

Thus, both tree species depend on a few lemur species for seed removal and potential dispersal (Table 5).

Though the same lemur species fed on fruits of both investigated tree species, there was a considerable difference between tree species in the proportion of seeds swallowed and thus removed (Fig. 1). This is due to the facts that firstly, lemur body size correlates with the size of their food trees (RICHARD, 1985; GANZHORN, 1988, 1989) and, in addition, there is a positive correlation between tree size and fruit production across species ($F_{1,11} = 7.09$, $p = 0.02$; this study). Secondly, the maximum seed size to be swallowed and thus the probability of being dispersed is correlated with gape size (WHEELWRIGHT, 1985; LEVEY, 1987; DOWSETT-LEMAIRE, 1988). Since the larger lemur species, *E. fulvus* and *P. verreauxi*, are more often found in larger trees such as *P. sylvatica* than the smaller lemur species *C. medius* and *L. ruficaudatus*, and since the larger species may and actually do swallow seeds more easily than the smaller species, seed removal was higher in the larger *P. sylvatica* than in *B. discolor*.

The fate of dropped or defecated seeds is uncertain because seeds deposited on the forest floor do not necessarily remain untouched (CHAPMAN, 1989). For example, seeds are moved by wild pigs [*Potamochoerus larvatus* (ROHNER, 1988)] or rodents (*Hypogeomys antimena*) while others are killed by seed predators such as *Eliurus myoxinus*.

The results of the germination experiments revealed neither improved nor hindered germination for the differently handled seeds (Table 6). However, in our germination experiments we had to remove the fruit husk and pulp of the fallen fruits to avoid moulding. Also the fruit pulp often contains chemical compounds which inhibit germination (HLADIK and HLADIK, 1967). Therefore it is possible, as previously shown for fruits of the Malagasy rain forest (DEW and ASQUITH, 1991; DEW and WRIGHT, in prep.), that under natural conditions chewed or defecated seeds germinate faster than seeds with adhering fruit pulp and thus have a better chance of establishing themselves.

According to our own and previous (GANZHORN, 1986) observations on *E. fulvus*, seeds or markers take between three and nine hours to pass their digestive tract. Considering the size and morphology of their digestive tract, even longer passage times can be postulated for *P. verreauxi*. Since the mean daily travel distance exceeds 100 m in both species (RICHARD, 1977; SUSSMAN, 1977), it is likely that at least these two lemur species are primary dispersers and thus play an important role in forest regeneration (RALISOAMALALA, 1996).

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SEED DISPERSAL IN THE TREE *COMMIPHORA GUILLAUMINI*: A COMBINATION OF ORNITHOCHORY AND MYRMECOCHORY IN A DRY TROPICAL FOREST IN WESTERN MADAGASCAR

K. BÖHNING-GAESE, J.F. BURKHARDT and J. SCHMID

Résumé: Dissémination des graines de *Commiphora guillaumini*: une combinaison d'ornithochorie et de myrmécochorie dans une forêt tropicale sèche de l'ouest de Madagascar

L'étude de l'écologie de dissémination de l'"Arofy à grandes feuilles" (*Commiphora guillaumini*), un arbre de la forêt sèche de l'ouest de Madagascar, laisse entrevoir un système inhabituel.

1. *C. guillaumini* est une grande espèce arborescente dont les diaspores sont disséminées par myrmécochorie. Jusqu'ici, ce mode de dissémination était seulement connu dans le cas d'arbrisseaux, d'herbacées pérennes, d'espèces annuelles ou rudérales, de graminées, de plantes grimpantes, d'hémiparasites, de parasites et d'épiphytes (BEATTIE, 1983).
2. Dans la concession forestière du CFPF, une seule espèce de fourmi, *Aphaenogaster swammerdami* amasse les diaspores. On admettait jusqu'ici que la myrmécochorie ne procédait que d'une faible spécificité, la dissémination étant alors le fait d'un rassemblement de fourmis (BUCKLEY, 1982, BEATTIE, 1985).
3. Les colonies de *A. swammerdami* sont associées de façon significative à *C. guillaumini*. On trouve habituellement une colonie de *A. swammerdami* sous chaque couronne de *C. guillaumini*, ce qui indique que les diaspores de ce dernier représentent une importante source de nourriture pour *A. swammerdami*.
4. Les avantages de la dissémination des diaspores de *C. guillaumini* par *A. swammerdami* ne résident pas dans la soustraction aux prédateurs, au feu ou à la concurrence (BEATTIE, 1985).
5. Les propriétés du fruit indiquent en premier lieu l'ornithochorie. La dissémination a lieu aussi bien par des oiseaux que par des fourmis.

