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FRUIT SELECTION AND EFFECTS OF SEED HANDLING BY FLYING FOXES ON GERMINATION RATES OF SHEA TREES, A KEY RESOURCE IN NORTHERN BENIN, WEST AFRICA

Bruno A. Djossa[1,2], Jakob Fahr[2], Elisabeth K. V. Kalko[2,3] & Brice A. Sinsin[1]

[1] Laboratoire d'Ecologie Appliquée-FSA/UAC/Bénin
[2] Institute of Experimental Ecology, University of Ulm, Germany
[3] Smithsonian Tropical Research Institute, Balboa, Panama

Abstract. Many tropical plants depend on seed dispersal by animals for their natural regeneration. Our results reveal that in the Pendjari Region, Benin (West Africa), fruits of shea trees (*Vitellaria paradoxa*) constitute a key resource for flying foxes (Chiroptera: Pteropodidae). Furthermore, handling of *Vitellaria* seeds by flying foxes can lead to an increase in germination success. We propose that seed dispersal by flying foxes is crucial for the long-term maintenance of this socio-economically important tree, which is not yet cultivated by local populations in traditional agroforestry systems. *Accepted 9 May 2008.*

Key words: *bats*, *Chiroptera*, *conservation*, *Pendjari National Park*, *seed dispersal*, *seed germination*, Vitellaria paradoxa.

INTRODUCTION

Seed dispersal by animals is the most common mode of seed dispersal for the majority of plant species in the tropics (Fleming & Heithaus 1981, Bollen *et al*. 2004). This ecological service is a key process in plant regeneration (Balcomb & Chapman 2003). Seed dispersal away from the parent tree is important for the successful establishment of seedlings (e.g., Janzen 1970, Connell 1971, Howe & Smallwood 1982, Terborgh *et al*. 2001). Thus animal-dispersed plant populations require regular visits from frugivorous animals to secure recruitment (Tellería *et al*. 2005). However, in many parts of the world, hunting pressure and changes in land use cause dramatic reductions in the population of seed-dispersing animals, particularly larger vertebrates (Tutin *et al*. 1991, Whitney & Smith 1998, Poulsen *et al*. 2002). As an example, degraded landscapes in Asia already lack many important dispersal agents such as gibbons and hornbills (Corlett 1998). The same holds true for Africa, where changes in land use and hunting for bushmeat (Fa *et al*. 2005, Thibault & Blaney 2003) are leading to a serious decline in large to medium-sized seed dispersers, including elephants, antelopes, and primates. Presumably, flying foxes (Chiroptera: Pteropodidae) are among the few remaining important groups of small to medium-sized vertebrate seed dispersers in many areas of the Paleotropics that are also heavily exploited by humans.

Old World fruit bats (flying foxes) are highly mobile (Webb & Tiedemann 1996) and potentially disperse seeds over long distances. Maximum dispersal distances of small seeds, which can be retained in the guts of fruit bats, are estimated to exceed 100 km (Shilton *et al*. 1999). At least 300 plant species of nearly 200 genera are known to rely on flying foxes for either pollination and/or seed dispersal (Marshall 1983, Fujita & Tuttle 1991). In addition, fruit handling by bats can have a positive effect on seed germination (Soriano *et al*. 1991, Sosa & Soriano 1993, 1996 in Naranjo *et al*. 2003, Entwistle & Corp 1997) although this is somewhat debated as some studies did not find measurable effects of seed manipulation by flying foxes on germination success (Bollen & van Elsacker 2002, Izhaki *et al*. 1995).

In the village areas surrounding the Pendjari Biosphere Reserve, Benin, where this study was carried out, the shea tree (*Vitellaria paradoxa*) represents a socio-economically important resource for the local human populations (Djossa *et al*. 2008). Household income from shea tree use may exceed those from

e-mail: djosbruno@yahoo.fr

cash crops like cotton (Agbahungba & Depommier 1989). Shea fruits yield a high economic value because of their oil-rich seeds. They are harvested intensively by women for sale and for butter making. The oil obtained from its kernel constitutes the first cooking oil that was produced and used in this region (Hyman 1991, Hall *et al.* 1996, Boffa 1995). However, this plant species has not yet been cultivated despite its high socio-economic importance for the local populations. This is at least in part due to a lack of knowledge about the recruitment requirements of the species, which has, in conjunction with other factors, precluded cultivation so far.

It is known that flying foxes disperse the fruits of shea trees (Jaeger 1962). Among small mammals, flying foxes are likely to be the most important group of dispersers due to their high mobility, while the contribution of primates and birds to seed dispersal remains to be shown. Seed dispersal is ensured through frequent and regular visitation of fruiting shea trees. In contrast to small fruits, where small seeds are usually swallowed by bats during feeding (Fleming & Heithaus 1981, Naranjo *et al.* 2003), the seeds of shea fruits are too large to be ingested. In general, flying foxes carry large fruits, like those of shea, away from the parent tree and process them at feeding roosts (Ebigbo 2004, BD & JF pers. obs.). Subsequently, the seeds are dropped underneath the feeding roost. Since shea trees rely on natural regeneration for reproduction, we asked whether handling of large seeds by flying foxes might increase germination rates, similar to the positive effect of gut passage on small seeds shown for other fruit bats (e.g., Fleming & Heithaus 1981, Entwistle & Corp 1997, Naranjo *et al.* 2003, Ebigbo 2004).

