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A QUANTITATIVE ASSESSMENT OF BIRD DIETS IN THE BRAZILIAN ATLANTIC FOREST, WITH RECOMMENDATIONS FOR FUTURE DIET STUDIES

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Resumo. – Avaliação quantitativa da dieta de aves na Mata Atlântica brasileira, com recomendações para futuros estudos de dieta. – Neste estudo, descrevemos quantitativamente a dieta de 22 espécies de aves passeriformes presentes na Mata Atlântica do sudeste do Brasil, com base em 253 amostras de regurgitação obtidas com tártaro emético. Adequação amostral foi verificada através de curvas cumulativas com re-amostragem aleatorizada, o que nos permitiu identificar 13 espécies cuja diversidade alimentar foi adequadamente amostrada durante o período de estudo. Dez amostras foram suficientes para descrever adequadamente a dieta da maioria das espécies. Ao descrever a composição das dietas, usamos um índice quantitativo que incorpora informação tanto sobre a abundância quanto sobre a occorrência das categorias alimentares. Nós sugerimos o uso deste índice em estudos de dieta como uma alternativa mais informativa do que índices de abundância relativa. As categorias alimentares mais importantes em geral foram Coleoptera, Formicidae e outros Hymenoptera, adultos e larvas de Lepidoptera, Araneae, ovos de insetos, ootecas de Blattodea, Homoptera, frutos e sementes. Afiliação em guildas e diferenças entre espécies pertencendo às mesmas guildas são discutidas.

Abstract. – This study presents quantitative information on the diet of 22 passerine bird species occurring in an area of Atlantic forest in Southeast Brazil, based on the analysis of 253 regurgitation samples obtained with tartar emetic. Sampling adequacy was verified by cumulative curves with randomized re-sampling, what allowed identifying 13 species for which diet diversity was adequately sampled during the study period. Ten samples were sufficient to adequately describe the diet diversity of most species. We used a quantitative index to describe diet composition that incorporates information on both abundance and occurrence of diet categories, and we propose the use of this index in bird diet studies as a more informative alternative than the usually adopted indices of relative abundance. The most important diet categories overall were Coleoptera, Formicidae, non-ant Hymenoptera, adult and larval Lepidoptera, Araneae, insect eggs, Blattodea oothecae, Homoptera, fruits, and seeds. Guild affiliation and intraguild differences in the diet of the bird species are discussed. *Accepted 30 November 2004*.

Key words: Atlantic forest, Brazil, diet, trophic guilds, methodology, Neotropical birds, tartar emetic.

INTRODUCTION

Diet studies deal with a fundamental aspect of the biology of organisms and provide important information for an array of evolutionary, ecological, and conservationist questions. Such studies identify food resources that provide necessary nutrient and energy contents,

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and which may be consumed in a more or less selective manner in relation to their availability (Davies 1977, Levey & Martínez Del Rio 2001, Rodway & Cooke 2002). Diet requirements may limit populations and structure communities (Loiselle & Blake 1991, Rosselli 1994, Malizia 2001), act on the evolution of physiology, life history, and behavior (Hespenheide 1971, Sherry 1990, van Heezik & Davis 1990, Brändle *et al.* 2002), and influence patterns of habitat use as well as intra- and interespecific interactions (Morse 1974, Beaver & Baldwin 1975, Sherry 1984, Chapman & Rosenberg 1991, Pérez & Bulla 2000). Finally, identifying food resources that are critical for particular species can guide the development of wildlife management plans (Hess & James 1998).

Our knowledge of the diet and feeding behavior of Brazilian birds is still inadequate. Anecdotal and non-quantitative observations remain as unique reports for many species (e.g., Moojen *et al.* 1941, Hempel 1949). Available detailed studies emphasize mostly frugivores (Marini 1992, Galetti & Pizo 1996, Marini & Cavalcanti 1998); many simply list birds foraging on a single plant species (Motta-Júnior & Lombardi 1990, Pineschi 1990, Oniki *et al.* 1994, Argel-de-Oliveira *et al.* 1996). In contrast, only a handful of studies describe the diet of insectivorous species (Schubart *et al.* 1965, Willis & Oniki 1992, Gomes *et al.* 2001, Lopes 2001, Mallet-Rodrigues 2001). Moreover, most studies are largely qualitative (but see Gomes *et al.* 2001, Mallet-Rodrigues 2001). Thus, there is a gap to be filled concerning detailed, quantitative studies on bird feeding ecology in Brazil.

Direct analysis through fecal, stomach, or regurgitation samples allows detailed, quantitative characterization of diet which is not easily obtained by observational data, mainly for arthropod prey items (Wooller & Calver 1981, Chapman & Rosenberg 1991, Poulin *et al.* 1994a, 1994b; Chesser 1995, Mallet-Rodrigues 2001). Here, we present a quantitative analysis of the diets of a bird assemblage occurring in an area of Atlantic forest in Southeast Brazil, using a chemical, the tartar emetic, to obtain regurgitation samples. The study was limited to a single rainy season, therefore should be taken as an assessment of a seasonal component of the diet over the complete annual cycle of the species. Still, this study probably represents the most extensive report on Atlantic forest birds' diets to date, especially for insectivorous species. Additionally, we offer recommendations for future studies on bird diets, such as the use of randomization techniques for verification of sampling adequacy and the use of a descriptive index that integrates information both on abundance and occurrence of diet categories.

METHODS

Study area. The study was conducted in the Barreiro Special Protection Area (19º50'S-43º50'W, 1070-1220 m a.s.l), Belo Horizonte municipality, Minas Gerais state, Brazil. Barreiro is a 1406-ha area located on the western slope of the Cachimbo hills in the Espinhaço mountain range, and is included in the Serra do Rola-Moça State Park. The region lies in the transition zone between Cerrado and Atlantic forest ecosystems (Veloso 1966, Ab'Saber 1977), sharing faunistic and floristic elements with both biomes (R. Durães pers. observ.). In the study area, formations of cerrado, rupestrian fields, gallery forests, and mesic forests alternate according to soil fertility and elevation (Centro Tecnológico de Minas Gerais 1993). Data were collected in two mesic-forest fragments (50 and 200 ha) embedded in a cerrado matrix. These fragments are in an advanced stage of succession (~ 150 years), have a relatively open understory and a canopy layer of 20 m with emergent trees up to 30 m high (Centro Tecnológico de Minas Gerais 1993). The climate in the region is characterized by a wetter and hotter season between October and March, and a drier and milder season between April and September. Average monthly temperatures vary from 18° to 26° C. Total monthly precipitation ranges from 14 to 324 mm, with a monthly mean of 124 mm and annual total around 1500 mm (Anonymous 1992).

