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Seed dispersal in *Palicourea rigida*, a common treelet species from neotropical savannas

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ABSTRACT. The dispersal system of *Palicourea rigida* (Rubiaceae), a common woody species of neotropical savannas, was studied in a seasonal Venezuelan savanna. Production and consumption of fruits, dispersal agents, feeding behaviour, transport and effects on seed viability, were investigated by field observations, cage experiments and viability tests. To compare different dispersers, quantitative and qualitative dispersal parameters were calculated. About 59% of the fruit crop was dispersed successfully by birds. Although 10 different bird species consumed the fruits of *Palicourea rigida*, three bird species dispersed 79% of the fruits (*Tyrannus melancholicus*, *Molothrus bonariensis* and *Elaenia chiriquensis*). *T. melancholicus* (Tyrannidae) was the most important dispersal agent, with more than 39% of dispersed seeds. In contrast to the predictions of the specialization vs. generalization paradigm, this system achieves high effectiveness by means of predominantly unspecialized traits in both the plant and the dispersers.

RESUMEN. Se estudió el sistema de dispersión de *Palicourea rigida* (Rubiaceae), una leñosa común de las sabanas neotropicales, en una sabana estacional de Venezuela. Mediante observaciones de campo y experimentos en jaulas y en el laboratorio, se estudiaron paramétros tales como producción, transporte y consumo de frutos, los agentes dispersores y su comportamiento y los efectos sobre la viabilidad de las semillas. Para comparar los agentes de dispersión se estimaron paramétros cualitativos y cuantitativos. Cerca del 59% de la cosecha total de frutos fue dispersada existosamente por pájaros. Aunque los frutos fueron consumidos por diez especies de aves, el 79% de los frutos fueron dispersados por solamente tres especies (*Tyrannus melancholicus*, *Molothrus bonariensis* y *Elaenia chiriquensis*). *T. melancholicus* (Tyrannidae) fue el más importante agente dispersor con más del 39% del total de semillas dispersadas. En contraste con el paradigma de especialización vs. generalización, este sistema alcanza alta efectividad pero se caracteriza por rasgos poco especializados, tanto en la planta como en los dispersores.

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INTRODUCTION

In spite of the wide distribution of neotropical savannas, and the important role of the tree component in savanna functioning (Sarmiento *et al.* 1985) there is little information about seed dispersal of tree species in these areas. In savannas from Brasilia, Oliveira & Moreira (1992) found that 41% of woody species belonging to 10 different families were anemochoric. They also reported a decrease in number of anemochoric species and their relative importance along tree-cover gradients and conclude that this dispersal syndrome is the most efficient in open savannas.

Palicourea rigida is a widespread species in neotropical savannas (Sarmiento 1983) suggesting very effective dispersal and regeneration mechanisms. In this paper we present field results concerning both the dispersal agents, and the quantity and quality of seed dispersal in *P. rigida*. Furthermore, we estimated the dispersal agent's effectiveness, representing the contribution of a disperser to the fitness of a plant and characterized the dispersal system of this tree species. The results are discussed in the context of the specialization vs. generalization paradigm (Howe 1993, McKey 1975).

MATERIALS AND METHODS

The species

Palicourea rigida H.B.K. (Rubiaceae, 'chaparrillo') is a distylous treelet species that grows up to 3 m tall. It is abundant in the study site with an average of 187 individuals ha^{-1} (García-Nuñez *et al.* 1996). Here, the majority of adult trees flower asynchronously at the end of the dry season (March–April), and fruits ripen and are dispersed until August. The fruit is a near spherical coenocarp drupe, dark violet when ripe, 5–8 mm in length and 4–5 mm in diameter, with a fleshy and very juicy pulp. Seeds are small, weigh less than 0.5 g and have a hard coat.

Study site

The investigation was conducted at Hato Palma Sola, a farm with natural savanna vegetation under extensive cattle ranching at an altitude of 300 m, in the western llanos of Venezuela, about 10 km west of Barinas (08°38′N and 70°12′W). The climate is strongly seasonal with an average 1500 mm of annual precipitation, concentrated between April and November. Mean temperature is 27 °C throughout the year. Fire occurs almost every year during the dry season. The physiognomy of the vegetation lies between open and parkland savanna (Sarmiento *et al.* 1971). Frequent scattered evergreen trees are *Palicourea rigida*, *Byrsonima crassifolia* (L.) Kunth, *Curatella americana* L., and less abundant *Byrsonima coccolobifolia* Nied. and *Bowdichia virgilioides* Kunth. In the grass layer, the most common species are *Andropogon semiberbis* (Nees) Kunth, *Axonopus canescens* (Nees ex Trin.) Pilger, *Elyonurus adustus* (Trin.) Ekman, *Leptocoryphium lanatum* Nees, *Sporobolus cubensis* Hitchc. and *Trachypogon plumosus* Nees.

