

SEED DISPERSAL BY FRUGIVOROUS TREE VISITORS IN THE MALAGASY TREE SPECIES *COMMIPHORA GUILLAUMINI*

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Abstract. We quantified fruit production, tree visitation, crop removal, and seed dispersal rates for the Malagasy tree species *Commiphora guillaumini*. We investigated six individual trees for 28 to 33 days, using fruit traps that covered the entire crown area, combined with 156 hours of tree observations. *C. guillaumini* produced relatively constant but low numbers of large-seeded, lipid-rich arillate fruits, over an extended fruiting season. During observations, trees were visited by four bird and one lemur species, which consumed 89.7% of the fruit crop. Two of the bird species were specialized frugivores, two were insectivores feeding opportunistically on the fruits of *C. guillaumini*. The dispersal rate (measured by number of seeds taken away from the immediate vicinity of the tree) was only 9.0%. Nearly all seeds dispersed involved the Lesser Vasa Parrot *Conocopsis nigra* leaving the trees while still handling seeds in its beak. Accepted 25 April 1995.

Key words: *Commiphora guillaumini*, fruit production, bird visitation, crop removal, seed dispersal, Madagascar.

INTRODUCTION

Seed dispersal by birds and mammals is one of the most important mutualistic animal-plant interactions (reviewed in Howe & Smallwood 1982, Janzen 1983, Howe 1986, Jordano 1992, Stiles 1992, Willson 1992). Nevertheless, very little quantitative information exists about the ecological and evolutionary consequences that these interactions have for the species involved (Begon *et al.* 1990). One of the reasons for this lack of understanding is the scarcity of quantitative data on the structure of dispersal systems (Howe & Smallwood 1982, Howe 1986, 1993, Schupp 1993).

The dispersal systems of Madagascar are particularly little known. This is unfortunate because of the unique evolutionary history of Madagascar. Malagasy plant and animal species have evolved rather independently from African species for at least 120 million years, leading to particularly high levels of endemism. Thus, the objective of this study was to quantify fruit production, tree visitation, crop removal, and seed dispersal rates for the Malagasy tree species *Commiphora guillaumini*.

One of the few hypotheses about the evolutionary outcome of frugivore-plant interactions is the para-

digm of specialized versus generalized dispersal systems, first formulated by Snow (1971) and McKey (1975), and later developed by Howe & Estabrook (1977), Howe & Smallwood (1982), and Howe (1993). According to the paradigm, specialized dispersal systems involve mostly large-seeded but highly nutritious fruits that are produced in low numbers over long periods of time, with overall annual fecundity being low (< 5000 fruits). These fruits are supposed to be removed consistently by few, often large, specialized frugivorous bird species that reliably disperse a high proportion of seeds away from the parent tree (Howe 1993).

In contrast, generalized dispersal systems involve mostly small-seeded but energy-poor fruits that are produced in superabundance during a short, sharply-peaked fruiting season with high overall annual fecundity (> 20 000 fruits). In generalized dispersal systems, fruits are supposed to be removed by many opportunistic species of birds and often mammals. Nevertheless, total fruit removal and seed dispersal rates are typically quite low (Howe 1993).

Although the paradigm is controversial (e.g., Wheelwright & Orians 1982, Herrera 1985, 1986, Howe 1993, Levey *et al.* 1994), it provides a valuable conceptual framework for understanding the evolution of frugivore-plant interactions. By comparing the results of our investigation with the theoretical frame-

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work of the paradigm, we sharpen our perception and improve our understanding of the dispersal system of *C. guillaumini*.

Study site. The study was conducted from the middle of February until the end of March 1993 in a dry deciduous forest of western Madagascar. The study site was the Forêt de Kirindy, a 10 000-ha forestry concession of the Centre de Formation Professionnelle Forestière de Morondava (CFPF) located 60 km north of Morondava. The forest has been used for selective logging, which in this case has had very little negative impact on the vegetation or the abundance and distribution of animals (Ganzhorn *et al.* 1990). In the study area, precipitation ranges between 300 and 1400 mm per year with an average of 770 mm (Ganzhorn *et al.* 1990). The rains start in November and last till April with heavy rains in January and February. A brief description of the area is given by Covi (1988) and Nicoll & Langrand (1989). Within the forestry concession the study was conducted in block "CS7" (Ganzhorn *et al.* 1990), a control area not used for selective logging and with high abundance of *C. guillaumini* trees (Böhning-Gaese, unpublished data).

