

## Differential fruit consumption of two Melastomataceae by birds in Serra da Mantiqueira, southeastern Brazil

Cristina Oishi Gridi-Papp<sup>1</sup>, Marcos Gridi-Papp<sup>1</sup> and Wesley Rodrigues Silva<sup>2</sup>

<sup>1</sup> Curso de Pós-graduação em Ecologia, Instituto de Biologia, Universidade Estadual de Campinas, 13083-970 Campinas, SP, Brasil.

<sup>2</sup> Laboratório de Interações Vertebrados-Plantas, Departamento de Zoologia, Universidade Estadual de Campinas, 13083-970 Campinas, SP, Brasil.

Correspondence to Marcos Gridi-Papp, Universidade Estadual Paulista – UNESP, Departamento de Zoologia – Instituto de Biociências, Av. 24 A, 1515, Caixa Postal 199, 13506-900 Rio Claro, São Paulo, Brasil. E-mail: mgpapp@rc.unesp.br

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**RESUMO. Consumo diferencial de frutos de duas espécies de Melastomataceae por aves na Serra da Mantiqueira, sudeste do Brasil.** O consumo por aves de frutos de duas espécies sintópicas de Melastomataceae foi observado em Monte Verde, Minas Gerais, Brasil. As guildas de frugívoros foram identificadas e caracterizadas pelos métodos de captura e consumo dos frutos. Foram obtidas também informações sobre abundância, fenologia das plantas e características dos frutos das duas espécies de Melastomataceae. As 13 espécies de aves observadas formaram dois grupos estatisticamente distintos de frugívoros com diferenças taxonômicas e comportamentais. Cinco entre sete espécies que se alimentaram dos frutos de *L. aff. sublanata* pertencem a subfamília Thraupinae e a maioria dos frutos foram mascados antes de serem engolidos. Quatro entre oito espécies de aves frugívoras que visitaram *M. cinerascens* pertencem à subfamília Turdinae e todos os frutos consumidos foram engolidos inteiros. Apenas duas espécies de ave visitaram ambas espécies de Melastomataceae. Este estudo mostra que os frutos de duas espécies de Melastomataceae semelhantes foram explorados diferencialmente pelas aves frugívoras de Monte Verde.

**PALAVRAS-CHAVE:** frugivoria, aves, comportamento alimentar, Melastomataceae.

**ABSTRACT.** In this study we report on the consumption of two syntopic Melastomataceae species by birds in a lower montane forest in Monte Verde, southeastern Brazil. The species of frugivores were identified and characterized by their methods of capture and consumption of fruits. We also provide information on abundance, phenology of plants and fruit characteristics of the two Melastomataceae species. The 13 observed species of birds formed two statistically distinct frugivorous groups with taxonomic and behavioral differences. Five of seven bird species that fed on *L. aff. sublanata* fruits belong to the subfamily Thraupinae and most fruits were mashed before swallowed. Four of the eight bird species that visited *M. cinerascens* belong to the subfamily Turdinae and all fruits were swallowed whole. Only two bird species were common visitors of both Melastomataceae species. Our findings show that fruits of the two Melastomataceae species with similar morphological characteristics were exploited differently by frugivorous birds.

**KEY WORDS:** frugivory, birds, feeding behavior, Melastomataceae.

Studies on the interactions between fruiting plants and frugivorous birds have helped to explain the population dynamics of plants and birds in a variety of habitats (Herrera 1998, Brown and Hopkins 2002, Kitamura *et al.* 2002, Manhães 2003, Melo *et al.* 2003). In the tropics, a substantial portion of birds feeds on fruits produced by shrubs and trees (Stiles 1985). By consuming fruits, frugivores obtain energy and nutrients while plants may benefit from having their seeds dispersed.

Among plant families that produce fleshy fruits, only a few provide the bulk of the fruits eaten by frugivorous birds (Fleming 1991). Melastomataceae is among the most important families of plants in the diets of Neotropical frugivorous birds (Hilty 1980, Snow 1981, Wheelwright *et al.* 1984, Rodrigues 1991, Stiles and Rosselli 1993, Galetti and Stotz 1996, Polin *et al.* 1999, Marcondes-Machado 2002, Manhães 2003).

