SYMPOSIUM PAPERS

ORNITOLOGIA NEOTROPICAL 15 (Suppl.): 117–126, 2004

FRUGIVORY AND HABITAT USE BY FRUIT-EATING BIRDS IN A FRAGMENTED LANDSCAPE OF SOUTHEAST BRAZIL

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Resumo. – Frugivoria e uso do habitat por aves frugívoras em uma paisagem fragmentada no sudeste do Brasil. – Para investigar o movimento de sementes transportadas por aves frugívoras em uma paisagem agrícola altamente fragmentada na Mata Atlântica do sudeste do Brasil, registrei as principais aves dispersoras de sementes neste ambiente e como usavam os habitats disponíveis (pequenos fragmentos e capões de mata nativa, cercas vivas, árvores isoladas e pastos) onde provavelmente depositavam as sementes. A importância relativa das aves como vetores de sementes foi avaliada baseada no número de espécies de frutos consumidas, número de visitas e taxa de visitas às plantas com frutos. O uso de habitat foi investigado registrando-se os habitats onde as aves eram vistas ou ouvidas durante várias transecções conduzidas pela área de estudo. Dezesseis espécies de plantas foram observadas durante 308,3 horas-planta. Quarenta e duas espécies de aves foram registradas em um total de 830 visitas às árvores com frutos. Sanhaço-cinza (*Thraupis sayaca*) e Sabiá-de-cabeça-cinza (*Turdus leucomelas*) consumiram o maior número de espécies de plantas, foram os visitantes mais freqüentes em termos de número e taxa de visitas e usaram todos os habitats disponíveis. Estas duas espécies e Jacupemba (*Penelope superciliaris*), capaz de dispersar sementes grandes que aves menores são incapazes de ingerir, têm provavelmente uma grande contribuição para o movimento das sementes por esta paisagem degradada.

Abstract. – To investigate the movement of seeds transported by fruit-eating birds in an agricultural, fragmented landscape of the Atlantic forest of southeast Brazil, I asked which bird species are the main seed dispersers in such environment, and how they use the available habitats (small forest fragments, forest thickets, live fences, isolated trees, and active pastures) where they are most likely to drop the seeds they swallow. The relative importance of fruit-eating birds as seed vectors was evaluated based on the number of fruit species eaten, the number of visits, and visitation rate to fruiting plants. Habitat use was accessed by recording the habitats where birds were seen or heard during walks conducted throughout the study area. Sixteen plant species were observed during 308.3 plant-hours. Forty-one bird species were observed eating fruits in a total of 830 visits to fruiting plants. Sayaca Tanagers (*Thraupis sayaca*) and Pale-breasted Thrushes (*Turdus leucomelas*) ate the greatest number of fruit species, were the most frequent plant visitors in terms of number and rate of visits, and had a broad range of habitat use. These two species and the Rusty-margined Guan (*Penelope superciliaris*), which is able to swallow large fruits with large seeds that smaller bird species cannot eat, likely have a great contribution to the movement of seeds throughout this highly degraded landscape. *Accepted 16 December 2003*.

Key words: Agricultural landscape, Atlantic forest, forest fragmentation, frugivory, habitat use, seed dispersal.