Study system. The "Arofy à grandes feuilles", *Commiphora guillaumini* (H. Perr. 1944, Schwitter 1984) is the most abundant of five species of *Commiphora* (Burseraceae) that are known to occur in the forestry concession (Rakotonirina, pers. comm.). *C. guillaumini* is the dominant canopy tree species, representing 42% of the trees > 40 cm DBH (Hunziker 1981). The trees grow to 20 m in height with a trunk diameter of up to 80 cm DBH (de la Bathie 1946, Rohner & Sorg 1986). The species is dioecious, with flowering taking place from October to November and fruiting from January to April (Rohner & Sorg 1986).

The roundish fruits (diameter 20 to 25 mm) are borne in small clusters at the ends of 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 (*sensu* Howe & Smallwood 1982). The diaspore consists of a brilliant black kernel (about 13 x 8 x 6 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. Because the aril is very tough, it can be removed from the kernel

only with difficulty. In most instances 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.

METHODS

Fruit traps. In order to trap the fruit coverings and kernels we installed under six trees (O1–O6) large nets for four to five weeks from the middle of February until the end of March (Fig. 1). Nets were installed after fruit production had started and were removed before fruit production ended. The nets covered the entire crown area of the trees and were inspected four times daily (at dawn between 05:50–06:20 h, in the morning: 09:30–10:30 h, in the afternoon: 14:00–15:00 h and at dusk: 18:15–18:45 h), with the exception of two periods of three days each. At each inspection the number of coverings and seeds was counted and the bill and tooth marks left on the seeds by frugivorous tree visitors were identified.

The coverings collected in the nets gave the number of ripe fruits produced per day. As each fruit has two coverings and one seed, the percentage of seeds removed could be obtained by calculating the difference between the number of seeds expected and the number of seeds found in the nets. We defined seeds that were transported away from the crown, and therefore did not drop in the nets, as having been dispersed.

As fruit production varies daily, and fruit coverings and seeds do not drop simultaneously, seed dispersal rates could not be calculated precisely. For example, in the net of tree O2, we found 1141 coverings, corresponding to 570.5 fruits, and 576 seeds. Thus, we found five to six seeds more than we expected from the number of ripe fruits produced. Hence, seeds were not "exported" but "imported", resulting in a negative dispersal rate for tree O2 (Table 1). Although a negative dispersal rate is biologically meaningless, we did not report it as zero because this would have biased further statistical analysis, e.g., the value for average dispersal rate calculated over all six trees.

The bill and tooth marks left on the seeds by tree visitors were identified using a key obtained during tree observations (see below). We observed no rodents or ants removing seeds from the nets.

Tree observations. In order to identify which frugivorous tree visitors visited the trees, to determine their

relative frequency, and to describe their behavior, the same six trees were watched for two days each. Observations were conducted in blocks: in the morning from 05:50–10:00 h, at midday 10:00–14:30 h and in the afternoon 14:30–18:45 h (sum of observations 156 hours). Observation blocks began and ended in correspondence to the four regular inspections of the fruit traps (see above). The observation blocks were randomly distributed over the study period. Observations were conducted from hides as the most frequent tree visitors, the vasa parrots (*Coracopsis* spp.), were hunted and therefore shy. All visits by animals were recorded. For each visitor we noted the seed handling behavior and the time spent in the tree, and we counted the number of seeds dropped in the nets. Analysis was limited to individuals for which foraging for arils had been observed.

RESULTS

Phenology of fruit production. The trees produced ripe fruits over the entire study period of 28 to 33 days (depending on the tree) (Fig. 1). Fruit production peaked in trees O1 and O5 in the middle of March, in tree O2 fruit production increased towards the end of March (Fig. 1). Trees O3, O4 and O6 produced fairly constant numbers of fruits over the entire study period. Trees O1 to O4 and O6 produced on average between 8.7 and 17.5 ripe fruits per day. Tree O5 had a much larger crown area and produced on average 108.9 ripe fruits per day. During the study period the trees produced from 284 to 3276 fruits. From the number of coverings found on the ground before the fruit traps were installed, and the number of fruits remaining on the trees after the fruit traps were removed, the overall annual fecundity of the trees could be estimated: from 345 to 4591 fruits per tree.