L'écologie de dissémination inhabituelle de *C. guillaumini* pourrait représenter une adaptation aux conditions particulières des forêts tropicales sèches. La combinaison des modes de dissémination par les oiseaux et par les fourmis est en effet commune dans le cas d'espèces australiennes d'*Acacia*. Il se pourrait que les oiseaux soient les agents de dissémination favoris, quoique peu fiables par climat sec, les fourmis jouant un rôle de sauvegarde.

Abstract

The investigation of the dispersal ecology of the tree "Arofy à grandes feuilles" (*Commiphora guillaumini*) in the dry tropical forest of western Madagascar yielded insights into an unusual dispersal system:

1. *C. guillaumini* is a large tree species exhibiting myrmecochory. So far only shrubs, herbaceous perennials, annuals, ruderals, grasses, vines, hemiparasites, parasites, and epiphytes have been reported to be myrmecochorous (BEATTIE, 1983).
2. The diaspores are collected in the forestry concession of the Centre de Formation Professionnelle Forestière mainly by a single ant species, *Aphaenogaster swammerdami*. Myr-

mecochory has thus far been reported as having low specificity, with dispersal taking place always by an assemblage of ants (BUCKLEY, 1982, BEATTIE, 1985).

3. Colonies of *A. swammerdami* were significantly associated with *C. guillaumini* trees: usually below the crown of a *C. guillaumini* tree one *A. swammerdami* colony could be found, indicating that the diaspores of *C. guillaumini* are an important food source for this species.
4. The benefits of *A. swammerdami* dispersal for *C. guillaumini* diaspores are neither predator-, nor fire-, nor competition-avoidance (BEATTIE, 1985).
5. The fruit characteristics are primarily ornithochorous. Dispersal takes place by both birds and ants.

The unusual dispersal ecology of *C. guillaumini* might be an adaptation to the special conditions found in tropical dry forests, as the combination of bird and ant dispersal is also common in Australian *Acacia* species. Birds might be the favoured but unreliable dispersal agents in dry climates, whereas ants could act as safeguards of adequate dispersion.

1. Introduction

Trees of dry tropical forests face problems similar to those of wet tropical and deciduous forests. Seeds have to escape predation, pathogens, herbivory, intra- and interspecific competition, and be able to survive under minimum levels of light. Additionally, they must cope with an extended dry season which is especially stressful to seedlings (WALTER, 1984). One means of overcoming these conditions might be the special adaptation of the mode of seed dispersal which will ensure maximum survival of the seeds and seedlings (e.g., GENTRY, 1983; DAVIDSON and MORTON, 1984; WESTOBY et al., 1990).

The dominant upper story trees of the dry forest within the forestry concession of the Centre de Formation Professionnelle Forestière (CFPF) are "Arofy à grandes feuilles" (*Commiphora guillaumini* Perr. 1944; SCHWITTER, 1984a), representing 42 % of the trees > 40 cm DBH (HUNZIKER, 1981). They are the most important group of timber species, yielding 80 to 90% of the commercially used wood (SCHWITTER, 1984a). Because of its dominance and economical importance, we chose *C. guillaumini* for an investigation of the seed dispersal strategy of a tropical dry forest tree species.

2. Morphology and phenology of *C. guillaumini*

C. guillaumini is the most abundant of the five species of *Commiphora* (Burseraceae), that are known to occur in the forestry concession (see RAKOTONIRINA, 1996). The trees grow up to a height of 20 m with a trunk diameter of up to 80 cm DBH (PERRIER DE LA BATHIE, 1946; ROHNER and SORG, 1986). The species is dioecious, with flowering taking place from October to November and fruiting from January to April (ROHNER and SORG, 1986).

