Nectarivory by Endemic Malagasy Fruit Bats During the Dry Season[1]

Daudet Andriafidison[2,3], **Radosoa A. Andrianaivoarivelo**[2,3], **Olga R. Ramilijaona**[2], **Marlène R. Razanahoera**[2], **James MacKinnon**[4,5], **Richard K. B. Jenkins**[3,4,6], and **Paul A. Racey**[4]

[2]Department of Animal Biology, Faculty of Sciences, University of Antananarivo, Antananarivo (101), Madagascar

[3]Madagasikara Voakajy, B.P. 5181, Antananarivo (101), Madagascar

[4]School of Biological Sciences, University of Aberdeen, Aberdeen AB24 2TZ, UK

[5]Wildlife Conservation Society, B.P. 8500, Antananarivo (101), Madagascar

ABSTRACT

Madagascar has a distinctive fruit bat community consisting of *Pteropus rufus*, *Eidolon dupreanum*, and *Rousettus madagascariensis*. In this study, we observed fruit bat visits to flowering baobabs (*Adansonia suarezensis* and *Adansonia grandidieri*) and kapok trees (*Ceiba pentandra*) during the austral winter. *Eidolon dupreanum* was recorded feeding on the nectar of baobabs and kapok, *P. rufus* was observed feeding on kapok only and no *R. madagascariensis* were seen. Three mammals species, two small lemurs (*Phaner furcifer* and *Mirza coquereli*) and *E. dupreanum*, made nondestructive visits to flowering *A. grandidieri* and are therefore all potential pollinators of this endangered baobab. This is the first evidence to show that *A. grandidieri* is bat-pollinated and further demonstrates the close link between fruit bats and some of Madagascar's endemic plants. *Eidolon dupreanum* was the only mammal species recorded visiting *A. suarezensis* and visits peaked at the reported times of maximum nectar concentration. *Pteropus rufus* visited kapok mostly before midnight when most nectar was available, but *E. dupreanum* visited later in the night. These differences in timing of foraging on kapok can be explained either by differing distances from the roost sites of each species or by resource partitioning. We advocate increased levels of protection, education awareness, and applied research on both mammal-pollinated baobab species and fruit bats, and suggest that both baobabs and bats are candidate "flagship species" for the threatened dry forests of Madagascar.

RESUME

Madagascar a une remarquable communauté de chauves-souris frugivores comprenant *Pteropus rufus, Eidolon dupreanum* et *Rousettus madagascariensis*. Dans le cadre de la présente étude, nous avons observé les visites que les chauves-souris effectuent sur les baobabs (*Adansonia suarezensis* et *Adansonia grandidieri*) et les kapokiers (*Ceiba pentandra*) en floraison durant l'hiver austral. *Eidolon dupreanum* a été observé se nourrissant du nectar des baobabs et des kapokiers, *Pteropus rufus* a été observé en train de se nourrir des kapokiers uniquement, et aucun *Rousettus madagascariensis* n'a pu être recensé. Trois espèces de mammifères, deux lémuriens *(Phaner furcifer, Mirza coquereli)* et *Eidolon dupreanum,* effectuant des visites non destructives des fleurs d' *A. grandidieri* et sont, de ce fait, des pollinisateurs potentiels de cette espèce de baobab en danger. Il s'agit de la première preuve qu' *A. grandidieri* est pollinisé par les chauves-souris. Cette observation démontre aussi le lien étroit qui existe entre les chauves-souris frugivores et quelques-unes des plantes endémiques de Madagascar. *Eidolon dupreanum* est la seule espèce observée sur *Adansonia suarezensis* et les visites sont plus fréquentes aux heures de concentration maximale de nectar. *Pteropus rufus* visite les kapokiers, surtout avant minuit, lorsque les nectars sont encore disponibles. En revanche, la visite effectuée par *Eidolon dupreanum* a lieu plus tard dans la nuit. Cette différence d'heures de fourrage sur les kapokiers pourrait être justifiée par l'inégalité de la distance des gîtes de chaque espèce ou par le partage des ressources. Aussi recommandons-nous le renforcement des mesures de protection, des activités d'IEC et de la recherche appliquée aux espèces de baobab pollinisées par des mammifères et les chauves-souris frugivores. Nous suggérons l'intégration des baobabs et des chauves-souris dans la liste des espèces *"flagship"* pour les forêts caducifoliées en danger à Madagascar.

