SEED DISPERSAL BY FRUGIVORES: TREE VISITORS IN THE MALAGASY TREE SPECIES COMMIPHORA GUAILLUMINA

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Abstract: We quantified fruit production, tree visitation, crop removal, and seed dispersal rates for the Malagasy tree species Commiphora guillamina. We investigated an individual tree for 28 to 33 days, using fruit traps that covered the entire crown area, combined with 168 hours of tree observations. C. guillamina produced relatively constant but low numbers of large-seeded, fleshy drupe fruits, over an extended flowering season. During observations, trees were visited by fruit-bird and one kind of species, which consumed 89.7% of the fruit crop. Two of the fruit species were specialized frugivores, one was insectivorous feeding opportunistically on the fruits of C. parviflora. The dispersal rate (measured by number of seeds taken away from the immediate vicinity of the tree) was only 0.96. Nearly all seeds dispersed involved the Lesser Vaya Parrot, C. guillamina. We observed the tree while still handling seeds in its trunk. Accepted 20 April 1995.

Key words: Commiphora guillamina, fruit production, bird visitation, crop removal, and seed dispersal.

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, Seil 1992, Wilkun 1993). Nevertheless, very little quantitative information exists about the ecological and evolutionary consequences that these interactions have for the species involved (Héran et al. 1990). One of the reasons for this lack of understanding is the scarcity of quantitave data on the structure of dispersal systems (Howe & Smallwood 1982, Howe 1986, 1993, Schupp 1993).

The dispersal systems of Madagascar are particu-larly little known. This is unfortunate because of the unique evolutionary history of Madagascar. Malagasy plant and animal species have evolved rather inde-pendently from African species for at least 120 mil-lion years, leading to particularly high levels of endem-ism. Thus, the objective of this study was to quantify fruit production, tree visitation, crop removal, and seed dispersal rates for the Malagasy tree spe-cies Commiphora guillamina.

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 McCoy (1975), and later developed by Howe & Enquist (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 flowering season with high overall annual fecun-dity (> 20 000 fruits). In generalized dispersal systems, fruits are supposed to be removed by many opportunistic species of birds and other mammals. Nevertheless, total fruit removal and seed dispersal rates are typically quite low (Howe 1995).

Although the paradigm is controversial (e.g., Wheelwright & Ortia 1982, Herura 1985, 1986, Howe 1993, Lamy et al. 1996), 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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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 forest concession of the Centre de Formation Professionnelle Forestière de Morondava (CFPM) 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 (Gurnham et al. 1990). In the study area, precipitation ranges between 300 and 1400 mm per year with an average of 770 mm (Gurnham 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 Cossi (1988) and Noss & Langrand (1989). Within the forest concession the study was conducted in block "C5" (Gurnham et al. 1990), a control area not used for selective logging and with high abundance of C. guinaeae trees (Böhning-Gaese, unpublished data).

Study system. The "nephel à grandes feuilles", Cornuophora guinaeae (H.Prov. 1944, Schwartz 1984) is the most abundant of five species of Cornuophora (Balaracidae) that are known to occur in the forest concession (Rakotondravina, pers. comm.). C. guinaeae is the dominant canopy tree species, representing 42% of the trees > 40 cm DBH (Hambito 1981). The trees grow to 20 m in height with a trunk diameter of about 80 cm DBH (de la Beche 1946, Rohner & Sorg 1986). The species is diocious, 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-red fleshy outer covering (scarp and mesocarp) that splits when mature into two halves, exposing a single drupelet (Cossio Hone & Smillwood 1982). The drupelet consists of a brilliant black kernel (about 13 x 8 x 6 mm), which is partially surrounded by a cup-like red fleshy pericarp (van der Walt 1973, p. 55, van der Puij 1982, p. 144).

The pericarp (in the following "sep") is rich in lipids and palatable, whereas the outer covering is full of secondary compounds and unpalatable. Because the Sep is tough, it can be removed from the kernel only with difficulty. In most instances the covering splits from the tree and drops off, leading to a display of the drupelet so fragrant usually tree viowits. If the tree is not visited, drupelets can accumulate over several days.