The importance of Melastomataceae fruits to frugivorous birds might be related to the species richness, high density of

individuals and characteristics of the fruiting biology of the family. Melastomataceae is the seventh largest family among angiosperms, with most of the species occurring in the Neotropics. Especially in the understories of lowland and mid-elevation forests, Melastomataceae is among the predominant families (Gentry and Emmons 1987). Approximately half of the about 4500 described Melastomataceae species produce fleshy fruits that mainly contain water and carbohydrates (Renner 1993). In some habitats, Melastomataceae species may be considered an important resource during periods of fruit scarcity (Galetti and Stotz 1996, Polin *et al.* 1999).

Despite its importance, frugivory on Melastomataceae species as well as on other fleshy-fruited plants is still undescribed in many Neotropical habitats.

In 1995 the fruit consumption by birds of Melastomataceae species was investigated in a southeastern lower montane forest. In Monte Verde, Minas Gerais state, Brazil, two species seemed particularly interesting for an investigation of the relationship between fruiting plants and frugivores.

*Miconia cinerascens* (Miq.) and *Leandra* aff. *sublanata* (Cogn.) occur in the same area and have similar height, fruit display, fruit color, size and nutrients but differ in seed size and the fruiting strategies (Gridi-Papp 1997). *Miconia cinerascens* produces a large amount of fruits with large seeds, available for a short time while *Leandra* aff. *sublanata* produces a small amount of fruits with small seeds, throughout the year.

The aim of this study is to characterize the abundance and fruit production of these two plants, the assemblage of frugivorous birds visiting the plants and their feeding behavior.

## MATERIAL AND METHODS

**Study site.** The fieldwork was carried out in the district of Monte Verde, municipality of Camanducaia, state of Minas Gerais, southeastern Brazil. It is located in the Serra da Mantiqueira, at elevations of 1600 m to 2000 m. The vegetation is characterized by a mosaic of pine forest and secondary lower montane forest (*sensu* Brasil 1983). In 1996, the average annual temperature was 14.7°C and the total rainfall was 1417 mm, measured at the nearest meteorological station at Fazenda Levantina, 17 km from the study site.

**The plants.** Two Melastomataceae species were studied, *Miconia cinerascens* and *Leandra* aff. *sublanata*, both with similar heights (3–6 m). For each species, plant abundance, production of ripe fruits over the year, fruit and seed dimensions and nutritional composition were estimated.

Plant abundance was estimated in May 1998, along an 800 m trail (Selado trail), from 1860 m to 1978 m of altitude, where 20 points at 40 m intervals were marked. From each point, a 30 m line, oriented towards NE 30° on the compass, was set out. Individual melastomes taller than 1.5 m (minimum height of individuals bearing fruits observed in the area) were counted within 1 m of each side of the 30-m lines, obtaining a total sampled area of 1200 m<sup>2</sup>.

To estimate fruit production, 15 *L. aff. sublanata* and 15 *M. cinerascens* were randomly chosen among the individuals bearing fruits along the Selado trail. Once a month, during one year, all ripe fruits in each plant that were visible from the trail using binoculars were counted, and the total number of fruits on each individual was estimated. For each monitored plant, at least 50% of the crown was visible.

To characterize the fruits and fruit display of the two melastomes, five fruits from each of the 10 *L. aff. sublanata* and 10 *M. cinerascens* plants of the Selado trail were collected. The following characteristics of ripe fruits were recorded: color, maximum length (distance between base and top of the fruit), maximum width, number of seeds, fresh weight, and position of the fruits in the crown. Seed measures were: maximum length, width and fresh weight. Seed maximum length was defined for *M. cinerascens* as the maximum distance of the flat side of the seed. Seed width was the maximum distance perpendicular to the length of the seed. Seed fresh weight was obtained for *L. aff. sublanata* by averaging samples of 50 seeds, due to their small size. For *M. cinerascens*, seeds were weighed individually.

