INFLUENCE OF SEED DISPERSAL BY BROWN LEMURS ON REMOVAL RATES OF THREE *GREWIA* SPECIES (TILIACEAE) IN THE DRY DECIDUOUS FOREST OF MADAGASCAR

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Résumé. Influence des Lémurs Bruns dans la dissémination des graines de trois espèces de *Grewia* (Tiliaceae) dans la forêt décidue sèche de Madagascar. Le but de cette étude était de déterminer les effets de la densité des graines et de leur passage dans le système digestif des Lémurs Bruns (*Eulemur fulvus rufus*) dans la prédation et la dissémination secondaire des graines de trois espèces d'arbres sympatriques du genre *Grewia* (Tiliaceae) dans la Forêt Kirindy/CFPF, une forêt décidue sèche de l'ouest de Madagascar. La perte de graines par la prédation ou la dissémination a été déterminée dans trois types de parcelles de 1 m²: 1) parcelles ouvertes témoins, 2) parcelles accessibles aux rongeurs et invertébrés mais filtrés aux plus grands prédateurs de graines ou disséminateurs ("semi-perméables"), et 3) parcelles accessibles aux seuls invertébrés ("imperméables"). Des graines "disséminées" (qui ont transité par l'intestin des lémuriens) et des graines "non disséminées" (cueillies sur l'arbre) des trois espèces d'arbres ont été déposées dans les parcelles, soit à faible densité, soit à haute densité, permettant ainsi de disposer de 36 groupes expérimentaux différents (trois espèces, trois types d'enclos, deux densités, deux traitements [déféqués et non-déféqués]), chacun étant répliqués neuf ou 12 fois. La densité des graines n'a eu d'effet sur aucune espèce, ni sur les traitements. Les graines de *G. cyclea* n'ont subit ni la prédation par des rongeurs ni la dissémination secondaire par les invertébrés alors que les graines non déféquées ont subit la prédation par des insectes. Les graines de *G. lavanalensis* ont subit la prédation par des rongeurs et des insectes; des graines non déféquées ont eu une plus grande probabilité de souffrir de prédation que les graines déféquées. Il n'y avait pas de signes de dissémination secondaire. Les graines non déféquées de *G. glandulosa* n'avaient pas subit la prédation par des rongeurs alors que les insectes se nourrissaient de la pulpe des fruits en détruisant les graines. Un tiers des graines non déféquées ont également été disséminé secondairement par des fourmis. Les graines déféquées n'ont été touchées ni par des prédateurs ni par des disséminateurs. Ainsi, dans le genre *Grewia*, le passage des graines dans le système digestif des lémuriens les rend-elles sans attraits pour des prédateurs et des disséminateurs secondaires.

Abstract. The goal of this study was to determine the effects of seed density and seed passage through the digestive tract of Brown Lemurs (*Eulemur fulvus rufus*) on seed predation and secondary dispersal of seeds of three sympatric tree species of the genus *Grewia* (Tiliaceae) in the Kirindy Forest/CFPF, a dry deciduous forest in western Madagascar. Seed predation or dispersal was determined in three types of 1 m² exclosures: 1) open controls, 2) exclosures that were accessible for rodents and invertebrates, but not for larger seed predators or dispersers ("semipermeable"), and 3) exclosures that were only accessible to invertebrates ("impermeable"). "Dispersed" seeds (= defecated seeds passed through the gut of lemurs) and "non-dispersed" seeds (= non-defecated seeds collected directly from the tree) of the three tree species were deposited in the exclosures at either low or high density. This resulted in 36 different experimental groups (three tree species, three types of exclosures, two treatments [defecated and non-defecated], two densities), each with nine or 12 replica. Seed density had no effect in any of the species or treatments. Defecated seeds of *G. cyclea* experienced neither predation by rodents nor secondary dispersal by invertebrates; undefecated seeds experienced some predation by insects. Defecated seeds of *G. lavanalensis* experienced predation by rodents and by insects; undefecated seeds had a higher probability of being predated than defecated seeds. There was no evidence for secondary dispersal; defecated seeds of *G. glandulosa* were not touched by predators or by secondary dispersers; undefecated seeds were not predated by rodents but the pulp was eaten by insects who also destroyed the seeds; one third of the undefecated seeds were also dispersed secondarily by ants. Thus, within the genus *Grewia*, seed passage through the digestive tract of lemurs renders the seeds unattractive for predators as well as for secondary dispersers. *Accepted 15 November 1999.*