The aim of our study was first to assess the importance of shea fruit in the diet of flying foxes. Shea trees dominate the agroforestry parklands of our study areas, but their population structure is significantly affected by increasing human land use in the region around the protected areas of the Pendjari Park (Djossa *et al.* 2008). Second, we wanted to show whether and how manipulation of seeds by flying foxes might contribute to the recruitment of this plant species, because up to now shea trees have not yet been cultivated and their propagation continues to rely on natural regeneration. We performed germination tests of seeds processed by flying foxes and compared them with unprocessed seeds from ripe fruits. The results of this study are essential to assess the ecological importance of flying foxes with regard to tree recruitment of shea trees, and to gather crucial information for the development of meaningful conservation and management plans involving flying foxes as seed dispersers.

METHODS

Study site. Our study took place in the vicinity of and within the Pendjari Biosphere Reserve (RBP) (FIG. 1c). The region is located in the northwest of Benin in the District of Atacora (10°40'–11°28'N and 0°57'–2°10'E) (Fig. 1 a,b). It covers an area of 4661 km^2 and consists of the Pendjari National Park (2660 km^2), the Pendjari hunting zone (1750 km^2), and Konkombri hunting zone (251 km^2). The Pendjari River is the only permanent watercourse, while smaller streams desiccate in the dry season. The dominant vegetation type is savanna interspersed by some patches of dry forests with deciduous trees (Sokpon *et al.* 2001).

The border of Pendjari Biosphere Reserve is lined with many small villages. Agriculture forms the main economic activity of the local population, in addition to Fulani herders, who keep the largest groups of livestock (cattle). Women mainly exploit non-timber forest products like fruits of shea trees.

Climate. Temperature varies from around 21°C during the night up to around 40°C during the day. The annual mean varies from 25° to 28°C during the cooler period of the dry season and 30° to 33°C during the hot period of the dry season. Relative humidity varies between 17 and 99 % (PAG2 2005). The park is located in the Sudanian Zone with a single wet season from April–May to October and one dry season from November until March. Average annual precipitation is 1000 mm, with 60 % falling between July and September (Sinsin *et al.* 2002). During the wet season large parts of the park are flooded.

Study tree. *Vitellaria paradoxa* C.F. Gaertn. (Sapotaceae), the shea tree, is a source of vegetable fat that is second in consumption by humans only to palm oil in West Africa. Shea trees occur in a savanna belt stretching across Africa from Senegal to the Sudanian/Ethiopian border (Hall *et al.* 1996). A wide variety of useful products are made from this tree. Oil derived from the kernels of the shea fruits ("shea butter") is by far the most important product. Traditionally, it is extracted by women through a laborious and time-consuming process. This oil has been an important product in international trading activities in West Africa since the fourteenth century (Busson

