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A COMPARISON OF THE EFFECTIVENESS OF METHODS OF DETERRING PTEROPODID BATS FROM FEEDING ON COMMERCIAL FRUIT IN MADAGASCAR

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Abstract: We compared the effectiveness of methods of deterring *Pteropus rufus* from feeding on commercial fruit in east central and southeastern Madagascar in 2012–2013 during the *Litchi chinensis* harvest. Two of the three methods used, installing plastic flags and ringing bells in the trees, were derived from those used by litchi growers in the southeast. We improved and standardized these methods and compared their effectiveness with an organic product made from dried blood and vegetable oil (Plantskydd®) with a taste and odour aimed at deterring mammal feeding. The bats damaged from 440–7,040 g of litchi fruits per tree and two of the three methods reduced the fruit lost to bats: the plastic flags and the organic deterrent. There were significant differences in the damage levels between the study sites and between our three methods of deterrence. The plastic flags and bell ringing methods were significantly less effective in reducing the fruit bat damage compared to the taste deterrent. The latter was most effective when it had enough time to dry and adhere to the fruits after spraying and before rain. Its effectiveness was further demonstrated in flight cage experiments during which *Rousettus madagascariensis* avoided litchis treated with Plantskydd®. Analysis of bat faecal samples revealed no feeding preference but the collected samples contained large numbers of *Ficus* seeds, suggesting that the bats feed extensively on *Ficus* fruits rather than on fruit of economic importance. Apart from fruit ripeness, tree productivity or other phenological factors did not affect the amount of fruit eaten by the bats. More fruits were damaged by birds than bats at both study sites.

Keywords: Bat-human conflict, bells, deterrents, litchi, Plantskydd®, plastic flags, Pteropus.

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Author Contributions: TEAR collected field data at both study sites, analysed it using R-statistics and wrote the first draft of the report to the funding agency. JLMR was also involved in data collection at both study sites and used it for his Master's thesis. PAR edited the original research report into a journal paper, coordinated the improvements to successive drafts and steered the paper through the publication process. RAA was project manager for the research. He successfully sought funding and contacted the stakeholders involved during the study. He assisted and supervised the team in the field, advised and taught the statistical methods used in the paper. He commented and improved on previous versions of this manuscript.

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INTRODUCTION

As a result of habitat destruction and associated loss of the native plant species which comprised the diet of Old World fruit bats, there is growing evidence that exotic plants have become an important food resource for these bats (Aziz et al. 2016). In Madagascar, the Flying Fox Pteropus rufus, has a wide diet including some economically important introduced species such as Tamarindus indica leaves (Raheriarisena 2005), Agave sisalana pollen and nectar (Long & Racey 2007), Dimocarpus longan (Andrianaivoarivelo et al. 2007) and Litchi chinensis fruits (Andrianaivoarivelo et al. 2012). The Madagascar Rousette Rousettus madagascariensis also feeds on litchi fruits and banana (Goodman 1999), and the straw-coloured fruit bat Eidolon dupreanum includes guavas and passion fruit in its diet (Picot et al. 2007).

As a result, these three Madagascar fruit bat species, all endemics, are considered to be pests by some litchi growers because they feed on ripe fruit. Litchis are also eaten by birds, although there has been no comparison of the loss to different pest species. Aziz et al. (2016) reviewed methods of mitigating damage by fruit bats and concluded that netting was the only effective method of protecting fruit. Although lights, aversive smells and tastes have been used to deter bats, there have been no systematic tests of their effectiveness.

Litchis were introduced to Madagascar by 1802 and grow well in the southeastern and eastern parts of the island which has become the world's third largest litchi producer (Menzel 2002). Litchis contribute significantly to improving the income of many Malagasy and losses to pests decreases that income. The primary aim of our study was to compare visual, sonic and biological deterrents which might be used to reduce the impact of bats on litchi fruit. In particular, we tested the hypothesis that an aversive taste deterrent, widely used in the northern hemisphere to discourage grazing and browsing herbivores would deter P. rufus from feeding on litchis. We also predicted that bats would feed on taller and more productive litchi trees. Our work also provided an opportunity to compare the damage to fruits by bats and other vertebrates.