Bird sampling. Birds were captured during the wet season, between October 1999 and February 2000, corresponding to the main breeding season in the region, and also to the period of higher productivity, mainly for insects (Davis 1945, Marini & Durães 2001). Ten to 15 mist-nets (12 x 2.5 m, 36-mm mesh) were set daily in one of 11 transects (six transects in the 200-ha fragment and five in the 50-ha fragment) located in the interior and on the edges of the forest. Transects were sequentially sampled, each being sampled once or twice a month, totaling 3640 net-h. Nets were operated from dawn until 14:00 h.

Regurgitation samples were obtained by administration of a 1.2% solution of potassium antimony tartrate solution (tartar emetic) in a dosage of 0.8 ml per 100 g of body mass (Kadochnikov 1967 *fide* Kelso 1967, Tomback 1975). The solution was given orally through a 2-mm silicon tube connected to a c. 1-ml syringe. The tube was slowly inserted until the end of the esophagus to avoid injection of liquid into the respiratory tract. The emetic was then administered at an approximate rate of 0.02-0.03 ml/s. The birds were maintained in a dark, ventilated box until regurgitation (boxes were checked periodically) or for a maximum of one hour. Average time elapsed between emetic administration and regurgitation was 19 ± 10 min. Birds were then released near the point of capture. Regurgitated material was preserved in 70% alcohol. Birds that died during the study were dissected as soon as possible to avoid post-mortem digestion and stomach contents were preserved in 70% alcohol. These birds are stored in the ornithological collection of Universidade Federal de Minas Gerais, Brazil. Investigators planning to adopt the method of the tartar emetic should be aware that this is an invasive technique and may have variable results for different trophic guilds; for a detailed discussion about the performance of the method as applied in this study, including mortality and post-treatment recapture rates, see Durães & Marini (2003).

In the laboratory, regurgitation samples were examined under a stereoscopic microscope. Diet items were identified, counted, and grouped in the following diet categories: a) arthropods, mostly at order-level, subdivided by life stages (adults, larvae, and eggs; due to their unique morphological and behavioral characteristics among the Hymenoptera, the Formicidae were considered as a distinct category); b) seeds, grouped in operational taxonomic units (O.T.U., i.e., seeds considered as belonging to the same species based on morphological similarity); c) other infrequent categories were: flowers, plant material, or fruits (mostly pulp). When pulp and seeds occurred together in the sample, only the seeds were recorded. If pulp material occurred without seeds, the pulp was recorded as one single item, unless there was evidence of ingestion of more than one type of fruit (e.g., pulp material of two different colors). Arthropods were usually fragmented in regurgitation samples and were quantified by association among body parts. Fragments were combined to form complete body parts (wings, heads, etc.), and these body parts were combined to give an estimate of the minimum number of individual prey (diet items) in the sample. All associations were based on similarities in color, size and shape.

Data analysis. It is desirable in quantitative assessments of diets to include an evaluation of how adequate the samples are in representing the diversity of diet categories, a point commonly ignored in bird diet studies in general (but see Sherry 1984, Chapman & Rosenberg 1991, Mallet-Rodrigues 2001). In this study, sampling adequacy was assessed for each species by two different methods: cumulative curves of diet diversity and cumulative curves of the coefficients of variation associated with these diversity estimates. Cumulative curves were constructed using randomization procedures (EstimateS Version 5, Colwell 1997). The Shannon index (Magurran 1988) was used to estimate diet diversity (some authors consider that richness and evenness are more informative when taken separately; however, using diet richness, instead of diet diversity, produced very similar results, which are not presented here.). To construct cumulative curves of diet diversity, a first sample was selected, and the diversity of diet categories in this sample estimated; then a second sample was selected, and the cumulative diversity of these two samples pooled was estimated. This was repeated until all samples were included in a cumulative diversity measure. The samples were added in random order, without replacement. This procedure was repeated 100 times for each species, and a cumulative curve was produced with mean values of diet diversity per sampling size. Sampling adequacy was evaluated by visual inspection of curve stabilization. Additionally, coefficients of variation (CV) associated with the diversity estimates were plotted in a cumulative curve. Sampling was considered adequate if CV stabilized at low levels (15%). A value of 15% was chosen as the cutoff because species with larger sample sizes, whose diversity curves clearly stabilized, also presented CV stabilized below 15%.

The importance of each category in the diet of different bird species was estimated by a modified version of the Kawakami-Vazzoler index of alimentary importance (Kawakami & Vazzoler 1980), originally applied to the study of fish diets. Because this index integrates information both on relative abundance and occurrence of diet categories, it has the advantage of correcting the importance of items that occur abundantly but sporadically, or items registered frequently but always in small amount. For this analysis, the 35 registered seed types were lumped as a single diet category. Thus, the importance of different fruit species in the diets was not assessed in this study, but rather the overall relative importance of fruits in the diet. To calculate this index, first the relative occurrence RO_i of each diet category i is estimated, where RO_i is the number of samples where category i occurs relative to n, the total number of samples per species. Second, the relative abundance RA_i of each diet category i is estimated for each sample separately, where RA_i is the number of diet items belonging to category i relative to the total number of diet items in that sample. Then, the mean relative abundance $\overline{RA}_i$ of each diet category i is obtained by adding the relative abundances of each category among the samples and dividing the total by n. Finally, relative occurrence and mean relative abundance are merged in the index of alimentary importance (AI_i), which provides the overall relative importance of each diet category for a given species, expressed as a percentage:

$$AI_i = \left(RO_i \times \overline{RA}_i / \sum_{i=1}^{n}(RO_i \times \overline{RA}_i)\right) \times 100.$$

