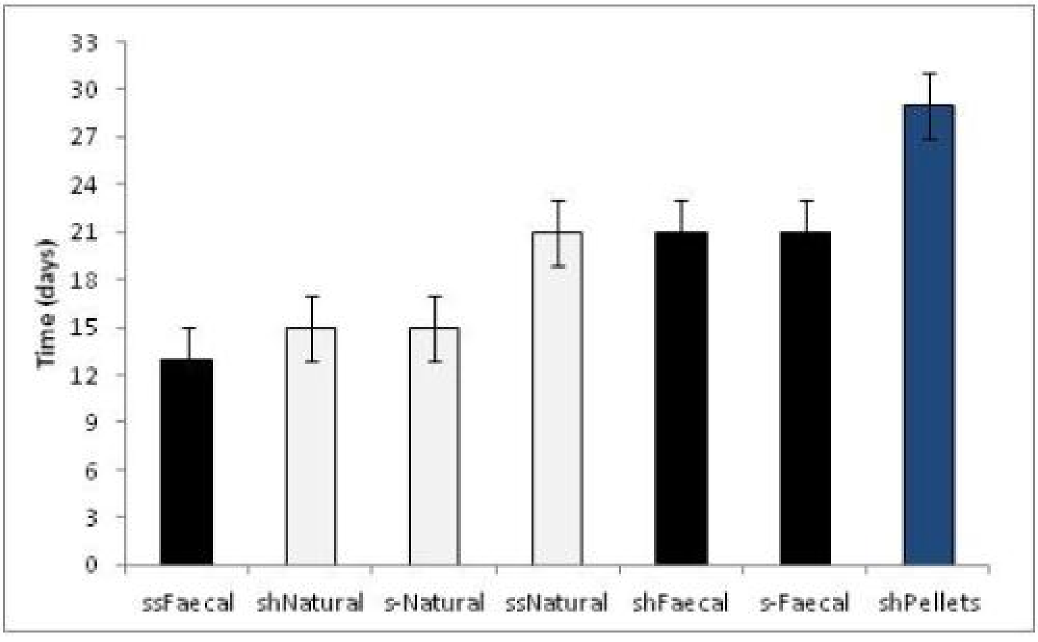

Fig.9. Median start of germination across the treatments. The bars represent standard error.

The seeds in ssFaecal germinated on a 13th day of the experiment (Fig.9.) followed by shNatural (15th day). The longest to germinate were shPellets seeds (29th day) with no success in sPellets and ssPellets.