Frugivorous tree visitors

Tree visitors during tree observations. The arils of *C. guillaumini* were eaten by four bird and one primate species: the vasa parrots *Coracopsis nigra* and *C. vasa*, the Common Jery *Neomixis tenella*, the White-headed Vanga *Leptopterus viridis* and the diurnal lemur *Propithecus verreauxi*. The most frequent tree visitor (with 64 individuals) was the Lesser Vasa Parrot *C. nigra* (Psittacidae, body length 35 cm; Fig. 2). *C. nigra* was observed in all six trees. It visited the trees individually or in small flocks of up to five individuals. *C. nigra* is characterized as a frugi- and granivore (Langrand

1990). Most often, the parrots picked the diaspores with their beaks and nibbled off the arils using beak and tongue. As the aril is tough and difficult to remove, handling times ranged between 15 and 25 s. While handling the diaspores the parrots climbed through the crown, already looking for fresh ones. After arils had been nibbled off, seeds were usually dropped directly under the crown. In at least 11 out of 64 visits (17%) we observed the parrots taking off with a seed still in their beaks, thereby dispersing it. Average duration of *C. nigra* visits was 115 ± 102 s (range = 25 s - 8 min, $n = 33$) with 3.9 ± 5.8 seeds (range = 0 - 34, $n = 42$) dropped in the net per individual.

Of all visiting species, *C. nigra* consumed by far the largest proportion of arils. After 156 hours of tree observation we found 307 seeds in the fruit traps, of which 298 (97.1%) could be "identified" because the visitors left characteristic bill or teeth marks or because the arils had not been eaten at all. On an average of 82.6% ($n = 6$ trees) of these 298 seeds, the arils had been eaten by *C. nigra* (Fig. 3).

The Common Jery *N. tenella* (Timaliidae, 10 cm), with 53 visits, was the second commonest tree visitor (Fig. 2). *N. tenella* is similar in size, plumage color and behavior to Old World leaf-warblers. *N. tenella* is usually insectivorous (Langrand 1990). However, we observed *N. tenella* foraging on arils in five of the six trees. It visited trees singly or in groups of two or three individuals. *N. tenella* nibbled on the exposed arils, frequently while hanging head down. Thus the diaspores stayed attached to the twig and a single aril was frequently fed upon for up to 10 min, over several visits. In some cases the diaspore became detached during handling and dropped under the crown. *N. tenella* did not disperse the seeds of *C. guillaumini*. Although *N. tenella* was a frequent tree visitor, the arils of only 5.5% ($n = 6$) of the seeds that were found in the fruit traps after observations had been eaten by it (Fig. 3).

The Greater Vasa Parrot *C. vasa* and the White-headed Vanga *L. viridis* visited the trees only occasionally. The eight visits by *C. vasa* (Psittacidae, 50 cm), a frugi- and granivore, in two of the trees were probably made by two individuals that stayed in the study area for a few days. The handling of diaspores was similar to that by *C. nigra*, but slower and less efficient. The arils of only 1.1% ($n = 6$) of the seeds had been eaten by *C. vasa* (Fig. 3). The five visits of *L. viridis* (Vangidae, 20 cm) in two of the trees were probably also made by a single pair of birds. *L. viridis* is usually