Key words: Adansonia; baobabs; *Ceiba; Eidolon;* Madagascar; lemurs; nectar; *Pteropus;* resource use.

OLD WORLD MEGACHIROPTERA PLAY AN IMPORTANT ROLE IN TROPICAL ECOSYSTEMS by transferring pollen (*e.g.*, Law & Lean 1999, Singaravelan & Marimuthu 2004), dispersing seeds (*e.g.*, Rainey *et al.* 1995, Shilton *et al.* 1999), and facilitating germination (*e.g.*, Entwistle & Corp 1997a). For some isolated oceanic islands, this has led to the concept of "keystone species" being applied to Megachiroptera (Cox *et al.* 1991). The fruit bats of the western Indian Ocean have received conservation attention in recent years but few studies have been conducted in Madagascar, with most effort concentrated on the smaller islands of Pemba, Rodrigues, and the Comoros (*e.g.*, Entwistle & Corp 1997ab; Granek 2002; Powell & Wehnelt 2003; Sewall *et al.* 2003).

Madagascar's distinctive megachiropteran assemblage consists of the three endemic species *Pteropus rufus* (Madagascar flying fox), *Eidolon dupreanum* (Madagascar straw-colored fruit bat), and *Rousettus madagascariensis* (Madagascar Rousette) and thus has genera of both African and Asian origin (Eger & Mitchell 2003). The continuing fragmentation of Madagascar's remaining forests reduces the opportunity for forest-dependent primate and bird species to contribute to seed and pollen distribution between fragments. Fruit bats that use a mosaic of habitats, including natural forest fragments, over wide areas, represent the most viable extant agents for facilitating interfragment genetic exchange for many plants in Madagascar (Conservation Breeding Specialist Group 2002).

Analysis of *P. rufus* feces from Madagascar has revealed a highly variable diet, including a wide range of endemic plants but also some exotic species (Bollen & van Elsacker 2002, Long 2002). In a

survey of plants consumed by pteropodids in Madagascar, Hutcheon (2003) noted that only 4 of 18 species (22%) were used for flower-related resources, with most foraging associated with fruits. However, studies that use only macroscopic fecal analysis may underestimate the contribution made by nectar and pollen to the feeding ecology of fruit bats. For example, from a sample of *ca* 118 taxa identified in the diet of *P. rufus* and *E. dupreanum* across Madagascar, 64 and 48 percent, respectively, of the plant taxa were identified solely from pollen grains in the feces (J. MacKinnon, pers. obs.). Since nectar or pollen may therefore play a more important role in the nutrition of fruit bats in Madagascar than previously documented and some trees possess the distinct floral characteristics (*e.g.*, large, white, and musky smelling flowers that open at night) considered to be attractive to nocturnal mammals (Baum 1995, Hutcheon 2003), close links may exist between endemic bats and certain plants in Madagascar.

In a comprehensive review of the floral biology and pollination of the genus *Adansonia,* Baum (1995) related flower structure, phenology, and nectar production to pollination biology. The five baobab species in the Longitubae section (four Malagasy and one Australian) are all pollinated by nocturnal hawk moths, whereas the two Malagasy species that constitute the Brevitubae section (*Adansonia suarezensis* and *Adansonia grandidieri*) are pollinated by mammals. Baum (1995) suggested that fruit bats are the major pollinators of *A. suarezensis* whereas nocturnal lemurs may have the same function for *A. grandidieri* and he advocated more research on the relative contribution made by lemurs and fruit bats to pollination of Brevitubae baobabs. As poor recruitment is one of the major threats, along with deforestation, to the long-term survival of many *A. suarezensis* and *A. grandidieri* populations further studies on their reproductive biology are required.

The nectar of Brevitubae baobabs (*A. suarezensis* and *A. grandidieri*) and kapok (*Ceiba pentandra*) is likely to be an important food source for bats in Madagascar because both trees flower during the dry season when fruits are scarce. Knowledge on the temporal patterns of resource use by Old World fruit bats in general is limited, but recent work on foraging patterns of Megachiroptera in India showed that peak bat activity is related to periods of maximum nectar production and sugar concentration (Elangovan *et al.* 2000, Singaravelan & Marimuthu 2004). The pollination biology of baobabs and kapok in Madagascar is incompletely known (Baum 2003), as is the foraging ecology of pteropodids (Hutcheon 2003). In this article, we describe the temporal patterns in nectarivory by two endemic fruit bat species and assess the conservation implications of the baobab–bat relationship.

