Ararajuba 3:27-32
dezembro de 1995

Spatial distribution and food utilization among tanagers in southeastern Brazil (Passeriformes: Emberizidae)

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Recebido em 2 de março de 1993; aceito em 5 de março de 1995

RESUMO. **Distribuição espacial e alimentação de traupíneos no sudeste do Brasil (Passeriformes: Emberizidae).** Foram estimadas a sobreposição de nicho alimentar e espacial entre treze espécies de traupíneos da Mata Atlântica na Fazenda Intervales, Estado de São Paulo. Durante um ano de observações, tal sobreposição foi baseada em três parâmetros principais: substrato no qual as presas eram capturadas, estrato da vegetação e o tipo de alimento (artrópodes ou frutos). Todas as espécies apresentaram uma dieta mista de frutos e artrópodes, sendo o néctar um elemento também importante. Houve alta sobreposição ecológica em relação ao substrato no qual as presas eram capturadas e ao estrato da vegetação em que as aves forrageavam. Entretanto, houve pouca sobreposição em relação às espécies de frutos utilizadas. A dieta frugívora foi o fator mais importante para redução da competição entre as espécies.
PALAVRAS-CHAVE: aves, comportamento alimentar, Mata Atlântica, sudeste brasileiro, sobreposição de nicho, Thraupinae.

ABSTRACT. The food utilization and the degree of food overlap of 13 species of tanagers (Emberizidae, Thraupinae) was estimated based on its feeding behavior. The observations were done over one year and estimated niche overlap was based on three main axes: substrate of prey capture, vertical feeding zones, and food type (arthropods and fruits). Nearly all species had a mixed diet of insects and fruits; nectar was also an important food source for some species. Overlap among tanagers was high for both foraging substrate and vertical foraging height, but was relatively low for fruit species included in the diet. Overall niche overlap was low for all species. Fruit diet was the most important axis in reducing overlap among species.
KEY WORDS: Atlantic Forest, birds, feeding behavior, niche overlap, Southeastern Brazil, tanagers.

Studies of resource utilization by birds form the basic issues of the theory of community ecology since the classical work of MacArthur (1958) (see Cody and Diamond 1975, Wiens 1989).

The objective of this paper is to quantify resource utilization poorly known group of Neotropical birds, the tanagers. Tanagers form a guild of forest birds that typically feed on foliage insects and small fruits. These birds make up an heterogeneous subfamily (Thraupinae) in the Emberizidae. Although they are common and conspicuous birds, few studies have dealt with resource utilization and niche overlap values obtained from several dimensions (resources axes) (see Snow and Snow 1971 and references in Isler and Isler 1987).

STUDY SITE AND METHODS

The Fazenda Intervales is a reserve of 38,000 ha near the city of Capão Bonito (24°11'S, 48°32'W) in southern São Paulo State, Brazil. The altitudinal range is from 60 m to 1100 m a.s.l. Observations on tanagers feeding were made in patchy forest from about 800 to 900 m. Annual mean rainfall is nearly 1800 mm. The area is covered by primary and secondary growth evergreen cloud forest (see Willis 1989). Bird-dispersed fruits of shrubs and trees located along edges and forest are available throughout the year (Alvares and Rodrigues 1991), with a peak of fruit diversity from December to February (pers. obs.).

According to Isler and Isler (1987), 33 species of tanagers may occur in the study area. In this paper I gathered data for the 13 most common forest tanagers.

During 13 months (January 1989 through January 1990), I recorded the feeding behavior of tanagers while walking on roadsides and paths in the forest. For each individual bird encountered that exhibit that feeding behavior, I recorded height at which it foraged, relative vegetation layer (low-story, middle-story, canopy) and the substrate of prey capture (branches, leaves, epiphytes, moss, ground, air, army-ants), or fruit and flower species as well. I recorded only the first foraging move per individual encountered in order do avoid bias (see references in Morrison *et al.* 1990).