METHODS Fruit traps. In order to trap the fruit coverings and kernels we installed under six trees (01-06) large nets for five 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 ceased. 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 leaf and shoot marks left on the fruits by fragrant tree vitisors were identified. The coverings collected in the nets gave the number of ripe fruits produced per day. At each fruit hit two coverings and one seed, the percentage of seed removed could be calculated by dividing 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. At fruit production varies daily, and fruit coverings and seeds do not drop simultaneously, seed dispersed rates could not be calculated precisely. For example, in the net of tree O2, we found 1144 coverings, correspond- ing to 575 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 "labelled" but "imprinted", resulting in a negative dispersed rate for tree O2 (Table 1). Although a negative dispersed 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 trees.

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

Tree observations. In order to identify which fragrant tree vitisors visited the Sep, to determine their
relative frequency, and to describe their behaviour, the same six trees were watched for two days each. Observations were conducted in blocks in the morning from 09.50 - 11.00 h, at middle 10.00 - 14.50 h and in the afternoon 14.30 - 18.45 h (sum of observations 156 hours). Observation blocks began and ended in correspondence to the forest regular inspections of the fruit traps (see above). The observation blocks were randomly distributed over the study period. Observations were conducted from hides at the most frequent tree visitors, the Vista parrot (Cyanopsitta sp.), were burned and therefore they did. All visits by animals were recorded. For each visitor we noted the handling behaviour and the time spent in the trees, 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 35 days (depending on the tree) (Fig. 1). Fruit production peaked in tree O3 and O5 in the middle of March, in tree O2 fruit production increased to the end of March (Fig. 1). Trees O3, O4 and O6 produced fairly constant numbers of fruits over the entire study period. Trees O3 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. 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 first traps were removed, the overall annual fecundity of the tree could be estimated from 345 to 4591 fruits per tree.

Fragileuess tree visitors
Tree visitors during tree observations. The arils of C. guianense were eaten by four bird and one primate species: the vista parrot Cyanopsitta sp. and C. noae, the Common Jery Nesiotis atene, the White-headed Vanga Lepidosparva vanga and the diurnal lorimer Prophilocho emisma. The most frequent tree visitor (with 56 individuals) was the Litera Vista Parrot C. signa (Pimandaceae, body length 35 cm; Fig. 2). C. signa was observed in all six trees. It visited the trees individually or in small flocks of up to five individuals. C. signa is characterized as a frugivorous and granivorous (Langrand 1990). Most often, the parrots picked the diaspora with their bills and nibbled off the arils using beak and tongue. As the arils is tough and difficult to remove, handling times ranged between 15 and 25 s. While handling 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 use of 64 visits (17%) we observed the parrots taking off with a seed still in their beak, thereby dispersing a. Average duration of C. signa visits was 115 ± 102 s (range 25 ± 8 min, n = 33) with 3.9 ± 5.8 seeds (range 0 - 34, n = 42) dropped in the net per tree. Of all visiting species, C. signa consumed by far the largest proportion of seeds. After 156 hours of tree observation we found 307 seeds in the fruit traps, of which 298 (97%) could be "identified" because the visitors left characteristic bill or teeth marks or because the arils had not been eaten at all. On average of 82.6% (n = 6 trees) of these 298 seeds, the arils had been eaten by C. signa (Fig. 3).

The Common Jery Nesiotis atene (Timaliidae, 10 cm), with 53 visits, was the second commonest tree visitor (Fig. 2). N. atene is similar to the previous species, plumage color and behavior to Old World finches. N. atene is usually incommunicadus (Langrand 1990). However, we observed N. atene foraging on arils in five of the six trees. It visited trees singly or in groups of two or three individuals. N. atene nibbled on the exposed arils, frequently while hanging head down. Thus the diaspora exposed to the rufous and a single aril was frequently fed upon for up to 10 min, over several visits. In some cases the diaspora became detached during handling and dropped under the crown. N. atene did not disperse the seeds of C. guianense. Although N. atene was a frequent tree visitor, the arils of only 1.5% (n = 10) of the seeds that were found in the fruit traps after observations had been eaten by it (Fig. 3).