To determine the chemical composition of ripe fruits, additional samples of five fruits were collected from the plants used to characterize the fruits. Fruit samples were stored at: -5°C until they were analyzed. For *Leandra* fruits, skin, pulp and seeds together were analyzed, due to the difficulty in separating the tiny seeds from the pulp. For *M. cinerascens*, pulp and skin were analyzed separately. Protein concentration was estimated by quantifying the amount of nitrogen in the sample using the Kjeldahl method (Horwitz 1980). Lipid content was determined by the Bligh and Dyer method (1959). Water content was determined by subtracting dry weight from fresh weight of samples (Horwitz

1980), and carbohydrate concentration was inferred by subtraction of all other components (protein, lipid and ash contents). The analysis was restricted to one sample per Melastomataceae species.

**The frugivores.** From October 1995 to May 1997 the study site was visited twice a month to observe the visits of frugivores to melastomes with the aid of binoculars, from 6:00 to 9:00 and from 16:00 to 18:00. Using the “focal-sampling” method (Altmann 1974), 60 h of observation were accumulated on eight individuals of *L. aff. sublanata* and 44 h on 12 *M. cinerascens*. A “visit” is here defined as the period during which a bird remained in the focal tree feeding on fruits. For each visit the bird was identified and we recorded the number of fruits consumed, the bird feeding behavior (fruit captured from a perch or on the wing), and the fruit handling technique (fruit swallowed whole immediately after removal from the branch or mashed before being swallowed).

To compare the visitation patterns exhibited by frugivores, two groups were considered: the visitors of *M. cinerascens* and the visitors of *L. aff. sublanata*. Chi-square tests were used to compare the number of visits corrected by the number of hours of observation, and the number of fruits consumed by the two groups of visitors. Differences in the method of fruit capture and ingestion were also tested using contingency tables.

In addition to these analyses, three simulations in Matlab (Mathworks Inc.) were performed to evaluate if the visitation of the two Melastomataceae species was better explained by: (H<sub>0</sub>) a simple pattern where each Melastomataceae species had a fixed proportion of the total number of visits independent of the bird species, (H<sub>1</sub>) two distinct visitation patterns among the different bird species or (H<sub>2</sub>) three visitation patterns: the ones tested in H<sub>0</sub> and H<sub>1</sub>. The goal of this simulation was to find out if there was variation, among bird species, in the proportion at which they exploited each species of plant.

In the first simulation, the following assumption was made (H<sub>0</sub>): the visitation rates were the same among bird species visiting the melastomes. The field data was used to calculate the average probability of a bird visiting *M. cinerascens*, which was the sum of *M. cinerascens* visits by all birds divided by the total number of visits for both Melastomataceae, calibrated for the number of hours of observation. Then 1000 repeats of a simulation were performed, where a random number was multiplied by the average probability of a bird visiting *M. cinerascens*, to assign each bird visit to either *M. cinerascens* or *L. aff. sublanata*.

For each bird species, as many visits as the total visits observed in the field were assigned. Then the visits obtained in each repeat of the simulation were compared with the visits observed in the field and recorded the number of visits that were assigned to the right plant. The sum of all correctly assigned visits for all bird species was obtained for each repeat as an index of fit.

The same procedures were used for the second simulation, except that the visitation patterns could be described as bird species visiting mostly *M. cinerascens* or *L. aff. sublanata*. Each bird species was assigned to either the *M. cinerascens* or the *L. aff. sublanata* group, whichever was the most visited in the real data. Within each frugivorous group the probability of visiting a species of plant was defined as the sum of visits to that plant divided by the sum of visits to both plant species. A third simulation was also performed using the two groups defined in the previous simulation plus one group where bird species could exhibit the intermediate visitation pattern described in the first simulation.

The indexes of fit of the simulations 1 vs. 2 and 2 vs. 3 were compared using t-tests with unequal variances to evaluate which model best explained the observed visitation patterns. All three simulations were also repeated using the numbers of fruits consumed instead of visits. Finally the whole analysis was repeated using theoretical values for visitation rates instead of values derived from our data. The values were 1, 0.5 and 0 representing extreme bias (1 and 0) for one of the plants or no bias (0.5).

To evaluate the acceptance of Melastomataceae fruits by birds and compare with data obtained in the field, melastome fruits were offered to birds of the same species observed in the field and to close relatives. Fruits of *L. aff. sublanata* were offered to one individual of the following species: *Tangara cayana*, *T. desmaresti*, *Tachyphonus surinamus* and *Turdus rufiventris*. Fruits of *M. cinerascens* were offered to one individual of the following species: *Tangara cayana*, *T. cyanocephala*, *T. cyanopygia* and *Turdus rufiventris*. The individual of *Tangara cayana* was the same for both *L. aff. sublanata* and *M. cinerascens* fruit tests.