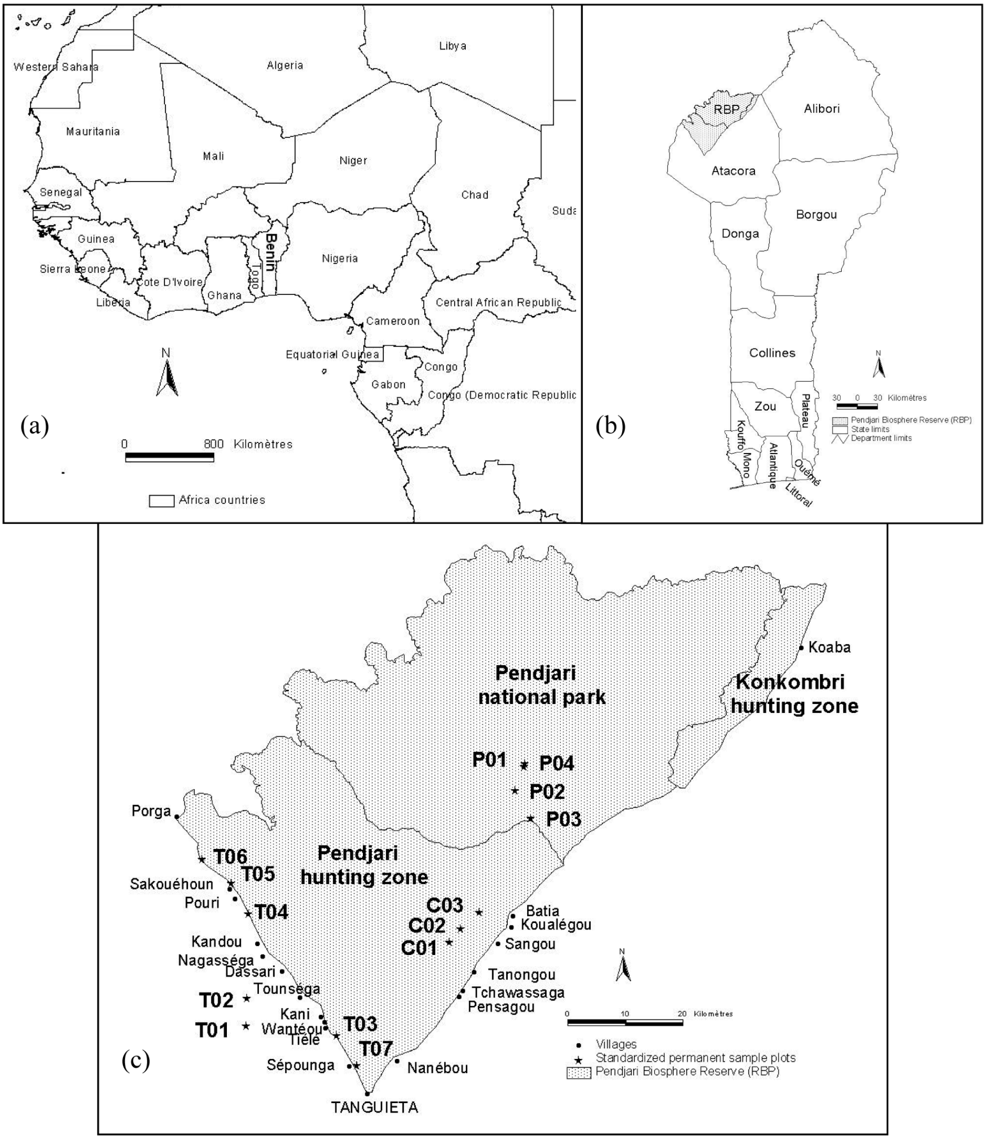

FIG. 1. Study area. a) Benin in West Africa, b) Benin with the location of the Pendjari Biosphere Reserve (RBP), and c) location of the plots within the RBP. T stands for plots in the village territory, C for plots in the hunting zone, and P for plots in the Pendjari National Park. Source: soil map of Borgou (Benin), scale 1/100 000.

1965). After the First World War, shea butter contributed substantially to the flourishing trade between West Africa and Europe, where the butter was used in the production of margarine and in candle making (Dudgeon 1922).

From central to northern Benin, this tree species constitutes the most important source of non-timber resources for the rural population. Fruits and butter from shea trees form a large portion of the income of local households (Agbahungba & Depommier

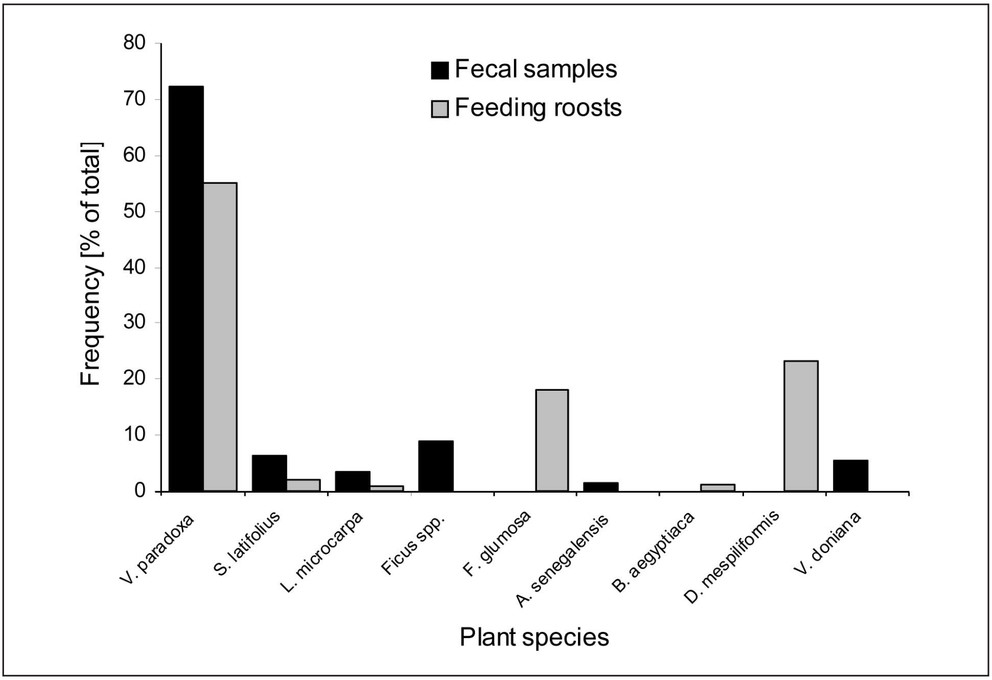

FIG. 2. Resource use by flying foxes based on fruit species identified from fecal samples (n = 337), and fruit species identified from ejecta pellets and seeds dropped under feeding roosts (n = 124).