The Greater Vista Parrot C. noae and the White- headed Vanga L. viridis visited the trees only occasionally. The white Vanga L. viridis (Pititridae, 50 cm; Fig. 2) C. signa was observed in all six trees. It visited the trees individually or in small flocks of up to five individuals. C. signa is characterized as a frugivorous and granivorous (Langrand 1990).
FIG. 1. Fruit production of six C. gallinacea trees during the study period. Day 1: 15.2, day 20: 71.3, day 40: 31.3. Notice variable scaling of ordinates.
in offshoots (Langford 1990). We observed L. viridis taking deposits with their bills, then holding them with one foot and nibbling off the arils. The seeds were dropped under the crown. The arils of 1.9% (n = 6) of the seeds had been eaten by L. viridis (Fig. 3). Neither C. nigra nor L. viridis was ever seen to disperse a seed.

The linens P. remota was the only primary observed using fruits of C. sabulettii (five visits in two trees, Fig. 2). It used two foraging techniques. Sometimes lemurs put several ripes exposed deposits 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 covering 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 dislodged with its mouth still full of seeds. P. remota, therefor, can be regarded as occasionally dispersing the seeds of C. sabulettii. However, because of its low visitation rate its impact was much lower than that of C. nigra (see below). The arils at an average 4.8% (n = 6) of the seeds found in the fruit traps after observation had been eaten by P. remota (Fig. 3).

In summary, none of the true visitors we observed dispersing seeds by swallowing them. Occasionally, seed dispersal took place because individuals of P. remota and, especially, C. nigra left the crowns, 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 96% (mean = 0.19/fruit; n = 6; range = 0.08–0.51) of the number of seeds trapped over the day (mean = 1.98/fruit; n = 6; range = 0.64–7.53). None of the seeds found in the nets at dawn had characteristic bill and tooth marks, suggesting that they had been 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 true observations has also for the entire study period from fruit trap data. C. nigra, N. scelid and P. remota 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 observation periods, but also the seeds that were removed from the fruit traps during the daily inspections over the entire study period. While during observations 97.7% of the 302 seeds could be "identified" because of the presence of characteristic bill or tooth marks, or because the arils had not been eaten at all, during the regular inspections of fruit traps identification of only 39.8% of the 4920 seeds was possible, because arils visiting the fruit traps foraged on arils, thereby destroying the characteristic frugivores identification marks.
Comparing the relative frequency of tree visits 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 (Figs. 3 and 4). This was especially obvious for the percentage of seeds whose arils had been eaten by C. nigra, N. serra and P. vernacu. However, the variation 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% (± 20.0%) n = 60 of the seeds had been eaten by C. nigra, whereas for the entire study period the figure was 80.7% (± 7.5%) 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. nigra 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 dispersion. Over the entire study period on average 9.9% (range = 1.0 – 15.2%; n = 6) of the seeds were dispersed by frugivorous tree vipers (Table 1). Tree OS5, with high fruit production and high variation rates, did not differ in the percentage of seeds dispersed from trees with relatively low fruit production (Table 1). However, in tree OS5 a higher absolute number of seeds were dispersed. In the rest of tree OS2, 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 of the visitation rates of the potential seed dispersers C. nigra and P. vernacu on the rate of dispersed seeds. For each tree we correlated the per centage of dispersed seeds with the strength of seed dispersal by C. nigra and P. vernacu (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; R² = 92.0%; n = 6; t = 6.78; P = 0.003). However, no significant relationship with the percentage of seeds dispersed by P. vernacu could be found (Y = 0.81 (P. vernacu) + 5.12; R² = 45.4%; n = 6; t = 1.82; P = 0.14).

Combining the visitation rates of C. nigra and P. vernacu to predict seed dispersal in a multiple regression, only the influence of C. nigra was significant (Y = 0.71 (C. nigra) + 0.37 (P. vernacu) + 65.81; R² = 93.2%; n = 6; C. nigra: t = 4.66; P = 0.02; P. vernacu: t = 0.72; P = 0.50). 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 trap became smaller as 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% ± 6.2%; range = 77.3 – 90.9%; n = 6). Hence, on average 11.3% (range = 1.3 – 19.3%) n = 60 of the seeds handled by C. nigra got dispersed (Table 3). 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 (107) and the percentage of seeds dispersed (9.9%) as 307 x 0.091/311.3 = 30. As 306 seeds got dispersed during 64 visits by C. nigra we can 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 parent in most instances obscured the view.