The caged birds had been kept in captivity for more than one year. Five ripe fruits of one of the Melastomataceae species were offered to each bird before its regular morning meal (fruits and vitamins). Fruits were placed in the same containers where the birds were fed daily. Each trial lasted 15 min during which we recorded the number of fruits consumed and the ingestion behavior. Uneaten fruits were discarded after each trial.

*The plants.* From a total of 167 individuals, *M. cinerascens* was more abundant (70.1%) than *L. aff. sublanata*, which accounted for 29.9% of the individuals. *Miconia cinerascens* had a short fruiting period but a large fruit production whereas *Leandra aff. sublanata* showed a long fruiting period but had few ripe fruits available at any time (figure 1).

Ripe fruits in both species are purple, located on terminal branches and well exposed in the external part of the tree crown. Fruits of *L. aff. sublanata* are slightly wider, longer and heavier than *M. cinerascens* fruits, containing numerous tiny seeds, whereas *M. cinerascens* seeds are larger and occur in small numbers per fruit (table 1). Hairs are present on the skin of *L. aff. sublanata* fruits but not on *M. cinerascens* fruits.

Regarding chemical composition, *M. cinerascens* and *L. aff. sublanata* contain mostly water (81% and 85% respectively) and carbohydrates (18% and 13% wet weight), and low concentrations of nitrogen (1% wet weight) and lipids (1% and 3% dry weight).

*The frugivores.* During the study, eight bird species fed on *M. cinerascens* fruits in 69 visits, totaling 44 hours of observation from April to May 1996, during the fruiting peak of this species. Seven species fed on *L. aff. sublanata* fruits in 62 visits and 60 hours of observation (table 2) from October 1995 to May 1996. The only frugivore species that visited both plants were *Turdus albicollis* and *Elaenia mesoleuca*, although most of the visits were directed to *M. cinerascens*. In proportion to the number of hours of observation, *M. cinerascens* had more visits ( $c\delta^2 = 5.76$ ,  $p < 0.05$ ) and more fruits consumed ( $c\delta^2 = 17.71$ ,  $p < 0.001$ ) than *L. aff. sublanata*. The segregation into two distinct groups of birds was confirmed by the simulation analysis using parameters based on field observations (simulation 1 vs. 2, visitation  $t = -275$ ,

Table 1. Size and weight of fruits and seeds of two Melastomataceae species of Monte Verde ( $x \pm SD$ ).

Plant species	<i>M. cinerascens</i>	<i>L. aff. sublanata</i>	t	p
Fruits				
N	47	28		
Width (mm)	5.77 $\pm$ 0.56	6.81 $\pm$ 0.89	5.56	<0.001
Length (mm)	4.69 $\pm$ 0.48	7.05 $\pm$ 0.92	12.63	<0.001
Weight (mg)	124.00 $\pm$ 28.41	188.48 $\pm$ 72.89	4.48	<0.001
N seeds	5.13 $\pm$ 1.36	160.21 $\pm$ 46.26	17.74	<0.001
Seeds				
N	50	50		
Width (mm)	2.34 $\pm$ 0.24	0.51 $\pm$ 0.11	-52.60	<0.001
Length (mm)	1.47 $\pm$ 0.45	1.14 $\pm$ 0.11	-5.09	<0.001
Weight (mg)	3.78 $\pm$ 1.18	0.10 $\pm$ 0.01	-22.05	<0.001

$p < 0.001$ ; consumption  $t = -402$ ,  $p < 0.001$ ) and theoretical values (simulation 1 vs. 2; visitation  $t = -292$ ,  $p < 0.01$ ; consumption  $t = -475$ ,  $p < 0.001$ ). The simulations with three groups of frugivores did not explain significantly better the observed data than simulations with two groups in any of the conditions tested.