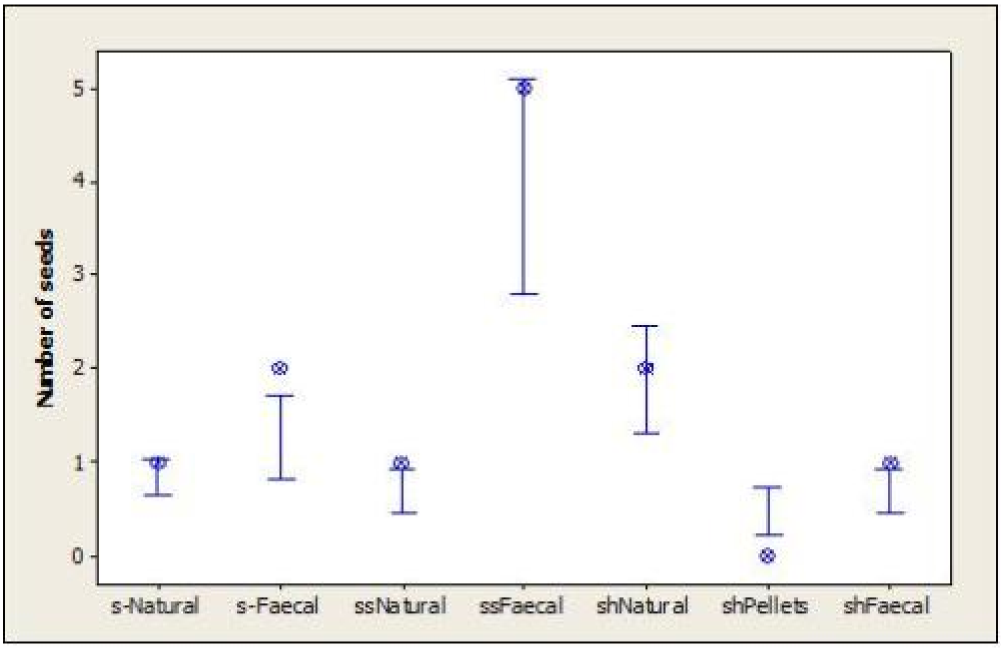

Fig.10.Median number of germinated seeds. The bars represent 95% CI for the mean. Treatment codes: s- sun; ss- semi-shade; sh- shade.

The median number of germinated seeds (Fig.10.) for ssFaecal was the highest among all treatments and significantly different from sFaecal and shNatural (Mann-Whitney test, p=0.0019; W= 477.5 and p= 0.0126; W= 456.5 respectively). Statistical difference was also apparent when comparing median germination rate (Fig.11.) of ssFaecal to shNatural and sFaecal (Mann-Whitney test, p= 0.0072; W= 418.5 and p= 0.0019; W= 477.5 respectively).

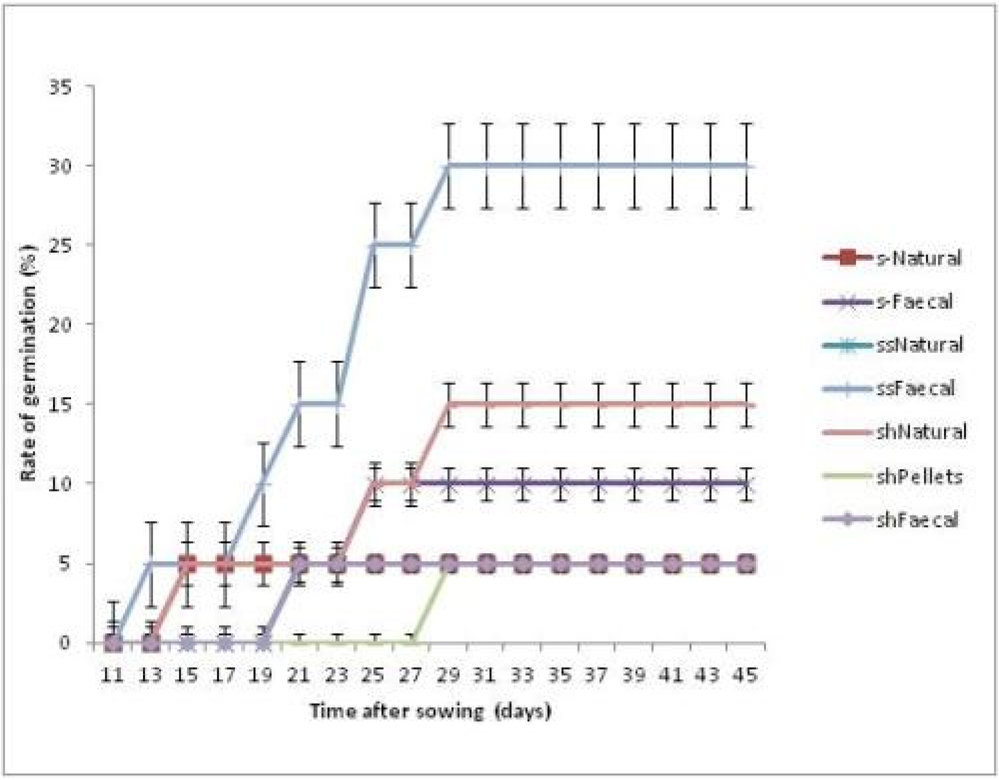

Fig.11. Germination rate (taken from the median) of seeds as a proportion of germinated seeds at given day after sowing. The bars represent standard errors.

Seed dispersal

Observations on bats' dispersal abilities showed that as many as over 220 droppings can be found on 3x5m plastic sheeting placed under a feeding tree after one night. Apart from droppings, hundreds of spat-out pellets can be found around a single tree. On a single night as many as 400 pellets could be found on 3x5m sheet. The bats dispersed seeds in the form of fruits, pellets and faecal samples as far as 50m beyond the trunk of the tree they fed on. As many as 60 bats have been seen between 19.00h and 23.00h feeding on a single tree.