Key words: Seed dispersal, seed predation, passage time, dispersal distance, Grewia, Eulemur fulvus, lemurs, primates, Madagascar.

INTRODUCTION

It has been repeatedly hypothesized that dispersal of seeds away from the parent tree improves the probability of seeds and seedlings escaping predation by

vertebrate and invertebrate seed predators (Janzen 1970, Connell 1971; for a recent review see Thery *et al.* 1998). According to this hypothesis, seeds ought to attract more predators when they occur in high densities (i.e., under the parent tree) than at low densities (such as after dispersal away from the parent

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tree). In the dry deciduous forest of western Madagascar the importance of seed dispersal seems pronounced. Bird-dispersed and ant-dispersed seeds of *Commiphora guillaumini* do much better when transported beyond the area covered by the crown of the parent tree (Böhning-Gaese *et al.* 1995, 1996); seedlings of some tree species do not become established in the vicinity of conspecific trees (Deleporte *et al.* 1996), and regeneration of mammal-dispersed tree species is suppressed when the main dispersers are absent from the forest (Ganzhorn *et al.* 1999).However, in the case of animal-dispersed seeds, these findings incorporate at least three different factors that can vary simultaneously: the distance to the parent tree (which might represent a landmark for a reliable food resource), the density of potential food resources, and the manipulation of seeds by primary dispersers.

In order to separate the effects of these confounded variable we conducted a series of experiments on the role of vertebrate and invertebrate seed predators in seed mortality. In the first series of experiments no distance effect on the removal rates of seeds could be demonstrated for the mammal-dispersed tree species *Strychnos decussata* (Loganiaceae) (Dausmann 1997, Dausmann *et al.* submitted). In the second series, presented here, we manipulated the density of seeds and whether or not seeds had been passed through the digestive tract of *Eulemur fulvus rufus* (Spehn 1998). This 2.2 kg primate species is considered to be the most important seed disperser in the dry deciduous forest of Madagascar (Ganzhorn *et al.*

1999). Due to the high seasonality of the dry deciduous forest, seeds of *S. decussata* were no longer available for the second set of experiments presented here. We therefore used three species of *Grewia* (Tiliaceae); with different seed characteristics; that are also dispersed by *E. f. rufus*.

MATERIAL AND METHODS

Study site. The study was carried out in near-primary deciduous dry forest of the forestry concession of the Centre de Formation Professionnelle Forestière de Morondava (CFPF) in western Madagascar during the dry season from May to September 1997. The study site "N5" is part of a large (> 12,000 ha) tract of the Forêt de Kirindy/CFPF, 60 km north of Morondava (20°03'S, 44°39'E). The climate is highly seasonal with about eight months without rain per year, during which time most trees shed their leaves. Fruit is available year-round (Sorg & Rohner 1996). A general introduction to the forest is given by Ganzhorn & Sorg (1996).

Tree species. Three tree species of the genus *Grewia* (Tiliaceae) were selected for the experiments: *G. cyclea*, *G. lavanalensis*, and *G. glandulosa* (Table 1). Fruits of all three species are consumed whole by *Eulemur fulvus rufus* and are then dispersed from the parent tree. Seeds of all three tree species pass through the digestive tract of *E. f. rufus* physically undamaged.

The size of *G. cyclea* fruits is about 14 mm; the hard kernel contains two seeds and is surrounded by

TABLE 1. Tree species used for experiments and the influence of digestion by *Eulemur fulvus rufus* on fruit/seed size and weight (n = 100 for fruits and seeds, except for fruits of *G. glandulosa*).