Species considered adequately sampled were assigned to diet guilds based on the following criteria: 1) insectivores, i.e., those with diet exclusively or almost exclusively composed by arthropods ($AI_{arthropods} \geq 90\%$); 2) omnivores, i.e., those with mixed diet, composed by significant proportions of arthropods, fruits, and seeds ($AI_{arthropods}$ and $AI_{fruits+seeds} \geq 10\%$ each); 3) frugivores, i.e., those with diet exclusively or almost

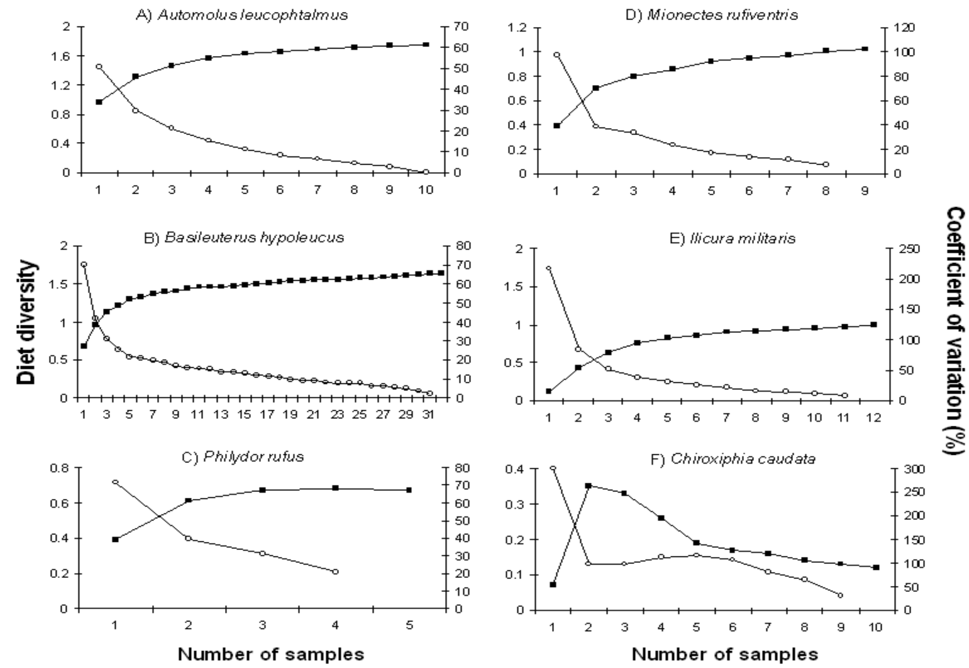

FIG. 1. Cumulative curves of mean diet diversity (black squares) and coefficient of variation (open circles) for six passerine species present in an area of Atlantic forest, during the wet season of 1999–2000. Patterns were similar for other species: all but one species with at least 10 diet samples (*C. caudata*, graph F) were considered adequately sampled by both methods. Graphs for insectivores are in the left, and for omnivores (*M. rufiventris*) or frugivores (*I. militaris*, *C. caudata*) in the right. A, B, D, and E: both curves showed stabilization. C: the diet diversity curve suggested stabilization, but the curve for coefficient of variation accused undersampling. F: neither curves stabilized. Note differences in scale among graphs.

exclusively composed by seeds and fruits ($AI_{\text{fruits+seeds}} \geq 90\%$).

In order to verify whether the above classification reflected true differences among species, and to identify finer intraguild diet differences, we performed a correspondence analysis (CA) where bird species were ordinated according to the relative importance of different diet categories. Extremely rare diet categories (total AI summed across all species ≤1%) were excluded from this analysis. The use of CA is appropriate since the data supported the assumption of unimodal distribution, as verified by performing a detrended correspondence analysis (DCA) and checking the length of the gradient (ter Braak & Šmilauer 1998). Detrending was not necessary as the ordination diagram did not show an arch effect (Hill & Gauch 1980), and regular CA was able to explain a larger portion of the total variance on the diet data than DCA. Analyses were carried out in CANOCO Version 4.0 (ter Braak & Šmilauer 1998) using symmetric scaling of ordination scores, with no data transformation and equal weighting for all species and diet categories.

RESULTS

A total of 283 identifiable regurgitation sam-

TABLE 1. Diet categories present in bird regurgitation samples, ranked by decreasing order of relative occurrence (RO) and relative abundance (RA). Indices values are for the pooled 207 samples from 13 species considered adequately sampled (see text). A = adults; L = larvae; otherwise indicated, categories refer to adult instars.

Diet categories	Relative occurrence (Rank)	Relative abundance (Rank)
Coleoptera (A)	73.9 (1)	24.5 (2)
Formicidae	37.7 (2)	11.1 (4)
Non-ant Hymenoptera	32.8 (3)	6.6 (5)
Lepidoptera (A)	15.9 (4)	1.7 (8)
Seed	13.0 (5)	13.5 (3)
Homoptera	13.0 (5)	5.9 (6)
Araneae	11.6 (6)	2.4 (7)
Lepidoptera (L)	11.6 (6)	1.5 (10)
Diptera	9.7 (7)	1.7 (8)
Heteroptera	9.7 (7)	1.3 (11)
Fruit	9.2 (8)	1.5 (9)
Insect egg	5.3 (9)	24.8 (1)
Coleoptera (L)	3.9 (10)	1.7 (8)
Hemiptera	3.4 (11)	0.6 (12)
Ootheca	3.4 (11)	0.4 (13)
Neuroptera (A)	1.4 (12)	0.2 (14)
Gastropoda	1.4 (12)	0.2 (14)
Neuroptera (L)	1.0 (13)	0.1 (15)
Isoptera	0.5 (14)	0.1 (15)
Blattodea	0.5 (14)	0.1 (16)
Plecoptera	0.5 (14)	0.1 (16)
Embioptera	0.5 (14)	0.1 (16)
Flower	0.5 (14)	0.1 (16)
Plant material	0.5 (14)	0.1(16)

ples were obtained after excluding those samples containing only liquid (indicative of empty stomach) or excessively fragmented parts not allowing identification of diet items. These samples encompassed 39 bird species from 11 families. Fourteen species were considered adequately sampled by visual inspection of diet diversity curves; all but one of these 14 species (*Philydor rufus*) were considered adequately sampled according to the criterion of stabilized coefficients of variation (Fig. 1, Appendix 1). Thus, the two methods used to evaluate sampling adequacy provided similar results. The 13 species considered adequately sampled were represented by 9 to 32 diet samples (total: 207 samples).