1989), particularly between harvests of other agricultural products such as maize, sorghum, beans, and yam.

Bat captures and seed collection. Flying foxes were mist-netted from September 2004 to August 2006. Mist nets (R. Vohwinkel, Velbert, Germany) measured 12 m x 2.8 m and had five shelves (16-mm mesh; 70 denier/2-ply netting). Bat sampling was conducted each trimester during a five to six week period in a standardized configuration where 12 mist nets were set in a rectangle on a 2-ha plot with nets spaced about 50 m apart. Netting took place from 19:00–19:30 until 00:00 h and again from 04:00 to 06:00 h. Nets were closed during heavy rain. Bat species were identified based on Hayman & Hill (1971) and Bergmans (2002). The animals were weighed with Pesola spring balances (precision 1 g) and their forearm length was measured with callipers (precision 1 mm).

Parallel to mist-netting, we searched for feeding roosts and collected ejecta pellets and fresh seeds dropped by bats underneath these roosts. To identify fruit pulp in the feces of flying foxes, we established a reference collection where we fed identified fruits *ad libitum* to 3–4 individuals of *Epomophorus gambianus* and *Micropteropus pusillus*, which were the most abundant flying foxes at our study site. They were individually and temporarily kept for 24 hours in a flight cage (1.2 m x 1 m x 0.7 m). After we had fed a number of identified fruits to the bats, we collected the fecal material, noted its characteristics including color, texture, smell, and consistency, thereby creating our reference collection. Only a few fecal samples (5 %) could not be identified according to these characters. To obtain fecal material from wild-caught bats we usually kept them for 20–30 min in a clean cloth bag.

Seed germination tests. To investigate the effect of fruit handling by flying foxes on seed germination rates, we carried out two germination tests (trial I & II): one in the period from May until June in 2005 (trial I) and the second from August until September in 2006 (trial II). In the first period, we collected fresh seeds at feeding roosts that had been processed and dropped by flying foxes, as well as ripe fruits randomly

TABLE 1. Germination tests of shea tree seeds.

Year	Category of seeds		Germination rates Processed seeds	Control	Comparison (χ^2, Yates correction)
2005 trial I	processed seeds collected from several feeding roosts	control: seeds from ripe, unprocessed fruits collected from several trees	84 %	60 %	χ^2 = 9.10, d.f. = 1, P = 0.0226, n = 140
2006 trial II	processed seeds from ripe fruits of one shea tree fed to flying foxes in cages	control: seeds from ripe, unprocessed fruits collected from same tree	89 %	84 %	χ^2 = 0.04, d.f. = 1, P = 0.844, n = 66

Control: seeds from ripe fruits collected from tree(s), pulp removed manually; Processed seeds: seeds from feeding roosts and seeds manipulated by flying foxes when they were fed with ripe fruits in flight cages.

collected from shea trees in the same area. For the second period, we sampled ripe fruits from only one tree and fed part of them to flying foxes in a cylindrical flight cage (diameter: 30 cm, height: 40 cm). Three flight cages were used where we kept up to two flying foxes (*E. gambianus* or *M. pusillus*) overnight. Within a period of five days we obtained 35 seeds handled by flying foxes.

We compared the germination rates of seeds handled by flying foxes with seeds where pulp had been removed (controls). For both experiments, we removed pulp manually from the control fruits and, provided there was some pulp left, also from the seeds that we had collected from the feeding roosts. All seeds were dried for two consecutive days in the open air to minimize water content. Intense radiation was avoided.

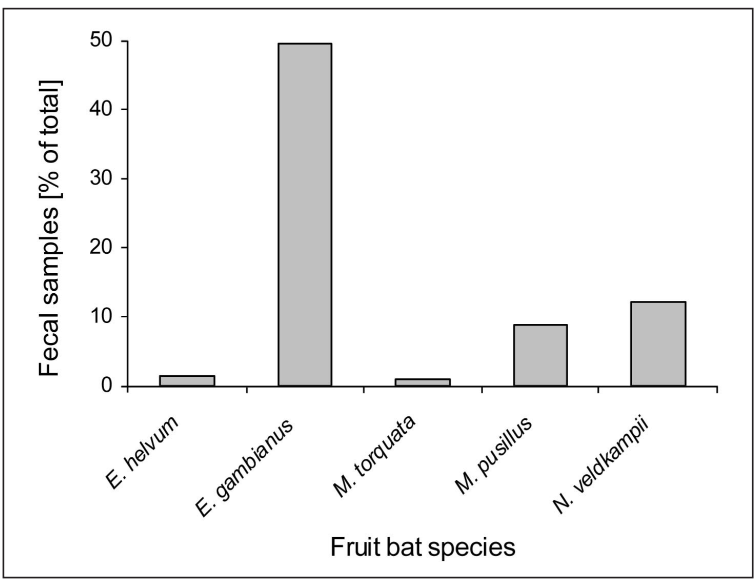

FIG. 3. Proportion of fecal samples containing pulp from shea fruit for the different species of flying foxes in RBP (n = 248).