Species	Size of fruits before digestion [mm]	Mass of fruits before digestion [g]	Mass of fruits/seeds after digestion [g]	Number of kernels per fruit	Number of seeds per kernel	Pulp thickness
G. cyclea	13.1 ± 1.1 x 14.4 ± 1.3 x 13.6 ± 1.2	1.16 ± 0.31	1.07 ± 0.24	1	2, not released	< 1 mm, fibrous
G. lavanalensis	8.3 ± 0.8 x 8.6 ± 0.7 x 7.8 ± 0.7	0.25 ± 0.08	< 0.1	4, isolated	1, not released	< 1 mm, soft
G. glandulosa	24.5 x 20.4 x 16.7	1.88	0.24 ± 0.07	4, isolated	2, not released	2–3 mm, soft, fibrous

a very thin (< 1 mm) pulp; seeds are not released from the kernel when passed through the lemur gut; average mass of the whole fruit is 1.16 g. After passage through the digestive tract of *E. f. rufus* the diaspore weighs 1.07 g; thus the fruit pulp available to lemurs is only 0.09 g per fruit. The unit of dispersal (diaspore) by *E. f. rufus* is represented by the two seeds enclosed in the hard kernel (Table 1).

Fruits of *G. lavanalensis* measure 8–9 mm and weigh on average 0.25 g. The fruit pulp is soft and about 1 mm thick; each fruit contains four isolated seeds; single seeds are 7 x 3 x 3 mm and weigh less than 0.1 g. For this species the unit of dispersal by *E. f. rufus* is the single seed.

The size of *G. glandulosa* fruits is about 25 x 20 x 17 mm (n = 100); average fruit mass is 1.88 g; each fruit contains four kernels with two seeds each that are surrounded by fibrous pulp of 2–3 mm; seed size is 8 x 7 x 7 mm; seed mass is 0.24 g. The unit of dispersal by *E. f. rufus* is the kernel containing two seeds.

Seedbank. To assess the availability of seeds in the seedbank, and the effect of lemur dispersal on seed density, the number of undamaged seeds were counted in seven 1 m² quadrats under each of five *G. cyclea* food trees and under each of four food trees for *G. lavanalensis* and of *G. glandulosa*. The density of seeds below trees where the animals defecated was counted in one m² per defecation site.

Distance of primary dispersal. Marked individuals of *E. f. rufus* were followed in the forest after they had fed on one of the three *Grewia* species. At the location where the animals defecated the seeds were marked and the distance to the food tree was measured. This could be done precisely if the animal had eaten different food items before and after the *Grewia* fruits in question. Seeds of different fruit species appeared in the feces in the same sequence in which they had been eaten. Therefore it was possible to assign the seeds reappearing in the feces to distinct food trees. This allowed the measurement of the distance between a given food tree and the location where its seeds had been deposited in feces and thus to calculate the area where the majority of *Grewia* seeds had been deposited.

Experimental setup
Types of exclosures. The experimental design concerning the contribution of predators to seed mortality follows that of Terborgh *et al.* (1993) and Dausmann (1997). The exclosures consisted of four wooden stakes at the corners of the 1 x 1 m = 1 m² quadrat

and were made out of wire mesh smaller than any of the *Grewia* seeds (mesh squares 1 mm). For the impermeable exclosures (Fig. 1a), the wire mesh covered the top with a roof 50 cm above the ground and all four sides of the quadrat. At the sides, the mesh was buried in the ground to prevent vertebrates from entering the exclosure. Arthropods were given access into the exclosure by cutting holes of approximately 1 cm into the wire mesh at the sides. Semipermeable exclosures (Fig. 1b) were constructed as the impermeable exclosures, but the wire mesh ended 3–5 cm above the ground thus allowing small vertebrates to enter. The base of the mesh was secured by additional stakes. At the bottom end of the wire mesh we attached sticky tape to collect hair from small mammals that passed underneath the wire. Control plots (Fig. 1c) had the same dimensions as the exclosures but were only covered with a roof made of wire mesh.