Visitors of *L. aff. sublanata* took more fruits from perches, defined as "picking" behavior by Moermond and Denslow (1985) than visitors of *M. cinerascens* ( $c\delta^2 = 6.85$ ,  $p < 0.01$ ). Only *E. mesoleuca* took fruits on the wing from both plant species (table 2). The visitors of *M. cinerascens* swallowed all the fruits whole, differing from most species visiting *L. aff. sublanata*, that mashed the fruits and swallowed the juicy pulp with the tiny seeds, discarding the skin (table 1) ( $c\delta^2 = 192.24$ ,  $p < 0.001$ ).

Captive birds did not reject nor have difficulties consuming the fruits of neither Melastomataceae species. The percentage of fruits eaten, all trials combined, was 95% for both Melastomataceae fruits. All captive birds mashed the fruits before swallowing them, sometimes discarding parts of the skin, pulp, and seeds, except for *Turdus rufiventris*, which swallowed the fruits whole. Most of the discarded parts of *L. aff. sublanata* fruits were skin and seeds. The much larger seeds of *M. cinerascens* were often dropped by the mashers.

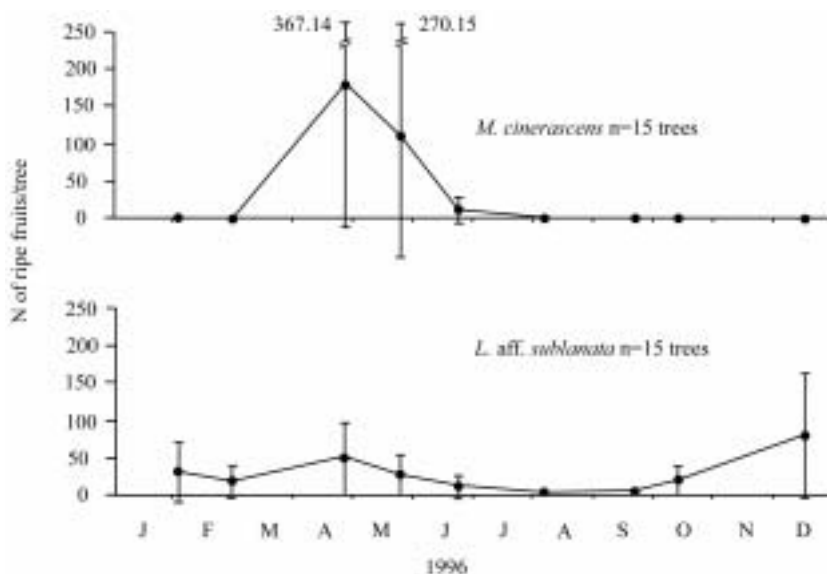


Figure 1: Monthly averages and standard deviation of ripe fruit production per tree of two Melastomataceae species in Monte Verde.

Table 2. Bird species recorded feeding on *M. cinerascens* and *L. aff. sublanata* fruits after 44 and 60 hours of observation, respectively.

<i>Miconia cinerascens</i>						
Family	Bird species	Visits	Fruit consumption	Fruits/visit ( $x \pm SD$ )	Feeding behavior	
					from a perch	on the wing
Tyrannidae	<i>Elaenia mesoleuca</i>	33	56	$1.82 \pm 1.13$	26	30
Muscicapidae	<i>Platycichla flavipes</i>	6	24	$4.00 \pm 5.48$	21	0
	<i>Turdus rufiventris</i>	9	50	$5.78 \pm 6.48$	47	3
	<i>T. amaurochalinus</i>	1	15	15.00	15	3
	<i>T. albicollis</i>	11	23	$2.27 \pm 1.42$	23	0
	<i>Ramphastos dicolorus</i>	3	9	$3.00 \pm 1.73$	9	0
Emberizidae	<i>Saltator similis</i>	3	10	$3.33 \pm 0.58$	10	0
	Not identified <sup>1</sup>	3	8	$2.67 \pm 0.58$	8	0
Total		69	195		159	36
<i>Leandra aff. sublanata</i>						
Tyrannidae	<i>Elaenia mesoleuca</i>	5	6	$1.20 \pm 0.45$	3	3
Muscicapidae	<i>Turdus albicollis</i>	2	4	$2.00 \pm 1.41$	4	3
Emberizidae	<i>Stephanophorus diadematus</i>	32	54	$1.81 \pm 1.03$	51	1
	<i>Pipraeidea melanonota</i>	5	9	$1.80 \pm 1.30$	4	1
	<i>Tangara cyanoventris</i>	2	3	$1.50 \pm 0.71$	3	0
	<i>T. desmaresti</i>	4	11	$2.75 \pm 0.96$	11	0
	<i>Poospiza thoracica</i>	12	19	$1.58 \pm 1.00$	18	0
Total		62	106		94	8

<sup>1</sup> The bird was identified as Emberizidae, although poor light conditions prevented the species identification.