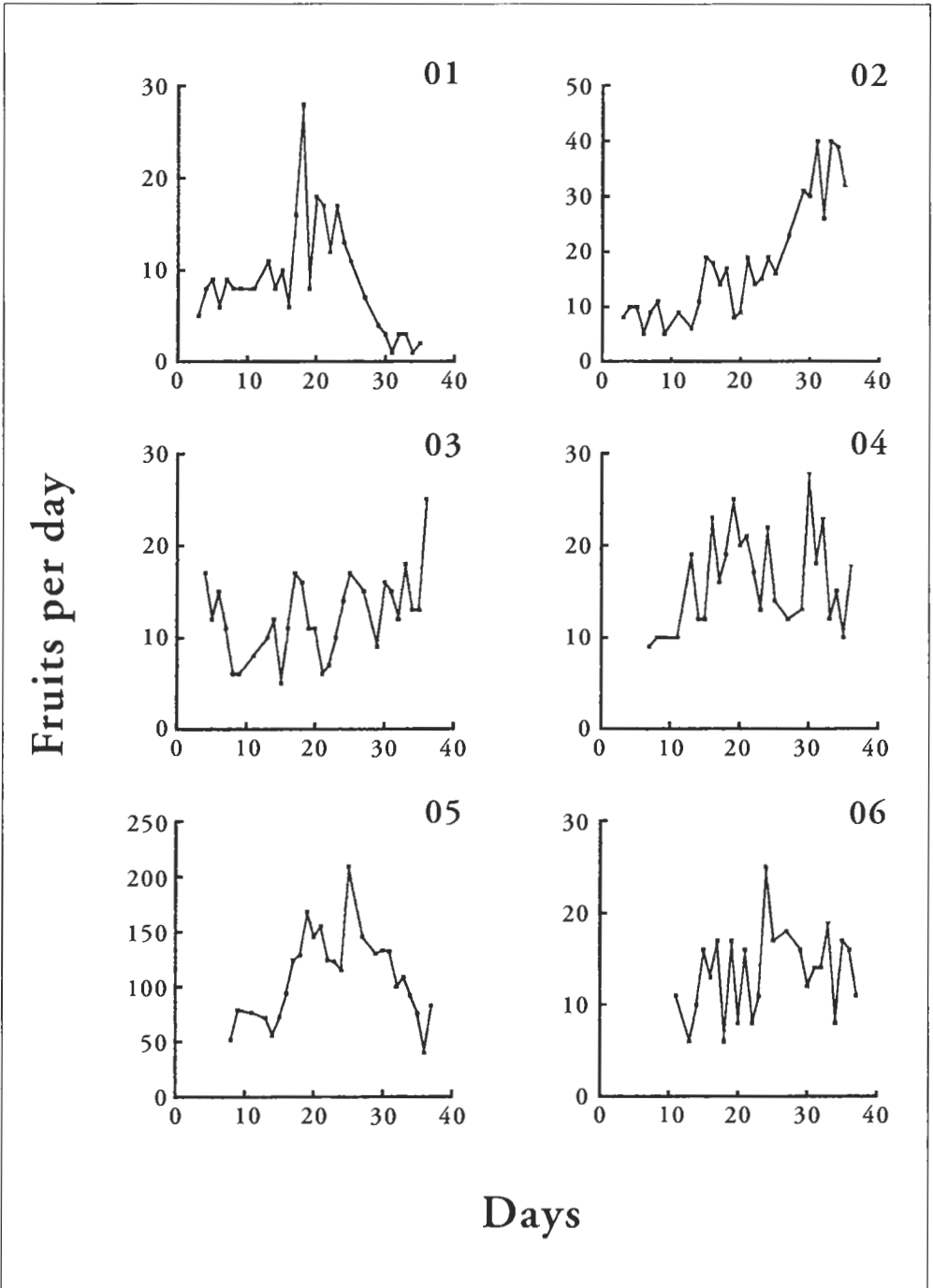


FIG. 1. Fruit production of six *C. guillaumini* trees during the study period. Day 1: 15.2., day 20: 11.3., day 40: 31.3. Notice variable scaling of ordinates.

insectivorous (Langrand 1990). We observed *L. viridis* taking diaspores with their bills, then holding them with one foot and nibbling off the arils. The seeds were dropped under the crown. The arils of 1.5% ($n = 6$) of the seeds had been eaten by *L. viridis* (Fig. 3). Neither *C. vasa* nor *L. viridis* was ever seen to disperse a seed.

The lemur *P. verreauxi* was the only primate observed eating fruits of *C. guillaumini* (five visits in two trees; Fig. 2). It used two foraging techniques. Sometimes lemurs put several ripe exposed diaspores in their mouths, chewed off the arils, spat the seeds out and thereby dropped them under the crown. On other occasions they ate the outer coverings of unripe closed fruits and, again, dropped the unripe pale seeds under the crown. In one instance, outside of the regular observation periods, we observed one individual moving off from the crown after having been disturbed with its mouth still full of seeds. *P. verreauxi*, therefore, can be regarded as occasionally dispersing the seeds of *C. guillaumini*. However, because of its low visitation rate its impact was much lower than that of *C. nigra* (see below). The arils of on average 4.8% ($n = 6$) of the seeds found in the fruit traps after observations had been eaten by *P. verreauxi* (Fig. 3).