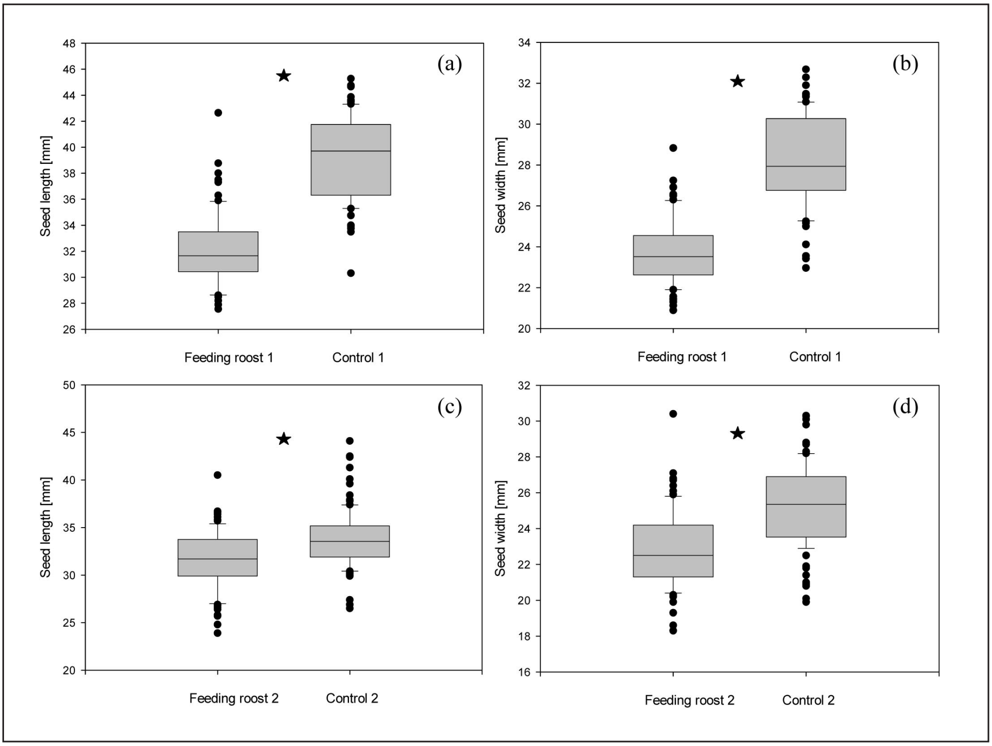

FIG. 4a-d. Length (a & c) and width (b & d) of shea seeds collected from feeding roosts in the field (feeding roost 1) and from ripe, unprocessed fruits randomly collected from shea trees where pulp was removed manually (control 1) in 2005, and of shea seeds from fruits collected from a single tree and fed to flying foxes in flight cages (feeding roost 2), and from ripe, unprocessed fruit sampled from the same shea tree (control 2) in 2006. Significant differences are marked with an asterisk (a: n = 140, t-test, t = -14.180, d.f. = 138, $p < 0.001$; b: n = 140, t-test, t = -13.591, d.f. = 138, $p < 0.001$; c: n = 205, t-test, t = -5.310, d.f. = 203, $p < 0.001$; d: n = 205, t-test, t = -8.308, d.f. = 203, $p < 0.001$).

For the germination experiments we used black polyethylene pots (20 cm long, 10 cm wide) that were filled with soil from farming areas where shea trees grew. They were set up in the open air near a tree to minimize solar radiation during midday. Pots were wetted completely before the seeds were planted for the germination test. They had small holes for drainage of excess water. A total of 140 seeds (70 handled by flying foxes and 70 controls) was obtained in the first study period and 66 seeds (35 handled by flying foxes and 31 controls) in the second study period. They were buried about 3–4 cm underneath the soil surface. As shea trees are adapted to mesic to semi-arid zones, water was only administered when the soil at the surface began to dry out in the pots.

The experiments were monitored daily. Germination of a seed was scored as positive as soon as the hypocotyl emerged from the skin (Marche-Machad 1965: pp. 316–318, Gorenflot 1992: pp. 165–196). Each germinated seed was then monitored for an additional two weeks on a daily basis to see if the seedling survived or died. Finally, in 2006 we measured seed mass of ripe fruits by weighing 235 ripe shea fruits before and after we had manually removed the pulp. Seed size (length and width) was measured with callipers (precision 1 mm).

Statistics. We used a chi-square test (STATISTICA 6.0) to compare germination rates of both experiments. Differences in seed size and seed mass were assessed with t-tests when the data passed tests of normality and homogeneity of variance, otherwise we employed Mann-Whitney U-tests (SigmaStat 3.1). Box plots show the median, the 25th and 75th percentiles (box), the 10th and 90th percentiles (whiskers), and outliers (dots).