Niche overlap in each dimension (substrate of prey capture, vertical occupation and food type) was calculated by the Morisita-Horn index (Horn 1966, see Krebs 1989 for review):

$$\alpha = 2.\Sigma p_{ij}\, p_{ik} / [\Sigma p^2_{ij} + \Sigma p^2_{ik}]$$

where P_{ij} and P_{ik} are the proportions of resource i of the total resource used by any two species.

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Overall niche overlap was calculated by:

$$P_{xi} P_{yi}(\Sigma h_{xij} \cdot h_{yij} \Sigma s_{xij} \cdot s_{yij}) + P_{xf} P_{yf}(\Sigma h_{xfj} \cdot h_{yfj} \Sigma F_{xfj} \cdot F_{yfj}) + P_{xn} P_{yn}(\Sigma h_{xnj} \cdot h_{ynj} \Sigma F_{xnj} \cdot F_{ynj}) = \alpha$$

Where P is the proportion of observations of species x or y using resource i (insects), f (fruits) or n (nectar); h is the proportion of observations of species x or y while using resource i, f or n in height class j; s is the proportion of observations of species x or y while foraging for insects on substrate class j, F is the proportion of observation of species x or y while foraging on flowers (n) or fruits (f). This equation includes height of flower type. As I did not measure this variable, I prefer to treat it as equal to 1 for all species. This results in an overestimation of diet overlap, but gives better results than excluding nectar feeding entirely. This procedure more accurately estimates values of multidimensional overlap than the sole use of "summation alpha" or "product alpha" (see May 1975).

RESULTS AND DISCUSSION

Niche overlap was calculated between 13 tanagers species based on three axes: substrate of prey capture (table 2 derived from table 1), vertical occupation (table 4 and 5 derived from table 3), and food type (table 7 derived from table 6).

Substrate of prey capture. The range of alpha (α) values for this parameter was 0.16 (*Trichothraupis melanops* x *Tangara seledon*) to 0.99 (*Cissopis leveriana* x *Dacnis cayana*). The mean value was 0.71.

Trichothraupis melanops was the most distinct species with overlap values below 0.5 in 11 out of 12 comparisons; this species was the only that regularly foraged at army-ant swarms.

The matrix in table 2 shows three groups: those using leaves as the principal substrate (*Cissopis leveriana, Dacnis cayana, Tachyphonus coronatus, Thraupis cyanoptera, Stephanophorus diadematus, Hemithraupis ruficapilla, Orthogonys chloricterus*), branch users (*Thraupis ornata, Tangara cyanocephala, Thraupis sayaca* and *Tangara seledon*) and one aerial forager (*Trichothraupis melanops*).

Overlap was low within congeners with two exceptions. Within the genus *Thraupis, T. sayaca* and *T. ornata* had high α values (0.89). However, these two species occupy different habitats (orchards and human settlements x forest edge, respectively; pers. obs.). The other exception is within the genus *Tangara* (*T. cyanocephala* x *T. desmaresti*, α= 0.92). Snow and Snow (1971) found that *Tangara* species of Trinidad are segregated by branch diameter. I found at Intervales that *T. seledon* prefers thicker branches than the other two congeners due to his non acrobatic behavior.

Trichothraupis melanops is a generalist species in relation to substrata of prey capture since it used all of them with exception of mosses and epiphytes (table 2).