INTRODUCTION

Human exploitation of natural environments creates a mosaic of habitats ranging from totally cleared lands to large, well-preserved fragments of the original vegetation (Forman 1995). Between these two extremes there are a variety of landscape elements whose value for the conservation of the biological diversity of the whole landscape is not negligible (Turner & Corlett 1996, Estrada *et al.* 1997, Graham & Blake 2001, Hughes *et al.* 2002). For instance, small forest fragments, forest thickets, live fences and isolated trees serve as habitats or stepping-stones for birds, helping to maintain the connectivity among isolated, undisturbed forest patches (Estrada *et al.* 2000, Fischer & Lindenmayer 2002). From the point of view of forest recovery, such landscape elements also play a role. Small forest fragments and forest thickets, for example, may serve as catalytic agents of forest recovery and accelerate the reversal of deforestation and fragmentation (Lugo 2002, Puyravaud 2003). Trees isolated in pastures, on the other hand, attract seed dispersal agents and act as recruitment foci for forest plant species (Guevara & Laborde 1993, Slocum & Horvitz 2000). Such possibilities are not unreal, but are taking place in some parts of the Neotropical region where lands, traditionally used for agriculture and cattle ranching, are being abandoned and naturally replaced by secondary forests. In the Brazilian Amazon, hundreds of hectares of abandoned pastures are slowly being converted to forests (Uhl *et al.* 1988), and even in the highly degraded and threatened Brazilian Atlantic forest (Morellato & Haddad 2000), a recent increase in forest cover has been observed in some parts of south and southeast Brazil (Vibrans 2003, Zorzetto *et al.* 2003; see Lugo 2002 for similar processes occurring in Puerto Rico).

Frugivorous birds, in conjunction with frugivorous bats (Galindo-González 1998), are key elements for the recovery of tropical forests because they act as seed dispersal agents, moving a variety of seeds throughout the landscape (Wunderle 1997). In other words, they dictate where and when which seeds land. However, frugivorous birds, especially medium-sized to large ones, are sensitive to habitat disturbance and often disappear from degraded lands, leaving plants devoid of important seed dispersal mutualists (Willis 1979, Silva & Tabarelli 2000). Silva & Tabarelli (2000) estimated that approximately 34% of the tree flora occurring in the highly fragmented Atlantic forest of northeast Brazil (Ranta *et al.* 1998) are threatened due to the disappearance of their seed dispersers, large, wide-gaped frugivorous birds. For the frugivorous birds that thrive in disturbed lands the available landscape is not homogeneous. While some bird species favor certain habitats (i.e., forest fragments, live fences, isolated trees, etc.) others avoid them (Estrada *et al.* 1993, Graham & Blake 2001). Studying interhabitat movement of frugivorous birds in an interface between second-growth forest and active and abandoned pastures in eastern Amazonia, Silva *et al.* (1996) noted that, of the 47 bird species recorded in the second-growth forest, 18 also frequented the adjacent abandoned pasture, and only three were found in the adjacent active pasture. Avoidance of degraded lands by frugivorous animals leads to seed limitation and represent one of the great barriers to forest regeneration (Nepstad *et al.* 1990, Duncan & Chapman 2001).

Therefore, to understand the course of natural regeneration of degraded lands and to properly manage this process, it is important to know (i) which bird species are the main seed dispersers in such environments, and (ii) how they use the available habitats. This work was designed to answer these questions in an agricultural, fragmented landscape located in the Atlantic forest of southeast Brazil.

TABLE 1. Fruit and seed characteristics of plant species observed during focal observations, and details of the sampling effort. Ten fruits and seeds were measured for each plant species.

Family	Species	No. of plants observed	Total observation time (h)	Mean fruit diameter ± SD (mm)	Mean seed diameter ± SD (mm)	Number of seeds per fruit
Anacardiaceae	*Lithraea mollioides*	2	3.1	5.0 ± 0.5	3.4 ± 0.2	1
	Schinus terebinthifolius	3	15.1	4.3 ± 0.4	3.9 ± 0.2	1
Boraginaceae	*Cordia sellowiana*	2	10.1	13.4 ± 1.3	5.0 ± 0.5	1
Burseraceae	*Protium heptaphyllum*	2	16.0	6.1 ± 0.2	4.7 ± 0.2	1
Erythroxylaceae	*Erythroxyllum deciduum*	17	43.7	7.0 ± 0.4	4.7 ± 0.3	1
Flacourtiaceae	*Casearia sylvestris*	22	102.3	3.2 ± 0.4	1.3 ± 0.1	1–4
Meliaceae	*Guarea macrophylla*	1	4.0	8.1 ± 1.3	8.0 ± 1.2	1
Moraceae	*Maclura tinctoria*	1	2.0	19.5 ± 1.9	2.1 ± 0.2	> 50
Myrsinaceae	*Myrsine umbellata*	9	30.3	4.7 ± 0.2	3.8 ± 0.1	1
Myrtaceae	*Myrcia floribunda*	1	1.7	9.0 ± 1.0	4.1 ± 0.3	1–2
	Myrcia tomentosa	1	0.7	7.7 ± 1.6	4.3 ± 1.0	1–2
	Sizygium cumini[a]	1	5.2	14.5 ± 1.2	7.8 ± 0.9	1
Rosaceae	*Rubus urticifolius*	1	11.4	9.7 ± 1.9	1.2 ± 0.2	10–50
Sapindaceae	*Pseudina frutescens*	9	23.6	15.4 ± 2.5	10.5 ± 2.2	1–2
Solanaceae	*Cestrum sendtenerianum*	5	23.9	6.4 ± 0.5	2.7 ± 0.3	3–6
Verbenaceae	*Aegiphila sellowiana*	4	15.2	5.2 ± 0.2	3.7 ± 0.3	1