Field observations

Animals visiting 20 marked trees of *P. rigida*, were observed from nearby concealed locations from 06h00–13h00 and 16h00–19h00 on different days from April to August 1995, totalling 76 observation hours. On several overcast days, observations were continued throughout the day. For each observation, we recorded the visiting species, time and duration of visit, number of fruits eaten and feeding behaviour. Duration of visits was recorded to the nearest 5 s for visits lasting less than 30 s, to the nearest 10 s for visits lasting 30–60 s, and to 30 s when visits lasted more than one min. Scientific and common names of birds follow Schauensee & Phelps (1978).

Cage experiments

For a closer look at the birds' feeding behaviour we conducted cage experiments with birds previously captured with mist nets in the study site. These experiments allowed us to classify species as gulpers with high probability to disperse seeds or as mashers, which do not disperse any or only a part of the consumed seeds (Levey 1987, Schupp 1993). A total of 55 captured individuals of 18 species of birds were kept temporarily (2 d on average) in cages and given fruits of *P. rigida* to consume. We monitored and recorded individual behaviour, the handling procedures and the time spent. Regurgitated and defecated seeds were collected and their viability was tested and compared to the viability of undispersed seeds, using the standard tetrazolium method (Moore 1973). Number of seeds used in these tests depended on the number of seeds collected during the cage experiments (Table 6) and no replicates were feasible.

Fruit consumption

To measure fruit consumption, the fruit crop of 20 trees was estimated at the beginning of the dispersal period (end of April), counting the berries of each infrutescence (to the nearest 10 berries). Exact fruit counting was not possible due to the high amount of fruits per infrutescence (up to 400) and removal of fruits was impractical. At the end of the dispersal period (end of July), fruits remaining in the tree and fruits that had dropped to the ground were counted to estimate the number of fruits removed from each tree.

Effectiveness

Based on Howe & Estabrook (1977), an effectiveness value was calculated for each bird species to compare the relative importance of the different dispersers of *P. rigida*. Effectiveness can be considered as the product of quantity and quality (Schupp 1993). Quantity is the number of seeds dispersed per bird species and was calculated as the species' fraction of fruit consumption multiplied by the fraction of seeds that were not excreted under the treelet but carried away. Quality depends on the treatment given a seed and on the seed deposition. As the quality of seed deposition (microsite, germination conditions and probability of survival) could not be considered in this study, the qualitative component of the effectiveness value refers here only to the fraction of seeds that remain viable after bird treatment. On this basis, the following equation was used:

$$E = F_C \,.\, F_{CA} \,.\, S_V \tag{1}$$

where F_C = fraction of fruits consumed on the tree; F_{CA} = fraction of fruits removed, and S_V = fraction of seeds that remain viable after excretion.

Fractions of fruits consumed or carried away were calculated from field observations and the viability of excreted seeds was obtained from the cage experiments. Since we could not capture the least frequent species *Mimus gilvus* and *Myiodynastes maculatus*, we assumed the viability of their excreted seeds as equal to the average of all other viability results.

RESULTS

Only birds were observed handling and eating *P. rigida* fruits. No other animal species was observed on the trees that could be related to fruit dispersal. No signs of mammal fruit predation were observed during the inspections to the trees. Of the 56 bird species observed at the study site, 14 were recorded visiting *P. rigida* but only eight species were observed feeding in field conditions (Table 1), and another two fed in the cage experiments (*Thamnophilus doliatus* and *Icterus nigrogularis*) (Table 3).

Over two-thirds (69%) of all visits were made by the eight frugivorous species, though proportions differed among species (Table 1). These frugivorous species ate fruits on 56–100% of visits (mean 77%, Table 1). Over 40% of all visits were made by *Tyrannus melancholicus* (tropical kingbird), the most frequent feeder observed. *Elaenia chiriquensis* (lesser elaenia), *Tangara cayana* (burnished-buff tanager) and *Thraupis episcopus* (blue-gray tanager) consistently visited *P. rigida* throughout the whole period, whereas *Molothrus bonariensis*

Table 1. Total number of visits and feeding visits of frugivorous bird species observed feeding on *Palicourea rigida* fruits whilst visiting the tree, and the fraction of total feeding events corresponding to each species.