The roundish fruits (diameter 20-25 mm) are borne in small clusters at the ends of the branches. The fruits consist of a greenish-reddish fleshy outer covering (exocarp and mesocarp) that splits when mature into two halves, exposing a single diaspore (see HOWE and SMALLWOOD, 1982). The diaspore consists of a brilliant black kernel (about 13x8x6 mm), which is partially surrounded by a cup-like red fleshy pseudaril (VAN DER WALT, 1973, p. 55; VAN

DER PIJL, 1982, p. 144). The pseudaril (in the following "aril") is rich in lipids and palatable, whereas the outer covering is full of secondary compounds and unpalatable. In most cases the covering splits on the tree and drops off, leading to a display of the diaspore to frugivorous tree visitors. If the tree is not visited, diaspores can accumulate over several days (RAKOTONIRINA and PRELAZ, 1982).

3. Evidence for bird dispersal

The fruit shows characteristics typical of the "bird dispersal syndrome" (VAN DER PIJL, 1982; HOWE, 1986): bicolored with a fleshy red aril and a black seed greater than 10 mm. Correspondingly, birds were observed to be the main seed dispersers. However, seed dispersal was not very efficient. Only 7.9 % of the seeds were carried for distances more than 30 m away from the crown (BÖHNING-GAESE et al., 1995).

The Lesser Vasa Parrot (*Coracopsis nigra*) was the most important seed disperser, accounting for 92.5 % of the dispersal events. Usually the birds nibbled off the aril and dropped the seeds directly under the crown. Seed dispersal took place when a parrot took off while still handling a seed in its beak (BÖHNING-GAESE et al., 1995).

Other bird species observed to feed on the fruits of *C. guillaumini* were the Common Jery (*Neomixis tenella*), the White-headed Vanga (*Leptopterus viridis*), the Greater Vasa Parrot (*C. vasa*), the Madagascar Bulbul (*Hypsipetes madagascariensis*), and the Crested Drongo (*Dicrurus forficatus*). Although *H. madagascariensis* and *D. forficatus* dispersed seeds, they were responsible for only 7.5 % of the dispersal events. Similar seeds of South African *Commiphora* spp. are eaten by hornbills, starlings, orioles, tits, and white-eyes (PALMER and PITMAN, 1972).

Besides birds, the only other species observed feeding on the fruits of *C. guillaumini* was the diurnal lemur *Propithecus verreauxi*. However, it dispersed seeds only very rarely (BÖHNING-GAESE et al., 1995). We did not observe any nocturnal animals (nocturnal lemurs, fruit bats) feeding on the fruits of *C. guillaumini*.

4. Evidence for ant dispersal

After the diaspores drop to the ground, 48.3 % of them were secondarily dispersed by ants (BÖHNING-GAESE, unpublished manuscript). *Aphaenogaster swammerdami* (see OLSON and WARD, 1996; BURKHARDT et al., 1996) was the most important secondary seed disperser, accounting for 93.0 % of the dispersal events. *A. swammerdami* is an omnivorous ant species (length 12 mm) which builds conspicuous mounds up to 1 m in diameter. The workers carry the diaspore into their colony, remove the aril and discard the seed undamaged on the refuse piles at the edge of the colony. Evidence obtained from excavated colonies indicated that no seeds are stored below ground (RAKOTONIRINA and PRELAZ, 1982). When the trees produce fruit, on average 166 seeds (range 1-545, n = 12 trees) can be found piled up at the edge of the associated colony.

One other ants species (*Pheidole* sp. 1; minors 3 mm, majors 5 mm) was also observed to disperse the seeds of *C. guillaumini*. It accounted, however, for only 7.0 % of the dispersal events (BÖHNING-GAESE et al., unpublished manuscript).

Of the seeds that drop to the ground, 51.7 % are not secondarily dispersed. Careful examination of the litter in 1 m² plots under the canopies of 12 *C. guillaumini* trees yielded on average 6.4 seeds/m² (range 1.5-16.9). The seeds found below the canopy had their arils removed by other smaller ant species that were not able to carry the diaspore (mostly *Pheidole* spp.). Thus within a couple of hours the diaspore is either carried off by *A. swammerdami* or *Pheidole* sp. 1, or the aril is eaten by another ant species.