[a]Exotic plant species.

STUDY AREA AND METHODS

The study was conducted in private lands located in the rural zone of Itatiba (22°57'S, 46°44'W; 800 m a.s.l.), São Paulo state, SE Brazil, in an area of approximately 300 ha. The region was originally covered by semideciduous Atlantic forest (*sensu* Morellato & Haddad 2000), which was fragmented many decades ago to give place to pastures and agricultural fields. Embedded in this human-derived matrix, one can find four distinct habitats: (i) small forest fragments (1–30 ha) in different successional stages, (ii) forest thickets [i.e., small groups (clumps) of trees < 0.05 ha], (iii) live fences (140–450 m long, 6–12 m wide) composed of native vegetation left by land owners along the boundaries of their properties, and (iv) isolated trees in pastures. Climate is seasonal, characterized by a hot-wet season from September to March, and a dry-cold season from April to August. An ongoing bird survey recorded 165 species in the area (M. A. Pizo unpubl. data).

From August 2002 to August 2003, I made focal observations on plants with fleshy fruits, recording the bird species that visited them to eat fruits, as well as their fruit handling behavior (i.e., if they swallow the whole fruit or only parts of it). Observations were conducted in the morning (06:00–10:00 h), and late afternoon (16:00–18:00 h) from observation points, concealed whenever possible, located at least 15 m from the focal plant. Plants were selected for observation according to their availability, irrespective of the habitat where they occurred. Because fruit and seed size represent important constraints for fruit handling by birds (Levey 1987), fruit and seed diameters were measured with calipers to the nearest 0.1 mm, from at least ten fresh fruits and seeds of each plant species.

The relative importance of each bird species as seed disperser was based on three

TABLE 2. Bird species recorded eating fruits at the study site. Within families, bird species are arranged in alphabetical order.

Family	Species	Diet[a]	No. of fruit species eaten[b]	No. of visits to fruiting plants	Mean visitation rate ± SD (visits/ 10 h)
Cracidae	*Penelope superciliaris*	F	3	2	0.09 ± 0.24
Columbidae	*Columba cayenensis*	G	2	2	0.06 ± 0.17
	Columba picazuro	G	2	6	0.31 ± 1.00
	Columbina talpacoti	G	1	2	0.04 ± 0.17
	Leptotila verreauxi	G	1	3	0.13 ± 0.51
	Zenaida auriculata	G	1	1	0.04 ± 0.17
Psittacidae	*Aratinga leucophtalmus*	F	1	5	0.63 ± 0.46
Cuculidae	*Crotophaga ani*	I	2	8	0.45 ± 1.58
	Guira guira	I	1	2	0.01 ± 0.05
Picidae	*Celeus flavescens*	IF	4	3	0.07 ± 0.19
	Colaptes campestris	I	2	5	0.19 ± 0.53
	Melanerpes candidus	I	1	1	0.02 ± 0.06
	Veniliornis spilogaster	I	2	2	0.04 ± 0.10
Tyrannidae	*Camptostoma obsoletum*	I	2	8	0.10 ± 0.35
	Elaenia flavogaster	FI	4	12	0.22 ± 0.61
	Empidonomus varius	IF	2	15	0.22 ± 0.82
	Myiarchus ferox	IF	4	23	0.33 ± 0.78
	Myiodynastes maculatus	IF	3	12	0.48 ± 1.36
	Myiozetetes similis	IF	4	5	0.10 ± 0.33
	Pachyramphus validus	I	1	2	0.03 ± 0.12
	Pitangus sulphuratus	O	6	19	0.60 ± 1.35
	Tyrannus melancholicus	IF	3	13	0.17 ± 0.48
	Tyrannus savanna	IF	3	93	0.88 ± 2.10
	Xolmis velata	I	2	23	0.30 ± 1.00
Corvidae	*Cyanocorax cristatellus*	O	4	12	0.70 ± 1.56
Mimidae	*Mimus saturninus*	O	3	3	0.19 ± 0.51
Muscicapidae	*Turdus amaurochalinus*	FI	2	2	0.02 ± 0.06
	Turdus leucomelas	FI	11	136	4.79 ± 6.17
	Turdus rufiventris	FI	8	28	0.84 ± 1.27