METHODS

Study sites

The study was conducted during 2012 and 2013 at two widely separated sites (Image 1). Site 1 was at

Amborabao Village in Tolagnaro District (24°19'30.8"S, 47°07'16.5"E, Commune Rurale Mahatalaky, Anosy Region, southeastern Madagascar), where up to 50 litchi trees occurred 2km from a P. rufus roost inside a small forest fragment: a sacred place called Kibory situated to the east of the village. This site is close to the large forest fragment: the Tsitongambarika Reserve that is managed jointly by the local communities (COBAs) and the Asity Organization. Site 2 was in eastcentral Madagascar at Ampasimaneva (19°23'00"S & 48°20'00.0"E, Anosibe An'ala District, Alaotra Mangoro Region). This region is characterized by scattered forest fragments with midaltitude humid climate (Andrianaivoarivelo et al. 2007) and includes a roost of P. rufus. The fruiting season of litchis at Site 2 was two to three weeks later than at Site 1. The straight-line distance separating the two sites is 607km.

Litchi productivity

We measured the crown diameter as the furthest distance between the two extremities in the horizontal plane for every litchi tree studied. Tree height was calculated by trigonometry. The GPS coordinates for each sampled litchi tree were also recorded. Total fruit productivity per tree was estimated by counting the number of fruits in one panicle and multiplying that by the total number of fruit-bearing panicles. This method was a development of that proposed by Sud et al. (2015). Although we reduced potential observer bias largely through maintaining the same survey team, it was still difficult to count the litchi fruits because some may have remained hidden from view. To allow for this, counts were repeated nine times by three observers, and we established that about 30% of the observed fruits could not be seen and counted. To correct for our underestimate, we added 30% to the total number of litchi fruits subsequently counted.

Methods of deterring fruit bats from feeding on litchis

We used three different methods of deterring fruit bats from feeding on litchis and tested the success of each. Two of these methods were inspired by those previously used by litchi farmers especially at Site 1 and were improved and standardized. The farmers at Site 2 used no deterrent apart from waving a long wooden stick to kill *R. madagascariensis* (Andrianaivoarivelo et al. 2007), which fed on their longan trees (*D. longan*).

(a) Visual Method: plastic flags

In 2007, at Site 1, at least 10 households were seen using coloured plastic flags attached near the most





Image 1. Localities of the two study sites in Madagascar with country map

clustered ripe fruits to scare bats attempting to land on litchi branches. We standardized the size (1m x 0.5m) and colour of the plastic flags and selected branches carrying a similar number (100–150) of litchi fruits. The clapping sounds produced by the plastic flags blowing in the wind and their bright pink colour contrasted with the background green leaves (Musyoki 2014). We selected 37 focal fruit groups and randomized the samples observed during the study (Image 2). A fruit group consists of four to 10 panicles grouped in the same place, randomly chosen in a tree as a sample unit.

(b) Sonic method: bells

A bell 12cm in diameter at the open end was attached to the branch approximately 1m from the focal groups of litchis. We rang the bell by means of a string, with one end attached to the bell and the other pulled down by the observer (Image 3). When a flying fox was seen flying around the litchi fruit groups, we allowed the

bat to land and approach the fruits and then rang the bell up to six times (with a five second interval between consecutive rings) to disturb the bat attempting to feed on the litchi. We stopped ringing the bell if the bat did not take off after six bell rings. We used six bells, four in one tree and two in another and we changed their places three times. The bell was left in place on the branch for four consecutive nights. Bell ringing sessions were conducted after sunset from 18:00hr until 22:00hr.

(c) Biological control: Plantskydd®

Plantskydd® is a water-soluble powder which deters some mammals such as rabbits or deer from feeding on crops (Wagner et al. 2001). The active ingredient is foodgrade dried blood (porcine or bovine) with vegetable oil added by the manufacturers to act as a binder to the crop being protected. Plantskydd® works by emitting an odour that repels animals before they eat the plant. We tested the effectiveness of Plantskydd® to control



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Image 2. (a) Two coloured plastic flags and (b) the possible area covered when they were blown by the wind.

bat damage to litchis. The Plantskydd® adheres to the exocarp of the litchi and does not permeate it so does not affect the taste of the fruit.

A kilogram of Plantskydd® was added to 18.6 litres of water. We sprayed the resulting solution onto the target litchi fruit groups with a garden sprayer attached on a long wooden stick (Image 4a). A total of 46 fruit groups with one to two fruit groups per tree were treated (Image 4b). Each group contained 60 to 125 fruits and the Plantskydd® was applied when the fruits were at a green-red unripe status (around 15 days before they became ripe). If the solution is allowed to dry for six hours after the application it is considered by the manufacturers to be effective for to up to six months in summer even after heavy rainfall (http://www.plantskydd.com).

We used 53 fruit groups or samples as controls, with 21 at Site 1 and 32 at Site 2 where the deterrence methods were on trial.



