ORNITOLOGIA NEOTROPICAL 17: 373–382, 2006

DIET OF THE RUSTY-MARGINED GUAN (*PENELOPE SUPERCILIARIS*) IN AN ALTITUDINAL FOREST FRAGMENT OF SOUTHEASTERN BRAZIL

William Zaca[1], Wesley Rodrigues Silva[2,4], & Fernando Pedroni[3]

[1]Programa de Pós-Graduação em Ecologia e Conservação de Recursos Naturais, Universidade Federal de Uberlândia, Campus Umuarama, 38400-902, Uberlândia, MG, Brasil. *E-mail*: wzaca68@hotmail.com

[2]Laboratório de Interações Vertebrados-Plantas, Departamento de Zoologia, Instituto de Biologia, Universidade Estadual de Campinas, 13083-970, Campinas, SP, Brasil. *E-mail*: wesley@unicamp.br

[3]Departamento de Ciências Biológicas e da Saúde, Universidade Federal de Mato Grosso, 78698-000, Pontal do Araguaia, MT, Brasil. *E-mail*: fpedroni@cpd.ufmt.br

Resumo. – Dieta do Jacupemba (*Penelope superciliaris*) em um fragmento de floresta altitudinal no sudeste brasileiro. – Neste trabalho estudamos a dieta do Jacupemba (*Penelope superciliaris*), entre Março de 1999 a Outubro de 2000, em um fragmento de Floresta Atlântica de altitude, no Parque Municipal do Itapetinga, Atibaia, SP. Estudamos os hábitats utilizados para alimentação, altura de forrageamento, sazonalidade da dieta e características morfológicas dos frutos consumidos. Foram coletadas 223 amostras fecais e registrados 25 eventos de alimentação, sendo o maior número no interior da mata e em alturas entre 5,1 a 10 m. A dieta foi composta por frutos de 52 espécies de plantas, além de folhas e flores. Myrtaceae, Rubiaceae e Solanaceae foram as famílias mais bem representadas nas amostras fecais. O consumo de frutos não foi sazonal e o de folhas e flores apresentou um aumento significativo nas estações secas. Bagas e drupas foram mais freqüentes na dieta. O Jacupemba é um frugívoro generalista de grande porte, que pode atuar como importante dispersor de sementes em fragmentos florestais com diferentes graus de degradação no sudeste do Brasil.

Abstract. – We studied the diet of the Rusty-margined Guan (*Penelope superciliaris*), from March 1999 to October 2000, in an altitudinal forest fragment in southeastern Brazil, located in the Parque Municipal do Itapetinga, in Atibaia, SP. We studied habitat use for feeding, strata occupied for foraging, diet seasonality and morphological characteristics of consumed fruits. We collected 223 fecal samples and recorded 25 feeding-bouts, mostly in the forest interior, and between 5.1 and 10 m high. The fruit diet was composed of 52 plant species, beyond leaves and flowers. Myrtaceae, Rubiaceae and Solanaceae were the family most represented in the fecal samples. Fruit consumption presented no seasonality in the study area, whereas flowers and leaves were consumed mainly in the dry season. Berries and drupes appeared more frequently in the diet. Rust-margined Guans are large-bodied generalist frugivores that can act as important seed dispersers in forest fragments with different degrees of degradation in the southeastern Brazil. *Accepted 25 January 2006*.

Key words: Cracidae, seed dispersal, frugivory, habitat fragmentation, altitudinal Atlantic forest.

[4]*Corresponding author.*

INTRODUCTION

Guans of the genus *Penelope* are important seed dispersers for many plant species in tropical forests (Howe 1984), as they usually pass seeds undamaged through their guts (Érard & Théry 1994), an interaction that is tremendously beneficial for both plants and animals in these forests (Janzen 1983, Jordano 1992). Furthermore, the Rusty-margined Guan (*Penelope superciliaris*) is one of the few large frugivore species that can be found in forest fragments of relatively small sizes in southeastern Brazil, a condition that underlies its role as a key component in the plant regeneration processes taking place in those habitats (Mikich 1996).