RESULTS

Resource use by flying foxes. We captured 1217 flying foxes during 605.5 nights of sampling, resulting in a total of eight species: *Epomophorus gambianus*, *Micropteropus pusillus*, *Nanonycteris veldkampii*, *Lissonycteris angolensis*, *Rousettus aegyptiacus*, *Myonycteris torquata*, *Eidolon helvum*, and *Hypsignathus monstrosus*. *Epomophorus gambianus* (604 individuals) was the most abundant flying fox in our study area followed by *M. pusillus* (306 individuals) and *N. veldkampii* (279 individuals). Five of the flying foxes species were captured in sufficiently high numbers to conduct a detailed analysis of fecal samples. Based on a total of 337 fecal samples collected during netting sessions, as well as fruit remains and seeds collected from 124 feeding roosts, we found that the bats fed on nine types of fruit (Fig. 2). The species composition of fruit plants was almost identical in fecal and feeding roost samples, with a dominance of *Vitellaria paradoxa* in both cases. The other species were *Sarcocephalus latifolius* (Rubiaceae), *Lannea microcarpa* (Anacardiaceae), *Ficus* spp. and *Ficus glumosa* var. *glaberrima* (Moraceae), *Annona senegalensis* (Annonaceae), *Balanites aegyptiaca* (Zygophyllaceae), *Diospyros mespiliformis* (Ebenaceae), and *Vitex doniana* (Verbenaceae). Based on fecal samples, shea fruits were used by five out of eight flying fox species (Fig. 3), which were *E. helvum* (n = 5), *E. gambianus* (n = 172), *M. pusillus* (n = 30), *M. torquata* (n = 1), and *N. veldkampii* (n = 40).

Seed size and the influence of seed manipulation on germination rates. In our germination tests, the seeds from both categories, trials I & II and controls, began to germinate after 12 days in 2005 and seven days in 2006. Although the size of seeds collected in 2005 at the feeding roosts was significantly smaller than the controls (i.e., fruits randomly collected under several shea trees; Fig. 4a & b), germination rates of the seeds handled by the bats were significantly higher (Table 1) than in the controls (trial I; 84 % vs. 60 %). In contrast, in 2006 germination rates did not differ significantly between seeds handled by flying foxes in the cages and the control (trial II; 89 % vs. 84 %) (Fig. 4c & d, Table 1). As in 2005, the shea seeds processed by flying foxes in 2006 were significantly smaller than the controls (Fig. 4c & d). Interestingly, comparison of the seeds collected at feeding roosts in 2005 and 2006 revealed that they were of similar length (Fig. 5a) but differed significantly in width (Fig. 5b). The seeds collected in 2005 were significantly wider than the seeds from the fruits sampled in 2006. Based on a random collection of shea fruits (n = 235), we showed a close and positive relationship between seed

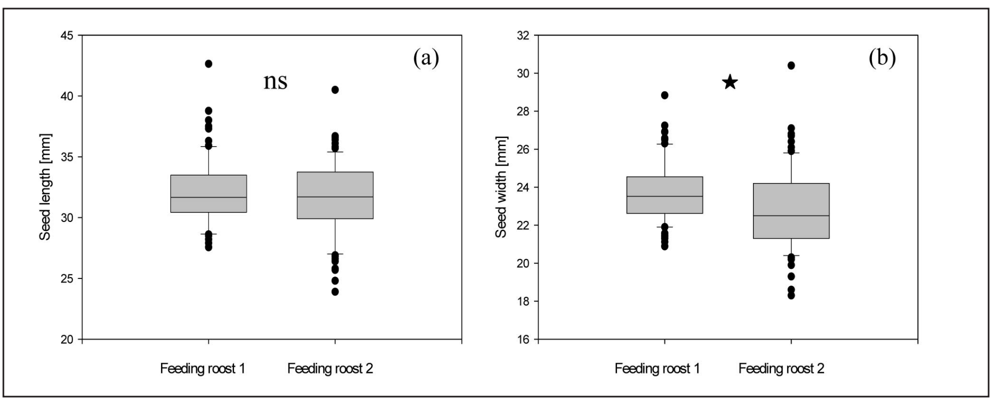

FIG. 5a & b. Length (a) and width (b) of shea seeds collected from feeding roosts from two different sites in 2005 (1) and 2006 (2). For details see FIG. 4. Significant differences are marked with an asterisk (a: n = 175, t-test, t = 1.246, d.f. = 173, p = 0.215; b: Mann-Whitney U-Test, T = 7359.5, $n_{f.roost1}$ = 70, $n_{f.roost2}$ = 105, p < 0.001).