Image 3. Bell used during the sound experiment

Damage to litchis

To quantify the level of damage to the fruit, we monitored the litchis early each day (from 06:00hr to 09:00hr), from when they were ripe until they were all collected by the farmers and no more were left on the sampled trees. Fruits that were considered damaged by animals (Image 5) were subdivided into four groups using the following criteria:

Bats: distinctive teeth marks, which were larger for *P. rufus* or *E. dupreanum* and smaller for *R. madagascariensis*. Bat teeth clearly showed unambiguous dual canine punctures (Andrianaivoarivelo et al. 2012), the distance between the puncture corresponding to the distance between the canine tips of each of the three species.

Birds: distinctive beak marks of *Acridothere tristis* or *Coracopsis* spp.

Other mammals: incisor marks of rats.

Humans: the exocarp was peeled by humans and left beneath the tree.

Faecal analyses

Faecal samples were collected using plastic sheeting (2 or 3m x1m) placed beneath the roost trees during the day (Stashko & Dinerstein 1988) (Image 6a). To prevent consumption or removal of pellets by terrestrial vertebrates, they were set 1m above the ground (Tang et al. 2007). We checked the roosts twice a week and collected the faecal samples which were then sun dried and stored in small paper envelopes for later identification of seeds. At our two sites, we obtained a total of 277 items (seeds, fibre, vegetable debris, and unidentifiable viscous items) in 126 faecal samples from *P. rufus* during the study, 54 from site 1 and 72 from site 2 (Image 6b).





Image 4. (a) Use of sprayer attached to a stick (December 2012) to cover the focus fruit groups with Plantskydd® and (b) fruits sprayed with Plantskydd® sold by a farmer in the local market at Site 1. The red exocarp is removed before the fruit is eaten.

Identification of seeds in faeces

We used three one kilometre transects for each site in the native forests in the vicinity of the *P. rufus* roost. Each site was visited twice and fruit samples were taken from identified trees along the transect and stored for later determination. The seeds from these collections were used as reference samples in the identification of those extracted from the faecal samples. Faecal samples were initially assessed visually and the seeds subsequently examined with a binocular microscope (magnification: 10 x 4).

Flight cage experiments

We also conducted experiments at Site 1 for six nights using Plantskydd® on fruit in a tent (2m x 2m x 1.5m) into which a single *R. madagascariensis* was introduced and could fly freely and choose between treated and untreated fruits. For each of six nights 46 litchi fruits were provided in the cage, 23 of which had been sprayed with Plantskydd® and 23 left untreated. Three bananas fruits without Plantskydd® were also left in the cage as alternative food. The bat was left alone in the tent throughout the night and released where it was captured two hours before sunrise, and the remaining fruits with and without Plantskydd® were counted and recorded. Fruits sprayed by Plantskydd® were distinctively coloured red-brown.

Statistics

The three studied covariates were, the control groups, the groups impregnated with Plantskydd® and those protected with plastic flags. Linear models

and ANOVA were used to investigate the effects of treatments.

RESULTS

The diet of Pteropus rufus

Faecal samples (n=277) collected from the two study sites were similar in composition so the results were pooled. They consisted of vegetable fibre (28.5%; n=66), seeds (22.0%; n=61) and consistent viscous components (19.5%: n=47). Many of the samples were green and had a pasty consistency (30.0%; n=54). The viscous matter appeared smoother and slightly transparent, but the pasty matter was compact and dense.

From these observations and the reference samples, six principal plant species were found to be eaten by *P. rufus* during the study period (Fig. 1). Two were introduced: *Litchi chinensis* (19.0%), which is commercially important and *Syzygium jambos* (5.0%). Three were fig species indigenous to the sites: *Ficus polita*, *F. pyrifolia*, and an unidentified *Ficus* sp., which made up 41.3% of the items in the faeces. Two plant species in the diet could not be identified.

Comparison of damage by fruit bats to litchis with different methods of deterrence: plastic flag and Plantskydd®

(1) Site 1

Bat damage to litchi fruits varied significantly according to the method of deterrence used (Table 1). The level of damage when fruit groups were protected



Image 5. Damage to litchis: a - Bird-damaged fruits; b - fruit damaged by the common myna *Acridothere tristis*; c - *Pteropus rufus* tooth marks; d - damaged by *Rattus* sp.: incisor marks are apparent; e - insect damage; f - naturally dried and split fruit





Image 6. a - Plastic sheeting used for collecting faeces of P. rufus; b - faecal sample of P. rufus with Ficus sp. seeds,

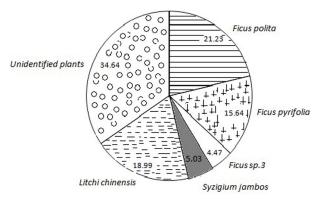


Figure 1. Proportion of the principal plant species presents in the *Pteropus rufus* faecal samples at Sites 1 and 2.