Species	Family	Visits	Feeding visits	% feeding visits
Tyrannus melancholicus	Tyrannidae	44	28	41.8
Elaenia chiriquensis	Tyrannidae	17	11	16.4
Tangara cayana	Thraupidae	18	10	14.9
Thraupis episcopus	Thraupidae	8	7	10.4
Molothrus bonariensis	Icteridae	7	6	9.0
Myiodynastes maculatus	Tyrannidae	5	3	4.5
Mimus gilvus	Mimidae	1	1	1.5
Rampphocelus carbo	Thraupidae	1	1	1.5
Total		101	67	100

Table 2. Relative fruit consumption, fruits of *Palicourea rigida* consumed per feeding visit and rate of consumption for the eight frugivorous birds observed.

Species	Family	Per cent of fruit consumed	Mean number of fruits consumed per feeding visit	Fruits consumed $\min^{-1}$
Molothrus bonariensis	Icteridae	21.2	5.2	5.6
Mimus gilvus	Mimidae	2.1	3.0	6.0
Tangara cayana	Thraupidae	19.2	2.8	3.9
Thraupis episcopus	Thraupidae	13.0	2.7	4.6
Ramphocelus carbo	Thraupidae	1.4	2.0	8.0
Tyrannus melancholicus	Tyrannidae	30.1	1.6	3.1
Elaenia chiriquensis	Tyrannidae	10.3	1.4	3.9
Myiodynastes maculatus	Tyrannidae	2.7	1.3	4.8
Average		12.5	2.2	4.0

(shiny cowbird) was observed only in July, the month with the highest supply of ripe fruits. These five species were the most important fruit consumers, representing over 90% of all feeding visits (Table 1).

Fruit consumption varied widely among birds (Table 2). From a total of 146 fruits consumed by the birds, *T. melancholicus* ate nearly a third. This species fed slowly and ate few fruits per feeding visit. On the other extreme, *M. bonariensis* was a more intense consumer, eating more than a fifth of the total at a high rate per visit and per minute.

Most species were observed gulping fruits (Table 3). In fact, 39% of all seeds were gulped during the cage experiments. *T. melancholicus*, *M. bonariensis* and *E. chiriquensis* swallowed the complete fruit, including the seed. These species may be categorized as gulpers with a high probability to disperse seeds (Levey 1987, Schupp 1993). Also, *Myiodynastes maculatus* (streaked flycatcher) and *Mimus gilvus* (tropical mockingbird) were observed in the field to gulp fruits but since these species could not be captured, they were not included in the cage experiments. Six species defecated seeds after consumption, whereas only one species (*T. melancholicus*) was observed regurgitating the seeds (Table 3).

Some birds gulped whole fruits, while others mashed fruits and let the seeds fall to the ground. *Tangara cayana* gulped only a few entire fruits but mashed

Table 3. Observed feeding behaviour of birds on *Palicourea rigida* trees and in the cage experiment. G, gulps the whole fruit; F, eats flesh, lets seed fall; GD, gulps the whole fruit and defecates seeds; GR, gulps the fruit and regurgitates the seeds.

Species	Behaviour on tree	Behaviour in cage
Elaenia chiriquensis	G	GD
Icterus nigrogularis	—	F
Molothrus bonariensis	G	GD
Mimus gilvus	G	—
Myiodynastes maculatus	G	—
Ramphocelus carbo	F	F
Tangara cayana	G, F	F, GD
Thamnophilus doliatus	—	F, GD
Thraupis episcopus	G, F	GD, F
Tyrannus melancholicus	G	GD, GR

Table 4. Comparison between retention time of seeds in the gut (from cage experiments) and duration of feeding visit (observed in the field).

	Retention time (min:s)			Feeding visit (min:s)		
Species	n	mean	minimum	n	mean	minimum
Elaenia chiriquensis	5	18:18	16:30	11	0:21	0:50
Molothrus bonariensis	14	27:02	22:20	6	0:42	1:10
Tangara cayana	5	27:30	20:00	10	0:34	1:40
Thraupis episcopus	33	42:30	40:00	7	0:33	1:50
*Tyrannus melancholicus**	8	13:25	12:30	28	0:39	2:30

n, number of cases.
* Retention time of regurgitated seeds; defecation lasted longer but could not be measured.

most with its beak, swallowing 39% of seeds and dropping the rest. Similarly, *Thamnophilus doliatus* (barred antshrike), which could not be observed feeding in field, dropped 74% of the seeds. In contrast, *Ramphocelus carbo* (silver-beaked tanager) and *Icterus nigrogularis* (yellow oriole) mashed fruits and dropped all the seeds. In the field, *Thraupis episcopus* was observed gulping most of the fruits, but rarely let seeds drop, and usually the birds flew away with a berry in the beak.