In the roost forest of Amborabao, the bats' droppings are very abundant on the vegetation. As local people pass through the forest daily, the bats move along forest edges and disperse seeds all over the trees.

Artificial feeding sites

Table.2. Summary of animal activity around feeding sites as a number of visits in each site, percentage among visitors in each site and among all the sites. Scientific names are listed in the Appendix.

Animal	No. of visits in each site					Total no. of visits	Per cent in each site					Per cent among all
	Site1	Site2	Site3	Site4	Site5		Site1	Site2	Site3	Site4	Site5	
Owl	23	27	11	23	22	106	32.86	32.14	18.97	29.87	30.99	29.44
Insectivorous bat	20	25	15	14	19	93	28.57	29.76	25.86	18.18	26.76	25.83
Brush warbler	9	11	8	22	21	71	12.86	13.10	13.79	28.57	29.58	19.72
Falcon	10	5	8	14	6	43	14.29	5.95	13.79	18.18	8.45	11.94
Madagascar Nightjar	1	14	6		3	24	1.43	16.67	10.34	0.00	4.23	6.67
Gray mouse lemur	1		3			4	1.43	0.00	5.17	0.00	0.00	1.11
Long tailed cormorant				4		4	0.00	0.00	0.00	5.19	0.00	1.11
Collared nightjar	3					3	4.29	0.00	0.00	0.00	0.00	0.84
Straw-coloured flying fox		1	2			3	0.00	1.19	3.45	0.00	0.00	0.83
Unknown birds (Sagoaky and Trangalovaky)	1	1				2	1.43	1.19	0.00	0.00	0.00	0.56
Greater dwarf lemur	1					1	1.43	0.00	0.00	0.00	0.00	0.28
Ring-tailed mongoose	1					1	1.43	0.00	0.00	0.00	0.00	0.28
Crested coua			1			1	0.00	0.00	1.72	0.00	0.00	0.28
Rat			1			1	0.00	0.00	1.72	0.00	0.00	0.28
Cuckoo			1			1	0.00	0.00	1.72	0.00	0.00	0.28
Read-billed teal			1			1	0.00	0.00	1.72	0.00	0.00	0.28
Lemur			1			1	0.00	0.00	1.72	0.00	0.00	0.28

During 31 days of monitoring the feeding sites, an owl scored the highest percentage of visits among all animals (29.44%; Tab.2.) followed by insectivorous bats (25.83%) and brush warbler (19.72%). The straw- coloured flying fox (*Eidolon dupreanum*) was seen six times (0.83%). No *Pteropus rufus* was seen around the sites, although it was known that the species visits Mandena forest.

No dispersed seeds were seen around artificial feeding sites.

GPS study

From four collared bats data were obtained from one for a period of 11 nights (Fig.12.). The collar fell off a second bat just after the first night while it was feeding on a fig tree (*F. polita*) most likely due to a wrong attachment, and two bats went missing just after the tags were attached to them. No RF signal was found around the roost and in places where bats were known to visit.

However, the downloaded data from one bat shows that the bat was feeding exclusively around the roost in a radius of ca. 2km. Small forest fragments across the agricultural were visited nightly, often the bat roost in the fragments, away from the colony. Due to the high density of fig trees (over 50 within 2km radius from the roost) food seems to be easily accessible to the bats during the dry season. They were also seen to feed on kapok trees (*Ceiba pentandra*) which were still in flower at the beginning of August, as well as coffee trees abundant in the area and in bloom during August. From mid-November the site is rich in mango and lychee fruits which are included in the bat diet.