In summary, none of the tree visitors was observed dispersing seeds by swallowing them. Occasionally, seed dispersal took place because individuals of *P. verreauxi* and, especially, *C. nigra* left the crown, while still handling seeds in their mouths or beaks. None of the frugivorous tree visitors was observed cracking seeds, thereby destroying them.

We did not observe any nocturnal animals feeding on arils during 15 hours of night observations in February and March 1994. Additionally, the number of seeds found in the nets at dawn was only 9.6% (mean = 0.19/hour; $n = 6$; range = 0.08–0.31) of the number of seeds trapped over the day (mean = 1.98/hour; $n = 6$; range = 0.61–7.53). None of the seeds found in the nets at dawn had characteristic bill and tooth marks, suggesting that they had dropped by themselves and had not been handled by animals.

Frequency of tree visitors over the entire study period. Tree visitation rates could not only be calculated from tree observations but also for the entire study period from fruit trap data. *C. nigra*, *N. tenella* and *P. verreauxi* left characteristic bill or tooth marks on the seeds (see description of handling behavior above). Therefore, we were able to "identify" not only the seeds that dropped into the nets during the observa-

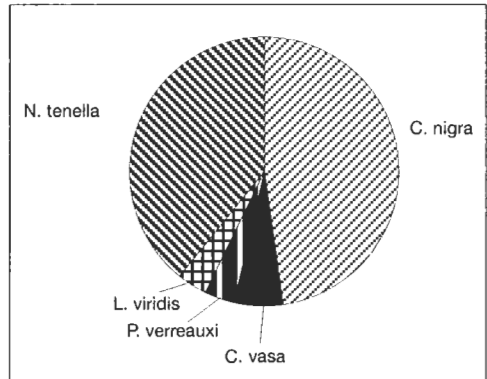


FIG. 2. Percentage of 135 visits by four bird and one lemur species to six *C. guillaumini* trees during 26 hours of observation per tree (sum 156 observation hours).

tion periods, but also the seeds that we removed from the fruit traps during the four daily inspections over the entire study period. While during observations 97.1% of the 307 seeds could be "identified" because of the presence of characteristic bill or teeth marks, or because the arils had not been eaten at all, during the regular inspections of fruit traps identification of only 59.8% of the 4920 seeds was possible, because ants visiting the fruit traps foraged on arils, thereby destroying the characteristic frugivore identification marks.

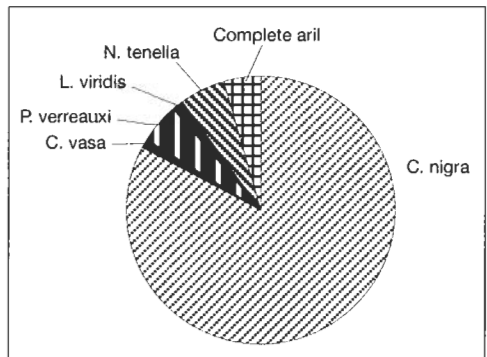


FIG. 3. Percentage evidence of consumption by four bird and one lemur species on 298 seeds whose marks could be identified following tree observations. Complete arils include those that had not been eaten or seeds that dropped as whole fruits.

Comparing the relative frequency of tree visitors as calculated from fruit trap data that were gathered after tree observations, and those that were collected over the entire study period, revealed close similarity between the two data sets (Fig. 3 and 4). This was especially obvious for the percentage of seeds whose arils had been eaten by *C. nigra*, *N. tenella* and *P. verreauxi*. However, the variance among the six trees was considerably lower for the data collected over the entire study period as compared to the data gathered after tree observations. For example, after tree observations the arils of 82.6% ($\pm 20.0\%$; $n = 6$) of the seeds had been eaten by *C. nigra*, whereas for the entire study period the figure was 80.7% ($\pm 7.9\%$; $n = 6$). The higher variance after tree observations was caused by the data being averaged over only two days, whereas for the entire study period the data were averaged over 28 to 33 days. The percentage of seeds whose arils had been eaten by *C. vasa* and *L. viridis* was probably underestimated for the entire study period because neither species left characteristic bill marks.

The percentage of seeds that dropped as whole fruits, or whose arils had not been eaten at all, was very low (4.6% after tree observations, 10.3% for the entire study period; Figs. 3 and 4).