The relative importance of diet categories for the 22 species with a minimum of four diet samples, expressed by the AI index, is presented in the Appendix 1. A total of 2823 diet items distributed in 27 diet categories were identified in these samples. Overall, the diet categories with the highest importance were Coleoptera, Formicidae and other Hymenoptera, adult and larval Lepidoptera, Araneae, insect eggs, Blattodea oothecae, Homoptera, fruits, and seeds.

Indices of relative occurrence and abundance were strongly correlated for 19 of 21 species (r_s = 0.638–0.969, $P < 0.05$; not significant for *P. rufus* and *Sclerurus scansor*; small number of diet categories for *Turdus leucomelas* prevented statistical test). Some categories, however, presented large discrepancies between their relative occurrence and abundance. This is illustrated in Table 1, which ranks the diet categories pooled for all 13 species in terms of their relative occurrence and relative abundance: insect eggs were ranked as the first more important diet category in regard to their abundance, but only as the ninth more important in terms of relative occurrence; on the other hand, larval and adult lepidopterans were ranked high according to their occurrence, but lower in regard to their abundance in the samples. Examples of discrepancy between frequency of occurrence and abundance of diet categories are also found for individual species (see Appendix 1); e.g., the high frequency in which adult coleopterans and larval lepidopterans were found in *Conopophaga lineata* samples was not mirrored by their relative abundance. Another example is given by *Trichothrapis melanops*: Hymenoptera and Coleoptera were more frequent in the

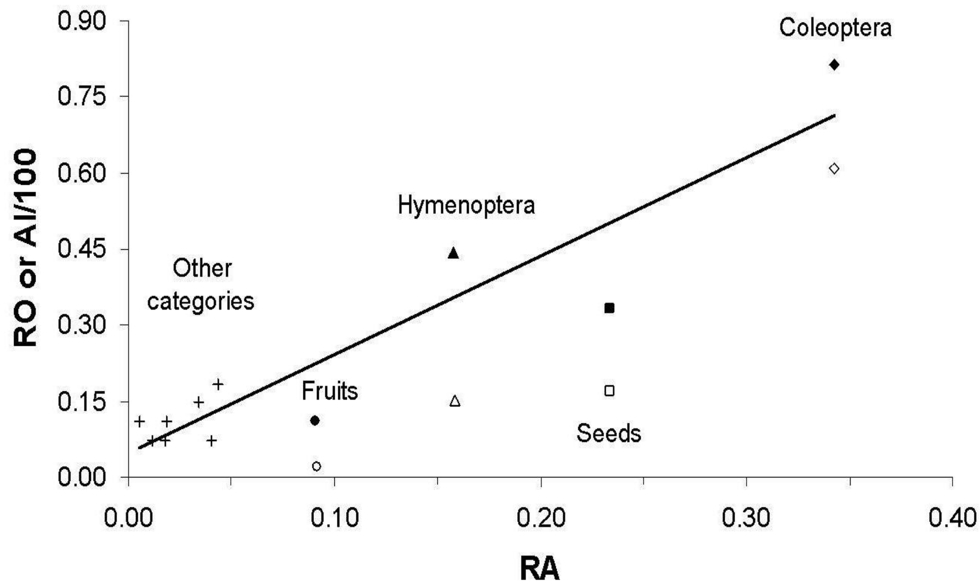

FIG. 2. Relationship between the relative abundance (RA) and the relative occurrence (RO) of diet categories consumed by *Trichothraupis melanops*, and its effect on the index of alimentary importance (in this case presented as proportion, AI/100). Diet category symbols: adult coleopterans (diamonds), non-ant hymenopterans (triangles), seeds (squares), fruits (circles), and others (crosses); closed symbols and crosses depict the relationship between RA and RO; open symbols depict the relationship between RA and AI for the four depicted diet categories.

diet than abundant, what caused the AI values for these categories to be reduced; likewise, seeds and fruits were more abundant than frequent, also downweighting their corresponding AI values (Fig. 2).

Nine species were classified as exclusive insectivores: *C. lineata*, *Dysithamnus mentalis*, *Thamnophilus caerulescens*, *Automolus leucophtalmus*, *Lathrotriccus euleri*, *Leptopogon amaurocephalus*, *Platyrinchus mystaceus*, *Basileuterus flaveolus*, and *Basileuterus hypoleucus*. Adult coleopterans were the most important diet category for eight of these species. Other important categories were Formicidae, non-ant Hymenoptera, adult and larval Lepidoptera, Heteroptera, Homoptera, Blattodea oothecae and other insect (mainly Lepidoptera) eggs. Four species (*B. flaveolus*, *B. hypoleucus*, *D. mentalis*, and *T. caerulescens*) consumed a very small proportion (< 2.5%) of seeds, fruit, plant material, and/or flowers.

The only species classified as exclusive frugivore was *Ilicura militaris*. Consumed items other than fruits and seeds were Araneae and Formicidae. Three different seed morphotypes were found in the diet samples, but most samples contained only fruit pulp, and not seeds.

Three species (*Mionectes rufiventris*, *Turdus albicollis*, and *T. melanops*) were classified as omnivores. These species consumed 14 different diet categories, of which 12 were arthropods (adults, larvae, or eggs). They consumed 15 different seed morphotypes (seven for *T. melanops*, six for *M. rufiventris*, and four for *T. albicollis*), with only two morphotypes shared between *T. melanops* and *T. albicollis*. The relative importance of animal versus veg-

TABLE 2. Eigenvalues and explained variance (per axis and cumulative) produced by a correspondence analysis ordering 13 bird species based on the importance of diet categories consumed.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.842	0.406	0.266	0.105
% explained variance	47.1	22.7	14.9	5.8
% cumulative variance	47.1	69.8	84.7	90.5

etal categories varied greatly among these species: *T. albicollis* consumed >75% seeds and fruits and *T. melanops* consumed >80% arthropods, while *M. rufiventris* consumed roughly equal proportions of both category types (54.5% arthropods, 45.5% seeds/fruits).