Gulped seeds can be deposited under the parent tree when retention time is shorter than duration of visits. However, the comparison between retention time and the time spent feeding on the tree for the five most important species, shows that even the maximum duration of visits is always 5 to 20 times smaller than retention time (Table 4). Although retention time of *M. gilvus* and *M. maculatus* could not be measured, their maximum duration of visits was even smaller than the other species, so the probability of releasing the seeds during the visits must be small. Therefore, we can assume that every gulped seed is carried away from the parent tree.

Seed survival

When compared to undispersed seeds, the viability of seeds defecated by *E. chiriquensis* and seeds regurgitated by *T. melancholicus* decreased only slightly with respect to intact seeds (Table 5). Seeds defecated by the latter species showed decreased viability, but the number of seeds tested was small. The other four species decreased seed viability from 17 to 31%.

Table 5. Per cent of seeds that remained viable after defecated by birds during the cage experiment. Viability of intact seeds was 81%.

Species	n	% viable
Elaenia chiriquensis	100	97.3
Tyrannus melancholicus	15 (100*)	65.3 (98.5*)
Molothrus bonariensis	100	82.5
Thraupis episcopus	51	80.1
Thamnophilus doliatus	17	72.6
Tangara cayana	100	68.9

n, number of seeds tested.
* Regurgitated seeds.

Effectiveness

The calculated effectiveness value allows the determination of the relative importance of each species in seed dispersal (Table 6). *T. melancholicus* is the most important disperser with nearly 40% of dispersed seeds, followed by *M. bonariensis* and *E. chiriquensis*. These three species together account for nearly 80% of dispersed seeds and more than half (54.7%) of all fruits consumed by birds. *R. carbo* did not disperse at all or only by accident. The other four species only dispersed 14.3% of the consumed fruits and account for 20% of dispersed seeds.

The addition of effectiveness values results in a high value (0.690) which means that more than two-thirds of all fruits consumed by birds are dispersed. Since we estimated an 86% of the fruit crop consumed by birds, the effective fraction of total seeds dispersed by this system would be 59.3%.

DISCUSSION

We conclude that the dispersal system of *Palicourea rigida* is ornithochory. From a guild of 10 frugivorous bird species, eight participated in seed dispersal, while two pulp eaters did not disseminate the seeds. *Tyrannus melancholicus* was the most effective disperser, followed by *Molothrus bonariensis* and *Elaenia chiriquensis*. These three species together are responsible for about 80% of dispersed seeds. They have been described as common inhabitants in savannas and savanna-like communities in most of the neotropical region (Schauensee & Phelps 1978).

Most previous studies show consumption values under 66% (Chapman & Chapman 1996, Herrera 1995, Howe 1990, Sallabanks & Courtney 1993), although in *Erythroxylum havanense* all fruits were consumed (Gryj & Domínguez 1996). Consequently, our results showed a very high fruit consumption by birds in *Palicourea rigida*.

The small number of fruits consumed per visit (2.2 fruits per feeding visit) may reflect the short duration of visits (34 s) and the low consumption rate (only 4.0 fruits per minute in comparison to 10.9 and 8.9 found by other systems) (Graham *et al.* 1995). *M. bonariensis* had a rate of consumption slightly

Table 6. Calculated values for absolute and relative effectiveness of frugivorous birds, according to Eqn (1).