TABLE 2. Continuation.

Family	Species	Diet[a]	No. of fruit species eaten[b]	No. of visits to fruiting plants	Mean visitation rate ± SD (visits/ 10 h)
Vireonidae	*Cyclarhis gujanensis*	IF	3	3	0.12 ± 0.27
	Vireo olivaceus	IF	2	10	0.09 ± 0.24
Emberezidae	*Pseudoleistes guirahuro*	I	1	2	0.01 ± 0.05
	Dacnis cayana	O	5	16	0.42 ± 0.98
	Tachyphonus coronatus	FI	4	20	0.88 ± 2.91
	Tangara cayana	FI	7	37	1.27 ± 3.85
	Tersina viridis	FI	1	1	0.02 ± 0.06
	Thraupis sayaca	FI	17	231	26.03 ± 72.26
	Coryphospingus cucullatus	GI	1	1	0.04 ± 0.16
	Saltator similis	FI	4	14	0.48 ± 1.46
	Volatinia jacarina	GI	3	29	0.77 ± 2.38
	Zonotrichia capensis	IG	4	18	0.55 ± 1.12

[a] Diet categories based on personal observations and on the literature (Moojen *et al.* 1941, Schubart *et al.* 1965, Willis 1979). Codes: F = frugivorous, G = granivorous, I = insectivorous, O = omnivorous (i.e., more than two diet categories). When two codes were applied to the same bird species, the first code refers to the predominant diet category.

[b] In addition to the 16 plant species observed during focal observations (see Table 1), three plant species (*Psidium guajava* – Myrtaceae, *Solanum granuloso-leprosum* – Solanaceae, *Lantana camara*, and *Lantana* sp. – Verbenaceae) were recorded in non-systematic observations.

parameters: (i) number of fruit species eaten, (ii) number of visits to fruiting plants, and (iii) visitation rate. The first parameter was derived not only from the focal observations, but also from non-systematic records of birds eating fruits. The number of visits and visitation rate are important components of the effectiveness of seed dispersal, being usually positively correlated with the number of dispersed seeds (Schupp 1993, Jordano & Schupp 2000). Visitation rates were averaged over all observed plant species and presented as number of visits/10-h observation.

To investigate habitat use by frugivorous birds (i.e., those recorded during focal observations), I recorded the habitats (i.e., forest fragments, clumps of trees, live fences, isolated trees; see above) where birds were seen or heard during several walks conducted throughout the study area. I did not consider the number of individuals; therefore, birds alone or in flocks were treated equally in the analysis of habitat use. I also recorded the presence of birds in the predominant matrix of active pastures. This procedure permitted to infer where the different species of birds were more likely to deposit the seeds they swallow.