Seventy-two exclosures were installed at 25 m intervals within the forest. The different types of exclosures were assigned to sites at random. Two experimental plots were installed with 12 replicas of each type of exclosure. Experiments were alternated between the two plots to reduce the possible effects of learning. The part of the forest where the the exclosures had been installed was structurally and floristically homogeneous to the human eye. It is likely that differences existed on a microhabitat scale, but since exclosures were assigned to any give locality at random it is unlikely that the data suffered from systematic sampling errors.

Treatment. The term treatment defines whether fruits and the enclosed seeds had been eaten by and passed through the digestive tract of *E. f. rufus* or not. Fruits of the three *Grewia* spp. were collected from fruiting trees, checked for insect damage and divided into two parts. One half was kept untreated and the other half was fed to captive *E. f. rufus*. Diaspores and seeds (referred to as "seeds" hereafter) of all three *Grewia* species fed to captive animals passed through the digestive tract of *E. f. rufus* within one to two hours. Seed passage time was two to four hours for wild lemurs (see Results). Defecated seeds were not cleaned but simply dried in the sun and subsequently used in the experiments. It was not necessary to dry the fresh seeds since the fruits of all three species of *Grewia* have a dry, fibrous pulp. Storage time for untreated and defecated seeds was between one and five days before the seeds were used in the experiments.

Density effects. For each of the three *Grewia* species fresh or defecated seeds were deposited at either low

or high density within each of the three exclosure types. Densities used in the experiments attempted to mimic seed densities in the seedbank on the forest floor under the parent trees (high density) and at the defecation sites (low density). In the experiments with *G. lavanalensis* and *G. glandulosa* the number of seeds available limited this approach. Low densities were 10 seeds in the case of *G. cyclea* and *G. glandulosa* and 30 seeds for *G. lavanalensis*. High densities were 20 seeds for *G. cyclea* and *G. glandulosa* and 60 for *G. lavanalensis*. In experiments involving *G. lavanalensis*, seeds were deposited in groups of three. This was done to compensate for the much smaller size and thus possible low attractiveness of their seeds.

Twelve replica per treatment and type of exclosure could be run in the experiments with *G. cyclea* and *G. lavanalensis*. Due to the shortage of seeds for *G. glandulosa* only nine replica could be run for this species. This resulted in 36 different experimental groups (three species; three types of exclosures; two treatments [defecated and non-defecated]; two densities). Experiments with *G. cyclea* took place mainly between May and July, with *G. lavanalensis* from June to September, and with *G. glandulosa* from August to September, corresponding to their respective fruiting periods.

Potential seed dispersers and seed predators after primary dispersal by E. f. rufus. During the dry season the principal secondary seed dispersers for small seeds are ants (Böhning-Gaese *et al.* 1995, 1996) and small rodents (*Eliurus myoxinus*: adult body mass 82 ± 10 g and *Macrotarsomys bastardi*: adult body mass 33 ± 3 g).

These species, plus the larger rodent *Hypogeomys antimena* (adult body mass 1100–1300 g), act also as seed predators. Bush pigs (*Potamochoerus larvatus*) also feed on fallen seeds, but their impact on seeds of the different tree species in not known. Ants could enter all three types of exclosures. The two small rodent species could enter the control plus the semipermeable exclosures. *H. antimena* also entered the semipermeable exclosures by digging their way underneath the wire mesh. All of these species and the bush pig had access to the control plots.

Insect predation. After termination of the experiments, all seeds were collected from the exclosures and checked for signs of insect predation, which was scored when a seed showed entrance/exit holes caused by the drilling action of insects. Only seeds from the impermeable exclosures are considered here as none of them was removed by vertebrates.