Despite the importance of this large frugivore as part of the many fragile and fragmented forest habitats along its area of distribution, few studies provide information on their ecology and natural history, leading to management and conservation efforts (Strahl & Grajal 1991), especially in the highly deforested region of southeast Brazil (Galetti *et al.* 1997, Mikich 2002).

This study aims to contribute to the knowledge of the feeding biology of Rusty-margined Guans in an altitudinal forest fragment of the Atlantic forest domain in southeastern Brazil, assessing the relative importance of different vegetable items in the diet.

METHODS

Study site. Field work was carried out in the Parque Municipal do Itapetinga, located in Atibaia, São Paulo state (23°07'–23°12'S, 46°49'–46°32'W), in the mid slope of the Serra do Itapetinga, a 245-ha protected area ranging in altitude from 900 to 1400 m. The climate is characterized by two well-defined seasons. The dry-cold season extends from April to September, and the wet-hot season lasts from October to March. The annual mean temperature is 18.7°C, July is the coldest month (mean = 14.5°C) and February is the warmest (mean = 21.7°C). The annual mean precipitation is around 1500 mm, with the monthly mean precipitation ranging from 37 mm in August to 244 mm in January (Centro de Pesquisa Agrícola – Cepagri – Unicamp, unpubl.). The main vegetation type of the park is the altitudinal semi-deciduous forest, with trees of 10–15 m high. A few coffee trees remain in the understory of the forest in some areas because a coffee plantation existed in this local around 60–70 years ago. Granite outcrops are scattered throughout the area, especially in the hilltops, where the forest is replaced by rocky fields (Meira Neto *et al.* 1989). In the outer limits of the park there are anthropic areas, including pastures and agricultural fields.

The bird. Rusty-margined Guan is a mid-sized cracid (55–73 cm and 750–800 g) (del Hoyo 1994), being the smaller in its genus. The characteristic bare, red, dewlap is more prominent in males, which are also larger than females (Delacour & Amadon 1973, Sick 1997). The species ranges from south of Amazon and Madeira rivers to the northeast, south central, southeast, and south Brazil, extending until Paraguay and far north Argentina (Guix 1997, Sick 1997). In Brazil, this guan species inhabits the border of forest formations in the domain of the semi-deciduous forest of the southeast, as well as in riparian forests of the Cerrado and Caatinga biomes (del Hoyo 1994, Sick 1997).

Feeding data. Between March 1999 and October 2000, we made 54 field visits, 2 days a week, both in the morning (06:00–12:00 h) and in the afternoon (15:00–18:00 h). We set these sessions of observations according to previous knowledge of guans behavior in the study site. Sample effort totalized 374 h of

field observation: 206 h in forest (52 ha), 105 h in open areas (22 ha, rocky outcrops, roads and old fields with isolated trees), and 63 h in "capoeira" (16 ha, usually an early to mid successional stage in forest regeneration). Two methods were employed to record the observation of birds feeding upon a food source: feeding-bouts in transects (6 km) through definite routes (forest, edges and trails) and observations on focal-trees. In the first, several routes were established in the study site and walked slowly by the observer trying to spot birds feeding on fruit trees. In the second, the observer stayed at a convenient distance from a fruiting plant, trying to record guan visits to that plant.

Feeding-bouts (*sensu* Altmann 1974) are here defined as the observation of one or more individuals consuming fruits, flowers or leaves from an individual plant. A new feeding-bout was recorded if the observed bird moved to another plant. We also recorded habitat types where feeding-bouts occurred. The stratum where foraging birds were observed was divided into four categories: ground, < 5 m, 5.1–10 m, > 10 m. Detectability of feeding birds were similar in forest and capoeira habitats, but greater in open areas. Fruits eaten by guans were identified at the species level, and characterized by their general morphological type (berry, drupe, multiple fruit, arilate seed, nucoid and syconium, (see Barroso *et al.* 1999). The largest and smallest diameter of ripe fruits were taken with a caliper to the nearest millimeter from a sample of 30 fruits taken randomly from 4–5 plants of those species that were accessible along the study.