![Image](37x605 to 412x1198)

FIG. 4. Percentage evidence of consumption by four birds and one lizard on 2944 seeds whose seeds could be identified on the entire study period. Complete arils include those which had not been eaten or seeds that dropped as whole fruits.
TABLE I. Seed dispersal and vegetation rates by C. nigra and P. tremuloides for six C. pellamnioides trees over the entire study period.

<table>
<thead>
<tr>
<th>Year</th>
<th>01</th>
<th>02</th>
<th>03</th>
<th>04</th>
<th>05</th>
<th>06</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fruits in net</td>
<td>285.5</td>
<td>579.5</td>
<td>398.0</td>
<td>456.5</td>
<td>3726.0</td>
<td>379.5</td>
</tr>
<tr>
<td>Seeds in net</td>
<td>249</td>
<td>576</td>
<td>381</td>
<td>388</td>
<td>3004</td>
<td>322</td>
</tr>
<tr>
<td>Dispersed seeds</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number</td>
<td>34.5</td>
<td>5.5</td>
<td>17.0</td>
<td>68.5</td>
<td>272.0</td>
<td>57.5</td>
</tr>
<tr>
<td>Percentage</td>
<td>12.2</td>
<td>-</td>
<td>4.3</td>
<td>15.0</td>
<td>8.3</td>
<td>15.2</td>
</tr>
<tr>
<td>Percentage seeds in net whose arils had been ingested by C. nigra</td>
<td>75.2</td>
<td>90.9</td>
<td>89.8</td>
<td>74.0</td>
<td>80.7</td>
<td>74.6</td>
</tr>
<tr>
<td>by P. tremuloides</td>
<td>0.6</td>
<td>0.0</td>
<td>0.0</td>
<td>11.5</td>
<td>8.6</td>
<td>8.5</td>
</tr>
<tr>
<td>Percentage seeds handled by C. nigra</td>
<td>77.3</td>
<td>90.8</td>
<td>90.2</td>
<td>77.9</td>
<td>82.5</td>
<td>78.4</td>
</tr>
<tr>
<td>Percentage seeds dispersed by C. nigra</td>
<td>15.7</td>
<td>-1.1</td>
<td>4.7</td>
<td>19.3</td>
<td>10.1</td>
<td>19.3</td>
</tr>
</tbody>
</table>

1 Number of seeds in net whose arils had been ingested 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).
2 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. pellamnioides belongs to the group of trees with a specialized dispersal system. The seeds were large (length 1.3 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. Only fruit production year was low but relatively constant over an extended flowering 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 one in some aspects in agreement with the paradigm of specialized versus generalized dispersal systems. The observations that just a small group of four bird and one lemur species fed on the arils of C. pellamnioides appears to fit the paradigm. However, the number of frugivorous bird species in the dry deciduous forests of western Madagascar is low. Fruits of 116 bird species that are known to occur in the Forêt de Kirindy and an area of 5000 ha are mainly, and non-paritally frugivorous (Langrand 1998). Two of the four main frugivorous bird species, the Greater and Lesser Vasa Parrots, C. osae and C. nigra, were observed feeding on the arils. The two other species, the Madagascar Green Pigeon and the Madagascar Bulbul Pycnonotus madagascariensis, were not recorded. T. andrei and H. madagascariensis have been observed in the immediate area, although with low abundance. P. tremuloides represents one of eight lemur species known to occur in the forest (Harcourt & Thorburn 1995. Schmid & Kopperl, unpubl. data). All eight lemur species are potentially frugivorous. The Greater Vasa Parrot C. osae and the dominant lemur visitor, the Lesser Vasa Parrot C. nigra, also fitted into the paradigm. They are both large-bodied and specialized frugivores (Langrand 1993). During our studies we observed C. nigra feeding on the fruits of only three other plant species (A. Hampa, unpubl. data). In contrast, the two other bird species observed, N. troile and L. uvula, are normally exclusively insecivorous (Langrand 1996). During our study they fed opportunistically on the arils of C. pellamnioides. Nevertheless, N. troile was the second commonest species observed (33.9% of all individuals, Fig. 2). C. pellamnioides 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 (Harcourt, 1986).

In strong contradiction to the paradigm however, was
the unusually low seed removal and dispersal rate of 9.0%. The seed removal rate was even considerably lower than the 27.8% reported for Tempanisia pana-
menio, one of the "classic" generalized dispersal systems (Howe 1980). The low dispersal rate in C. drossieri was caused by the unusual dispersal mechanism. The seeds were dispersed anecdotally, but not in the crop - or the gut of the disperser. The tough arils forced the -fruits- to soil handling times, which had the effect that the trees were deserted while the frugivores still had seeds in their "banks", as in the case of dispersal by kensou, in their "melonbanks".