Statistical analyses. Any seed that had been eaten, damaged or removed from the exclosure during the seven days of exposure was scored as "removed". This classification does not distinguish between predation and secondary dispersal. Predation of seeds by insects that either entered or left the seeds while the seeds remained at the place where they had been deposited in the exclosures was recorded separately. Each exclosure was considered as one independent data point. Analyses are based on the percentage of seeds present in the enclosures after seven days. Since data differed significantly from a normal distribution, nonparametric tests were used (Siegel & Castellan 1988). SAS/STAT (1987) was employed in the analyses.
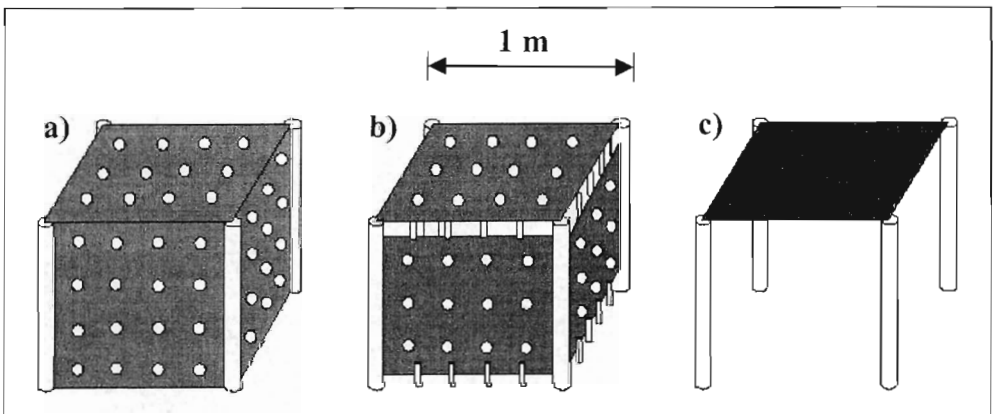

FIG. 1. Schematic diagram showing the exclosures used (modified from Dausmann 1997); a) impermeable exclosure, b) semipermeable exclosure, and c) control plot.

RESULTS

Seedbank

Seed densities below parent trees were 24 ± 25 seeds/m^2 (N = 35 m^2), 189 ± 236 seeds/m^2 (N = 28 m^2), and 173 ± 83 kernels/m^2 (N = 28 m^2) for *G. cyclea*, *G. lavanalensis*, and *G. glandulosa* respectively. At sites where the animals defecated the seeds, densities were 11 ± 12 seeds/m^2 (N = 18 m^2) for *G. cyclea*, 23 ± 5 seeds/m^2 (N = 12 m^2) for *G. lavanalensis*, and 29 ± 36 kernels/m^2 (N = 12 m^2) for *G. glandulosa*.

Distance of primary dispersal

After ingestion at the parent tree, *Eulemur fulus rufus* transported seeds of *Grewia cyclea* on average for 123 ± 78 m (n = 6), seeds of *G. lavanalensis* for 169 ± 66 m (n = 4), and seeds of *G. glandulosa* for 96 ± 68 m (n = 4). This corresponds to gut passage times for wild *E. f. rufus* of 178 ± 49 min, 283 ± 105 min, and 281 ± 23 min respectively.

Vertebrate predation and secondary dispersal

Density effects. The percentage of seeds that were still present after seven days did not differ significantly in any of the possible comparisons within species and treatments (Mann Whitney U tests: $P > 0.05$ for all comparisons). Since there was no density effect, data from different densities were pooled for further analyses.

Treatment effects. Fruits and seeds of *G. cyclea* suffered almost no predation from vertebrates and were not subject to secondary dispersal during the experiment (Fig. 2). No seeds were destroyed or disappeared from the semipermeable or impermeable exclosures. Seeds disappeared in 3 of the control plots for undefecated seeds and in 4 of the control plots with defecated seeds (Kruskal Wallis analysis of variance for comparisons between types of exclosure; undefecated seeds: Chi-square = 6.17, $P < 0.05$; defecated seeds: Chi-square = 8.34, $P < 0.02$). There was no difference in the number of defecated or undefecated seeds removed. *Eliurus myoxinus* did not consume seeds of these three *Grewia* trees during feeding experiments conducted at the research station. No feeding experiments were carried out with *Macrotarsomys bastardi* and *Hypogeomys antimena*.

