

Interacting effects of forest fragmentation and howler monkey foraging on germination and dispersal of fig seeds

Juan Carlos Serio-Silva and Victor Rico-Gray

Abstract We studied changes in germination rates and dispersal distance of seeds of *Ficus perforata* and *F. lundelli* dispersed by howler monkeys (*Alouatta palliata mexicana*), in a small (40 ha) 'disturbed' and a larger (>600 ha) 'preserved' tropical rainforest in southern Veracruz, Mexico. The interaction between *A. p. mexicana* and *Ficus* (*Urostigma*) spp. is beneficial for the interacting species and has important implications for their conservation. Howler monkeys gain from the ingestion of an important food source, germination rates of *Ficus* seeds are improved by passage through the monkeys' digestive tract, and the seeds are more likely to be deposited in a site suitable for germination and development. Seed dispersal distances are relatively larger in the preserved site, with both the size of the forest area and the spatial pattern of *Ficus* affecting the dispersal process.

In a large forest fragment with 'regularly' distributed *Ficus* individuals the howler monkeys move away from the seed source, increasing the probability that the seeds are deposited on a tree other than *Ficus*, which is important for the germination and future development of a hemiepiphytic species. In a small forest fragment with trees distributed in clumps howlers repeatedly use the same individual trees, and faeces containing seeds may be dropped on unsuitable trees more often. These are key issues when addressing conservation policies for fragmented forests.

Keywords *Alouatta palliata mexicana*, *Ficus*, fragmentation, howler monkeys, interspecific interactions, Mexico, seed germination, tropical forest.

Introduction

Recent studies suggest that one of the most important aspects to be considered in programmes for the conservation of tropical forests is the identification of ecological interactions among the important species in the ecosystem (Thompson, 1994; Howe & Miriti, 2000) and the evaluation of how these processes are altered by habitat fragmentation (Nathan & Muller-Landau, 2000). Given the current rate of tropical forest clearing, an important conservation issue is how forest fragments are altered by changes in the seed dispersal activities of the frugivores that the fragments support. Understanding the cascading effects of fragmentation will assist in the construction of informed management plans for such habitats.

Figs (*Ficus* spp., Moraceae) are an important food source for invertebrates and vertebrates, including bats, birds and monkeys, all of which may be seed dispersal agents (Banaccorso, 1979; Janzen, 1979; Gautier-Hion

et al., 1985; de Figueiredo, 1993). Frugivore strategies and the interactions between fruiting plants, including figs, and primate dispersers have been documented for *Pongo pygmaeus* in Asia (Galdikas, 1982), for *Papio anubis* and *Gorilla gorilla gorilla* in Africa (Lieberman *et al.*, 1979; Tutin *et al.*, 1991), and for *Alouatta palliata mexicana*, *A. p. palliata*, *Cebus capucinus*, *Saguinus mystax* and *S. fuscicollis* in the neotropics (Howe, 1980; Estrada & Coates-Estrada, 1984, 1986, 1991; Garber, 1986). Figs are one of the most important food sources for primates (Milton, 1980; Terborgh, 1986; Serio-Silva, 1996; Silver *et al.*, 1998), particularly during periods of general food scarcity (Terborgh, 1983, 1986; Wrangham *et al.*, 1993). Fig trees contribute young and mature leaves, and particularly fruits, to the diet of howler monkeys (*Alouatta* spp.) (Milton, 1980; Serio-Silva, 1996, 1997; Silver *et al.*, 1998). However, the specific associations between these primates and *Ficus* species have been little studied (but see de Figueiredo, 1993; Wrangham *et al.*, 1993), and we do not know how seed dispersal and germination are altered by changes resulting from forest fragmentation, and how this knowledge can be applied to tropical forest conservation programmes.

Figs occur in tropical and subtropical areas worldwide, and the genus *Ficus* is one of the most numerous in species (c. 800) among woody plants. Many of these species (c. 280), within the subgenus *Urostigma* (Putz & Holbrook, 1986), are hemiepiphytic 'stranglers'; their

Juan Carlos Serio-Silva¹ (Corresponding author) and Victor Rico-Gray
Departamento de Ecología Vegetal, Instituto de Ecología, A.C., Apdo. 63,
Xalapa, Veracruz, 91070 México

¹ Present address: División Académica de Ciencias Biológicas, Universidad Juárez Autónoma de Tabasco, Km. 0.5 carretera Villahermosa-Cárdenas, Villahermosa, Tabasco 86039, México. E-mail: serioju@ecologia.edu.mx

Received 29 January 2001. Revision requested 11 June 2001.