\* In all events, the bird flew away from the plant before ingesting the fruit.

## DISCUSSION

During the observations of this study, *Miconia cinerascens* and *L. aff. sublanata* were visited at the study site by frugivorous birds that exploited them differently, comprising two groups that varied in species composition and feeding patterns. Five out of seven species that fed on *L. aff. sublanata* fruits belong to the subfamily Thraupinae, a group that commonly mashes the fruits (“mashers”) before swallowing them (Moermond and Denslow 1985). Four out of eight bird species that visited *M. cinerascens* belong to the subfamily Turdinae, which swallow fruits whole (“gulers”).

These taxonomic and behavioral differences in fruit consumption, however, probably do not prevent mashers from eating *M. cinerascens* fruits or gulers from eating *L. aff. sublanata* fruits in Monte Verde. Captive birds, mashers and gulers ingested both Melastomataceae fruits without any apparent difficulty. Therefore, although fruit and seed sizes were statistically different, these differences may not be ecologically limiting to the birds.

Nutritional composition of the two Melastomataceae fruits was also similar at a macronutrient level, although we did not investigate the nutritional value of the fruits to the different bird species. As suggested by Levey and Martínez Del Rio (2001), differences in digestive and metabolic processes among bird species can influence fruit preferences.

Many studies have also investigated the basis of fruit

choice among birds, suggesting an interaction between the morphological, physiological and behavioral features of the bird and features of the plant, such as abundance of fruiting trees, fruit display, fruit and seed characteristics, spatial and temporal variation of fruit abundance (Moermond and Denslow 1985, Levey 1987, Loiselle and Blake 1990, 1991, 1993, Fuentes 1994, Witmer 1998, Githiru *et al.* 2002, Kitamura *et al.* 2002, Stanley and Lill 2002, Manhães 2003). Variation in fruit preferences has been described among bird species and even among individuals of the same species (Wheelwright *et al.* 1984, Loiselle and Blake 1990, Rodrigues 1991, Jung 1992, Sallabanks and Courtney 1993, Willson 1996, Herrera 1998, Manhães 2003), reflecting the complexity of fruit-frugivore systems.

The Melastomataceae-birds relationship in Monte Verde offers a good opportunity to focus the poorly understood aspects of the fruit-frugivore interactions in tropical habitats, though only some of the possible factors influencing the fruit consumption by birds were explored in this study. From the plants' point of view, compared to *L. aff. sublanata*, *M. cinerascens* fruits are consumed by large birds that remove many fruits and swallow large but few seeds, moving them far away from the parent-tree. If the fruits of *M. cinerascens* were mashed by the frugivores that visited *L. aff. sublanata*, the seeds would most likely fall under the parent-tree as observed in captivity. *Leandra aff. sublanata* fruits, on the other hand, have more but smaller seeds per fruit, per-

haps at a cost of lower germination success and a higher chance of being swallowed by mashers. As defined by Schupp (1993), the effectiveness of seed dispersal should depend on such factors as the number of visits made by the disperser to the plant, the number of seeds dispersed per visit, the quality of the treatment given in the mouth and in the gut, and the quality of seed deposition. The visiting pattern of birds observed in Monte Verde might be reflected in the higher abundance of *M. cinerascens* compared to *L. aff. sublanata*.