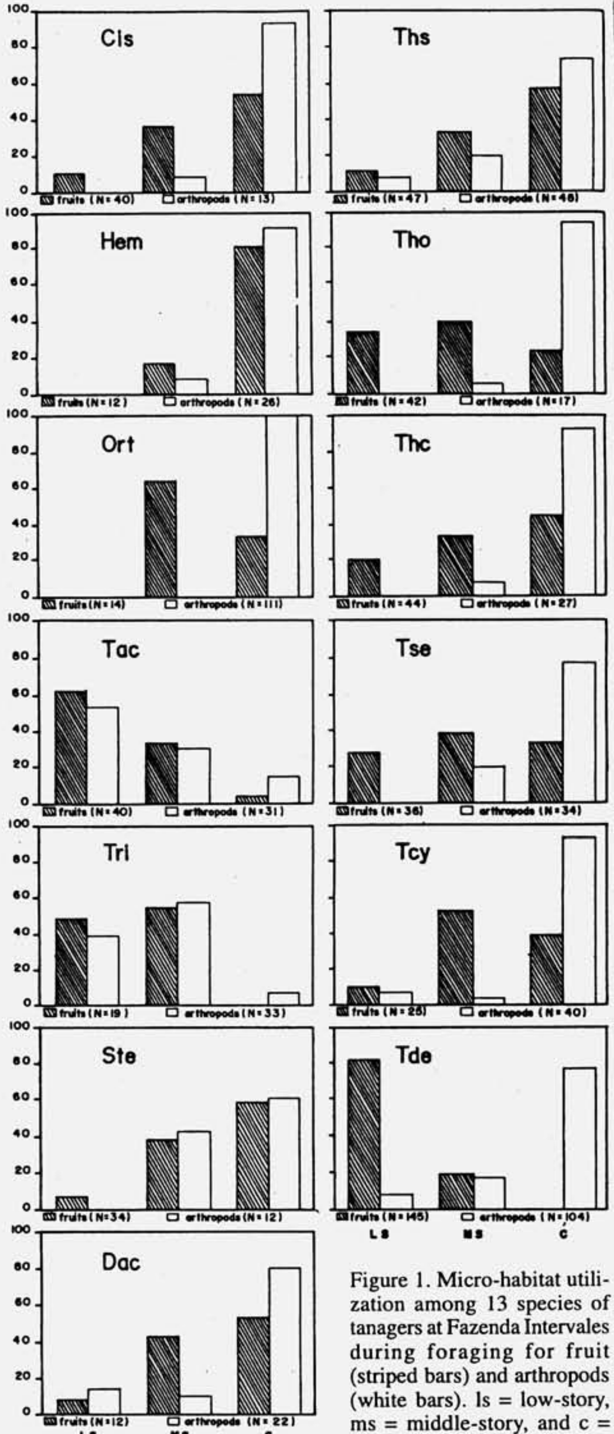

Figure 1. Micro-habitat utilization among 13 species of tanagers at Fazenda Intervales during foraging for fruit (striped bars) and arthropods (white bars). ls = low-story, ms = middle-story, and c = canopy (species names are listed in table 2).

Vertical occupation. The results show that some tanagers occupy different vertical forest zones according to food type (figure 1). Some species forage primarily for insects in the canopy and come down to the understory to search for fruits. This pattern is expected since in neotropical forests most of the understory trees and shrubs are bird-dispersed as opposed to canopy species (Stiles 1985).

Table 1. Arthropod foraging frequencies in seven substrates used by 13 tanagers of Fazenda Intervales (number in parentheses shows percentages).

Species	n	leaves	branches	moss	epiphytes	ground	army-ants	air
Cissops leveriana	13	9 (96)	4 (31)	–	–	–	–	–
Hemithraupis ruficapilla	26	25 (96.1)	1 (3.9)	–	–	–	–	–
Orthogonys chloricterus	111	75 (67.6)	13 (11.7)	–	23 (20.7)	–	–	–
Tachyphonus coronatus	31	20 (64.5)	6 (19.4)	1 (3.2)	–	4 (12.9)	–	–
Trichothraupis melanops	33	7 (21.2)	2 (6.1)	–	–	2 (6.1)	9 (27.2)	13 (39.4)
Thraupis sayaca	48	11 (22.9)	22 (45.8)	8 (16.7)	2 (4.2)	–	–	5 (10.4)
Thraupis ornata	17	4 (23.5)	11 (64.7)	2 (11.8)	–	–	–	–
Thraupis cyanoptera	27	15 (55.6)	6 (22.2)	2 (7.4)	2 (7.4)	–	–	2 (7.4)
Stephanophorus diadematus	12	6 (50)	3 (25)	1 (8.3)	–	–	–	2 (16.7)
Tangara seledon	34	4 (11.8)	17 (50)	12 (35.3)	1 (2.9)	–	–	–
Tangara cyanocephala	40	16 (40)	22 (55)	–	2 (5)	–	–	–
Tangara desmaresti	104	60 (57.7)	38 (36.5)	6 (5.8)	–	–	–	–
Dacnis cayana	22	16 (72.7)	5 (22.7)	–	–	–	–	–
Total	518	268 (51.7)	150 (29)	32 (6.2)	31 (6)	6 (1.2)	9 (1.7)	22 (4.2)