Fecal samples. Feces were collected as they were found along the transects where the observations were made, each individual pellet considered as one sample. No regurgitated seeds from guans were found in the study site. These samples were bagged and kept under soft refrigeration until the analysis in the lab, where feces were washed and inspected under a 10× stereomicroscope. Fecal contents were identified and quantified on a monthly basis, being all samples pooled together to determine the frequency of occurrence of the different items. Seed identification from feces was made possible with the aid of a reference collection from the study site.

The monthly diversity of seed species, as appeared in the feces, was calculated using the Simpson's diversity index (Krebs 1999), as follows: $D = \Sigma\ pi^2$, where D = Simpson's diversity index; pi = proportion of fecal samples containing the plant species i.

Differences among habitats, strata occupied by foraging birds, diet seasonality and morphological fruit types consumed were compared by the Chi-square test using the Yates correction (Zar 1999).

RESULTS

Of the 25 feeding-bouts recorded, 14 were recorded in the forest (56%), 9 in open areas (36%) and 2 in capoeira (8%) ($\chi^2 = 5.78$; $P < 0.05$). Guans fed significantly more often at mid level in the vegetation: 13 records between 5.1–10 m, 4 below 5.0, and 4 at upper 10 m high ($\chi^2 = 9.72$; $P < 0.05$).

We collected 223 fecal samples. From this total, 153 (68.6%) were gathered in forest habitats, 49 (22%) in open areas, and 21 (9.4%) in capoeira. None of the fecal samples had invertebrate remains.

During the dry seasons of 1999 and 2000, we collected 135 fecal samples of the Rusty-margined Guan: 67 with only seeds, 61 with seeds and remains of leaves, and 7 with only flowers. In the wet seasons of the same years, we collected 88 samples, all with seeds but no leaves or flowers remains. Fruits were consumed year round, with no significant differences between dry and wet seasons ($\chi^2 = 3.16$; $P > 0.05$). On the other hand, the consump-

TABLE 1. Characteristics and frequency of occurrence of fruit species consumed by Rusty-margined Guans (*Penelope superciliaris*) in an altitudinal Atlantic forest fragment in Atibaia, south-eastern Brazil (ND = not determined).

Families	Species	Freq. occurrence (%)	Life forms	Fruit types
Anacardiaceae	*Schinus terebinthifolius*	1.79	Tree	Drupe
Aquifoliaceae	*Ilex* sp.	1.79	Tree	ND
Araliaceae	*Didymopanax angustissimum*	9.21	Tree	Drupe
Boraginaceae	*Cordia sellowiana*	1.35	Tree	Drupe
Ebenaceae	*Diospyros inconstans*	0.45	Tree	Berry
Erythroxyllaceae	*Erythroxylum argentinum*	9.87	Tree	Drupe
Euphorbiaceae	*Alchornea triplinervia*	1.35	Tree	Arilate
	Sapium glandulatum	0.45	Tree	Arilate
Flacourtiaceae	*Casearia sylvestris*	0.45	Tree	Arilate
Lauraceae	*Ocotea diospyrifolia*	1.35	Tree	Berry
	Persea pyrifolia	0.45	Tree	Berry
Leguminosae	*Copaifera langsdorffii*	0.90	Tree	Arilate
Liliaceae	*Smilax* sp.	0.45	Liana	ND
Loganiaceae	*Strychnos brasiliensis*	0.45	Shrub	Berry
Melastomataceae	*Miconia cinnamomifolia*	7.17	Tree	Berry
Moraceae	*Ficus enormis*	1.79	Tree	Syconium
	Ficus sp2	2.69	Tree	ND
Myrsinaceae	*Myrsine coriacea*	1.35	Tree	Drupe
Myrtaceae	*Calyptranthes clusiaefolius*	0.90	Tree	Drupe
	Campomanesia guazumaefolia	1.35	Tree	Berry
	Eugenia brevipedunculata	2.24	Tree	Berry
	Eugenia involucrata	1.79	Tree	Berry
	Eugenia uniflora	1.79	Tree	Berry
	Eugenia uvalha	2.69	Tree	Berry
	Eugenia sp1	0.90	Tree	Berry
	Myrcia rostrata	0.45	Tree	Berry
	Myrcia sp.	5.38	Tree	ND
	Myrtaceae sp1	1.35	ND	ND
	Myrtaceae sp2	3.34	ND	ND
Nyctaginaceae	*Guapira opposita*	3.59	Tree	Nucoid
Rosaceae	*Prunus sellowii*	2.69	Tree	Drupe
	Prunus myrtifolia	0.45	Tree	Drupe
	Rubus rosaefolius	5.38	Herb	Multiple
Rubiaceae	*Amaioua guianensis*	0.45	Tree	Drupe
	Coccocypselum sp.	0.45	Herb	ND
	Coffea arabica	9.42	Shrub	Drupe
	Guettarda viburnoides	3.59	Tree	Drupe
	Psychotria sessilis	1.79	Shrub	Drupe
	Rudgea jasminoides	0.90	Tree	Drupe
Rutaceae	*Zanthoxylum rhoifolium*	0.45	Tree	Multiple
Sapindaceae	*Allophyllus* sp.	0.45	Tree	ND
	Cupania vernalis	3.59	Tree	Arilate
Sapotaceae	*Pouteria* sp.	0.45	Tree	ND