Substantial percentages of *G. lavanalensis* seeds disappeared from the control and semipermeable exclosures (Fig. 3). The differences between different types of exclosure were significant for undefecated and for defecated seeds (Kruskal Wallis analysis of vari-
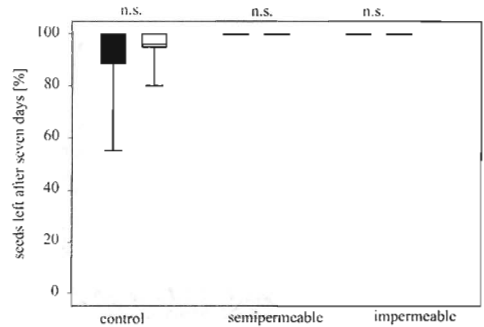

FIG. 2. Percentage of seeds of *Grewia cyclea* that were still present in the different types of exclosure after seven days. Values are medians, quartiles and minima–maxima of 24 exclosures per treatment. Significance levels for differences between seeds that had not passed through the gut (black), and those that had passed through the gut of *Eulemur fulvus rufus* (white) are listed above the pairwise comparisons.

ance; undefecated seeds: Chi-square = 20.92, $P < 0.001$; defecated seeds: Chi-square = 34.61, $P < 0.001$). Much higher percentages of undefecated seeds disappeared from the control and semipermeable exclosures than of seeds that had passed through the digestive tract of *Eulemur fulvus rufus* (Mann-Whitney-U test: controls: $P < 0.001$; semipermeable exclosures: $P = 0.05$; impermeable exclosures: not significant).

Two rodent species (*H. antimena* and *E. myoxinus*) were identified as visitors by hair caught by the hair
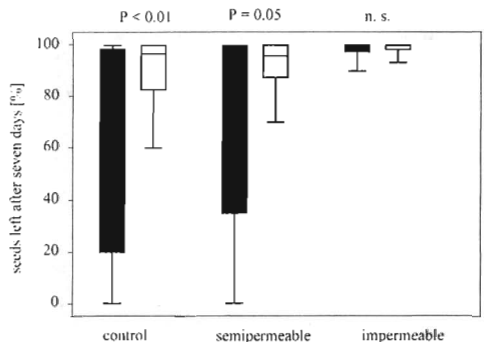

FIG. 3. Percentage of seeds of *Grewia lavanalensis* that were still present in the different types of exclosures after seven days (N = 24 exclosures per treatment). For further information see Fig. 2.
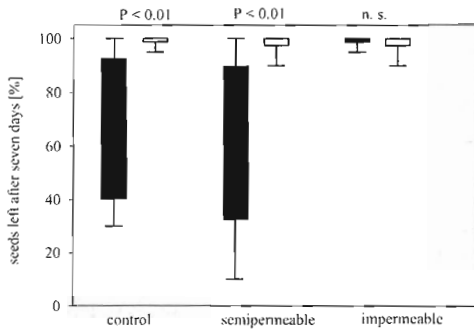
FIG. 4. Percentage of seeds of *Grewia glandulosa* that were still present in the different types of exclosure after seven days (N = 18 exclosures per treatment). For further information see Fig. 2.

traps on the semipermeable exclosures. Some of the seeds in these plots also showed rodent gnaw marks.

As in *G. lavanalensis*, untreated seeds of *G. glandulosa* disappeared at a higher rate from the control and semipermeable exclosures than seeds that had passed through the digestive tract of *E. f. rufus* (Fig. 4; Mann-Whitney-U test: controls: *P* < 0.001; semipermeable exclosures: *P* < 0.001; impermeable exclosures: not significant). However, for *G. glandulosa* the differences between different types of exclosures were significant

only for undefecated seeds (Kruskal Wallis analysis of variance: Chi-square = 26.79, *P* < 0.001). Defecated seeds were hardly touched in any of the exclosures (Chi-square = 0.18, not significant).