Table 2. Matrix of niche overlap values related to substrate of prey capture (species names are: Hem= *Hemithraupis ruficapilla*, Cis= *Cissops leveriana*, Ort= *Orthogonys chloricterus*, Tac= *Tachyphonus coronatus*, Tri= *Trichothraupis melanops*, Ths= *Thraupis sayaca*, Tho= *Thraupis ornata*, Thc= *Thraupis cyanoptera*, Ste= *Stephanophorus diadematus*, Tse= *Tangara seledon*, Tcy= *Tangara cyanocephala*, Tde= *Tangara desmaresti*, and Dac= *Dacnis cayana*).

	Cis	Ort	Tac	Tri	Ths	Tho	Thc	Ste	Tse	Tcy	Tde	Dac
Hem	.90	.91	.90	.34	.39	.35	.83	.77	.20	.58	.82	.94
Cis		.93	.97	.39	.68	.68	.95	.92	.49	.86	.98	.99
Ort			.93	.38	.53	.47	.94	.85	.32	.70	.88	.96
Tac				.21	.62	.85	.95	.91	.43	.78	.94	.97
Tri					.40	.23	.49	.60	.16	.32	.38	.39
Ths						.89	.74	.80	.91	.90	.80	.62
Tho							.66	.69	.90	.94	.74	.59
Thc								.97	.54	.83	.96	.96
Ste									.58	.83	.94	.90
Tse										.76	.63	.41
Tcy											.92	.80
Tde												.96
Dac												

The α values in vertical occupation (table 4 and 5) are high due to the few strata divisions (only three classes), and this overinflates the data in one or another resource class. In fact, only two species are typical of the understory (*Trichothraupis melanops* and *Tachyphonus coronatus*).

The data show that vertical occupation is not a good parameter to define isolation in species of tanagers with the above exceptions. This was also found by Snow and Snow (1971).

Feeding behavior and micro-habitat selection. Feeding behavior is an important parameter in which bird species may decrease overlap and partition resource (Cody 1974). Although it has not been quantified here, some general statements can be made.

When foraging for arthropods on leaf surfaces, *Cissops leveriana, Stephanophorus diadematus* and *Trichothraupis melanops* capture their preys more slowly through the vegetation. Prey items taken by these species are most likely stationary ones (relatively cryptic insects). *Cissopis leveriana*, however, may forage in groups and this may increase the vulnerability of cryptic prey (Powell 1985). *Trichothraupis melanops* follows mixed flocks of birds, monkeys and army-ants, and there is evidence that it benefits from insects frightened away. The other foliage gleaners (*Hemithraupis ruficapilla, Orthogonys chloricterus, Tangara cyanocephala, T. desmaresti,* and *Dacnis cayana*) forage with fast movements. This behavior allows individuals to find new feeding patches quickly, which facilitates the capture of exposed rather than cryptic prey.

Table 3. Number of observations related to species vertical occupation between 13 species of tanagers at Fazenda Intervales. Species names are listed in table 2.

Species	fruit			arthropod		
	Ls[a]	Ms	C	Ls	Ms	C
Hem	–	2	10	–	2	24
Cis	4	15	21	–	1	12
Ort	–	9	5	–	–	111
Tac	25	13	2	17	9	5
Tri	9	10	–	13	18	2
Ths	5	15	27	3	10	35
Tho	15	17	10	–	1	16
Thc	9	15	20	–	2	25
Ste	2	13	19	–	5	7
Tse	10	14	12	–	7	27
Tcy	2	13	10	2	1	37
Tde	118	27	–	7	18	79
Dac	1	5	6	3	2	17

[a] Ls = low-story; Ms = middle-story; C = canopy.