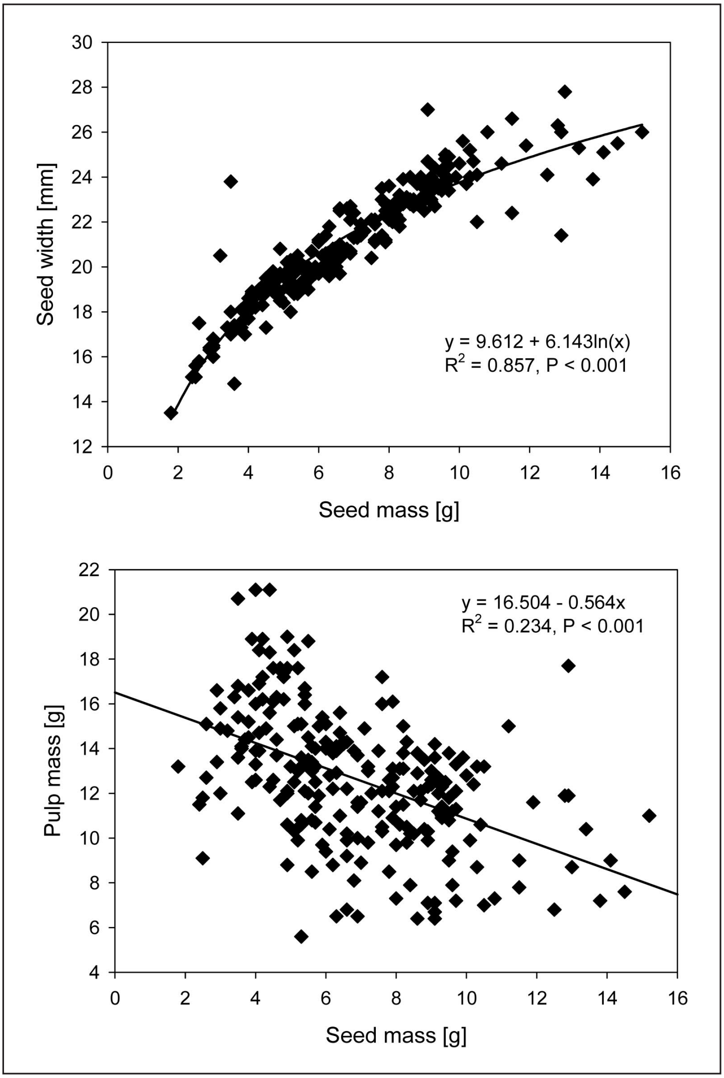

FIG. 6a & b. Relationship between (a) seed mass and seed width and (b) seed mass and pulp mass of shea fruits (n = 235) randomly collected from several trees.

width and seed mass (Fig. 6a, and also between seed length and seed mass, data not shown). Surprisingly, there was a negative, albeit loose relationship between seed mass and pulp mass, hence fruits containing smaller seeds had more pulp (Fig. 6b).

DISCUSSION

We recorded fruits of nine plant species in the diet of flying foxes during our study, all of which were known to be consumed by flying foxes in West Africa (Funmilayo 1979, Marshall & McWilliam 1982, Thomas 1982, Ebigbo 2004). Among those plants, shea fruit constituted a key resource for flying foxes in our study area. Indeed this plant species is very common in savannas inside the Pendjari Biosphere Reserve and also dominates fallows and farmed lands in disturbed areas (Schreckenberg 1999), mainly because they are specifically fostered by agroforestry practices (Maranz & Wiesman 2003). Pulp of shea fruits was recorded from the majority of flying foxes species (five out of eight species). The three most abundant flying foxes (*E. gambianus*, *M. pusillus*, and *N. veldkampii*) captured in the study area were all feeding on this plant to various degrees.

Flying foxes, like all fruit bats, are characterized by a high energetic demand coupled with fast gut passage (Thomas 1984, Delorme & Thomas 1999). Probably, the high consumption rate of shea fruits by *E. gambianus* (average body mass: 130 g) is related to the higher energetic demands of this rather large species compared with the smaller species *M. pusillus* (mean body mass: 24 g) and *N. veldkampii* (mean body mass: 22 g), the latter feeding somewhat less on this fruit. Migrating species (*Eidolon helvum* and *Myonycteris torquata*; Thomas 1983) also fed on shea fruits. These bat species occur in the study region only during the wet season, which coincides with the peak fruiting period of shea trees. Richter & Cumming (2006) reported a similar pattern for *E. helvum* in Kasanka National Park, Zambia, where the relative abundance of this species also increased during the peak fruiting period of key resources. Resource-driven increases in relative abundance of flying foxes has likewise been documented in Malaysia (Hodgkison *et al.* 2004).