Accepted 7 February 2002.

seeds germinate on a host or support tree, and the young plants later send roots to the soil. Howler monkeys use the forest canopy for their daily activities, and so faeces containing seeds of *Urostigma* are deposited on host trees (e.g. in branch forks, depressions and on bark).

As a result of their phenology figs are regarded as keystone species in many tropical rainforests, representing a source of food and shelter in times when other species are scarce (Terborgh, 1986; McKey, 1989), although this may not be true under all circumstances (Gautier-Hion & Michaloud, 1989). It has been suggested that, as a consequence of flowering asynchrony, figs are particularly vulnerable to forest fragmentation and reduction in habitat area (Janzen, 1986; McKey, 1989). Other observations suggest that in fragmented forests figs, and especially hemiepiphytic figs, may be more vulnerable to extinction than other tropical forest tree species because their minimum viable population size is relatively large and adults often occur at low densities (McKey, 1989). When forests become fragmented frugivores often disappear (Andr n, 1994), and fig seeds thus lose their dispersal agents. Figs in fragmented forests are dependent on the behaviour of seed dispersers, which may alter the shape of the seed shadow (i.e. the spatial distribution of seeds following dispersal; McKey, 1989). If monkeys that are restricted to mature forest are important dispersal agents for a particular fig species, the seed shadow may be truncated by forest fragmentation, because these animals will remain in the forest fragment and no seeds will be carried elsewhere. Bats or birds, in contrast, may carry fig seeds from one forest fragment to another, with some seeds being dropped in unsuitable habitats between fragments (Galindo-Gonz lez, 1998).

It is generally accepted that fig seeds pass undamaged through the digestive tracts of many frugivores. However, few quantitative studies have been made on the role of howler monkeys as dispersal agents and their effect on the germination of fig seeds (Estrada &

Coates-Estrada, 1986; de Figueiredo, 1993). In this paper we address a part of the dispersal process, namely we analyze the effect of Mexican howler monkeys *Alouatta palliata mexicana* on the germination success and dispersal distances of seeds of the strangler figs *Ficus perforata* and *F. lundelli*, and how these interactions differ between a 'disturbed' and a 'preserved' habitat. We then discuss the potential role that this interaction plays in the complex process of forest regeneration (Zuidema *et al.*, 1996; Howe & Miriti, 2000), and in particular the effect of forest fragmentation on the interaction.

Methods

Field observations and seed sampling were carried out between January 1998 and June 1999 in a 'disturbed' and a 'preserved' site in south-eastern Veracruz, M xico (Fig. 1, Table 1). The disturbed site was a relatively small isolated forest patch (40 ha), modified by humans and used for extraction of plant species, agriculture and cattle raising, located in Playa Escondida, San Andr s Tuxtla, Veracruz, M xico (18 35'N, 95 03'W). The preserved site is a large, relatively undisturbed area, of

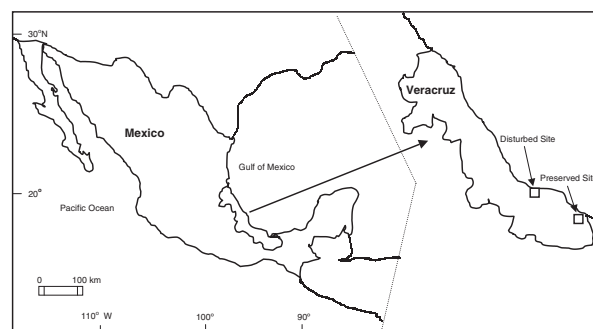


Fig. 1 Location of the two study sites in southern Veracruz, M xico: the 'disturbed' site at Playa Escondida and the 'preserved' site in the Carolino Anaya reserve.

Table 1 Characteristics of the two study sites.