The correspondence analysis produced four axes, which together depicted 90.5% of the variation contained on the diet of the 13 species, as described by the AI values for 14 diet categories (Tables 2 and 3, Fig. 3). The first axis separated species that rely on large amounts of fruits from species that are exclusively or predominantly insectivorous. A second axis separated *M. rufiventris* from all other species, due to the importance of Araneae in the diet of this species. A third axis separated *C. lineata* from all other species, given the very high importance of Formicidae and, at a least extent, insect eggs in its diet. Due to the high prevalence of adult Coleoptera in the diet of insectivores, all these species were grouped very close together along the first two axes. However, they were separated into two distinct groups along the third axis. One group (black circles on Fig. 3) is formed by species that fed relatively heavily on Hymenoptera, and also on Diptera (*P. mystaceus*, *B. flaveolus*), Hemiptera (*P. mystaceus*), or Homoptera (*B. flaveolus*). All species in this group but *B. flaveolus* forage predominantly by sallying (Fitzpatrick 1980, Maldonado-Coelho unpubl.). Species in the second group (white circles on Fig. 3, and also *C. lineata*) had as main characteristic the high importance of Formicidae in their diets (Tables 1 and 3). All species in this group but *L. euleri* forage predominantly by gleaning (M. Maldonado-Coelho unpubl.). The fourth axis explained little of the variation (< 6%) and hence will not be discussed.

DISCUSSION

Diet characterization. Partially or exclusively insectivores represented most of the species in this study. Although not all species in the Barreiro community (~ 115 forest-dwelling species, ~ 64% insectivores; M. Â. M. & M. Maldonado-Coelho unpubl.) were represented here, predominance of insectivores species is a recurrent characteristic of most forest bird communities worldwide (Karr 1971, Blake 1983, Terborgh *et al.* 1990, Malizia 2001). Additionally, arthropods can be important alternative food resources for frugivores and nectarivores, mainly during breeding (Poulin *et al.* 1992, Levey & Martínez Del Rio 2001). However, despite the importance of arthropods in fueling bird populations, community-level diet assessments are often restricted to frugivores (e.g., Loiselle & Blake 1990, but see Poulin *et al.* 1994a, 1994b).

In this study, the most important arthropod prey in the samples were also those usually most abundant in tropical forests, such as Coleoptera, Hymenoptera, Lepidoptera, and Homoptera (Janzen & Schoener 1968, Marinoni & Dutra 1991, Kumagai 1999). The importance of these prey categories for insectivores has been repeatedly confirmed (Schubart *et al.* 1965, Otvos & Stark 1985, Chapman & Rosenberg 1991; Poulin *et al.* 1992, 1994c; Chesser 1995, Gomes *et al.* 2001, Lopes 2001).

The guild classification adopted here was simple and separated species into three general categories (insectivores, omnivores, and frugivores). Moreover, sampling was concentrated during a single rainy season. Thus,

TABLE 3. Correspondence analysis scores (eigenvectors) for diet categories consumed by 13 bird species. A = adults; L = larvae.

Diet categories	Axis 1	Axis 2	Axis 3	Axis 4
Coleoptera (A)	-0.546	-0.019	-0.162	-0.195
Coleoptera (L)	-0.120	-0.314	-0.207	-0.019
Diptera	0.128	-0.443	-0.588	0.330
Formicidae	-0.565	-0.046	1.198	0.239
Non-ant Hymenoptera	-0.499	-0.040	-0.812	0.853
Heteroptera	-0.553	0.012	-0.075	-0.174
Homoptera	-0.385	-0.131	-0.675	-0.274
Hemiptera	-0.522	-0.066	-0.646	0.713
Lepidoptera (A)	-0.466	0.030	-0.341	-0.472
Lepidoptera (L)	0.217	-0.380	-0.312	0.957
Insect egg	-0.614	-0.093	1.500	0.276
Araneae	1.320	2.461	0.049	0.031
Fruit	1.824	-0.984	0.068	-0.069
Seed	1.492	0.0030	-0.025	-0.021

rather than offering definitive guild affiliations for the studied species, our classification, as well as the correspondence analysis, aimed to aid in the description of diets during the study period. The correspondence analysis supported some but not all aspects of the guild classification, and identified finer differences among species. Omnivores presented large differences in their diets and did not form a distinct group in the correspondence analysis. Rather, they encompassed a gradient from predominantly insectivorous (*T. melanops*, which was grouped with insectivores) to predominantly frugivorous species (*T. albicolis*, grouped with the only exclusive frugivore in this study, *I. militaris*). *Mionectes rufiventris*, maybe the only truly omnivorous species sampled, was separated from all other species. On the other hand, insectivores formed a very well defined group, mainly due to high predominance of Coleoptera in their diets. Yet, they could be subdivided in a group of species that forage mainly by sallying and consumed large proportions of hymenopterans and a group of species that forage mainly by gleaning and consumed large proportions of ants. Thus, diet differences among insectivorous species were in large extent related to differences in foraging behavior, but could not be inferred based only in this type of information (e.g., *B. flaveolus* and *L. euleri* were exceptions). While some studies have found correspondence between diet and foraging behavior in birds (Robinson & Holmes 1982, Sherry 1984), it is clear that sympatric species with similar foraging behavior can differ greatly in diet, and vice-versa (e.g., Beaver & Baldwin 1975, Chapman & Rosenberg 1991), what reinforces the importance of direct assessment of diets.