Table 4. Matrix of niche overlap related to vertical occupation when birds forage for arthropods (species names are listed in table 2).

	Cis	Ort	Tac	Tri	Ths	Tho	Thc	Ste	Tse	Tcy	Tde	Dac
Hem	1	.99	.27	.15	.96	1	1	.83	.98	1	.97	.97
Cis		.99	.27	.15	.96	1	1	.83	.98	1	.97	.97
Ort			.23	.08	.92	1	.99	.77	.95	.99	.94	.95
Tac				.89	.43	.26	.27	.46	.35	.29	.41	.44
Tri					.35	.13	.15	.54	.28	.14	.31	.28
Ths						.95	.96	.94	.99	.95	1	.98
Tho							1	.82	.97	1	.97	.97
Thc								.83	.98	1	.97	.97
Ste									.92	.80	.92	.86
Tse										.97	.99	.97
Tcy											.97	.97
Tde												.99
Dac												

Table 5. Matrix of niche overlap related to vertical occupation when birds forage for fruits (species names are listed in table 2).

	Cis	Ort	Tac	Tri	Ths	Tho	Thc	Ste	Tse	Tcy	Tde	Dac
Hem	.87	.64	.16	.14	.91	.50	.80	.89	.64	.72	.18	.84
Cis		.89	.45	.53	.99	.81	.98	1	.91	.96	.58	1
Ort			.44	.65	.83	.78	.84	.89	.84	.98	.81	.92
Tac				.93	.42	.87	.60	.39	.75	.51	.76	.46
Tri					.46	.90	.64	.48	.80	.66	.94	.55
Ths						.77	.97	.99	.88	.92	.50	.98
Tho							.90	.76	.97	.94	.63	.97
Thc								.96	.97	.94	.63	.97
Ste									.88	.95	.55	.99
Tse										.92	.77	.91
Tcy											.77	.98
Tde												.63
Dac												

Table 6. Fruit feeding bout of tanagers at Fazenda Intervales. Bird species names are listed in table 2.

Bird species	Plants *										
	7	8	12	14	15	19	20	22	26	27	28
Hem	0	0	0	0	0	0	0	0	0	0	18
Cis	0	2	0	2	0	1	0	0	0	0	0
Ort	0	0	0	0	0	1	0	0	8	0	0
Tac	1	0	0	7	0	4	0	0	0	0	1
Tri	0	2	0	0	0	0	0	0	0	0	3
Ths	0	0	0	0	0	6	6	1	0	5	0
Tho	1	1	0	1	0	6	3	0	0	0	3
Thc	0	0	0	1	0	0	0	2	0	0	9
Ste	1	0	0	0	0	24	0	2	0	2	0
Tse	0	0	0	0	0	0	0	0	0	0	0
Tcy	1	1	0	1	0	10	0	0	0	0	9
Tde	3	10	59	1	0	1	0	0	0	0	0
Dac	0	0	0	0	0	0	0	0	0	0	0

* 7= *Leandra barbinervis*, 8= *L. levigata*, 12= *L.* sp. 1, 14= *Miconia rigidiuscula*, 15= *Cabralea cangerana*, 19= *Rapanea ferruginea*, 20= *Gomidesia* sp. 1, 22= *Psidium catleyanum*, 26= *Solanum inodorum*, 27= *S. mauricianum*, 28= *Trema micrantha*.

Table 7. Matrix of niche overlap related to food type (fruit) eaten by tanagers (species names are listed in table 2).

	Hem	Ort	Tac	Tri	Ths	Thc	Tho	Ste	Tcy	Tde
Cis	0	.08	.51	.09	.80	.05	.78	.80	.60	.04
Hem		0	.11	.79	0	.93	.32	0	.59	0
Ort			.06	0	.05	0	.08	.12	.08	0
Tac				.10	.21	.21	.55	.47	.51	.03
Tri					0	.81	.38	0	.59	.09
Ths						.01	.51	.59	.32	.01
Thc							.37	.02	.63	0
Tho								.74	.86	.04
Ste									.69	.19
Tcy										.03
Tde										

Food type. Snow and Snow (1971) found that for Trinidadian tanagers there was greater overlap in the frugivorous diet than in the insectivorous one. My observations at Intervales were restricted to 28 plant species bearing flesh fruits in the forest edge. I verified that some fruits were not eaten by any tanager (table 6) and fruit overlap is lower than in the other resource axes (substrate of prey capture and vertical occupation) (table 7).