Table 1. Mean number of fruits damaged by fruit bats per fruit group throughout the study period at Site 1 with different methods of deterrence

Deterrent	Mean number of fruits damaged (%)	Standard deviation	N
Plantskydd®	0.63 (5.4%)	1.16	19
Plastic flags	3.94 (32.17%)	3.68	18
Control	5.24 (62.44%)	7.63	21

with Plantskydd® was significantly lower than when plastic flags were used, and damage to fruits in the control groups was highest (ANOVA, F=6.093, Df=2; p<0.05). When plastic flags were used, there was a positive relationship between the number of days from the beginning of the experiment and the number of litchi fruits eaten (Pearson's: r=0.48, t=3.25, Df=35, P=0.002) suggesting that the bats may become accustomed to the presence of the flags and ignored them after some time (Fig 2).

Flight cage experiments

Rousettus madagascariensis avoided feeding on litchi fruits sprayed with Plantskydd®. (Anova, F=10.537, Df=13, P<0.001). The total numbers of fruits remaining after the night's experiments were 89 (95%) with Plantskydd® and 2 (5%) without Plantskydd®. respectively.

(2) Site 2

The number of bat-damaged litchi fruits per fruit group varied significantly with the method of deterrence used (Anova, F=6.093, Df=2, P≤0.01). Damage was higher in control groups than in the groups in which plastic flags and Plantskydd® were used (control groups: mean number of damaged fruits per fruit group=11.3±19.1; n

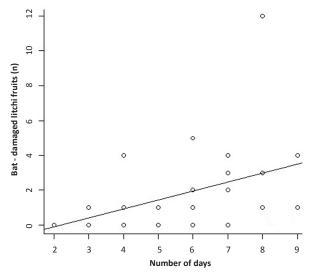


Figure 2. The relationship between the numbers of fruits protected by plastic flags which were damaged by bats and the number of days of data collection at Site1.

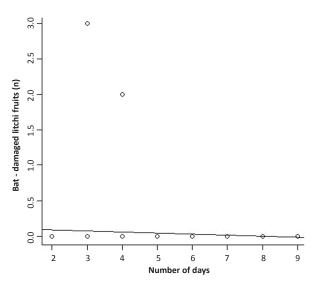


Figure 3. Correlation between the numbers of fruits damaged by the fruit bats which were protected with plastic flag and the number of the days of data collection at Site 2.

samples=32), (plastic flags: mean number of damaged fruits per fruit group=0.5±1.5; n samples=20) and (Plantskydd®: mean number of damaged fruits per fruit group=2.07±1.80 n samples=27) (Fig. 3a). However, in contrast to Site 1, there was no significant correlation between the number of data collection days and the number of litchi fruits damaged by bats in the vicinity of plastic flags (Pearson's: r=-0.1, P=0.22, Df=135) (Fig 3), meaning that regardless of the duration the flag was left with the litchi fruits, the fruit bats did not become accustomed to this deterrent and avoided feeding on

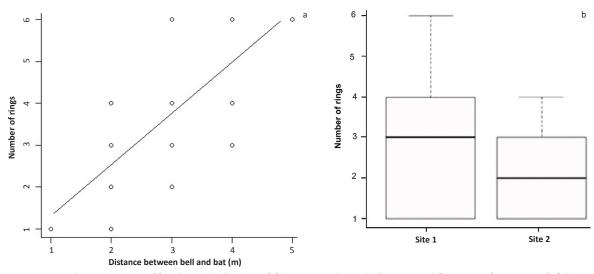


Figure 4. Disturbance response of fruit bats to bell ringing; (a) bats responding to bell ringing and flying away (*Pteropus rufus*) depending on its distance from the bell; (b) box plot showing the medians of the number of bell rings which were sufficient to make the bats fly away at the two sites.

the fruits.

Costs associated with the damage caused by fruit bats

The damage caused by bats to litchi fruits was assessed in plantations where no attempt had been made to deter bats. The maximum loss of litchi fruits to bats at Site 1 was 483 litchi fruits per day per tree. A single litchi fruit weighed from 12–18 g (average 16±4 g). The estimated average litchi productivity per tree was 4316±2101 fruits, range 1656–9425 fruits (n = 21). The fruits lost to bats amount to ca. 8kg per tree per night during the entire fruiting season. One kilogram costs approximately 700 Ariary for local purchasers, consequently the loss to the primary producer of litchi fruits due to fruit bats was around 5,600 Ariary or 2.00 USD per tree per night.

Predictions associated with fruit bat damage to litchis

At the beginning of our study, we predicted that two factors affected the bats' choice of litchi tree on which to feed—the productivity of the tree and its height. We assumed that the larger the number of fruits on a tree, the more the bats would be attracted to feed there. There was no significant correlation, however, between the number of fruits eaten by the bats and tree productivity (Pearson's: r=0.2, P=0.15, Df=180).