Myrmecochory had been reported as having low specificity, with dispersal taking place always by a multi-species assemblage (BUCKLEY, 1982; BEATTIE, 1985). In the *Commiphora-Aphaenogaster*-system, however, one tree species interacts mainly with only one ant species, making this a very interesting system for further studies.

5. Spatial distribution of *C. guillaumini* trees and *A. swammerdami* colonies

In order to gain a better understanding of the *Aphaenogaster-Commiphora* system, the spatial distribution and association of *C. guillaumini* trees and *A. swammerdami* colonies were investigated using the T-square sampling technique. First, the distance of a random point (R) to the nearest *C. guillaumini* tree (T1) was measured. Then, a line perpendicular to the line RT1 at T1 was made, and the distance from tree T1 to its nearest neighbour T2 beyond the "half-plane" created by this perpendicular was measured. The spatial distribution of trees could be determined by calculating an index C based on the ratio of the distances RT1 and T1T2. The value of C is approximately one-half for random patterns, significantly less than one-half for uniform patterns and significantly greater than one-half for clumped patterns (LUDWIG and REYNOLDS, 1988).

We measured the distribution of *C. guillaumini* trees (> 2 cm DBH) in two unlogged parts of the forest (N6: dry, CS7: wet). In N6 the trees were significantly clustered ($C = 0.70$, $z = 3.10$, $p = 0.002$, $n = 20$). The median distance of random points to the closest *C. guillaumini* tree was 18.0 m. In CS7 the median distance of random points to the closest *C. guillaumini* tree was 7.4 m with no significant deviation from a random spatial distribution ($C = 0.56$, $z = 0.93$, $p = 0.35$, $n = 20$).

The spatial distribution of the ant colonies, however, tended to be uniform. We found that in the two unlogged parts of the forest (CS7 and N6) the dispersion of the colonies was significantly uniform (CS7: $C = 0.33$, $z = -2.63$, $p = 0.009$, $n = 20$; N6: $C = 0.33$, $z = -2.63$, $p = 0.009$). This may indicate the interference of established colonies with the establishment of conspecific foundress queens (RYTI and CASE, 1992). Contrastingly, in CS5, a logged part of the forest, the spatial pattern was not significantly different from random ($C = 0.41$, $z = -1.39$, $p = 0.165$, $n = 20$).

Although the spatial distribution of *C. guillaumini* trees and *A. swammerdami* colonies were different, the ant colonies were significantly associated with the trees. In three parts of the forest (CS7, N6, CS5, see above), the median of the *C. guillaumini*-to-*A. swammerdami* colony distances was significantly smaller than the median of random point-to-colony distances (Table 1). An *A. swammerdami* colony could be found below the crown of almost every *C. guillaumini* tree. If two colonies existed under the same tree they were at opposite ends of the crown. As the turnover rate of *C. guillaumini* trees is much lower than that of ant colonies, *A. swammerdami* seems to establish its colonies preferentially under the crown of *C. guillaumini* trees. This suggests that the arils of *C. guillaumini* might be an important food source for *A. swammerdami*.

Table 1: Median distances of *C. guillaumini* trees and of random points to the closest *A. swammerdami* colony. Wilcoxon test. Numbers in parentheses are sample sizes.

Area	Median tree-to-colony distance (m)	Median random point-to-colony distance (m)	z	p
CS7	2.35 (36)	5.35 (20)	2.61	0.009
CS5	4.00 (20)	8.00 (20)	2.55	0.011
N6	3.00 (23)	5.90 (20)	1.99	0.047

6. Potential benefits of ant dispersal for *C. guillaumini*

Potential advantages of ant dispersal for plants have been summarized by BEATTIE (1985) in five hypotheses:

1. predator-avoidance (underground storage providing an escape from seed predators);
2. fire-avoidance (safe-haven from surface fires);
3. greater dispersal distance (the ants transport seeds away from the mother plant);
4. competition-avoidance (by being transported to ant colonies the seeds reach microenvironments with lower levels of interspecific competition); and
5. the nutrient hypothesis (ant colonies provide microenvironments with higher nutrient levels).