*Leandra aff. sublanata* could benefit from guppers consuming its fruits. For the birds visiting *M. cinerascens*, however, the availability of ripe fruits and the short distances separating fruiting trees may be an important factor influencing fruit choice (Levey *et al.* 1984). *Miconia cinerascens* fruits were available at higher quantities per tree than *L. aff. sublanata* fruits. The few ripe fruits of *L. aff. sublanata* trees could require a higher amount of energy to be captured, reducing their energetic value and perhaps rendering them unrewarding for *M. cinerascens*' visitors. For mashers, however, there was no apparent cost preventing them from eating *M. cinerascens* fruits, unless the fact that large seeds can make mashing a more costly task, a problem apparently overcome by the caged birds offered with *M. cinerascens* fruits. Although the seeds of *M. cinerascens* represent roughly 3% of the bulk of the whole fruit and the seeds of *L. aff. sublanata* only 0.05 % (table 1), in nature, this sixty-fold difference might reduce the interest of Thraupinae species (mainly mashers) in feeding upon the fruits of *M. cinerascens*.

Temporal variation in diet (Herrera 1998) and in the community species composition (Loiselle and Blake 1990) could have also influenced the segregation of birds into two distinct frugivore assemblages. Since the frugivory in *L. aff. sublanata* was recorded during a more extensive period of time than that of *M. cinerascens*, bird migration could have been responsible for the differences in the visiting pattern. Birds like *Stephanophorus diadematus* and *Poospiza thoracica*, however, the main visitors of *L. aff. sublanata*, were present when most of the observations on *M. cinerascens* took place. In addition, the birds visiting *M. cinerascens* were present during the fruiting peak of *L. aff. sublanata*. This suggests that, although migration could influence the composition of birds visiting these plants in Monte Verde, it seems unlikely that this factor alone could completely explain the segregation into two groups of frugivores.

Understanding the interactions between frugivorous birds and Melastomataceae fruits in Monte Verde and its ecological consequences will probably require further studies on a larger scale, including information on the several aspects of morphology and behavior of birds, as well as on the morphology, phenology and chemical constitution of fruits. Differences in fruit selection by birds may be related to many factors acting in concert. Ultimately, the comparison of the bird seed dispersal systems of other local Melastomataceae species would prove useful for the conservation of the lower montane forest vegetation in its associated avifauna in the southeastern Brazil.

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#### REFERENCES

- Altmann, J. (1974) Observational study of behavior: sampling methods. *Behavior* 49:227-267.
- Bligh, E. G. and W. J. Dyer (1959) A rapid method of total lipid extraction and purification. *Can. J. Biochem. Physiol.* 37:911-917.
- Brasil (1983) *Projeto Radam Brasil. Folhas SF 23/24 Rio de Janeiro/Vitória; Geologia, geomorfologia, pedologia, vegetação e seu potencial da terra.* Rio de Janeiro: Ministério das Minas e Energia.
- Brown, E. D. and M. J. G. Hopkins (2002) Tests of disperser specificity between frugivorous birds and rainforest fruits in New Guinea. *Emu* 102:137-146.
- Fleming, T. H. (1991) Fruit plant – frugivore mutualism: The evolutionary theater and the ecological play, p. 119-144. In: P. W. Price, T. M. Lewinsohn, G. W. Fernandes and W. W. Benson (eds.) *Plant-animal interactions: Evolutionary ecology in tropical and temperate regions.* New York: John Wiley and Sons, Inc.
- Fuentes, M. (1994) Diets of fruit-eating birds: what are the causes of interspecific differences? *Oecologia* 97:134-142.
- Galetti, M. and D. Stotz (1996) *Miconia hypoleuca* (Melastomataceae) como espécie-chave para aves frugívoras no sudeste do Brasil. *Rev. Brasil. Biol.* 56:435-439.
- Gentry, A. H. and L. H. Emmons (1987) Geographical variation in fertility, phenology, and composition of the understory of neotropical forests. *Biotropica* 19:216-227.
- Githiru, M.; L. Lens, L. A. Bennur and C. P. K. O. Ogot (2002) Effects of site and fruit size on the composition of avian frugivore assemblages in a fragmented Afrotropical forest. *Oikos* 96:320-330.
- Gridi-papp, C. O. (1997) *Frugivoria por aves em quatro espécies de Melastomataceae na Serra da Mantiqueira, MG.* Master's Degree thesis. Campinas: Universidade Estadual de Campinas.
- Herrera, C. M. (1998) Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecol. Monogr.* 68: 511-538.
- Hilty, S. T. (1980) Flowering and fruiting periodicity in a premontane rain forest in Pacific Colombia. *Biotropica* 12:292-306.
- Horwitz, W. (1980) *Official methods of analysis of the Association of Official Analytical Chemists.* Washington DC: The Association.
- Jung, R. (1992) Individual variation in fruit choice by American Robins (*Turdus migratorius*). *Auk* 109:98-111.
- Kitamura, S.; T. Yumoto, P. Poonswad, P. Chuailua, K. Plongmai, T. Maruhashi and N. Noma (2002) Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia* 133:559-572.
- Levey, D. J. (1987) Seed size and fruit-handling techniques of avian frugivores. *Am. Nat.* 12:471-485.
- Levey, D. J.; T. C. Moermond and J. S. Denslow (1984) Fruit choice in neotropical birds: the effect of distance between fruits on preference patterns. *Ecology* 65:844-840.
- Levey, D. J. and C. M. Martinez Del Rio (2001) It takes guts (and more) to eat fruit: lessons from avian nutritional ecology. *Auk* 118: 819-831.
- Loiselle, B. A. and J. G. Blake (1990) Diets of understory fruit-eating birds in Costa Rica: seasonality and resource abundance. *Stud. Avian Biol.* 13:91-103.