The second prediction was that *P. rufus* preferred to feed on higher trees. To investigate this, the litchi trees were categorized in three levels: low [5–8 m], medium [8–10] and high [10–14m]. There was no significant difference, however, in bat damage to fruit between these three height categories (ANOVA, Df=2, F=0.268

and P=0.76). These results suggest that neither the tree productivity nor the height of the fruits from the ground affected the bat feeding patterns.

Using bells to deter bats from feeding on fruit

During our bell ringing trials, we recorded 44 visits of *P. rufus* to our litchi target fruit groups over four consecutive nights. Two principal variables affected the effectiveness of the bell ringing method:

- (1) The distance between the bell and the branch on which *P. rufus* fed. This observation was made intensively at Site 1. There was a positive correlation (Spearman's correlation test r=0.85, N=23, P<0.001, df=21) between the number of bell strokes required to frighten the bats and the distance between the bell and the bats (Fig 4a). Consequently, the duration of bell ringing required to deter the bats increased proportionally with the distance between the bell and *P. rufus*.
- (2) The location of the site: bell ringing was more effective at Site 1 than at Site 2 (Anova, F=19.149, Df=1, N=238, P<0.001). The duration of ringing required to frighten the bats away from the target fruits averaged 17 ± 10 and 29 ± 26 seconds in Site 1 and Site 2 respectively (Fig. 4b).

There was no significant correlation between the number of bell rings required to deter the bats and the number of the days (n=4) over which the trial was conducted (Anova, Df=38, P=0.2). Thus, over the relatively short duration of this trial the bats did not become habituated to the noise of the bell. Bell ringing was effective as around 80% of the *P. rufus* individuals experiencing the ringing of the bells flew away.

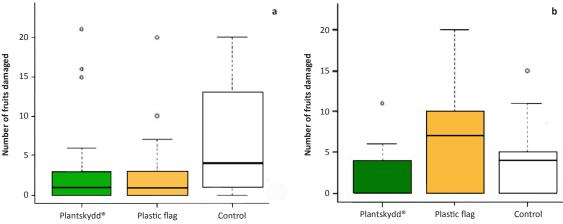


Figure 5. Box plots showing the medians of fruits damaged (a) by birds and (b) unknown animal feeders at Site 1.

Table 2. Mean number of fruits damaged per control fruit group by the three groups of feeders at the two study sites grouped together.

Species	Site 1	Site 2	Anova test	
Fruit bats	3.81±5.84	5.09±7.44	P=0.161	
Birds	4.67±6.34	14.12±12.31	P<0.001	
Unidentified mammals	4.21±4.87	3.24±4.86	P=0.25	

Other animal feeders

(1) Site 1: Regardless of the method of deterrence used, we found that birds fed on the studied fruit groups. Even though the average number of fruits damaged by birds in the control groups was high, there was no significant difference in the damage they caused (Anova, F=2.183, Df=2, P=0.132) between the three types of trials (fruit groups with plastic flag, with Plantskydd® and the control groups) (Fig 5 a). However, there was a significant variation in the damage to the fruit groups by unidentified feeders (especially mammals) between those three sample sets (Anova, Df=2, P=0.02). This was higher in the plastic flag experiments and control fruit groups than in fruit panicles impregnated with Plantskydd® (Fig. 5b).

(2) Site 2: The fruit groups where plastic flags were used were more heavily damaged by birds compared to those treated with Plantskydd® and the control fruit groups (Anova, df=2, P<0.05) (Fig. 6a). However, the unidentified animal feeders did not distinguish between the three samples of fruit groups (Anova, Df=2, P=0.79) (Fig. 6b).

Comparison between sites

Comparison of the numbers of fruit damaged in the control fruit groups revealed a significant difference between the two sites. It was higher at Site 2 (mean:

22.45 \pm 7.44, n=75), than at Site 1 (mean: 12.73 \pm 5.84, n=58) (Anova, Df=1, P<0.001) (Table 2).

No significant difference was apparent between the number of fruits damaged by bats or by other identified feeders between the two sites. In contrast, birds caused more damage at Site 2 than at Site 1. Consequently, the damage to litchi fruits could not only be attributed to bats but also to birds, with the latter causing high levels of fruit loss compared to bats at Site 2.

Assessing the natural damage to litchi productivity as a result of fallen fruits

Natural fruit fall (due to wind and/or rain) was assessed throughout the study period (as grounded fruit with no sign of animal damage) and was higher at Site 2 (n sampled trees=37) than at Site 1 (n sampled trees=57, ANOVA, Df=1, F=18.821, P<0.05). The total number of natural fruit falls (apart from animals' activity) per tree is summarized in Fig. 7.