Methodological issues and recommendations. As any diversity assessment, it is recommendable for quantitative diet studies to include verification of sampling adequacy, but this is a usually ignored point. Visual inspection of cumulative curves of diet diversity (Sherry 1984) or richness (Loiselle & Blake 1990, Mallet-Rodrigues 2001) has been used occasionally to check for sampling adequacy. This procedure can be highly improved with the incorporation of randomization techniques that provide associated deviation measures. The two methods used in this study (cumulative curves of diet

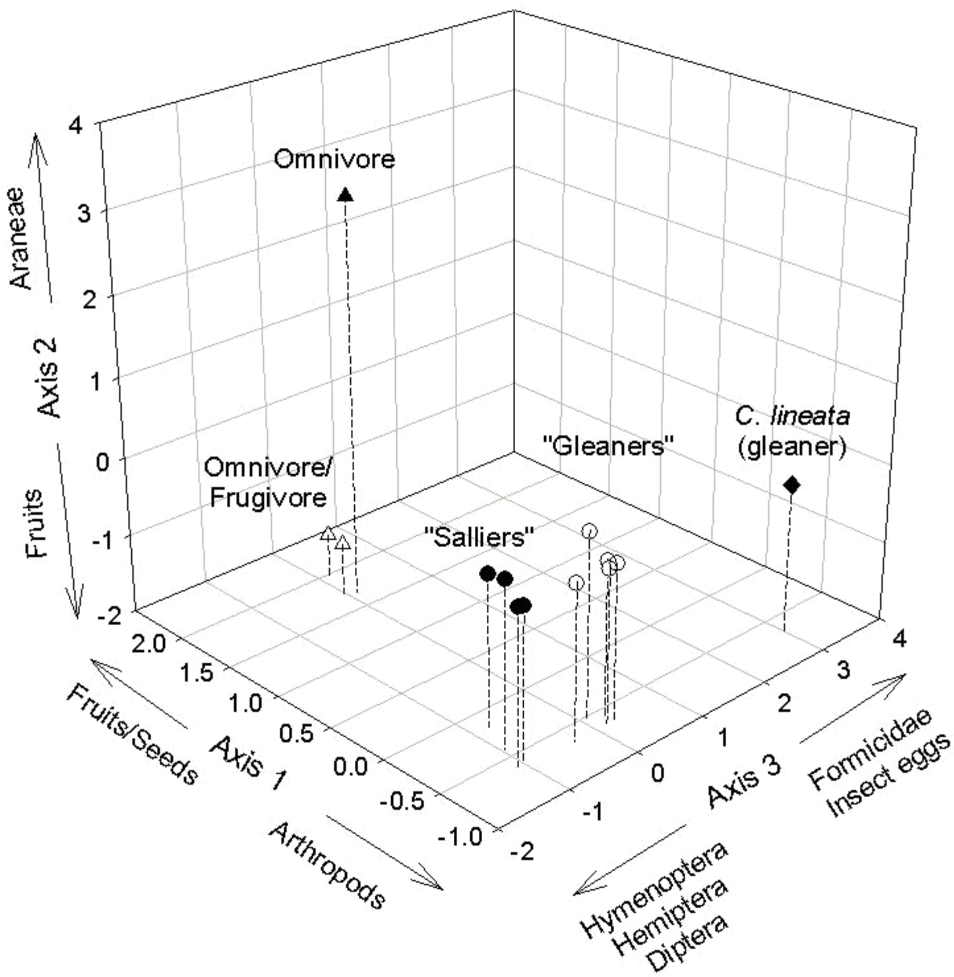

FIG. 3. Correspondence analysis ordinating 13 Atlantic forest bird species according to the importance of diet categories. Species symbols: white triangles, *I. militaris* and *T. albicollis*; black triangle, *M. rufiventris*; black diamond, *C. lineata*; white circles, *D. mentalis*, *T. caerulescens*, *A. leucophtalmus*, *L. euleri*, *B. hypoleucus*; and black circles, *L. amaurocephalus*, *P. mystaceus*, *B. flaveolus*, *T. melanops.*

diversity and cumulative curves of coefficients of variation) produced similar results for all but one species. During the study period and for all but one (*C. caudata*) of the sampled species, diet diversity could be adequately sampled with 10 regurgitation samples. Nevertheless, since the adequate number of samples can vary greatly due to temporal and spatial variability in resource availability and use, we stress that verification of sampling adequacy should not be overlooked.

If indices are utilized to describe diet data, these also must be chosen carefully. Most authors adopt indices of relative abundance to describe diets (Orians & Horn 1969, Gavett & Wakeley 1986; Poulin *et al.* 1994a, 1994c;

Mallet-Rodrigues 2001), but these indices can be misleading in some cases because they do not consider frequency of occurrence of diet categories. As the AI index integrates information about both occurrence and abundance of diet categories, it corrects the importance of categories occurring frequently but at low abundance or categories occurring rarely but at high abundance among the diet samples. Despite some evidence that relative abundance and occurrence of diet categories can be generally correlated (this study, Rodway & Cooke 2002; but see Clark 1982 for a counterexample with mammals), this relationship has been still poorly explored. Moreover, as demonstrated by this study, this is not true for all diet categories or species. The AI index can be especially advantageous when describing the diet of species feeding on large items that are taken at low numbers but frequently (i.e., caterpillars, large insects) or small items that are taken at large numbers but only occasionally (i.e., insect eggs and other items with clumped distribution).

A critical point in diet studies is how food items are identified and quantified. Fine taxonomic identification of prey items can be difficult due to their fragmented state, but a meaningful ecological characterization of prey items (e.g., with individualization of different life stages as eggs, larvae, and adults) is usually more relevant for diet studies (Cooper *et al.* 1990). The association among arthropod body parts provides a conservative method of quantification (Calver & Wooller 1982), being reasonably easy to perform after some practice. A special problem is posed by the quantification of insect eggs, since it is unknown whether the birds actively prey on these items, or whether eggs are secondarily ingested along with adult insects. However, the second alternative seems less likely since, in some instances where insect eggs were found in the regurgitation samples, there were no remains of adult insects, and it is not clear why only the eggs should remain undigested.