Species	Eaten	Removed	Viable	Absolute effectiveness	Relative effectiveness %
Tyrannus melancholicus	0.301	1.0	0.903*	0.272	39.4
Molothrus bonariensis	0.212	1.0	0.825	0.175	25.4
Elaenia chiriquensis	0.103	1.0	0.973	0.100	14.5
Tangara cayana	0.192	0.4	0.690	0.052	7.5
Thraupis episcopus	0.130	0.5	0.794	0.052	7.5
Myiodynastes maculatus	0.027	1.0	0.825	0.022	3.2
Mimus gilvus	0.021	1.0	0.825*	0.017	2.5
Total				0.690	100

Eaten, fraction of the total fruit crop eaten by birds; Removed, fraction of eaten fruits that were removed from the tree; Viable, fraction of seeds that remained viable after defecation.
* assumed values: median of determined values.

higher than the average, and a preference for the *P. rigida* fruits. Moreover, this is the only species for which we did not find a correlation between abundance and importance, since visits were restricted to less than a month during the peak of fruiting. In spite of this behaviour, *M. bonariensis* did not show specialization signs and did not have a dominant role in *P. rigida* dispersal system. The other dispersers were abundant throughout the fruiting season. Herrera (1995) and Jordano (1987) found a correlation between fruit consumption and the abundance of the frugivorous bird species in Mediterranean vegetation.

Eighty per cent of consumed fruits were carried away from the parent (69% of the total fruit production), and this is a considerable fraction. In *Byrsonima crassifolia*, another common savanna tree species, we found that only 23.4% of all fruits consumed by birds were carried away (authors' unpubl. data). The high value we found in *P. rigida* is due to the fact that most consumer species are gulpers (62.5%), which consumed 66.4% of all fruits.

The effect of frugivorous birds on the germination or viability of seeds can be variable. The seed passage through the digestive tract of a frugivorous animal can break dormancy and therefore enhance germination, or in seeds without dormancy, can reduce germination rate in different degrees up to destruction of all seeds (Krefting & Roe 1949). In our case, 86% of seeds survived the passage through the gut of the dispersal agents.

The relatively high effectiveness of *P. rigida* dispersal system could be considered as an indication of a specialized dispersal system according to the specialization vs. generalization paradigm (Howe 1993, McKey 1975). The low annual fecundity (< 5000 fruits), the relatively long fruiting season and high fruit removal by a small guild of dispersers present in the *P. rigida* system, are also considered traits of a specialized dispersal system (Howe 1993). In contrast to the paradigm, the dispersal system of *P. rigida* includes generalized traits as well (Howe 1993, Wheelwright *et al.* 1984). Among these traits are small seeds weighing less than 0.5 g and with a hard coat; juicy fruits high in water content and without the protection of a hard skin or spikes; and finally, seed/fruit ratio is low (0.16). Furthermore, dispersers are small, consume fruits only in addition to insects (at least the three most important species) and therefore do not possess adaptations of obligate frugivory, such as a reduced muscular gizzard. As indicated by the small number of fruits eaten per visit, observed species do not seem to be dependent on the fruits of *P. rigida*. Flycatchers (Tyrannidae), in particular, are primarily insectivorous, although they eat fruits regularly (Fitzpatrick 1985). Consequently, *P. rigida* seems to be largely dispersed by unspecialized birds as has been found by Snow (1981) for other *Palicourea* species.

Overall, we found that 59.3% of the total seed crop (> 2300 seeds per adult) was dispersed, suggesting a very effective dispersal system for *P. rigida*. Although this study did not include post-dispersal survival of seeds and seedlings, several aspects of the dispersal system should be remarked as indicative of the potential for recruitment success, invasion and range expansion, as pointed out by Nathan & Muller-Landau (2000). The high proportion of seeds carried away from the parent tree and the high rate of seed survival to the passage through the disperser gut should provide a high recruitment of seeds to the soil and an increased survival of removed seeds (Cain *et al.* 2000). The number of disperser species could buffer the effects of interannual fluctuations in the avian populations, specially considering the fact that *P. rigida* lacks a persistent soil seed bank (Garcia-Nuñez *et al.*, in press). Furthermore, the fact that at least the three more efficient disperser species are common inhabitants in savannas and savanna-like habitats and have a wide range of distribution in the neotropics (Schauensee & Phelps 1978), helps to explain the wide geographical occurrence of *P. rigida* in the neotropical savannas.

Wenny (2000) showed an example of a specialized disperser failing to provide high quality dispersal, contrary to the prediction from the specialization vs. generalization paradigm. Alternatively, our results indicate that *P. rigida* achieves an effective dispersal system with predominantly unspecialized traits, both in the plant and the birds, also contrary to the prediction from the specialization vs. generalization paradigm. This is consistent with the trend of rejections of the hypothesis of closed relationships and narrow co-evolution between specialized fruiting plants and dispersing animals as a requirement for effective dispersal (Fuentes 1994, Herrera 1995, Levey & Benkman 1999, Sallabanks & Courtney 1993).

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