Cost analysis of the different methods of deterring fruit

The costs and effectiveness of the three experimental deterrence methods are compared in Table 3.

Plantskydd® is effective for up to 16 weeks after treatment of the fruits and a single spray is sufficient to protect the fruits throughout the entire fruiting season. The litchi grower can procure this product in 1kg packages for 54.5 USD, equivalent to 137,340 Ariary, but it has to be imported from the US or Europe. The quantity required for one litchi tree is between 0.25–0.5 kg depending on the density of fruit on the tree and the price of Plantskydd® enough for one tree ranged from 27,000–34,000 Ariary or between 9.38 to 11.81 USD.

The capital cost for using bells is 108,000 Ariary

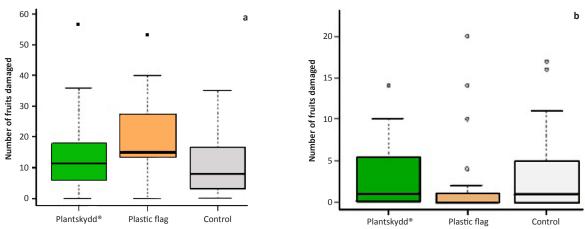


Figure 6. (a) box plots showing the medians of fruits damaged by birds; (b) unknown animal feeders at Site 2.

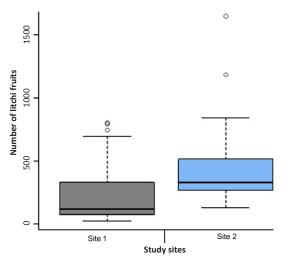


Figure 7. Box plot showing the total number of litchi fruits fallen and collected underneath the trees in the two study sites throughout the fruiting period.

per tree since a bell costs 27,000 Ariary. Farmers can store them after use and use them again in subsequent fruiting seasons and we assume they can be used for 20 years. The cost for using such a method per tree during a single fruit season is 1,664 Ariary or 0.57 USD.

Flags are made from plastic bags and are the cheapest method of deterrence (300 Ariary per flag without the installation cost). The flags tear after 21–28 days and have to be replaced. The flags need to be installed when the fruits start to ripen and attract mammals. The cost of six plastic bags was 1,800 Ariary or 0.63 USD for a single tree per fruit season.

The effective cost associated with each method was assessed from the data collected at Site 1 (Table 3). The average weight of litchi fruits was 16g, and the average litchi productivity was around 6316 fruits per tree, or

about 101kg. Consequently, the financial gain during a single litchi fruit season from using the three control methods was greatest using plastic flags, followed by bell ringing and lastly Plantskydd®

DISCUSSION

Flying fox diet

The results show that the Madagascar Flying Fox P. rufus feeds mainly on fruits and leaves with a diet similar to that of the two other Madagascar fruit bats: E. dupreanum and R. madagascariensis (Ratrimomanarivo 2003; Andrianaivoarivelo et al. 2012). Only three of the seven plant species collected along the transects were present in the faecal samples collected beneath the tree roosts and three species prevalent in the faecal samples were not observed on transects: two Ficus spp and F. pyrifolia. We therefore assume that our transect samples did not represent the complete range of bat food species available in our study area. Previous studies conducted at the two sites showed that apart from L. chinensis, the bats fed on other introduced and economically important plant species such as D. longan (Sapindaceae) which seemed to be one of the most important food resources of R. madagascariensis at Site 2 (Andrianaivoarivelo et al. 2007) as well as banana fruit (Musaceae) which were also eaten by this species in the south-east of the island (Goodman 1999). Pteropus rufus actively consumed the pollen and nectar of Agava sisalana (Agavaceae), three species of Ficus and other introduced species not economically important (Bollen & van Elsacker 2002; Raheriarisena 2005; Long & Racey 2007; Picot et al. 2007). Those findings coupled with ours suggested that the Moraceae (particularly Ficus) and the

Table 3. The effectiveness and the cost associated with the use of each of the three methods of deterrence. 1000 Ariary = 0.31 USD (March

Deterring methods	Durability: W: week Y: year	Unit price (Ariary)	Quantity/ tree	Cost/tree/ beneath season (Ariary)	Revenue: Fruit cost minus deterrent cost (Ariary)	Ratio: Revenue/ control method	Effectiveness	Time spent
Plantskydd®	16w	40,000Ar/kg	0.3–0.5 kg	10,000 -20,000	20,317–20,422	33–50 %	***	*
Bell ringing	20y	27,000Ar/Unit	4	5,400	24,917–35,022	13–18 %	*	***
Plastic flag	4w	300Ar	6	1,800	28,517–38,622	5-6 %	**	*

Sapindaceae are key food resources for Madagascar's three endemic fruit bat species.