- (1991) Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* 72:180-193.
- (1993) Spatial distribution of understory fruit-eating birds and fruiting plants in a neotropical lowland wet forest. *Vegetatio* 107/108:177-189.
- Manhães, M. A. (2003) Dieta de traupíneos (Passeriformes, Emberezidae) no Parque Estadual do Ibitipoca, Minas Gerais, Brasil. *Iheringia Sér. Zool. Porto Alegre* 93:59-73.
- Marcondes-Machado, L. O. (2002) Comportamento alimentar de aves em *Miconia rubiginosa* (Melastomataceae) em fragmento de cerrado, São Paulo. *Iheringia Sér. Zool. Porto Alegre* 92:97-100.
- Melo, C.; E. C. Bento, and P. E. Oliveira, (2003) Frugivory and dispersal of *Faramea cyanea* (Rubiaceae) in cerrado woody plant formations. *Braz. J. Biol.* 63:75-82.
- Moermond, T. C. and J. S. Denslow (1985) Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. *Ornithol. Monogr.* 36:865-897.
- Polin, B.; S. J. Wright, G. Lefebvre and O. Calderón (1999) Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama. *J. Trop. Ecol.* 15:213-227.
- Renner, S. S. (1993) Phylogeny and classification of the Melastomataceae and Memecylaceae. *Nord. J. Bot.* 13:519-540.
- Rodrigues, M. (1991) *Ecologia alimentar de traupídeos (Aves: Thraupinae) em uma área de mata atlântica do estado de São Paulo*. Master's Degree thesis. Campinas: Universidade Estadual de Campinas.
- Sallabanks, R. and S. P. Courtney (1993) On fruit-frugivore relationships: variety is the spice of life. *Oikos* 68:567-570.
- Schupp, E. W. (1993) Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107/108:15-29.
- Snow, D. W. (1981) Tropical frugivorous birds and their food plants: a world survey. *Biotropica* 13:1-14.
- Stanley, M. C. and A. Lill (2002) Importance of seed ingestion to an avian frugivore: An experimental approach to fruit choice based on seed load. *Auk* 119:175-184.
- Stiles, F. G. (1985) On the role of birds in the dynamics of neotropical forests, p. 49-59. In: A. W. Diamond and T. E. Lovejoy (eds.) *Conservation of tropical forest birds: proceedings of a workshop and symposium held at the XVIII World Conference of the International Council for Bird Preservation, 7, 8 and 10 August 1982, Kings College, Cambridge, England*. Cambridge: International Council for Bird Preservation.
- Stiles, F. G. and L. Rosselli (1993) Consumption of fruits of the Melastomataceae by birds: how diffuse is coevolution? *Vegetatio* 107/108:57-73.
- Wheelwright, N. T.; W. A. Haber, K. G. Murray and C. Guindon (1984) Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. *Biotropica*, 16:173-192.
- Willson, M. F. (1996) Fruit choices by captive American Robins. *Condor* 96:494-502.
- Witmer, M. C. (1998) Do seeds hinder digestive processing of fruit pulp? Implications for plant/frugivore mutualisms. *Auk* 115:319-326.