TABLE 1. Continued.

Families	Species	Freq. occurrence (%)	Life forms	Fruit types
Solanaceae	*Solanum granuloso-leprosum*	5.22	Tree	Berry
	Solanum sp2	5.12	ND	ND
	Solanum sp3	5.04	ND	ND
Styracaceae	*Styrax pohlii*	8.97	Tree	Berry
Symplocaceae	*Symplocos laxiflora*	0.45	Tree	Drupe
	Symplocos mosenii	7.04	Tree	Drupe
Thymeliaceae	*Daphnopsis brasiliensis*	0.45	Tree	Nucoid
Verbenaceae	*Aegiphila selloviana*	0.45	Tree	Drupe
	Vitex polygama	4,48	Tree	Drupe

tion of leaves and flowers was markedly different between dry and wet seasons, showing a distinct peak right in the middle of the dry season ($\chi^2 = 61.41$; $P < 0.001$).

Rusty-margined Guans ate the fruits of 52 plant species belonging to 27 botanical families at Serra do Itapetinga (Table 1). All were represented in the fecal samples, but only 12 species were also registered by directed observation (feeding bouts). Myrtaceae (11 species), Rubiaceae (6) and Solanaceae (3) were the most speciose families in the diet. The most frequent fruit species in the samples were: *Erythroxylum argentinum*,

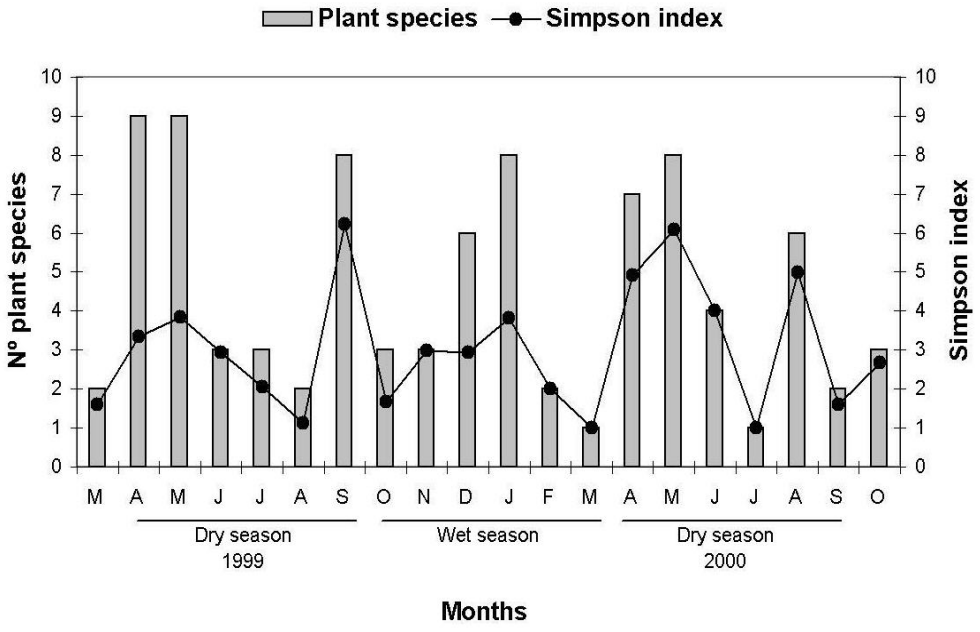

FIG. 1. Relation between species richness and species diversity of the seed content found in the fecal samples of Rusty-margined Guans (*Penelope superciliaris*), between March 1999 and October 2000 in Atibaia, southeastern Brazil.