Parameter	'Disturbed' site	'Preserved' site
Area	40 ha	600 ha
Climate	Warm, subhumid	Warm, humid
Annual precipitation	2,000 mm	2,500 mm
Temperature (max-mean-min)	39.5 – 25.1 – 9�C	43.5 – 25.5 – 18�C
Altitude	70 m	50 m
Vegetation type	Mostly patches of secondary forest	Primary forest
Major plant families	Moraceae, Cecropiaceae, Fabaceae	Moraceae, Rubiaceae, Orchidaceae, Fabaceae
Density of <i>Ficus perforata</i>	1.2 ha ⁻¹	0.2 ha ⁻¹
Density of <i>Ficus lundelli</i>	0.9 ha ⁻¹	0.1 ha ⁻¹
Number of howler troops	4	8
Howler density	1.05 ha ⁻¹ (4 troops, 42 ind.)	0.12 ha ⁻¹ (8 troops, 74 ind.)
Home range per troop	10 ha	75 ha

which 600 ha are protected from human activities; it is connected with other forested areas, and is one of the best preserved areas of tropical rainforest in southern Veracruz. This 600 ha area lies within the Carolino Anaya Reserve, near Coatzacoalcos, Veracruz, México (18°07'N, 94°18'W) (Fig. 1, Table 1).

In the disturbed site there are four howler monkey troops, and in the preserved site there are eight troops. We studied two troops at each site. The two troops selected for study in the disturbed site had eight and nine individuals, and those in the preserved site had eight and 10 individuals, respectively. To estimate the home range of the troops in each site we conducted a preliminary survey following the suggestions of Zucker *et al.* (1996). The howlers had larger home range sizes and occurred at a lower density in the preserved than in the disturbed habitat (based on estimations by Estrada & Coates-Estrada, 1984; Table 1).

We determined the spatial pattern of *F. perforata* and *F. lundelli* at both sites, using the Morisita Index of Dispersion (I_d , Brower *et al.*, 1989)

$$I_d = n[(\Sigma X^2 - N)/(N(N - 1))]$$

where n is the number of 0.5 ha plots (disturbed site $n = 20$, preserved site $n = 4$), N is the total number of individuals counted on all n plots, and ΣX^2 is the square of the number of individuals per plot, summed over all plots ($I_d = 1.0$ for a 'random' distribution, $I_d = 0$ for a 'regular' distribution, and $I_d = n$ at maximum aggregation).

Mature fruits of *F. perforata* and *F. lundelli* (c. 2.0 kg per species per site), and monkey faeces (30 samples per site) were collected from the forest floor. To determine the number of seeds of each fig species deposited in the faeces we selected, from only the most complete and least fragmented faeces, 11 samples containing *F. perforata* seeds and 9 containing *F. lundelli* seeds from each study site. Seeds from both faeces and fruits were observed under a microscope to confirm the presence of an embryo; those used by fig wasps (Agaonidae) were discarded. Seeds were washed, dried and weighed. For the germination trials, we randomly selected, from those seeds with confirmed embryos, 1,000 seeds of each species from fruits and 1,000 from faeces, from each study site, giving a total of 4,000 seeds for each species.

Seeds were placed in 9 cm Petri dishes covered with Whatman 42 filter paper. Forty Petri dishes (50 seeds in each) were allocated per *Ficus* species, for each study site; 20 dishes were used for seeds from faeces and 20 dishes for seeds from fruits. The Petri dishes were placed for 30 days in a thermostatically controlled chamber with a regime of 16 h at 27°C and 8 h at 30°C. Lids were kept in place to minimize evaporation, but distilled water was added at least every three days to maintain

humidity. Evidence of germination (appearance of the radicle) was noted every two days until no further germination was observed in seven successive counts. The position of the Petri dishes inside the controlled chamber was modified during each daily survey (one row at a time, from the front to the back of the chamber). We calculated the proportion of seeds germinating per treatment, per species.

To evaluate seed dispersal distance, i.e. from site of fruit ingestion to site of seed defecation, we selected individual trees of *F. perforata* and *F. lundelli* where a monkey troop was feeding and, after fruit ingestion, we followed the troop. We allowed for the evacuation of seeds from other trees ingested prior to feeding on the selected individual *Ficus*. The estimated digestive turnover of howler monkeys is c. 20 h (Milton *et al.*, 1980), so we followed the selected monkey troop for 24 h and, for each study site, we measured the linear distance in metres from site of fruit ingestion to site of defecation (9 measurements for *F. perforata* and 10 measurements for *F. lundelli*, per site) for seeds deposited after 20 h.

Differences in the proportions of seeds germinating between *Ficus* species, site and seed source were explored with ANOVA with a logit link function using the GLIM-4 statistical package (Francis *et al.*, 1993; Aitkin *et al.*, 1994). As a result of data overdispersion (adjusted scale parameter = 2.066), the goodness-of-fit was evaluated with an F -test, using a binomial error distribution, and the change in variance compared directly with F -tables to assess its significance (Crawley, 1993; Aitkin *et al.*, 1994). We used t -tests (Zar, 1996) to compare the seed dispersal distances between *Ficus* species and sites.