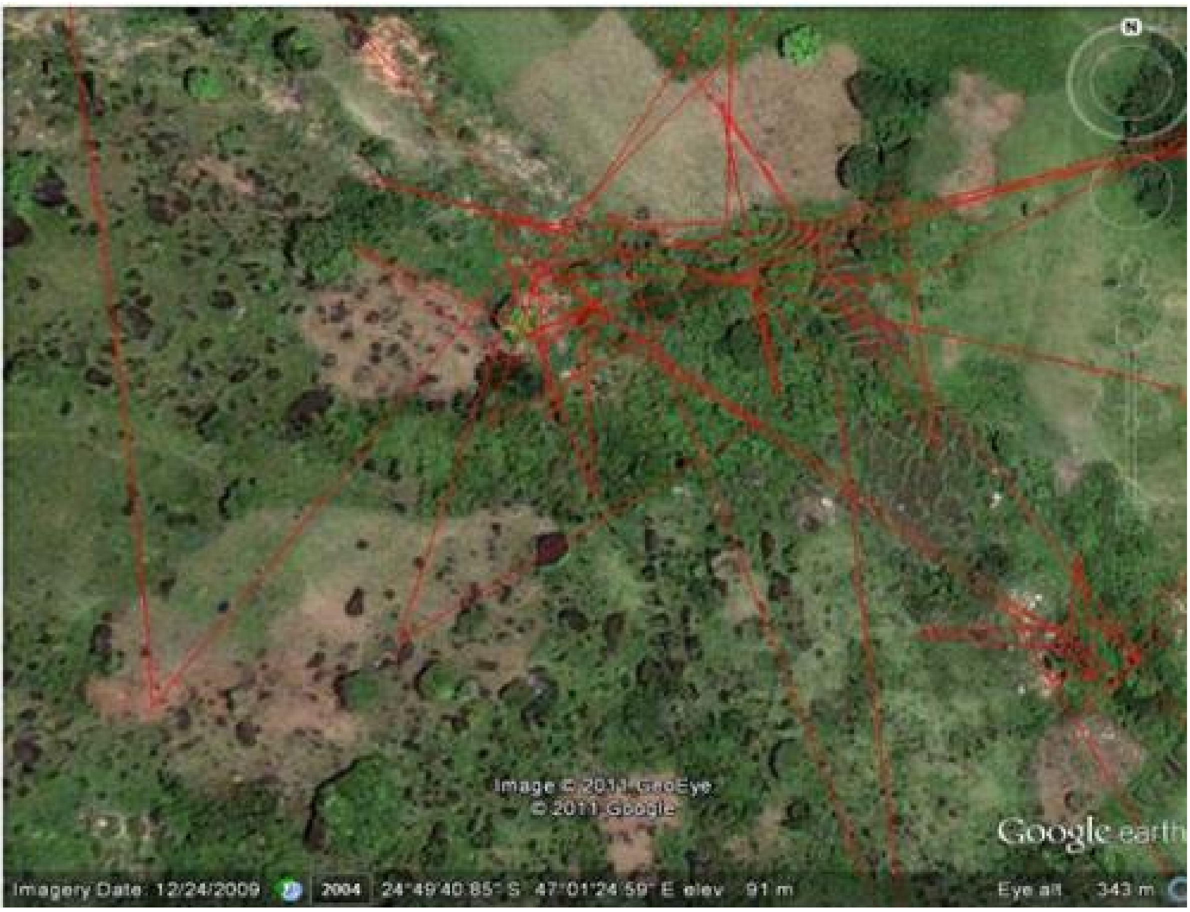

Fig.12. Bat movements across small forest patches. Partial data from the trial GPS-tracking study collected in September 2011. The bat's positions are plotted every 30 min intervals over a period of three days. The individual trees visited by bat can be resolved in the satellite image of the landscape

Discussion

Germination of bat processed seeds

The germination rate of seeds in all of the experiments varied greatly and seeds sown on filter paper had the best success. This may be due to a fact that *F. polita* is a strangler tree which usually starts to grow on a trunk of other trees (Arbonnier, 2004). Thus, seeds sown in the soil may show lower success.