Coffea arabica, *Didymopanax angustissimum*, *Styrax pohlii*, *Miconia cinnamomifolia* and *Symplocos mosenii* (Table 1).

Both the plant species richness and the species diversity in fecal samples were higher mostly during the dry season (Fig. 1). Although many plant species were represented in the diet, seeds from a few plant species were predominant in 72 fecal samples taken in those months: *S. pohlii* (51.8% of samples), *M. cinnamomifolia* (47.1%), *S. mosenii* (52%), and *E. argentinum* (40.9%).

Fruit diameter ranged from 3.5 ± 0.4 mm (*M. cinnamomifolia*) to 22.3 ± 2.5 mm (*Diospyros inconstans*). The average fruit diameter for the most consumed fruit species was between 4 and 16 mm. Drupes (42.5%) and berries (32.5%) were predominant in the guan diet, with no difference between them ($\chi^2 = 0.54$; $P > 0.05$).

DISCUSSION

Rusty-margined Guans can be found in a variety of habitats in Atibaia, but occur most frequently in the canopy of interior forest, a stratum often used by guans for foraging (Delacour & Amadon 1973, Mikich 1996, Guix 1997).

In this study, both the fecal analysis and the visual feeding records indicated a diet heavily based on fruits, like other cracids in the Neotropical region (Théry *et al.* 1992, Érard & Théry 1994, Galetti 1996). The lack of invertebrates in the fecal samples probably was due to the method employed to analyze the diet. Animal food items are most frequently found when birds are killed and have their stomachs opened (scrutinized) (Andrle 1967, Marion 1976, Théry *et al.* 1992, Caziani & Protomastro 1994). In the few studies that analyzed cracids diet with the same method used here, invertebrates were rarely found (González-García 1994, Merler *et al.* 2001).

The increased of leaf and flower consumption by Rusty-margined Guans only in the dry season may be related to the low fruit availability during that period. In fact, the number of plant species bearing zoochorous fruits in the dry season is markedly low in both the plateau and the altitudinal semideciduous forests in that part of São Paulo state (Morelatto & Leitão-Filho 1992). Many cracids diversify their diet during the dry season or the transition between wet and dry seasons (del Hoyo 1994), a behavioral shift also found in other frugivorous vertebrates during periods of fruit scarcity (Terborgh 1986). Merler *et al.* (2001) also found traces of leaf material in the feces of Dusky-legged Guan (*P. obscura*) in Argentina, but only during the winter. Some species of birds often include fibrous plant tissues as major dietary items doubtless because they are able to obtain a considerable fraction of energy from fiber to satisfy their maintenance energy requirements (Lopez-Calleja & Bozinovic 2000). On the other hand, as some fruits have usually low nitrogen content, frugivorous birds would tend to complement their diet ingesting leaves (Sun *et al.* 1997). The dominance of certain plant species in the fruit diet of Rusty-margined Guans can be explained by their local abundance in Atibaia. For instance, in the beginning of the dry season, *S. pohlii* seeds showed up in 51.8% of the fecal samples. This species was among those with the highest values of relative dominance and abundance in a previous phytosociological study (Grombone *et al.* 1990). *Miconia cinnamomifolia*, occurring in 47.1% of the fecal samples, although not particularly abundant (Grombone *et al.* 1990), fruited copiously during the whole dry season. *Miconia* fruits are well known for being consumed by a plethora of avian frugivores (Stiles & Rosselli 1993, Galetti & Stotz 1996), especially understory frugivorous birds (Loiselle & Blake 1990).