RESULTS

Sixteen plant species (81 individual plants) representing 13 plant families were observed for a total of 308.3 plant-hours (a plant-hour corresponds to one plant observed for one hour; Table 1). These plants were among the most common plant species at the study site, and produced fruits whose diameter ranged in size from 3 to 19 mm. Seed number and seed size varied greatly, from fruits with a large number of small seeds (e.g., *Maclura tinctoria*, Moraceae) to fruits with only one or two large seeds (e.g., *Pseudina frutescens*, Sapindaceae; Table 1).

Forty-one bird species (including six species of Columbidae and Psittacidae traditionally considered as seed predators; del Hoyo *et al.* 1997) were observed eating fruits in a total of 830 visits to fruiting plants (Table 2). Sayaca Tanagers (*Thraupis sayaca*) and Pale-breasted Thrushes (*Turdus leucomelas*) ate the greatest number of fruit species. These two species, plus the Fork-tailed Flycatcher (*Tyrannus savanna*), were the most frequent plant visitors, responsible for 54.8% of the visits recorded. Visitation rates were fairly variable among plant species, as denoted by the high values of standard deviations relative to means. Once again Sayaca Tanagers and Pale-breasted Thrushes presented the highest visitation rates to fruiting plants (Table 2).

Forest fragments were the most frequent habitats used for the top ten plant visitors, responsible for 74.1% of the recorded visits (Fig. 1). Sayaca Tanagers were frequently recorded in live fences, Fork-tailed Flycatchers and White-rumped Monjitas (*Xolmis velata*) in isolated trees, and Blue-black Grassquits (*Volatinia jacarina*) in pastures. In a qualitative analysis, Great Kiskadees (*Pitangus sulphuratus*), Fork-tailed Flycatchers, Sayaca Tanagers, and Pale-breasted Thrushes were the only to use all the habitats considered (Fig. 1).

DISCUSSION

Considering the number and frequency of visits to fruiting plants and the variety of fruit species eaten, Sayaca Tanagers and Pale-breasted Thrushes are among the most important avian seed dispersers in the fragmented, disturbed landscape studied. Moreover, these species used a variety of habitats likely having a great contribution to the movement of seeds throughout this landscape. In fact, both species are known to thrive in disturbed lands, and Sayaca Tanagers may fly for long distances between forest patches (Ridgely & Tudor 1989, Sick 1997, Isler & Isler 1999, Yabe & Marques 2001). In