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 1970s by Howe (e.g., Howe & Smallwood 1982). Although C. super was scored 47.4% of the tree visits and handled 82.8% of the seeds, it dispersed only 11.9% of the seeds handled and was still essentially the only seed disseminator. Thus, in order to determine the effectiveness of seed dispersers, visitation, consumption, and dispersal rates of all tree visitors have to be carefully documented (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. guianensis.

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 visiters, to watch their behavior and to inter-
pret the characteristic bill and teeth 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 indi-
vidual trees became more reliable. Furthermore, the low percentage of dispersed seeds could be calculated with high precision only by using trees that covered the entire crown area of the tree. Fruit traps that covered only parts of the crown area as e.g., by Rousse (1980) and Howe & Vanda Korikovich (1981) could not have been useful in our study system.

Our study is one of the first quantitative studies of Malagasy seed dispersal systems (but see Shachar 1991). The results were in many aspects unique. 1. Seed dispersal was performed by frugivorous only one bird species. 2. This species was unspecifically a passerine. In other dispersal systems studied, most of them in the Neomuscicapinae, passerine either do not disperse seeds (Howe 1977) or are even seed predators (Howe 1980, Janzen 1981, Galen & Rodrigues 1992, Galen 1993). 3. Regular seed dispersa by transport in the bill was, until now, never been observed (Howe 1986). The dispersive system of C. guianensis 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 Mada-
gascar either in historical or in palaeontological time (Lambert 1990, S. Goodwin, pers. comm.). There might have been lemurs species that dispersed the seeds of C. guianensis and which were extinct. However, the dispersion show characteristics typical of the bird dispersal syndromes (van der Pijl 1982, Howe 1986). Moreover, in agreement with our tree observa-
tions, one does not expect primates to be the "regular" disperser of C. guianensis seeds.

Additionally, there is no indication that the bird and lemur community in the Ivato de Kityana is impoverished compared with other forests along the west coast. The Ivato de Kityana is one of the largest forest fragments left in western Madagascar. It is one of Langrand's "recommended sites for observing the avifaunia of Madagascar" (Langrand 1990) because of its high bird species richness and the presence of rare forest species such as the White-breasted Mixta Melanotis leucogaster. Another explanation for the unusual dispersal system of C. guianensis might be that the Leonis Voas Parmas were just accidentally visiting C. guianensis trees. However, our observations suggest that the par-
aves fed frequently on the arils of C. guianensis and checked the trees in one area on a regular basis. C. super was visited very short (mean duration 165 s), they usually spent all their time in the trees foraging for arils, seeds handling appeared to be very efficient, and we observed in many instances that an individual either came from or left for another C. guianensis tree.

The unusual dispersal mechanism of C. guia-
nessi 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 ari without swallowing the whole seed. In all tree species that are traditionally cited to support the paradigm of speciali-
sed versus generalized dispersal systems (Howe & Smallwood 1982), the pulp covers the seeds com-
pletely. However, Howe (1977) reported for Cannaia corbyana, in which the arils do cover the seeds com-
pletely, that two species of parrots (Amazona autumn-
aites and A. farroh) also stripped arils with their
bells and dropped seeds in site. Thus, the unusual shape of the site and not the seeds are not the reason. C. guil- densteinii seeds were not swallowed.

Seeds dispersal systems in Madagascar might in general be very different from the ones in the Neotro- pics 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 no radiations of endemics that are extremely high in terms of both genera (24.6%) and species (53.0%; Lagrand 1990). Relatively low numbers of bird spec- ies and long periods of isolated evolution might have caused unusual dispersal systems. Although Madagas- car shares its independent evolution with archipelagos such as Hawaii or the Galapagos islands, it is consid- erably larger and includes major components of most tropical ecosystems, ranging from lowland rain forest to semi-deciduous (Gauthier & Kappeler 1993). This makes Madagascar an island that might be especially suited for understanding the evolution of dispersal systems. But before we can reach the point further thorough studies of Malagasy dispersal systems have to be conducted.

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