It is known that small neotropical frugivorous birds use many fruit species (Willis 1966, Snow and Snow 1971). These data led Howe and Estabrook (1977) to suggest that small frugivorous birds are not selective, choosing the fruits opportunistically. My data show that birds forage differentially and thus appear to prefer certain plant species. This contradicts the classical thought of frugivory that these small frugivorous-insectivorous birds (tanagers, saltators and manakins) do not select among fruits, rather choosing fruits randomly (Howe and Estabrook 1977, Fleming 1979, Worthington 1982). My results can probably be due to sample size (the number of plant species analysed and the fruits feeding bout). Moreover, the number of available fruit species is greater than the number of substrata of prey capture and vegetation strata. Consequently, this produces an overdispersion of the data within the food type axis, and would be expected to have a relative low overlap value compared to other resource axes. However, the data on frugivory was recorded in a restricted habitat (edge and forest) and this data overdispersion tend to be minimal. In a recent study, Loiselle and Blake (1990) showed that tropical understory frugivores partition fruit resources, and feeding decisions were constrained by morphology, feeding method, fruit type and display, and foraging height. Only detailed observations of each fruit species (Sorensen 1981, Snow and Snow 1988) can show if fruits are selected differentially by bird species.

Table 8. Overall niche overlap among the tanagers of Fazenda Intervales (species names are listed in table 2).

	Cis	Ort	Tac	Tri	Ths	Tho	Thc	Ste	Tse	Tcy	Tde	Dac
Hem	.118	.444	.070	.032	.111	.093	.318	.098	.061	.274	.201	.223
Cis		.166	.116	.015	.269	.271	.091	.333	.054	.202	.088	.212
Ort			.081	.015	.180	.114	.260	.139	.113	.327	.255	.296
Tac				.061	.084	.181	.078	.112	.033	.101	.149	.091
Tri					.036	.080	.125	.042	.013	.072	.046	.022
Ths						.208	.116	.107	.177	.257	.142	.180
Tho							.182	.134	.105	.327	.086	.123
Thc								.014	.090	.313	.133	.140
Ste									.062	.229	.115	.160
Tse										.208	.115	.087
Tcy											.220	.154
Tde												.152
Dac												

Overall niche overlap. The overall niche overlap was low for all the studied species (table 8). The highest overlap index was between *Hemithraupis ruficapilla* and *Orthogonys chloricterus* (0.444).

Trichothraupis melanops was the species with the lowest overlap among each pair. It is also so different from the other tanagers in all the studied axes because it occupies exclusively the understory, uses the air as the main substrate of prey capture, does not use nectar, and is mainly insectivorous (table 1, figure 1).

The most important axis reducing overlap among all the 13 species was the frugivorous diet (table 7) due the lowest index.

To answer if competition could explain this partition in food type axis, particular attention in future studies should be given to feeding decisions by birds and consequently fruit choice, as well as resource availability. This requires a detailed knowledge of the natural history of the organisms being studied.

ACKNOWLEDGMENTS

I thank J. Vielliard, D. Stotz, E. O. Willis, R. B. Cavalcanti, P. S. Oliveira, L. O. Marcondes-Machado, A. Rusczyck, F. Rocha, W. R. Silva, C. G. Machado, M. Galetti for suggestions on the manuscript. P. Moutinho helped with data analysis. S. M. R. Alvares, F. Olmos and civil servants of Fazenda Intervales helped with field work. I also thank S. M. R. Alvares for plant identification. I am indebted with A. Rusczyck for discussions during all the time. This work was partially financed by CAPES, Fundação para Produção Florestal de São Paulo and Fundação MB. I thank the Department of Zoology at UNICAMP for infrastructure.

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