The experiment using different substrates showed that natural, alcohol-washed seeds did best on the filter paper and among all the treatments, with relatively high germination success (85%) and these were also among the first to start germination. Additionally, they were the only seeds which showed germination across all the soil treatments. However, when sterilised seeds were excluded from analysis because they were the only ones manipulated through alcohol washing, seeds extracted from faecal samples did germinate batter in terms of seed number than natural ones. Although, the germination rate of faecal seeds was not statistically different from that of natural seeds ($p>0.05$), the number of germinated seeds among faecal samples was significantly higher than in natural seeds ($p=0.0012$). Greater success of seeds from faeces has been confirmed by the shade control experiment where faecal seeds did significantly better that natural seeds in terms of germination rate ($p=0.0072$) as well as the number of germinated seeds ($p=0.013$).

Higher success of bat-processed seeds has been previously suggested by Picot et al., (2007) where *Ficus* seeds processed by *Eidolon dupreanum* germinate better than unprocessed seeds. They achieved germination rate of 20% for *F. brachyclada* and 40% for *F. pyrifolia* while no seeds germinated form ripe fruits. Also, Entwistle and Corp (1997) recorded that the germination of *F. lutea* and *F. natalensis* seeds was higher after ingestion by *Pteropus voeltzkowi* compared with that of intact seeds. However, both studies had relatively small sample size and their germination experiments were just an addition to the study of bats' diet.

The shade control experiment also shown that the seeds grow best in semi-shade conditions which again may be due to a fact *F. polita* initiate germination between branches of other trees which is likely to be a more shaded environment. On the other hand, natural seeds did best in a strongly shaded environment, still with much lower success when compared to faecal seeds germinated in semi-shade.

Although, the number of germinated seeds was rather low in the shade control study when compared to experiment done in Petri dishes, this experiment took into account factors such as predation and atmospheric changes as the seeds were sown outside with no protection. Therefore, the seedlings were exposed to heavy rains and humidity fluctuations and were exposed to many invertebrates which feed on seeds and seedlings, where in Petri dishes they had a stable environment. This result show that bat-processed seeds do much better in a natural environment than unprocessed seeds. The strength of the seedling was not compared among the treatments, but it appeared that seeds extracted from bat faeces grow quicker and looked healthier. It would be essential to investigate those factors quantitatively in the future.

Seeds extracted from spat-out pellets had the lowest success. In most of the cases no germination or very low germination rates were evident. The spat-out seeds are mostly those already killed by fig wasp larvae which as a result lose their gelatinous coating which normally aids the passage of the seeds down the oesophagus of the bat along with the fruit juices. This makes it difficult for swallowing and bats reject the seeds along with the fibre and dump the pulp in the form of spat-out pellets (Utzurrum and Heideman, 1991). Similar findings were reported by Picot et al. (2007) who achieved no germination from spat-out seeds.

Seed dispersal

Observations on seed dispersal showed that bats can be very effective dispersal agents. They feed frequently in large groups and transfer many seeds to the ground. They disperse the seeds beyond the source tree in all the directions and some of them can travel with a fruit to a feeding tree up to 50m away. They seem to be very persistent with eating preferred fruits like figs and visit a tree as long as such fruits remain. The bats enhance germination success not only by ingesting the seeds but mainly due to a fact they separate the seeds from the pulp (Heer et al., 2010). The large number of bats feeding on fig trees at once also suggest that they are the main disperser for the species. As *F. polita* is a strangler fig, bats seem to be important dispersers for the plant. They deposit seeds wherever they feed as well as in the roosting areas. The forests in which bats roost were full of fig seeds which could be found all over the trees. That seems to improve the germination success of *F. polita* seeds when being deposited in the favourable place (on other trees). Also, the number of fig trees around the roost (over 50) may reflect the bats' success in dispersing the seeds. *Ficus* species are often described as keystone trees in tropical ecosystems as they produce fruits several times during a year. Therefore, they are often available when other fruits are scarce and many frugivores depend on them (Suleman et al., 2011; Heer et al., 2010). Due to the strangling habit of *F. polita*, the seeds dispersed in a dense forest like Mandena have a high chance of germination when deposited on other trees. Small, intact forest fragments benefit from this behaviour in particular, as fast-growing fig species dispersed by bats provide food for frugivores all year round.