A more serious problem is posed by differences in digestion rates among food categories (reviewed by Rosenberg & Cooper 1990). Although the action of the tartar emetic is independent from the type of food ingested (Zack & Falls 1976, Gavett & Wakeley 1986, Durães & Marini 2003), this technique is still subject to biases underestimating the importance of soft items (e.g., fruit pulp, non-chitinous arthropod parts, larvae) and overestimating that of hard items (e.g., Coleoptera elytra) (Levey & Karasov 1989, Major 1990). Without having applied a correction for differential digestion rates, we cannot rule out the possibility that the predominance of Coleoptera and Formicidae in the diet of the insectivorous species was partly due to these biases.

Quantification of fruits and seeds also suffer from methodological problems. Since pulp has short retention time (Levey & Karasov 1989, Major 1990) and its volumetric quantification can be very imprecise, consumption of fruits is measured mostly based on seeds. However, the seed/fruit ratio can be extremely variable among species, making the quantification of seeds in diets imprecise in the absence of a fruit collection. Wheelwright (1985) examined more than 200 bird-dispersed fruit species and observed that approximately half contained a single seed, while only 24% of the species had more than 10 seeds per fruit. During an extensive survey carried out in an area of Atlantic forest in São Paulo state, 131 fruit species were recorded in the diet of 51 passerine bird species; 48 (36.4%) of these fruit species were single-seeded, and 61 (46.6%) had a maximum of two seeds (Erica Hasui pers. com.). In this study, the number of seeds per diet sample varied largely, from 1 to 368. We assumed that most of the consumed fruit species have a low seed/fruit ratio, and that recording each seed as an item was a reasonable indicator of the relative importance of fruits in the diets. We acknowledge, however, that this procedure is far from ideal and that a representative reference fruit collection is necessary for more precise quantification. Additionally, a complete survey of diet of frugivores may require to be complemented by observational data, especially for "mashers" that mandibulate fruits and drop seeds (Moermond & Denslow 1985, Loiselle & Blake 1990).

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APPENDIX 1. Index of alimentary importance (AI, %) of diet categories consumed by 22 bird species in an area of Atlantic forest, during the wet season of 1999-2000. Below AI values, between parentheses, are values of relative abundance (RA, first number) and relative occurrence (RO, second number). Asterisks indicate that AI < 0.05%, or that RA or RO < 0.01. Species codes: Conopophagidae, CoLi = *Conopophaga lineata*; Thamnophilidae, DyMe = *Dysithamnus mentalis*, ThCa = *Thamnophilus caerulescens*; Furnariidae, AuLe = *Automolus leucophtalmus*, PhRu = *Philydor rufus*, ScSc = *Sclerurus scansor*; Dendrocolaptidae, LeFu = *Lepidocolaptes fuscus*, SiGr = *Sittasomus griseicapillus*; Tyrannidae, CnFu = *Cnemotriccus fuscatus*, LaEu = *Lathrotriccus euleri*, LeAm = *Leptopogon amaurocephalus*, MiRu = *Mionectes rufiventris*, PlMy = *Platyrinchus mystaceus*; Pipridae, ChCa = *Chiroxiphia caudata*, IlMi = *Ilicura militaris*; Muscicapidae, TuAl = *Turdus albicollis*; TuLe = *Turdus leucomelas*; TuRu = *Turdus rufiventris*; Emberizidae, BaFl = *Basileuterus flaveolus*, BaHy = *Basileuterus hypoleucus*, TaCo = *Tachyphonus coronatus*, TrMe = *Trichothraupis melanops*.

Diet categories	Species							
	CoLi	DyMe	ThCa	AuLe	PhRu[a]	ScSc[a]	LeFu[a]	SiGr[a]
Embioptera								
Isoptera								1.0 (.03/.25)
Plecoptera								
Psocoptera								
Coleoptera (adult)	28.9 (.25/.91)	78.3 (.52/1.0)	70.6 (.42/1.0)	66.8 (.47/.90)	91.5 (.72/1.0)	46.7 (.28/.75)	80.0 (.60/1.0)	61.9 (.45/1.0)
Coleoptera (larva)	0.1 (.01/.09)	0.4 (.02/.18)				11.7 (.21/.25)		1.7 (.05/.25)
Diptera				0.1 (.01/.10)				1.9 (.06/.25)
Formicidae	62.0 (.49/1.0)	10.8 (.13/.55)	16.6 (.20/.50)	14.7 (.19/.50)	2.6 (.10/.20)	4.6 (.08/.25)	6.2 (.19/.25)	1.9 (.06/.25)
Other Hymenoptera		1.5 (.04/.27)	2.4 (.05/.30)	0.3 (.02/.10)				
Hemiptera[b]		0.1 (.01/.09)	0.3 (.02/.10)					
Heteroptera	0.3 (.01/.18)	0.9 (.03/.18)	1.4 (.04/.20)	0.7 (.02/.20)	2.5 (.05/.40)	10.2 (.09/.50)		5.4 (.08/.50)
Homoptera		0.1 (.01..09)	0.7 (.02/.20)	1.0 (.03/.20)	3.4 (.13/.20)			1.7 (.05/.25)
Lepidoptera (adult)	* (*/.09)	0.4 (.02/.18)	3.1 (.05/.40)	9.4 (.10/.60)				

APPENDIX 1. Continuation.

Diet categories	Species							
	CoLi	DyMe	ThCa	AuLe	PhRu[a]	ScSc[a]	LeFu[a]	SiGr[a]
Lepidoptera (larva)	1.4 (0.2/.46)	2.2 (.04/.36)	0.5 (.01/.20)	0.4 (.01/.20)		11.0 (.10/.50)		
Neuroptera (adult)			0.3 (.02/.10)					
Neuroptera (larva)				0.7 (.02/.20)		1.0 (.02/.25)		
Orthoptera								
Blattodea (adult)								
Blattodea (ootheca)		0.4 (.01/.18)				5.5 (.10/.25)	13.8 (.21/.50)	24.5 (.24/.75)
Other insect eggs	7.2 (.21/.27)	4.7 (.17/.18)	1.4 (.08/.10)					
Araneae	0.1 (.01/.09)		0.2 (.01/.10)	5.8 (.12/.30)		2.8 (.05/.25)		
Diplopoda						6.5 (.06/.50)		
Gastropoda								
Fruits								
Seeds			2.5 (.07/.20)					
Plant material		0.1 (.01/.09)						
Flowers								
No. diet items	194	195	101	68	54	40	20	19
No. samples	11	11	10	10	5	4	4	4

APPENDIX 1. Continuation.