METHODS

STUDY SITE.—Our observations on *A. grandidieri* and *C. pentandra* were made in the Menabe region of western Madagascar approximately 100 km north of Morandava. Baobabs were observed at Marofandilia Forest (20°00′S, 44°30′E) and kapok trees near the village of Beroboka (19°76′S, 44°33′E–19°95′S, 44°36′E). *Adansonia suarezensis* has a very limited distribution and is known from only

a few localities in the north of Madagascar near Diego Suarez and we made our observations at Beantely Forest (12°10′S, 49°20′E), the same site visited by Baum (1995).

BAT OBSERVATIONS.—The study was carried out during the Malagasy dry season (June–July 2000) when baobab and kapok trees are in flower and nectar production is high (Baker & Harris 1959, Baum 1995). Observations of foraging bats were made at individual trees preselected during the day. During the course of each night, two observers moved slowly around the baobab trees, at a distance of approximately 20 m, to ensure all visible surfaces were sampled. Observers usually remained stationary during watches at kapok trees because the bats were prone to disturbance. A single tree was usually observed each night, from dusk (1800 h) to dawn (0600 h), although half-nights of observation (1800–0000 h or 0000–0600 h) were also sometimes used. The activity of bats and lemurs was noted by scanning the visible area of the tree with binoculars, flashlights, and an infrared imager (Omega Nightvision Systems). The two fruit bat species were distinguished in the field based on color and size differences. *Pteropus rufus* is a large (wingspan 100–125 cm, weight 500–750 g) species with distinctive dark orange fur around the head (MacKinnon *et al.* 2003). *Eidolon dupreanum* is a smaller bat (wingspan 75–95 cm, weight 250–340 g) with straw-colored fur around the neck and a longer tail than *P. rufus* (MacKinnon *et al.* 2003). The activity of bats and lemurs was measured as the total number of visits to each tree per hour. In using this approach, we estimated the overall activity rather than abundance. A random selection of focal animals was observed each hour, and the duration of each visit was recorded with a stopwatch (per flower for baobabs and per inflorescence for kapok). Counting bat visits to individual *C. pentandra* flowers was difficult because the flowers were small and grouped together, and we therefore timed visits to individual flowers for baobabs and each inflorescence for kapok. Estimates of activity were therefore number of tree visits per hour and the duration of each foraging bouts.

Bats visiting *C. pentandra* were observed on 7 nights between 2 and 30 July 2000 for a total of 77 h. For the two baobab species, 4 nights of observation were made on *A. suarezensis* (28 June to 1 July 2000) for a total of 48 h whereas *A. grandidieri* trees were observed on 7 nights for a total of 84 h (15–24 July 2000).

NECTAR MEASUREMENTS.—Three *C. pentandra* flowers were selected at random every hour from three trees and nectar was aspirated into micropipettes (5, 10, or 50 μl) until there was no more nectar available to measure the standing crop. It was not possible to measure the nectar production of baobab flowers because we were unable to safely and routinely access the high canopy (*ca* 20 m) and therefore we refer to Baum's (1995) published values.

STATISTICAL TESTS.—Differences in temporal patterns in flower and tree visitations were examined using repeated measures analysis of variance (ANOVA) (hour as the repeated measure) and Spearman rank correlation was used to investigate linear relationships between nectar and bat activity. Values are presented as mean ± SE.

RESULTS

FRUIT BATS, LEMURS, AND BAOBABS.—Although present in both the study areas, no *P. rufus* were observed on either species of baobab. Five Madagascar flying fox *P. rufus* roosts were found (mean distance from roost to study site = 19.6 km, range = 2–36 km) containing between 350 and 730 bats. At Marofandilia, the straw-colored fruit bat *E. dupreanum*, the fork-marked lemur *Phaner furcifer* and Coquerel's dwarf lemur *Mirza coquereli* were recorded feeding on four of the nine *A. grandidieri* trees. During foraging, the bats enveloped the flower with their wings, inserted their muzzle into the corolla, and licked nectar from the base of the calyx. A preference was noted for white, new flowers and the bats tended to ignore the older, browner flowers. Pollen transfer from the flower to the bat was assumed to occur because most foraging bouts involved contact between the bat and the flowers' reproductive parts.