Feeding sites

The artificial feeding sites showed very limited success in attracting bats to places they are not otherwise likely to visit. Although visits of two *E. dupreanum* were recorded six times over the period of 31 days, this made a minor contribution to overall activity of animals around the sites. As the sites were constructed during the dry season not many fruits were available for baiting the sites and none of them were actually in the recorded diet of *P. rufus*.

From the animals which have visited the sites owls were the most frequent. As the sites were constructed in the middle of cleared areas, it could be a good hunting spot for these birds. Additionally, insectivorous bats were very frequent probably due to a large number of insects which gathered around ripe fruits. Brush warblers were the third most frequent visitor and could potentially contribute some seeds falling around the site. The grey mouse lemur was seen eight times climbing up the artificial trees and feeding on fruits. The animal disperses small seeds and could contribute to the soil seed bank. A larger lemur (brown or bamboo lemur) was seen once which is unusual as these animals rarely go beyond forest edges.

GPS tagging study

Although only one out of four GPS tags provided clear data, the results from this aspect of the study provided valuable insights into the bats' foraging behaviour. The bat spent most of the time flying around the roost among the fig trees which are widely available in the area. The remaining forest fragments around the roost seem to be very important for bats as it visited them every night. The bat was found roosting along the edges of those fragments in the early morning, often moving back to the colony on afternoon. The availability of food could be a reason for the bat to feed only within ca. 2km from the roosts. As *P. rufus* was seen to feed around Mandena which is ca. 20km from the nearest roost (at Amborabao) it is highly likely that bats do sometimes travel this distance during the night.

A short radio-tracking study conducted by Long and Racey (2007) in Berenty reserve, south-east Madagascar showed that *P. rufus* flew between 7 to 17km to the feeding ground. Therefore, the distance of 20km could be within a feeding range of bats at Amborabao. Several large fig trees were found in the Mandena forest however none of them in were fruit. It would be essential therefore to visit the trees while fruiting to check whether the bats feed on them.

Conclusion

In general bats seem to improve germination success of *F. polita*. The analysis showed that bat-processed seeds are likely to germinate faster and with higher rates. Although the study was limited to one species of seeds which was the only one found in the faecal samples, it provides valuable information about bat-plant interactions. It will be informative to repeat the experiment with different plant species which are likely to be in the diet of *P. rufus*. It would also be useful to include further measures of the success of the seedlings as bat-processed seeds appeared to be stronger and healthier.

Studies with artificial feeding sites showed no clear evidence that they may be a successful tool in forest restoration. Although they do attract a variety of animals which potentially could contribute to the soil seed bank, no evidence seed dispersal by these visiting animals was obtained.

The GPS tagging study showed that bats may be very important in maintaining the remaining forest fragments in the wider agricultural landscape of Madagascar. They seem to visit such fragments every night while foraging, thus dispersing the seeds and contributing to the maintenance of those small ecosystems. They are also good dispersal agents, potentially flying long distances and dispersing seeds over a wide area. As *Ficus* species were the main food for bats during the study period (no other seeds found in faeces), the dispersal of their seeds even over a dense canopy is very likely to produce new fruiting trees important for a variety of frugivores. It would be valuable to continue the GPS study and collect more data about the foraging behaviour of the bats as they seem to travel along remaining forest fragments and have potential to cover great distances while searching for the food.

Appendix

Scientific names of the animals listed in Table 2:

Name	***Scientific name***
Owl	*Otus rutilus or Tyto alba affinis*
Brush warble	*Nesillas lantzii*
Falcon	*Falco peregrinus radama or Falco newtoni*
Madagascar Nightjar	*Caprimulgus madagascariensis*
Gray mouse lemur	*Microcebus murinus*
Long tailed cormorant	*Phalacrocorax africanus*
Collared nightjar	*Caprimulgus enarratus*
Straw-coloured flying fox	*Eidolon Dupreanum*
Greater dwarf lemur	*Cheirogaleus majo*
Ring-tailed mongoose	*Galidia elegans*
Crested coua	*Coua cristata*
Lemur	*Eulemur fulvus* or *Hapalemur meridionalis*
Cuckoo	*Cuculus rochii*
Red-billed teal-	*Anas erythrorhyncha*
Rat	Family: Nesomyidae Subfamily: Nesomyinae

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