Diet categories	Species							
	CnFu[a]	LaEu	LeAm	MiRu	PlMy	ChCa[a]	IlMi	TuAl
Embioptera								
Isoptera								
Plecoptera					0.1 (.01/.04)			

APPENDIX 1. Continuation.

Diet categories	Species							
	CnFu[a]	LaEu	LeAm	MiRu	PlMy	ChCa[a]	IlMi	TuAl
Psocoptera	0.6 (.02/.25)							
Coleoptera (adult)	76.6 (.64/1.0)	72.6 (.58/.96)	56.6 (.37/.62)		50.7 (.34/.74)			
Coleoptera (larva)		* (.01/.04)	0.2 (.01/.08)					0.3 (.01/.10)
Diptera	0.6 (.02/.25)	0.5 (.02/.17)	0.5 (.03/.08)		1.3 (.05/.13)	* (*/.10)		2.2 (.08/.10)
Formicidae	18.7 (.21/.75)	20.3 (.23/.67)	3.5 (.06/.23)	0.7 (.04/.11)	8.0 (.10/.39)		0.7 (.04/.08)	1.5 (.06/.10)
Other Hymenoptera	2.3 (.08/.25)	5.7 (.11/.42)	18.6 (.19/.39)		33.7 (.26/.65)	* (*/.10)		
Hemiptera[b]					0.8 (.04/.09)			
Heteroptera	0.6 (.02/.25)	0.1 (.01/.08)	1.4 (.04/.15)		* (*/.04)			
Homoptera	0.6 (.02/.25)	0.5 (.02/.17)	0.7 (.04/.08)		0.7 (.03/.13)			0.9 (.03/.10)
Lepidoptera (adult)		* (.01/.04)	0.1 (.01/.08)		3.6 (.08/.22)			0.9 (.03/.10)
Lepidoptera (larva)		* (*/.04)	13.3 (.17/.31)			1.0 (.05/.10)		8.2 (.15/.20)
Neuroptera (adult)			0.5 (.03/.08)					
Neuroptera (larva)								
Orthoptera								0.3 (.01/.10)
Blattodea (adult)								
Blattodea (ootheca)			0.1 (.01/.08)		0.3 (.02/.09)			
Other insect eggs					0.3 (.04.04)			
Araneae		0.2 (.02/.08)	4.4 (.06/.31)	53.8 (.41/.78)	0.4 (.02/.09)	* (*/.10)	0.7 (.04/.08)	
Diplopoda								
Gastropoda								
Fruits				11.2 (.20/.33)		27.7 (.35/.40)	61.8 (.50/.58)	50.4 (.31/.60)
Seeds				34.3 (.36/.56)		71.2 (.60/.60)	36.8 (.42/.42)	35.2 (.32/.40)

APPENDIX 1. Continuation.

Diet categories	Species							
	CnFu[a]	LaEu	LeAm	MiRu	PlMy	ChCa[a]	IlMi	TuAl
Plant material								
Flowers								
No. diet items	48	170	46	57	174	464	20	43
No. samples	4	24	13	9	23	10	12	10

APPENDIX 1. Continuation.

Diet categories	Species						No.
	TuLe[a]	TuRu[a]	BaFl	BaHy	TaCo[a]	TrMe	items/category
Embioptera				* (*/.03)			1
Isoptera				* (.01/.03)			3
Plecoptera							2
Psocoptera							1
Coleoptera (adult)		1.1 (.03/.17)	68.9 (.45/.93)	84.4 (.58/.91)	22.0 (.20/.80)	60.9 (.34/.82)	590
Coleoptera (larva)			0.5 (.03/.13)				58
Diptera			2.4 (.04/.33)	0.1 (.01/.06)		0.1 (.01/.11)	38
Formicidae			2.6 (.06/.27)	8.1 (.15/.34)		1.8 (.04/.19)	237
Other Hymenoptera			12.2 (.14/.53)	5.0 (.09/.34)		15.3 (.16/.44)	136
Hemiptera[b]				0.1 (.02/.03)		0.3 (.02/.07)	11
Heteroptera			0.4 (.02/.13)	0.8 (.03/.16)			35
Homoptera			6.9 (.13/.33)	0.4 (.02/.13)		1.1 (.03/.15)	121
Lepidoptera (adult)			5.6 (.10/.33)	0.4 (.02/.13)		0.4 (.02/.11)	34
Lepidoptera (larva)	10.0 (.25/.25)		0.1 (.01/.07)	0.1 (.01/.03)		0.2 (.01/.07)	33
Neuroptera (adult)				* (*/.03)			3
Neuroptera (larva)			* (*/*)				4

APPENDIX 1. Continuation.

Diet categories	Species						No.
	TuLe[a]	TuRu[a]	BaFl	BaHy	TaCo[a]	TrMe	items/category
Orthoptera					1.8 (.07/.20)		1
Blattodea (adult)							1
Blattodea (ootheca)				0.1 (.01/.06)			15
Other insect eggs				0.3 (.03/.06)		0.7 (.04/.07)	488
Araneae			0.1 (.01/.13)	0.1 (.01/.06)			52
Diplopoda							2
Gastropoda			0.2 (.01/.13)				2
Fruits	* (*/*)	47.7 (.50/.50)			1.8 (.07/.20)	2.2 (.09/.11)	51
Seeds	90.0 (.75/.75)	51.1 (.47/.50)	0.1 (.01/.07)	0.1 (.02/.03)	74.2 (.67/.80)	17.0 (.23/.33)	902
Plant material							1
Flowers			* (*/.07)				1
No. diet items	10	36	211	185	159	509	2823
No. samples	4	6	15	32	5	27	253

[a]Species considered insufficiently sampled in this study.
[b]Insects of Super-Order Hemiptera that could not be positively identified as Heteroptera or Homoptera.