A temporal peak in activity was evident and 61 percent of the flower visits were between 2100 and 2200 h with the earliest observation 2105 h and the latest 0025 h. Lemur visits were nondestructive. *Mirza coquereli* was recorded on seven occasions but was not observed making contact with the reproductive parts of the flower. *Phaner furcifer* made contact with reproductive parts on two of the six occasions observed.

No nocturnal lemurs were observed at Beantely Forest but 427 visits by *E. dupreanum* to *A. suarezensis* flowers were observed, although the timing of the visits varied significantly throughout the night (repeated measures ANOVA, $F_{1,2} = 19.78$, $P = 0.047$) with peak activity from 2000 to 2300 h (Fig. 1). The mean duration of fruit bat visits to each flower also varied significantly (repeated measures ANOVA, $F_{1,2} = 14.19$, $P < 0.05$) with the longest visits between 1900 and 2300 h (Fig. 1).

FRUIT BATS AND *C. PENTANDRA*.—*Eidolon dupreanum* and *P. rufus* were regular nocturnal visitors to *C. pentandra*. We assume that both species contributed to pollination because they made contact with the flowers' reproductive organs without significantly damaging the
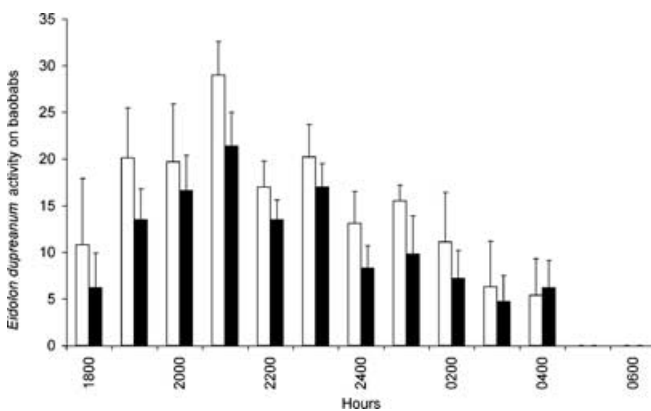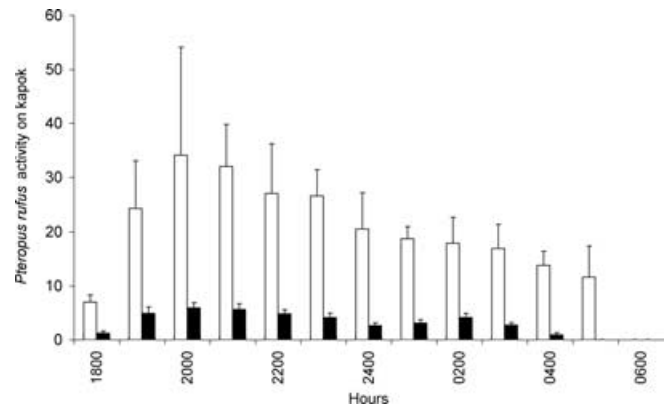

FIGURE 2. Activity of *Pteropus rufus* on kapok trees *Ceiba pentandra*: mean number of tree visits per hour + 1 SE (white) and mean duration of flower visits (sec) + 1 SE (black).

floral components. Mean activity of *P. rufus* was significantly higher than *E. dupreanum* (*P. rufus*, mean = 41.1 ± 7.2 visits per hour; *E. dupreanum*, mean = 7.9 ± 1.6, ANOVA $F_{1,24} = 20.00$, $P < 0.01$). The activity of *P. rufus* varied significantly throughout the night (repeated measures ANOVA, $F_{1,14} = 39.8$, $P < 0.01$) with peak activity from 1900 to 2100 h (Fig. 2). The mean duration of visits to each inflorescence also varied significantly (repeated measures ANOVA, $F_{1,4} = 532.6$, $P < 0.01$) with the longest visits between 2000 and 2300 h (Fig. 2). A significant difference in the timing of *E. dupreanum* activity was also found (repeated measures ANOVA, $F_{1,14} = 31.9$, $P < 0.01$), with peak activity after 2400 h (Fig. 3).