Seed dispersal. Over the entire study period on average 9.0% (range = -1.0 – 15.2%; $n = 6$) of the seeds were dispersed by frugivorous tree visitors (Table 1). Tree

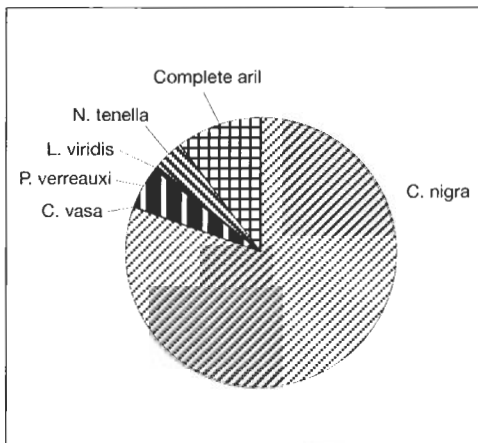


FIG. 4. Percentage evidence of consumption by four bird and one lemur species on 2940 seeds whose marks could be identified over the entire study period. Complete arils include those that had not been eaten or seeds that dropped as whole fruits.

O5, with high fruit production and high visitation rates, did not differ in the percentage of seeds dispersed from trees with relatively low fruit production (Table 1). However, in tree O5 a higher absolute number of seeds was dispersed. In the net of tree O2, 5.5 seeds more were found than expected from the number of ripe fruits produced (Table 1). This result lies within the variation we expected because fruit coverings and seeds do not drop simultaneously (see methods).

We tested the influence the visitation rates of the potential seed dispersers *C. nigra* and *P. verreauxi* had on dispersal rates. We correlated for each tree the percentage of dispersed seeds with the percentage of seeds dropped by *C. nigra* and *P. verreauxi* over the entire study period (Table 1). The percentage of dispersed seeds was a significant function of the percentage of seeds dropped by *C. nigra* (regression: $Y = -0.78 [C. nigra] + 72.17$; $R^2 = 92.0\%$; $n = 6$; $t = -6.78$; $P = 0.003$). However, no significant relationship with the percentage of seeds dropped by *P. verreauxi* could be found ($Y = 0.81 [P. verreauxi] + 5.12$; $R^2 = 45.4\%$; $n = 6$; $t = 1.82$; $P = 0.14$).

Combining the visitation rates of *C. nigra* and *P. verreauxi* to predict dispersal rates in a multiple regression, only the influence of *C. nigra* was significant ($Y = -0.71 [C. nigra] + 0.17 [P. verreauxi] + 65.81$; $R^2 = 93.2\%$; $n = 6$; *C. nigra*: $t = -4.6$; $P = 0.02$; *P. verreauxi*: $t = 0.72$; $P = 0.5$). This means that *C. nigra* was the only species with significant influence on seed dispersal. The relationship was negative because the percentage of seeds in the fruit traps became smaller the more seeds got dispersed.

The percentage of seeds handled by *C. nigra* could be calculated by adding the number of dispersed seeds to the number of seeds dropped by *C. nigra*. Doing this, the percentage of seeds handled by *C. nigra* was very similar among the six trees ($82.8 \pm 6.2\%$; range = 77.3–90.8%; $n = 6$). Hence, on average 11.3% (range = -1.1 – 19.3%; $n = 6$) of the seeds handled by *C. nigra* got dispersed (Table 1). The number of seeds dispersed by *C. nigra* during tree observations could be calculated from the number of seeds found in the nets after tree observations (307) and the percentage of seeds dispersed (9.0%) as $307 \times 0.09 / 0.91 = 30$. As 30 seeds got dispersed during 64 visits by *C. nigra* we conclude that on 47% of all visits a seed was carried away. This was a higher number than we actually observed (17%, see above). However, observations were not reliable because foliage or the body of the parrot in most instances obscured the view.

TABLE 1. Seed dispersal and visitation rates by *C. nigra* and *P. verreauxi* for six *C. guillaumini* trees over the entire study period.