No sign of rodent activity was recorded in *G. glandulosa* exclosures. The disappearance of these seeds from the control and semipermeable exclosures is likely to be caused by ants (*Aphenogaster swammerdami*). In the impermeable exclosures (impermeable for vertebrates but not for invertebrates), a high proportion of the non-defecated seeds were moved within the exclosure and deposited close to the wire mesh. In these cases, ants tried to remove the seeds but could not pass them through the wire mesh. If we score these dislocated seeds as "removed" (they would have disappeared from the exclosure due to secondary dispersal by ants if they had not been hindered by the wire mesh), the significant difference in the percentage of removed seeds between the three types of exclosure disappears (*P* = 0.08). It is therefore assumed that the *G. glandulosa* seeds that were missing from the control and semipermeable plots had been carried away by ants.

Insect predation. Table 2 lists the percentage of seeds infested by insects after seven days in the impermeable exclosures. Seeds from these exclosures had been pooled per density and treatment when collecting the seeds after seven days. Therefore analyses could not

TABLE 2. Insect infestation of seeds of three species of *Grewia* (Tiliaceae) exposed for seven days in exclosures that were impermeable to vertebrates but not to insects.

Species	No. of seeds per exclosure	No. of replica per type of exclosure	No. of seeds recovered after seven days	Gut passage	% infested seeds
G. cyclea	10	12	120	no	5.0
	20	12	240	no	10.4
	10	12	120	yes	4.2
	20	12	240	yes	5.0
G. lavanalensis	30	12	357	no	11.1
	60	12	720	no	3.8
	30	12	360	yes	0.3
	60	12	720	yes	0.0
G. glandulosa	10	9	90	no	6.7*
	20	9	178	no	1.7*
	10	9	89	yes	0.0
	20	9	178	yes	0.0

* insects in the pulp, not in the seeds

be based on exclosures but on the number of seeds. Since single seeds cannot be considered as independent data points, only a sign test was applied using the overall percentages given in Table 2. There was no systematic seed density effect, but seeds of all three *Grewia* spp. that had passed through the digestive tract of *E. f. rufus* showed lower infestation rates than seeds that had not been eaten (Sign test: $P < 0.05$, N = 6). In the case of *G. glandulosa* the seeds could be destroyed by larvae that lived in the pulp surrounding the seeds. When the attached pulp had been removed during gut passage no insect infestation took place on the remaining portion of the seeds.

DISCUSSION

In the tropics, most tree species are adapted for seed dispersal by vertebrates (Charles-Dominique *et al.* 1981, Howe & Smallwood 1982, Dirzo & Dominguez 1986, Chapman & Onderdonk 1998). Some benefits of seed dispersal include increased distance from the parent tree and lowered density of seeds and seedlings near the parent tree.However, these effects are not consistent across species (e.g., Terborgh *et al.* 1993, Gryi & Dominguez 1996, Julliot 1997, Dew & Wright 1998, Dausmann et al. submitted). In the Kirindy Forest/CFPF *Eulemur fulvus rufus* covered on average 128 ± 78 m between a food tree and deposition of its seeds with their feces. Dispersal by *E. f. rufus* reduced the density of potentially competing conspecific seeds in the seedbank by a factor of 2 in case of *G. cyclea* and by a factor of 6 to 8 in case of the other two *Grewia* species. Thus, our experimental design mimics the natural situation in case of *G. cyclea*, and approximates the seed densities after primary dispersal. But we underestimated the densities beneath the parent trees (i.e., the "high density situation") and thus the "dilution effect" of seed dispersal in the other two *Grewia* species. Therefore, for those two species, the lack of density dependence in our experiments could result from the fact that "low" and "high" seed densities were too similar. The distances over which seeds were dispersed in the present study match the distances of seed dispersal found for other primates (Estrada & Coates-Estrada 1986, Garber 1986), but differs from the situation in the humid forest of eastern Madagascar (Overdorff & Strait 1998). There, *Eulemur* spp. (including *E. f. rufus*) rested in the same tree after feeding and defecated before they moved to the next feeding site. Thus, in the humid forest, *Eulemur* spp. do not seem to be effective seed dispersers, while in the dry deciduous forest *E. f. rufus* is an

effective seed disperser for *Grewia* spp. (see also Ganzhorn *et al.* 1999).