Correlation analyses revealed no significant linear relationship between the activity (Spearman rank correlation $r_s = 0.44$, $P > 0.05$) or duration of visits (Spearman rank correlation $r_s = 0.42$, $P > 0.05$) of *P. rufus* and nectar standing crop on kapok. Nectar secretion in the first half of the night was on average double that of the second half (Fig. 4). The volume of nectar increased sharply from dusk until 2300 h and then leveled off around 0600 h. Although *P. rufus* was recorded feeding throughout the night, activity was highest

FIGURE 1. Activity of *Eidolon dupreanum* on the baobab *Adansonia suarezensis*: mean number of tree visits per hour +1 SE (white) and mean duration (sec) of flower visits + 1 SE (black).
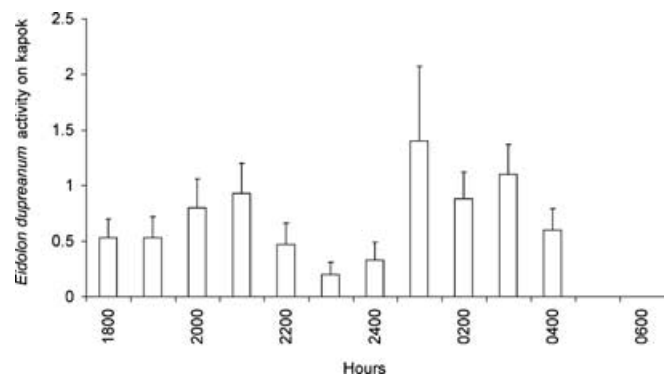

FIGURE 3. *Eidolon dupreanum* activity on kapok trees *Ceiba pentandra*: mean number of flower visits + 1 SE.
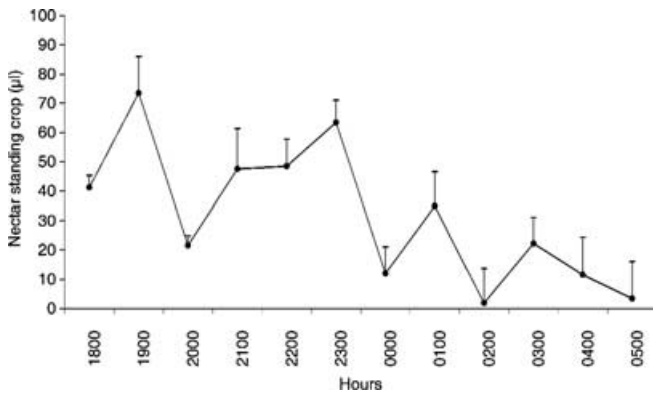
FIGURE 4.   Mean hour + 1 SE nectar standing crop (μl) from three *Ceiba pentandra* trees in the west of Madagascar.

before 0000 h and the bats may therefore be responding to the greater nectar production in the early night. *Eidolon dupreanum* peak foraging time was after that of *P. rufus* and generally commenced at 0100 h. There was no relationship between the activities of each species (Spearman rank correlation $r_s = 0.09$, $P > 0.05$) on *C. pentandra*, but *E. dupreanum* was most active on the study trees during the period following peak *P. rufus* activity (Figs. 2 and 3). When present on the same tree, *P. rufus* was most often observed feeding in the upper parts (crown 49% of observations, upper/mid branches 48%, and lower branches, 3%) and *E. dupreanum* was most frequently observed in the lower branches.

DISCUSSION

FRUIT BAT COMMUNITY.—We recorded two of three Madagascar's endemic fruit bat species during the study and although *R. madagascariensis* has been observed feeding on *C. pentandra* elsewhere in Madagascar (R.K.B. Jenkins, pers. obs.) and *Rousettus aegyptiacus* visits *Adansonia digitata* baobabs in Africa (Baum 1995), we did not record it during our study. *Rousettus leschenaulti* is an infrequent visitor to *C. pentandra* in India (Singaravelan & Marimuthu 2004) and it is likely that the proximity of favored day roosts (caves) to feeding sites influences the exploitation of nectar resources by *Rousettus* species. The distribution and abundance of *R. madagascariensis* is probably limited by the availability of suitable cave roosts (MacKinnon *et al.* 2003). Its absence from our study site where no caves are known and its high abundance 150 km to the north in Tsingy de Bemaraha National Park is further evidence that roost sites are probably a limited resource for this species.