The shift in bat feeding to introduced plant species such as litchi could be a response to habitat change. The damage to litchi fruits is assumed to be affected by their proximity to the bat roost and to the reduced availability of native fruits. Two reasons are presented to explain such findings.

Firstly, fruit bat foraging activity is influenced by food availability. Habitat destruction has resulted in the loss of native species which constituted the principal food of the bats and forced them to feed in the agricultural matrix. Rahaingodrahety et al. (2008) working also at Site 2 found that the population size of P. rufus was about 400 individuals, contrasting with our count in 2012-2013, when it had more than doubled, resulting in an increased demand for food. If native plants at the site are insufficient to meet that demand then the bats will feed on introduced plants regardless of their economic importance.

Secondly, results from other studies demonstrated that the flying foxes choose the most nutritious food. Andrianaivoarivelo et al. (2012) found that commercially important plant species were characterized by high levels of carbohydrates such as fructose compared to other forest or commercially unimportant fruit categories. The results from their feeding experiment on R. madagascariensis, however, showed that this species preferred to feed on economically unimportant forest plants which are richer in protein and lipid and this could also be the reason for the high proportion of Ficus sp. seeds we found in the P. rufus faecal samples collected during this study. For these reasons, the conservation of remaining forest and plantations of commercially unimportant plant species are recommended for mitigating the conflicts between fruit bats and litchi farmers.

Visual and biological bat deterrents

We found that the levels of success resulting from the use of the different means of deterrence we tested to reduce fruit bat damage were significantly different.

All three methods of deterrence investigated (visual and biological) are effective and could help the farmers to reduce fruit loss to fruit bats. Plantskydd® was the most effective especially at Site 1. The fact that the product was less effective at Site 2 was likely due to the higher rainfall there. The frequent and unpredictable rain appears to have washed the Plantskydd® from some of our target fruit groups and reduced its effectiveness especially when it was applied less than six hours before the rain. At Site 2, rain fell unpredictably, any time of the day and sometimes soon after we had sprayed the fruits with Plantskydd®, so we had to repeat the spraying.

Plastic flags were less effective at both sites than Plantskydd® but was the most commonly used method at Site 1, although after they have been used for several days, the bats become habituated to them. Also, P. rufus has well developed vision for some colours (Müller et al. 2007) and the plastic flags may act as a guide directing them to the litchi plantation and fruits. The data collected at Site 2 however demonstrated that the number of litchi fruits eaten by the fruit bats decreased when plastic flags were used. Here no deterrent had previously been used by the farmers apart from killing the fruit bats with sticks or shooting them (Andrianaivoarivelo et al. 2007) and hunting at the roost. At Site 2, plastic flags were almost as effective as Plantskydd®. The latter was much more effective at Site 1.

Bell ringing

Each of our bell ringing experiments lasted for four days but we found no evidence of bats habituating to the bell strokes and feeding on fruits near the bell and there was no significant correlation between the duration of the experiment and the duration of bell ringing. Bell ringing disturbed the bats and made them fly away from the fruits. The extent to which bells remain effective beyond four days should be investigated. Their effectiveness depended on the distance between the bell and the feeding bats and perhaps by the level of bat hunger or starvation.

In Australia, sound was initially effective but not recommended for long term use because flying foxes became habituated (Bicknell 2002). For this reason, we expect that after four or more days of rings, the number of rings needed to frighten away the flying foxes would increase and *P. rufus* would become accustomed to the sounds and continue feeding on the litchi fruits.

Overall, the fruit protection methods employed by the litchis growers were not reliably effective except for the biological method we tested—Plantskydd®. The majority of the households in a village in Kenya used a combination of two or more protection methods simultaneously such as guarding, scarecrows, beating on objects to make noises and also by harvesting immature crops (Musyoki 2014). None of the methods alone were 100% effective so the combined effect of such methods helped to increase their success for better controlling fruit loss due to the bats.

We also found that the level of success of each method varied between the sites. Several factors may interplay to explain this such as the climate, food availability and size of the bat population. The effectiveness of Plantskydd® at Site 2 was limited by the rain that washed the product off the fruit.

Other fruit pests

Fruit bats were not the only animal group feeding on litchi plantations. A large proportion of the damage to litchis was attributed to omnivorous and granivorous birds such as *Coracopsis* spp and the introduced *Acridotheres tristis* which were seen eating the litchis. We observed at Site 2 that *C. vaza*, *C. nigra* and *A. tristis* destroyed fruit which they ate only partially before they began to peel and tear apart another fruit. Such devastating bird activity was more prevalent at Site 2 than at Site 1. The birds fed on fruits treated with Plantskydd® so they were not deterred by its odour and taste.