Rusty-margined Guans may rely on fruits of a few plant species during the cold dry sea-

son, e.g., *Styrax* and *Miconia* in the study site. In Argentina, *Ligustrum sinense* and *L. lucidum*, although exotic species there, are important food resources for Dusky-legged Guan (*P. obscura*) during the winter (Merler *et al.* 2001). In Paraná state (south Brazil), Mikich (2002) observed that the palmito *Euterpe edulis* was the major food item for Rusty-margined Guans during the fruiting peak of this palm species, which occurred in the transition between wet and dry seasons (March to July).

On a diet basis, Rusty-margined Guans can be considered as generalist frugivores since they rely on locally abundant food items. This seems to be the case with the several Myrtaceae species abundantly found in the study site (Grombone *et al.* 1990). Fruits of this plant family have been pointed out as an important food item for cracids in similar studies (Théry *et al.* 1992, Galetti *et al.* 1997, Guix *et al.* 2001).

Solanaceae seeds were also frequent in the fecal samples of Rusty-margined Guans. These are usually second-growth plants in tropical habitats, becoming very abundant in disturbed areas or along the edges of forest fragments (Tabarelli *et al.* 1999). Although Rusty-margined Guans occur most frequently in the canopy of interior forest, seeds of Solanaceae species were the most important diet item in the study site. Besides fruits, Solanaceae leaves may also be part of the diet of this guan species (Mikich 2002) and Plain Chachalaca (*Ortalis vetula*) (Marion 1976, Christensen *et al.* 1978).

The size of fruits consumed by Rusty-margined Guans in this study falls between the size ranges observed for other cracids (Remsen Jr. & Cardiff 1990, Théry *et al.* 1992, Mikich 2002). Although fruits were not analyzed chemically in this study, most of the fruit species eaten by the guans are reported to vary greatly in their nutrient content, ranging from sugar rich berries like *Miconia* species (Schaefer *et al.* 2003) to lipid rich arils like those of *Alchornia* and *Cupania* species (Galetti *et al.* 2000). In Atibaia, Rusty-margined Guans can be considered as generalist frugivores, exploiting abundant fruits in the area and including in their diet a great variety of small to large fruits due to their wide gape. Since the gape size of frugivorous birds can limit the number of fruits included in their diet, a wide gape enables the birds to potentially disperse the seeds of a diverse array of plant species in the community (Moermond & Denslow 1985, Wheelwright 1985).

Implications for conservation. The Atlantic forest of southeast Brazil is one of the most threatened ecosystems in the world. Covering originally more than 1.3 millions of km^2, this biome is now reduced to 8% of its former distribution (Ministério do Meio Ambiente 2000). Most forest remnants are forest fragments of variable sizes (Brown & Brown 1992), as in the Atibaia region, and most of these forest fragments have experienced heavy vegetation and faunal impoverishments over the last decades, due to logging, illegal hunt and habitat destruction. Large frugivores are one of the bird guilds most affected by forest fragmentation in southeastern Brazil (Willis 1979, Anjos & Boçon 1999, Anjos 2002). However, Rusty-margined Guans seem to be the largest resilient frugivores to survive in small forest fragments (Aleixo & Vielliard 1995, Mikich 2002), probably because they include food items other than fruits in its diet, like flowers and leaves, and also because, in general, guans home range may be large enough to encompass a large amount of food resources (Guix & Ruiz 1997, Sánchez-Alonso *et al.* 2002).

Their capacity for ingesting a high number of fruit species with great variety of fruit types, and dispersing their seeds, is certainly a very important feature of such a bird species in these degraded forest fragments. In fact, the loss of wide-gaped avian seed dispersers

in small forest fragments in the Atlantic forest of northeastern Brazil can jeopardize the survival of many tree species that produce medium to large-sized fruits (Silva & Tabarelli 2000). Thus, the permanence of Rusty-margined Guans in small forest tracts in southeastern Brazil emerges as an effective protective measure to guarantee the maintenance of seed dispersal processes in those fragile communities.

ACKNOWLEDGMENTS

L. P. Bueno assisted in many aspects related to the fieldwork. J. Y. Tamashiro kindly helped with plant identification. M. C. M. Ribeiro provided valuable suggestions along the study and M. A. Pizo improved the early version of the manuscript with criticism and suggestions. W. Zaca was supported by grants from Fundação MB and CNPq.

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