Despite being common and abundant near both of the baobab study sites, we did not observe *P. rufus* feeding on either *A. suarezensis* or *A. grandidieri*. Baker and Harris (1959) reported that even when *C. pentandra* and *A. digitata* occurred in the same area *Eidolon helvum* ignored the baobabs in favor of the kapok. A similar explanation may be invoked to explain the absence of *P. rufus* feeding on baobab in Marofandilia. Although *P. rufus* is common in the Menabe area further survey work is required to establish the prox-

imity of bat roosts sites to baobabs. Citing Mickleburgh *et al.* (1992) as the source, Trewhella *et al.* (2001) report that *Pteropus seychellensis comorensis* feeds on *A. digitata* and *Adansonia madagascariensis* on the Comoros Islands. However, Mickleburgh *et al.* (1992) report a personal communication with J. F. Dahl that the bats probably feed on the baobab *A. madagascariensis* thus leaving some doubt as to whether *Pteropus* actually feed on the nectar of baobabs. Entwistle and Corp (1997a) used interviews with school students and villagers to supplement their dietary information on the Pemba Flying Fox *Pteropus voeltzkowi* and the baobab *A. digitata* was mentioned as a food plant. *Pteropus rufus* is a heavy bat (MacKinnon *et al.* 2003) and it may not be able to perch and climb on the thin outer branches of the baobabs in our study. Also possible is that the potential nectar reward on a given night on a baobab is less than what is available on kapok trees and the large-bodied *P. rufus* actively select the nectar producing trees that yield the most food resources per tree visit. There are also olfactory differences between baobab and kapok flowers (*e.g.*, Pettersson *et al.* 2004) and a follow-up study to incorporate a wider geographical area, sites with baobabs but few kapok and a longer duration would allow a better understanding of food selection by fruit bats in the west of Madagascar.

TEMPORAL PATTERNS IN FORAGING.—Most fruit bat visits to baobabs occurred during the first part of the night from 1900 to 2300 h. Baum (1995) reported that *A. grandidieri* nectar production started at anthesis and continued throughout the night at a constant rate until about dawn, but nectar concentration declined sharply after 2200 h. The timing of visits of *E. dupreanum* to baobabs in our study can therefore be interpreted as coinciding with the period of highest nectar concentration. This was not the case for *C. pentandra* where *E. dupreanum* peak foraging times were after the peak hours of nectar production.

In Brazil, Gribel *et al.* (1999) reported that *C. pentandra* flower orientation and bat behavior caused a rapid decline in the available nectar from 1900 h onward. In India, Singaravelan and Marimuthu (2004) also reported a sharp decline in nectar secretion and sugar concentration in *C. pentandra* throughout the night. In both of these studies, the highest bat visitation rates coincided with the period of maximum nectar production and sugar concentration. *Pteropus rufus* visitation rates in our study of *C. pentandra* were also highest during the first part of the night, suggesting that the bats are maximizing their nectar intake. *Eidolon dupreanum* visits peaked later, between 0100 and 0300 h. Possible explanations for this result include resource partitioning to avoid interspecific competition or roost site selection (distance between roosts and food source).

Spatial and temporal resource partitioning by pteropodids on *C. pentandra* nectar has already been reported by Singaravelan and Marimuthu (2004) in India. The species composition of Madagascar's pteropodids is distinctive and there are no data available on *Eidolon* and *Pteropus* foraging together. Our data provide evidence that resource partitioning occurs between pteropodids because *P. rufus* usually feeds before *E. dupreanum* and, when both species are present together, at greater heights in the tree. If kapok nectar is more rewarding than baobab nectar and the larger *P. rufus* has a competitive advantage over *E. dupreanum*, we would expect the

latter species to avoid either the time or the space occupied by *P. rufus.*

Roost site availability and proximity to suitable feeding areas may have important consequences for temporal patterns in foraging. The two Malagasy species in our study have distinct roosting requirements; *P. rufus* forms large colonies usually in natural forests with large trees and *E. dupreanum* aggregates in fissures and cliff over-hangs (MacKinnon *et al.* 2003). Thus the energetic requirements of travel to and from the roost may influence the foraging patterns by imposing limits on the location of the feeding site and duration of foraging bouts.