Tree	01	02	03	04	05	06
Fruits in nets	283.5	570.5	398.0	456.5	3276.0	379.5
Seeds in nets	249	576	381	388	3004	322
Dispersed seeds						
Number	34.5	-5.5	17.0	68.5	272.0	57.5
Percentage	12.2	-1.0	4.3	15.0	8.3	15.2
Percentage seeds in nets whose arils had been eaten						
by <i>C. nigra</i>	74.2	90.9	89.8	74.0	80.7	74.6
by <i>P. verreauxi</i>	0.0	0.0	0.0	11.5	8.6	8.5
Percentage seeds handled by <i>C. nigra</i> ^a	77.3	90.8	90.2	77.9	82.3	78.4
Percentage of seeds handled by <i>C. nigra</i> dispersed ^b	15.7	-1.1	4.7	19.3	10.1	19.3

^a Number of seeds in net whose arils had been eaten by *C. nigra* plus number of dispersed seeds (under the assumption that all seeds were dispersed by *C. nigra*) divided by number of seeds produced.

^b Number of seeds dispersed (under the assumption that all seeds were dispersed by *C. nigra*) divided by number of seeds handled by *C. nigra*.

DISCUSSION

All phenological fruit and fruit production data suggest that *C. guillaumini* belongs to the group of trees with a specialized dispersal system. The seeds were large (length 13 mm) and the arils oily and probably energy-rich. The annual fecundity was low. Even a large tree such as tree O5 produced fewer than 5000 fruits per year. Daily fruit production rate was low but relatively constant over an extended fruiting season of at least five weeks, most probably more than two months (Fig. 1).

The response of the avian community to this fruit display was only in some aspects in agreement with the paradigm of specialized versus generalized dispersal systems. The observation that just a small group of four bird and one lemur species fed on the arils of *C. guillaumini* appears to fit the paradigm. However, the number of frugivorous bird species in the dry deciduous forests of western Madagascar is low. Four out of 114 bird species that are known to occur in the Forêt de Kirindy are mainly, and ten partly frugivorous (Langrand 1990). Two of the four mainly frugivorous bird species, the Greater and Lesser Vasa Parrots *C. vasa* and *C. nigra*, were observed feeding on the arils. The two other species, the Madagascar Green Pigeon

Trogon australis and the Madagascar Bulbul *Hypsipetes madagascariensis*, were not recorded. *T. australis* and *H. madagascariensis* have been observed in the immediate area, although with low abundance. *P. verreauxi* represents one of eight lemur species known to occur in the forest (Harcourt & Thornback 1990, Schmid & Kappeler, *in press*). All eight lemur species are potentially frugivorous.

The Greater Vasa Parrot *C. vasa*, and the dominant tree visitor, the Lesser Vasa Parrot *C. nigra*, also fitted into the paradigm. They are both large-bodied and specialized frugivores (Langrand 1990). During our studies we observed *C. nigra* feeding on the fruits of only three other plant species (A. Hampe, *unpublished data*). In contrast, the two other bird species observed, *N. tenella* and *L. viridis*, are normally exclusively insectivorous (Langrand 1990). During our study they fed opportunistically on the arils of *C. guillaumini*. Nevertheless, *N. tenella* was the second commonest species observed (39.3% of all individuals; Fig. 2). *C. guillaumini* obviously attracted not only specialized but also opportunistic frugivorous species.

In good agreement with the paradigm was the high fruit consumption rate of 89.7%. This value is higher than any other reported so far (Howe 1986). In strong contradiction to the paradigm however, was

the strikingly low seed removal and dispersal rate of 9.0%. The seed removal rate was even considerably lower than the 27.8% reported for *Tetragastris panamensis*, one of the "classic" generalized dispersal systems (Howe 1980). The low dispersal rate in *C. guillaumini* was caused by the unusual dispersal mechanism. The seeds were dispersed zoochor, but not in the crop or the gut of the disperser. The tough arils forced the frugivores to long handling times, which had the effect that the trees were deserted while the frugivores still had seeds in their beaks or, in the rare case of dispersal by lemurs, in their mouths.

Our study demonstrated that in order to understand the evolution of dispersal systems it is extremely important to collect more thorough and quantitative data, a task already promoted since the late 1970's by Howe (e.g., Howe & Smallwood 1982). Although *C. nigra* provided 47.4% of the tree visitors and handled 82.8% of the seeds, it dispersed only 11.3% of the seeds handled and was still essentially the only seed disperser. Thus, in order to determine the effectiveness of seed dispersers, visitation, consumption, and dispersal rates of all tree visitors have to be carefully determined (Schupp 1993). Additionally, it is important to know the establishment success of dispersed versus non-dispersed seeds (Schupp 1993). This remains to be investigated for *C. guillaumini*.