The attractiveness of shea fruits may in turn help in dispersing its large-seeded fruit, similar to the fruits of an important Guinea savanna tree, *Cola cordifolia* (Sterculiaceae), studied by Ebigbo (2004) in Ivory Coast. With a high visitation rate by highly mobile dispersers like flying foxes, shea trees are likely to benefit for several reasons, thus achieving a higher success rate in the recruitment of seedlings (Tellería *et al.* 2005). Firstly, if the majority of seeds are dropped beneath the parent tree, they might be exposed to a high number of seed predators. Furthermore, seedlings are often out-shaded and particularly prone to pathogens. According to the escape hypothesis of Janzen (1970) and Connell (1971), transportation of seeds away from parent trees can substantially increase survival chances. Secondly, removal of seeds by flying foxes away from parent trees is of particular importance in the Pendjari Region and other areas used by humans where the plant's natural seed bank, i.e., ripe fruits fallen to the ground, is almost completely removed, here mainly by women who collect most of the fruits for multiple purposes. In village areas near the Pendjari Biosphere Reserve, where only a few scattered woody plants in fallows and farmed lands remain, feeding roosts of flying foxes are likely to be widely scattered. Potentially, because of their high mobility, flying foxes could transport seeds to places that are not regularly visited by collectors. There, those seeds may have a better chance of survival provided they are deposited at sites with suitable light and water conditions for germination, especially in rather open areas of lower land-use intensity such as fallows. In addition, the mechanical removal of pulp is known to speed up the germination of shea seeds (Hall *et al.* 1996). Since shea seeds are recalcitrant, they have to germinate quickly in order not to lose viability. It needs to be tested whether some chemicals mediated through the bats' saliva are responsible for the positive effect of flying foxes on seed germination, as the seeds do not pass through their alimentary tract and do not show any mechanical scarification, e.g., through teeth.

Seed size may also play a role in the selection and subsequent dispersal process mediated by flying foxes. It was surprising that bats consistently preferred smaller seeds in 2005 and 2006 compared with the controls. This could indicate a preference by flying foxes for a particular fruit size that might be best for handling, provided seed size is correlated with fruit size, but this relationship requires further testing. Another variable selected by the bats might be pulp mass, which correlates negatively with seed size/mass (Fig. 6b). Fruits with smaller seeds produce more pulp in relation to seed size.

Our results show that shea fruit handling by flying foxes can enhance germination success even though the seeds do not pass through their guts. This is in accordance with the study by Ebigbo (2004), who also found a positive effect of the handling behavior of flying foxes on germination rates of *Cola cordifolia*. However, it is also important to note that our second test in 2006 produced contradictory results, where we did not find significant differences in germination rates between seeds manipulated by flying foxes and controls.

One reason for the positive effect of flying foxes on germination rates of shea seeds in the first trial (2005; Table 1) could be due to a fruit choice by the bats, since we compared germination rates of seeds from feeding roosts with seeds from randomly collected fruits. Fruits attractive to flying foxes may contain higher numbers of mature and viable seeds than other fruits or fruit crops. However, this reasoning needs to be treated with caution as the second trial (2006) revealed high germination rates of both seeds processed by flying foxes and controls (Table 1) despite the fact that the bats were limited in choice as they were exposed to fruits from a single tree. It is remarkable that, in both trials, seed size of the fruits processed by the flying foxes was significantly smaller than the controls, suggesting a selection mechanism even within a fruit crop (Fig. 4a-d).

Given our somewhat inconclusive results, additional tests are necessary to find out what might guide fruit selection and to specify the effect of fruit handling by flying foxes on seed germination rates, since other studies have shown a generally high germination rate of shea seeds, which can be over 90 % (Booth & Wickens 1988).

Another unresolved topic concerns the time that shea seeds need for germination. In our study, seeds already started to germinate after 12 days in 2005 and seven days in 2006. Germination time in 2006 was considerably shorter than the two weeks reported by Hall *et al.* (1996) under natural conditions. One reason might be water supply. Even though we did not supply the pots with water on a daily basis, seeds were not grown under completely natural conditions as the soil never became fully dry, as it is often the case in these conditions. This may also be one of the reasons why germination rates of shea seed that are sown without any further watering tend to be low (Bonkoungou 1987).

Based on dietary composition and the potential effect of flying foxes on germination rates, we conclude that the interaction of flying foxes with shea trees is for the most part positive and probably of crucial importance for the maintenance of the trees. Because other small mammals (mainly rodents and primates) that also feed on shea fruits (Soladoyé *et al.* 1989) are often seed predators and frequently harvest and manipulate immature fruits, flying foxes stand out as dispersers that do not harm shea seeds (Tang *et al.* 2007) and mainly feed on ripe fruits, which are likely to have a higher germination rate than immature fruit. Larger mammals such as antelopes and elephants may feed on fruits that are partially consumed by flying foxes and thus can act as secondary dispersers. Scatter-hoarding rodents are likewise known to contribute to secondary seed dispersal (Jansen *et al.* 2006). However, the influence of seed dispersal by other frugivorous groups was not assessed by us and requires additional studies. Furthermore, flying foxes may play a particularly important role in areas of intensive land use because they transport at least some fruits and their seeds to places with less or no collecting activities by humans. However, to ensure their continued service as important seed disperser of this socio-economically valuable plant, adequate conservation measurements have to be put into place to ensure their survival. Flying foxes rely on a continuous fruit supply throughout the year and thus require areas with staggered resource phenology, i.e., additional fruit (and flower) resources outside the seasonal fruiting period of shea trees. Furthermore, they also require shea fruits for consumption, which means that they are likely to compete with human interests in areas of heavy land use. Here, conservation plans need to carefully balance the demands of humans and of seed dispersers. In this context, thorough environmental education is of the essence.

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