Baker and Harris (1959) reported *E. helvum* commence feeding in large numbers on kapok immediately after dusk. However, *E. helvum* frequently roosts in trees and in Baker and Harris' (1959) study the bats roosted very close to the flowering kapok trees, allowing early arrival and minimal energy travel demands. *Eidolon dupreanum* in our study may have arrived later than *P. rufus* because they had further to travel. Equally, we do not know the relative importance or spatial distribution of other food sources during the study; pteropodids also eat fruit, leaves, and pollen (*e.g.*, Law 1992) and it is likely that other food sources were simultaneously available within the normal flight range of the bats.

Trewhella *et al.* (2001) reported interference competition between *Pteropus livingstonii* and *P. s. comorensis* on the Comoros Islands with the larger *P. livingstonii* winning most encounters and differences in morphology, flight behavior, diet, reproductive activity, and roosting ecology between the two species were thought to facilitate coexistence. Given the differences in morphology and roosting ecology between *P. rufus* and *E. dupreanum*, a longer duration study would provide useful information on the extent to which there is overlap in the fruit component of the diet in the months when kapok nectar is unavailable.

POLLINATION OF BAOBABS.—Although local people reported that fruit bats use *A. grandidieri* baobabs, Baum (1995) was unable to verify this during his 2-wk study (Baum 2003). We observed *E. dupreanum* and *P. furcifer* feeding on the nectar of *A. grandidieri* and therefore demonstrate that both lemurs and bats are involved in the pollination of this species. Baum (1995) proposed that bats were the only pollinators of *A. suarezensis*, but both his study and ours were short and although we recorded no lemur visits to this baobab species, lemur pollination of *A. suarezensis* cannot be ruled out in other forests. Indeed, the pale color, strong scent, and sugar-rich nectar secretions of the accessible, nocturnal flowers of *A. grandidieri* and *A. suarezensis* suggest that they are both suited to pollination by bats and lemurs. Furthermore, as other external factors may determine the presence of mammal pollinators at a given forest or tree (*i.e.*, hunting by people, habitat fragmentation, and distance to roost site), it is possible that the relative contribution made by lemurs and bats will vary over a small spatial scale. As nectarivorous and frugivorous bats are subject to various forms of disturbance and can be sensitive to habitat degradation (*e.g.*, Quesada *et al.* 2003), more details on the effect of habitat change and human predation on the nocturnal pollinators of Brevitabue baobabs in Madagascar are now required. Lemurs probably do not visit baobabs that are

separate from other trees because they require crown access from the adjacent canopy and are unable to climb the large, smooth trunks of isolated baobabs. As all of our study sites were relatively disturbed, it would be profitable to compare bat and lemur visits to baobabs in intact forests in the west and north of Madagascar.

CONSERVATION SIGNIFICANCE.—The dry forests in the west of Madagascar have received much less conservation attention than the humid forests of the east (Baum 1996). The remaining populations of baobabs in Madagascar are widely threatened by direct destruction through uncontrolled bush fires, wood extraction, and poor recruitment (Baum 2003) and three of the six species are of particular conservation concern (Baum 1995). Forest fragmentation in western Madagascar has disrupted seed dispersal mechanisms for some tree species by limiting the movements of lemurs (Ganzhorn *et al.* 1999). The impact of habitat degradation on pollinators is not well understood in Madagascar but we believe that fruit bats are likely to be vital agents of pollen transfer in fragmented forests. Further effort is now required to assess the impact of deforestation on mammal pollinators of baobabs given the differing capacities of bats and lemurs to tolerate disturbance. The undeniably distinctive appearance of baobabs, especially in degraded areas where other large trees have been removed, is a powerful symbol of Madagascar's natural history and is widely used in promoting tourism. Baum (1996) proposed that baobabs are suitable candidates as flagship species for dry forests in western Madagascar. We concur with this assessment because they meet many of the "flagship" criteria (*e.g.*, endemism, endangered status, charismatic, culturally significant, and easily recognizable) of Bowen-Jones and Entwistle (2002). In addition, as fruit bats of the genus *Pteropus* have been successfully used elsewhere as flagships for conservation (*e.g.*, Entwistle & Corp 1997b) and because of the close relationship between fruit bats and the baobabs, we believe that there is potential for using both bats and baobabs as flagships for the conservation of Madagascar's dry forests.

ACKNOWLEDGMENTS

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