Our results were only obtained by using rigorous methods, i.e., the combination of fruit traps and tree observations. Tree observations enabled us to identify the tree visitors, to watch their behavior and to interpret the characteristic bill and tooth marks on the seeds they left behind. The fruit traps enabled us to extrapolate for each tree the data obtained during two days of observations to the entire study period of 28 to 33 days. By doing this, the variation between the trees was reduced considerably. Thus the data for individual trees became more reliable. Furthermore, the low percentage of dispersed seeds could be calculated with high precision only by using nets that covered the entire crown area of the tree. Fruit traps that covered only parts of the crown area as used, e.g., by Howe (1980) and Howe & Vande Kerckhove (1981) would not have been useful in our study system.

Our study is one of the first quantitative studies of Malagasy seed dispersal systems (but see Scharfe 1991). The results were in many aspects unique. 1. Seed dispersal was performed by essentially only one bird species. 2. This species was unexpectedly a parrot. In other dispersal systems studied, most of them in the Neotropics, parrots either do not disperse seeds

(Howe 1977) or are even seed predators (Howe 1980, Janzen 1981, Galetti & Rodrigues 1992, Galetti 1993). 3. Regular seed dispersal by transport in the bill has, until now, never been observed (Howe 1986).

The dispersal system of *C. guillaumini* might be unusual because the "right" dispersers might have gone extinct. However, there is so far no evidence for the extinction of frugivorous bird species on Madagascar either in historical or in paleontological time (Langrand 1990, S. Goodman, *pers. comm.*). There might have been lemur species that dispersed the seeds of *C. guillaumini* and which went extinct. However, the diaspores show characteristics typical of the bird dispersal syndrome (van der Pijl 1982, Howe 1986). Hence, in agreement with our tree observations, one does not expect primates to be the "regular" dispersers of *C. guillaumini* seeds.

Additionally, there is no indication that the bird and lemur community in the Forêt de Kirindy is impoverished compared with other forests along the west coast. The Forêt de Kirindy is one of the largest forest fragments left in western Madagascar. It is even one of Langrand's "recommended sites for observing the avifauna of Madagascar" (Langrand 1990) because of its high bird species richness and the presence of rare forest species such as the White-breasted Mesite *Mesitornis variegata*.

Another explanation for the unusual dispersal system of *C. guillaumini* might be that the Lesser Vasa Parrots were just accidentally visiting *C. guillaumini* trees. However, our observations suggest that the parrots fed frequently on the arils of *C. guillaumini* and checked the trees in one area on a regular basis. *C. nigra* visits were very short (mean duration 115 s), they usually spent all their time in the trees foraging for arils, seed handling appeared to be very efficient, and we observed in many instances that an individual either came from or left for another *C. guillaumini* tree.

The unusual dispersal mechanism of *C. guillaumini* might result from the fact that the arils do not cover the seeds completely. This might make it easier for birds and primates to nibble off the aril without swallowing the whole seed. In all tree species that are traditionally cited to support the paradigm of specialized versus generalized dispersal systems (Howe & Smallwood 1982), the pulp covers the seeds completely. However, Howe (1977) reported for *Casearia corymbosa*, in which the arils do cover the seeds completely, that two species of parrots (*Amazona autumnalis* and *A. farinosa*) also stripped arils with their

beaks and dropped seeds *in situ*. Thus, the unusual shape of the arils appears not to be the reason *C. guil-laumini* seeds were not swallowed.

Seed dispersal systems in Madagascar might in general be very different from the ones in the Neotropics or other regions of the world. The avifauna of Madagascar is relatively poor with 256 species. The long history of independent evolution, however, has led to rates of endemism that are extremely high in terms of both genera (24.6%) and species (53.0%; Langrand 1990). Relatively low numbers of bird species and long periods of isolated evolution might have caused unusual dispersal systems. Although Madagascar shares its independent evolution with archipelagos such as Hawaii or the Galapagos islands, it is considerably larger and includes major components of most tropical ecosystems, ranging from lowland rain forest to semi-deserts (Ganzhorn & Kappeler 1993). This makes Madagascar an island that might be especially suited for understanding the evolution of dispersal systems. But before we can reach this point further thorough studies of Malagasy dispersal systems have to be conducted.

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