The predator-avoidance hypothesis does not explain a potential benefit of *A. swammerdami* dispersal to *C. guillaumini*. On average 13.8 % (range 0-68 %) of the seeds on the edge of colonies ($n = 10$) had little holes and were emptied by small rodents (mainly *Eliurus myoxinus*, rarely *Macrotarsomys bastardi*). Also 10.7 % (range 0-59 %) of the seeds were cracked into two or more parts by the Giant Jumping Rat (*Hypogeomys antimena*). The predation rate on seeds in the refuse piles compared to the ones below the canopy was on average only 2.3 % lower for *E. myoxinus*-type predation (paired t-test, $n = 10$, $t = -0.17$, n.s.) and on average 3.8 % lower for *H. antimena*-type predation (paired t-test, $n = 10$, $t = -1.10$, n.s.). More thorough investigations indicated that in some years seed predation by both *E. myoxinus* and *H. antimena* might be even higher on the edge of the ant colonies than below the canopy (BÖHNING-GAESE et al., unpublished data).

The fire-avoidance hypothesis also fails to explain advantages of *A. swammerdami* dispersal. Firstly, the seeds of *C. guillaumini* are not buried. Additionally, fire is evidently not an important ecological factor in the forest of Kirindy as it is almost impossible to set the forest on fire (COVI, 1988).

Greater dispersal distance might be a benefit of *A. swammerdami* dispersal to *C. guillaumini*. Most colonies are situated below the crown (Table 1). Thus, in most cases the ants do not carry the diaspores further away from the mother plant than would be expected without dispersal agent. However in feeding experiments we observed *A. swammerdami* dispersing seeds to distances of up to 10.4 m (BÖHNING-GAESE et al., unpublished manuscript). Thus, occasionally some seeds may be transported further away.

Competition-avoidance does not appear to explain a potential benefit of *A. swammerdami* dispersal. Seeds that were dispersed by *A. swammerdami* ended up in dense conspecific aggregations. Seed density in close vicinity to *A. swammerdami* colonies was considerably higher than under the crown (BÖHNING-GAESE et al., unpublished manuscript). Furthermore,

A. swammerdami also dispersed the seeds of several other plant species. Dense seed aggregations might not only cause competition, but might also attract predators, pathogens, and herbivores.

Finally, *A. swammerdami* could benefit the seedlings of *C. guillaumini* because the soil surrounding colonies might have higher nutrient levels, better soil structure, or the colonies might be placed at spots with higher light levels. These factors remain to be investigated, though it appears that they may be the most probable explanation for the benefit of *A. swammerdami* dispersal.

An additional benefit of the passage through an ant colony might be higher germination rates (CULVER and BEATTIE, 1978, 1980; HORVITZ and BEATTIE, 1980). Germination experiments, however, showed that *C. guillaumini* seeds collected from refuse piles of *A. swammerdami* colonies did not have significantly higher germination success than mature black seeds collected below the canopy (SCHWITTER, 1984a,b).

7. Bird and ant dispersal?

All *Commiphora* species of Madagascar (PERRIER DE LA BÂTHIE, 1946) and South Africa (PALMER and PITMAN, 1972) have a similar type of fruit with considerable variation in size, shape, and color of the aril. The South African *Commiphora* spp. occur primarily in hot dry bushveld, desert, and semidesert (PALMER and PITMAN, 1972; VAN DER WALT, 1973). The *Commiphora* spp. of Madagascar are described by PERRIER DE LA BÂTHIE (1946) as trophophilic or xerophilic.

Thus, *Commiphora* is similar to the genus *Acacia* in both habitat requirements and dispersal ecology. O'DOWD and GILL (1986) showed that ants collect a wide array of diaspores of arillate Australian *Acacia* spp. including ornithochorous diaspores with brightly colored arils (yellow, orange, or red). DAVIDSON and MORTON (1984) hypothesized that the combination of ornithochory and myrmecochory might be beneficial if bird densities are variable and unpredictable. Birds might be favoured but unreliable dispersal agents, with ants acting as safeguards.