However, the consequences of simply dispersing the seeds away from the parent tree are not evident. The benefits of dispersal could be lowered when predators focus their search on the seeds in the feces, which must provide excellent olfactory cues for searching insects. The effects of seed passage through mammalian digestive tracts are highly variable. In some studies, predation rates of defecated seeds were high (Estrada & Coates-Estrada 1991, Hauser 1994, Wrangham *et al.* 1994) but in others rather low (Stiles 1992, Malo & Suárez 1995). Predation on seeds in the feces of animal dispersers has been studied experimentally for rodents (Janzen 1982, 1986) and insects (Traveset 1990, Levey & Byrne 1993). In the present study, neither defecated nor undefecated seeds of *G. cyclea* were predated by rodents (Table 3). But undefecated seeds suffered much higher predation rates by insects than seeds that had passed through the lemurs' digestive tract. Rodents consumed the seeds of only one of the tree species stuedied, *G. lavanalensis*. Seeds of this species have a thin, soft fruit-layer that contains the seeds, and are therefore easy to open for rodents. In the exclosures with access for large and small mammals, more undefecated seeds were consumed than defecated ones. The defecated seeds are small and might therefore be difficult to find for predators (Bradford & Smith 1977, Louda 1989, Greig 1993). Nevertheless, the surrounding dung provides an odorous marker that should help predators to locate the seeds. Insects also did not feed on the seeds once they had passed through the gut of *E. f. rufus*, but destroyed around 7 % of all seeds that had not been eaten by the lemurs.

For *G. glandulosa*, one third of all seeds that had not been eaten by *E. f. rufus* had disappeared from the two open exclosures after seven days. In contrast, almost all of the defecated seeds were encountered intact. Here there is evidence that the seeds that had not passed through the lemurs were dispersed by ants and not destroyed by rodents. Defecated seeds were less attractive to secondary dispersers due to the lack of fibrous pulp. Insects had an indirect effect on the survival of seeds because, in contrast to the two other species, they did not seem to attack the seeds but rather ate into the pulp surrounding them. Fruits that had been digested by the lemurs, and the seeds excreted, had lost the pulp and thus their attractiveness for insect predators. In the other two species of *Grewia*, passage through the lemur gut eliminated

TABLE 3. Summary of the effects of passage through the digestive tract of *Eulemur fulvus rufus* (= primary dispersal) on seeds of three species of *Grewia*, ranging from no effect (−) through small effect (+) to strong effect (++).

Species	Gut passage	Predation by rodents	Predation by insects	Secondary dispersal by ants
G. cyclea	no	−	++	−
	yes	−	+	−
G. lavanalensis	no	++	++	−
	yes	+	−	−
G. glandulosa	no	−	+[1]	++
	yes	−	−	−

[1] insects in the pulp, not in the seeds

predation by rodents and thus might be advantageous for the seeds. Passage through the lemur gut might have two diverging consequences in the case of *G. glandulosa*. On the one hand, seeds that had been digested by lemurs were no longer attractive for insect predators, while on the other, these defecated seeds were no longer attractive to secondary dispersers.

Thus in the dry deciduous forest of western Madagascar, seeds of the three *Grewia* species were subject to very different dispersal regimes and different predation pressures. Only the effect of the passage through the digestive tract of lemurs was consistent in reducing attractiveness for predators as well as for secondary dispersers. These experiments, carried out with the same dispersers during the same season in one plot of forest with similar fruits of three different tree species of *Grewia*, illustrate the variation in animal-seed interactions.

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