Results

We found no significant differences in the number of *Ficus* seeds in faecal samples between sites (*F. perforata*, $t = 0.615$, $df = 10$, $P = 0.552$; *F. lundelli*, $t = 0.519$, $df = 8$, $P = 0.618$) (Table 2). Seeds of both *Ficus* species germinated after 9–11 days, reached a maximum at about day 16, and ceased germination after 28–30 days. For both sites and species seeds from faeces had a higher germination success than seeds from fruit (Table 2). Seed source had the greatest influence on germination, explaining 87.9% of the variation in germination (Table 3). The species * source interaction also had a significant effect on seed germination (Table 3).

The *Ficus* population in the disturbed site exhibited a clumped spatial pattern (I_d , *F. perforata* = 1.25, *F. lundelli* = 1.18), whereas in the preserved site the spatial pattern was more 'regular' or uniform (I_d , *F. perforata* = 0.79, *F. lundelli* = 0.86).

Table 2 Mean number of seeds (\pm SEM) of both *Ficus* species in howler monkey faeces, germination percentage of seeds from faeces and fruit, and mean seed dispersal distances (\pm SEM) in the ‘disturbed’ and ‘preserved’ study sites. Numbers in parentheses are the sample sizes.

Parameter/Site	F. perforata		F. lundelli	
	Disturbed	Preserved	Disturbed	Preserved
Number of seeds in faeces	2224.8 \pm 111.5 (11)	2040.1 \pm 111.5 (11)	1917 \pm 110.3 (9)	1877.4 \pm 49.3 (9)
Seed germination (faeces)	78% (1,000)	72% (1,000)	59.5% (1,000)	68.1% (1,000)
Seed germination (fruits)	0% (1,000)	0.3% (1,000)	9.2% (1,000)	6.0% (1,000)
Dispersal distance (m)	72.71 \pm 21.42 (9)	172.25 \pm 15.64 (9)	57.48 \pm 7.9 (10)	248.3 \pm 15.74 (10)

Table 3 Analyses of germination proportions with ANOVA, using a logit model with a binomial error to test for differences in the germination of *Ficus* seeds as a function of species (*F. lundelli*, *F. perforata*), site (‘disturbed’, ‘preserved’) and source (fruits, faeces); overall $F_{1,152} = 3.84$, $P < 0.0001$.

Source of variation	Variance	df	Mean square	F	P
Species	1.545	1	1.55	0.750	0.387
Site	0.0002	1	0.0002	0.001	0.976
Source	2072.00	1	2072.00	1005.800	<0.001
Species * site	5.77	1	5.77	2.800	0.096
Species * source	119.3	1	119.30	57.900	<0.001
Site * source	7.44	1	7.44	3.610	0.059
Species * site * source	4.01	1	4.01	1.940	0.166
Error	147.14	152	0.96		
Total	2357.00	159			

The monkeys deposited seeds from both fig species farther away from the parent tree in the preserved than in the disturbed site (*F. perforata*, $t = 3.374$, $df = 8$, $p < 0.01$; *F. lundelli*, $t = 10.138$, $df = 9$, $p < 0.01$) (Table 2).

Discussion

Howler monkeys *Alouatta palliata mexicana* at the two study sites had positive and significant effects on the germination of *Ficus* seeds, as do *Papio anubis* (Lieberman *et al.*, 1979), *Saguinus mystax* and *S. fuscicollins* (Garber, 1986), *A. palliata* (Estrada & Coates-Estrada, 1991), and *Pan troglodytes* (Wrangham *et al.*, 1993, 1994). Although seed source explained most of the variation in seed germination, the significant source * species interaction showed that each species of *Ficus* has its own response to passage through the gut.