In the forestry concession, the number and density of frugivorous bird species is indeed low (BÖHNING-GAESE et al., 1995). This rarity seems neither caused by local nor by historical extinction. There is no indication that the bird and lemur community in the forestry concession is impoverished compared with other forests along the west coast (LANGRAND, 1990; BÖHNING-GAESE et al., 1995). Furthermore, there is no evidence so far for the extinction of frugivorous bird species on Madagascar either in historical or in paleontological times (LANGRAND, 1990; S. GOODMAN, pers. comm.). It appears, rather, that the number of frugivorous bird species in Madagascar is and has been generally low (FLEMING et al., 1987).

The general lack of frugivorous bird species on Madagascar might have favored the evolution of seed dispersal by ants. Correspondingly, *C. guillaumini* appears to have evolved special adaptations to encourage ant dispersal. Chemical analysis of arils revealed the presence of 1,2-Diolein (SCHMEER et al., unpublished manuscript), a chemical that has been demonstrated to elicit seed carrying behavior in ants (MARSHALL et al., 1979; BREW et al., 1989; HUGHES et al., 1994).

Furthermore, as seed dispersal by birds and ants works as a two stage process, evolving adaptations to encourage ant dispersal does not exclude bird dispersal. Thus, it gives *C. guillaumini* the "benefits of both worlds": the plant can profit from both the rare events of bird dispersal and the common events of ant dispersal.

THE ECOLOGY AND CONSERVATION OF THE BAOBABS OF MADAGASCAR

D. A. BAUM

Résumé: Ecologie et conservation des baobabs de Madagascar

Il y existe dans le monde entier huit espèces de baobabs (genre *Adansonia*), dont six sont des espèces endémiques de Madagascar. On trouve ces dernières avant tout dans les forêts caducifoliées de l'ouest et du sud du pays. Dans cet article, j'expose brièvement l'écologie des baobabs de Madagascar par une synthèse de la littérature qui existe déjà sur le thème et de mes propres recherches. Je décris les espèces malgaches d'*Adansonia* et fournis une clé de détermination. Par ailleurs, je me penche sur le rôle écologique joué par les baobabs dans les forêts caducifoliées malgaches, en particulier sur leurs interactions avec les animaux, notamment les visiteurs de fleurs. Les données présentées dans l'article suggèrent que les baobabs pourraient être des « mutualistes - clé de voûte » dans certains écosystèmes malgaches et que, de ce fait, les efforts de recherche entrepris au service de la conservation de la nature devraient se concentrer sur ces arbres. Je donne également un aperçu des interactions de l'être humain avec les baobabs, évalue les possibilités d'exploitation économique et éclaire le rôle potentiel de programmes d'éducation à la conservation d'*Adansonia*, à Madagascar.

Abstract

World-wide, there are eight species of baobab (genus *Adansonia*) of which six are endemic to Madagascar, occurring predominantly in deciduous forests in the west and south of the country. In this paper I summarize the ecology of baobabs in Madagascar, incorporating both the existing literature and my own field-research. I describe the Malagasy *Adansonia* species and provide a diagnostic key. The ecological role baobabs play in Malagasy deciduous forests is described with special attention to their interactions with animals, particularly flower-visitors. The data presented suggest that baobabs may constitute "keystone mutualists" in some Malagasy ecosystems and, hence, that they should be the focus of conservation research efforts. I also summarize human interaction with the baobabs, assess the possibilities for economic exploitation and highlight the potential role of *Adansonia* in conservation education programs in Madagascar.

1. Introduction

The baobabs (genus *Adansonia* L.) comprise eight species, six endemic to Madagascar. Like their well-known relative, the African baobab (*A. digitata* L.), the Malagasy baobabs are curious-looking trees, characterized by massive, often grotesquely swollen trunks and branches. They are widespread on the western slopes of Madagascar, from the very north to the extreme south, but are particularly numerous in the west and south-west. Baobabs are ecologically significant in many Malagasy ecosystems, and in some communities, appropriately named "baobab forests", they constitute the dominant tree species.

Despite their impressive appearance and ecological significance, the biology of the Malagasy baobabs is still poorly known. In this paper, my primary aim is to summarize the systematics,