According to Marsh et al. (1992), the effectiveness of plastic flags in deterring birds from feeding in litchi orchards is enhanced by loud distress sounds. Using only one method could ensure fruit protection but only for a limited time because the birds rapidly become habituated to the flags (Marsh et al. 1992). Birds feed actively on litchi fruits even though plastic flags are installed in the trees.

We also observed that fruits were missing as a result of the activity of unidentified feeders. This could partially be due to *R. madagascariensis*. During our nocturnal observation (data not collected), *R. madagascariensis*

individuals were occasionally observed eating the fruits but their feeding behavior was quite different to *P. rufus*. They hovered above the fruit panicle then quickly removed one fruit with their mouth and carried it away. Such behaviour was probably adapted to reduce the risk of predation or to minimize competition with other animals feeding on the same fruit panicle. No lemurs were seen during our investigation, and this may be due to the long distance separating the litchi trees and known lemur habitats.

Fruit predation by bats elsewhere

In Mauritius, litchis are grown in two situations, orchards and backyards. New orchards are pruned low and panicles are netted or nets thrown over the whole trees to protect the fruits from bats and birds. Backyard trees are too tall for netting and besides, the fruit of the tree is often sold each season to a merchant who owns it until it is picked and has little incentive to buy nets. In Thailand and Queensland Australia, the only method of crop protection that is really effective in preventing birds and mammals feeding on orchards is the use of physical barriers, such as full netting (Rigden et al. 2000; Aziz et al. 2016). This method is difficult to install in litchi plantations in Madagascar as it is costly and the litchis trees are not grouped to form an orchard and are not pruned, so that they reach heights of up to 20m. In conclusion, the use of aversive taste deterrents is the most effective method of reducing fruit loss to bats. In Madagascar, however, litchi farmers struggle with two main factors: they have no access to Plantskydd® and their choice of deterrent will be largely dictated by cost. Nevertheless, Plantskydd® should be tested in other countries and on other species of commercial fruit where full netting is impractical or unaffordable.

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French Abstract: Résumé: La fiabilité des méthodes utilisées pour minimiser la prédation des fruits économiques par les chauves-souris frugivores a été testée dans le Centre-est et Sud-est de Madagascar en 2012- 2013 pendant la période de moisson des lychees. Deux des trois méthodes utilisées, à savoir l'utilisation des drapeaux faits de sachets plastiques et celle utilisant les sons de cloches accrochées sur les arbres, sont dérivées des méthodes utilisées auparavant par les cultivateurs de lychees de la partie Sud-est de l'ile. Nous avons amélioré et standardisé ces méthodes et comparé leur efficacité par rapport à un produit biologique de synthèse composé principalement de sang séché et de l'huile végétale (Plantskydd®). Le Plantskydd® a le gout et l'odeur désagréable aux mammifères folivores et/ou frugivores. Il est susceptible de faire éloigner les mammifères nuisibles. Les fruits endommagés par les chauves-souris varient entre 440 g et 7040 g pour un pied de lychee et deux des trois méthodes s'avèrent efficaces pour réduire les pertes de fruits causées par les Renards volants : il s'agit des drapeaux fait de sachets plastiques et de l'agent biologique. Des variations significatives ont été observées sur le niveau de dommages selon les sites d'études et les méthodes de dissuasion. Pourtant, les méthodes utilisant les feuilles en plastique et les sons de cloches sont moins efficaces par rapport à la méthode olfactive. Cette derniere étant la plus efficace si le produit est pulvérisé et laissée un moment suffisamment long afin de permettre à celui-ci de s'assécher et d'adhérer complètement aux fruits. Son efficacité est également démontrée par l'expérience réalisée dans une volière, pendant laquelle, des individus de Rousettus madagascariensis évitent de manger les lychees imprégnés de Plantskydd®. L'analyse des contenus fécales des Renards volants ne révèle aucune préférence alimentaire pourtant les échantillons collectés contiennent largement des grains de Ficus, ce qui suggère qu'ils se nourrissent plus des fruits de Ficus que des autres fruits à valeur économique importante. Outre la maturité des fruits, l'abondance de fruits portés par pied et les autres facteurs phrénologiques ne semblent être des facteurs susceptibles d'affecter le nombre de fruits endommagés par les chauves souris. Les Oiseaux sont parmi les auteurs de dommages des fruits et affligent même plus de dégâts que les chauves souris frugivores.

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