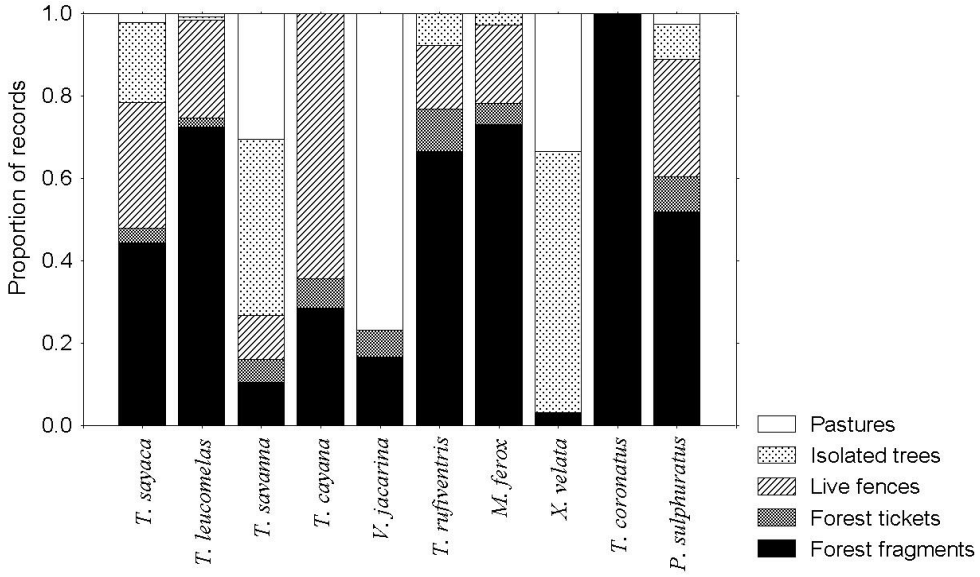

FIG. 1. Habitats used by fruit-eating birds at Itatiba, São Paulo, Brazil. On the X axis bird species are arranged in decreasing order of number of visits to fruiting plants. Bird species and number of records (between parentheses) are as follows: *Thraupis sayaca* (144), *Turdus leucomelas* (131), *Tyrannus savanna* (56), *Tangara cayana* (14), *Volatinia jacarina* (30), *Turdus rufiventris* (39), *Myiarchus ferox* (37), *Xolmis velata* (30), *Tachyphonus coronatus* (4), and *Pitangus sulphuratus* (42). See text for description of habitats.

a survey of 26 studies of avian frugivory in a variety of disturbed areas of south-southeast Brazil, Sayaca Tanagers and Pale-breasted Thrushes were also among the most frequent plant visitors and seed dispersers (M. A. Pizo unpubl. data).

Fruit-eating by predominantly insectivorous birds was frequently observed in this study. Although these species ate fruits of a few plant species, they frequent habitats not readily used by true frugivorous species (e.g., pastures by Fork-tailed Flycatchers, White-rumped Monjitas, and Blue-black Grassquits), and may be important seed vectors to such habitats which otherwise receive few seeds from fleshy fruits (Nepstad *et al.* 1990, Wijdeven & Kuzee 2000). What deserves further investigation is the quality of treatment these predominately insectivorous birds provide to the seeds they ingest, i.e., if they destroy or pass seeds intact through the gut, or even if they alter the germination success (see Schupp 1993, Traveset 1998).

Although rarely recorded in this study, the Rusty-margined Guan was the only species large enough (950–1150 g; del Hoyo *et al.* 1994) to swallow large fruits (> 15 mm diameter) with large seeds (e.g., *Pseudina frutescens*). This cracid is one of the few large avian frugivores able to survive in disturbed Atlantic forests, where it eats the fruits and disperse the seeds of a variety of plant species (Willis 1979, Mikich 2002). Moreover, this species can be considered for captive breeding and reintroduction programs (Pereira & Wajntal 1999). Thus, it should be carefully considered in conservation efforts to overcome the usual lack of large avian seed dispersers in fragmented forests (Silva & Tabarelli 2000). For large fruits with small seeds (e.g., *Maclura tinctoria*;

Psidium guajava, Myrtaceae), Sayaca Tanagers once again may act as seed dispersers. Being able to mash fruits in their bill and eat them piecemeal (Levey 1987), Sayaca Tanagers often dominate the visits to these plants. For instance, in *M. tinctoria* (whose seeds are also dispersed by bats; Fleming & Heithaus 1981) Sayaca Tanagers were responsible for 96.6% of the recorded visits (N = 59).

In summary, this study revealed that a variety of bird species eat fruits and likely disperse seeds in an agricultural, highly fragmented landscape in the Atlantic forest of southeast Brazil. Three bird species, however, should be highlighted: the Sayaca Tanager and the Pale-breasted Thrush, which eat a great variety of fruits, visit fruiting plants frequently, and have a broad range of habitat use, and the Rusty-margined Guan, the largest avian frugivore thriving in the study area, which is able to swallow and likely disperse the seeds of large fruits with large seeds that smaller bird species cannot eat.

ACKNOWLEDGMENTS

I am grateful to Bruno Turbiani, Paulo Rubim, Rafael Trevisan, Tadeu J. A. Guerra, and Vagner A. Gabriel for the kind help during the fieldwork. Comments by Mauro Galetti, Wesley Silva and Marcos Rodrigues greatly improved the manuscript. Special thanks are directed to the landowners who kindly permitted access to their lands. Financial support came from a fellowship from the Brazilian Research Council (CNPq, proc. PROFIX no. 540481/01-7). The facilities provided by the Departamento de Botânica of UNESP at Rio Claro made possible the preparation of this paper.

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