Dispersal distances differed between sites, being significantly greater in the ‘preserved’ site. To be sure that this result was not just a consequence of the larger size of this site, we calculated the ratio of dispersal distance (in metres) to number of *Ficus* individuals per site. This ratio was relatively larger for the preserved site (1.17 *vs* 0.78). This may be at least partly explained by the differences in distribution pattern of *Ficus* between the two sites. In the ‘disturbed’ site both *Ficus* species have a clumped distribution pattern, whereas in the preserved site they are more regularly distributed. Howler troops constantly move among *Ficus* trees to monitor

and cope with their asynchronous fruiting pattern (Milton, 1980; Serio-Silva, 1996), and troop displacements depend on social structure within a home range of flexible size (Zucker *et al.*, 1996). In the small disturbed site (40 ha) the four monkey troops must divide the fragment into small home ranges (*c.* 10 ha), and troops moving through neighbouring home ranges exhibit constant agonistic vocalizations (*pers. obs.*). The eight troops in the larger preserved site (> 600 ha) can occupy home ranges of up to 75 ha, and encounters between troops are rare (*pers. obs.*). Howler monkeys moved relatively shorter distances in the disturbed site, within clumps of *Ficus*. In the preserved site, however, they moved relatively larger distances among more regularly dispersed trees, and should be more effective in depositing seeds on sites suitable for germination and future establishment, *i.e.* away from the parent tree, and on tree species other than *Ficus* (Chapman, 1995).

Many tree species lose large proportions of seeds to the activity of seed predators, and *Ficus* trees are no exception, losing *c.* 50% of their seeds to agaonid wasps (Ramirez, 1976). The efficient dispersal (*sensu* Fleming & Sosa, 1994) of the remaining seeds is important for the conservation of *Ficus*. Primates are an important seed dispersal vector, because they make up 25–40% of the animal biomass of tropical forests, and in a typical day howler monkeys can ingest a relatively higher volume of *Ficus* (*Urostigma*) fruits and seeds than other frugivores such as bats or birds (Coates-Estrada

& Estrada, 1986). However, the effect of differences in digestion time and patterns of defecation amongst these vertebrates (e.g., Morrison, 1980; Fleming, 1988; Lambert, 1989a, b; Charles-Dominique, 1991; Midya & Brahmachary, 1991; Medellín & Gaona, 1999) on the dispersal and germination of *Ficus (Urostigma)* seeds has rarely been considered. Howler monkeys ingest and disperse more seeds per faecal unit deposited (2,015 seeds per individual in this study) than other sympatric vertebrate frugivores that also ingest *Ficus* seeds (e.g. bats 154 and birds 294 seeds per individual; Medellín & Gaona, 1999). Bats, birds and primates may all deposit seeds on the ground, but howler monkeys transport a greater number of seeds per individual and rarely leave the forest, whereas bats and birds transport a limited amount of seeds, and move outside the forested area where seeds may be deposited in unsuitable sites.

The interaction between *Alouatta palliata mexicana* and *Ficus (Urostigma)* spp. is beneficial for the interacting species and has important implications for their conservation. Howlers gain from the ingestion of an important food source (Milton, 1980; Terborgh, 1983; Serio-Silva, 1996), and *Ficus (Urostigma)* seeds attain greater germination success from passage through the digestive tract and are more likely to be deposited in suitable germination sites. Both the size of the forest and the distribution pattern of *Ficus* individuals can affect the dispersal process. A larger area of forest allows howler monkeys to move away from the seed source, increasing the probability that seeds be deposited on a tree species other than *Ficus*, which is important for the germination and future development of a hemiepiphytic species. In a small forest fragment howlers repeatedly use the same individual trees, and seeds may be more often dropped on unsuitable trees. These issues need to be considered when developing conservation policies for fragmented forests (Turner, 1996; Zuidema *et al.*, 1996), and it is increasingly important to understand how the interactions between trees and their dispersal agents change with increasing habitat fragmentation and decreasing area of forest.

Acknowledgements

We thank Albright and Wilson Troy de Mexico for permission to work in the Carolino Anaya Reserve, V.J. Sosa-Fernández, V. Parra-Tabla, R. Manson and two anonymous reviewers for their comments and suggestions on earlier drafts of this manuscript, and J. Bello-Gutiérrez for his help with the statistical analyses. Research was supported by Instituto de Ecología, A.C (902-16), equipment donation by *Idea Wild* and a CONACyT scholarship to JCSS.

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Biographical sketches

Juan Carlos Serio Silva is currently completing his PhD in Ecology and Management of Natural Resources at Instituto de Ecología, AC, Xalapa, Veracruz, México. His research since 1989 has mainly focused on primate behavioural ecology and conservation, especially animal-plant interactions.

Dr Victor Rico-Gray is a senior research scientist at the Plant Ecology Department of Instituto de Ecología, AC. With the late Elizabeth S. Watts, he was one of the pioneers of primate studies in the Yucatan Peninsula, México. Currently, his research focuses on the ecology of ant-plant interactions and their seasonal and geographic variation.