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HOW IMPORTANT ARE ARTHROPODS IN THE DIET OF FRUIT-EATING BIRDS?

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ABSTRACT.—In most dietary studies of fruit-eating birds, sampling methods consist of direct observations of foraging and fecal sample analyses, and the consumption of resource types is measured as the percent of occurrence in diet samples, or as counts (frequency) of ingested items. Since these measures are usually biased towards the overestimation of small and abundant resources, the amount of ingested mass is a more accurate measure of the crude energy and nutrients provided by a given food source. In this study, we use direct observations of foraging behavior to describe the diet of four frugivorous-insectivorous bird species during the breeding season in Southern Yungas forests, and we compare the number of ingested items and ingested dry mass as measures of fruit and arthropod consumption. In terms of ingested food dry mass, fruit consumption represented over 95% of the diet of the four bird species. The estimated proportion of fruit in the diet differed significantly among methods in three bird species. The comparison of two methods to quantify food consumption by birds allowed us to determine that, when gross amount of ingested matter is considered, the proportion of arthropods in the diet of frugivorous-insectivorous species is much smaller than previously reported. Our study suggests that the use of food dry mass is more appropriate than methods based on item counting to determine the importance of food items in the diet, since it avoids overestimation of resources which contribute comparatively little to the total energy and nutrients ingested. The comparison of these methods highlights the importance of using more reliable measurements of the contribution of different types of food to characterize the diet of frugivorous-insectivorous bird species. *Received 30 May 2016. Accepted 3 October 2016.*

Key words: avian diet analysis, food dry mass, foraging behavior, frugivory, insectivores, Southern Yungas forests.

Most fruit-eating birds also ingest insects and other arthropods, despite being functionally considered as frugivores (e.g., Levey and Karasov 1989, Fuentes 1994, Herrera M. et al. 2006, Hilty and Bonan 2016). Typecasting birds in a food category is controversial, since the relative importance of fruits and arthropods in the diet varies among bird species, season, and resource availability (Herrera 1998, Herrera M. et al. 2005, Carnicer et al. 2008). Moreover, trophic classification can be very sensitive to sampling biases, such as the temporal and spatial extent of sampling, and particularly to the sampling method used to determine the diet (Loiselle and Blake 1990, Herrera 1998, Naoki 2003, Rougès 2003).

The most used sampling methods in the study of the diet of fruit-eating birds are direct observation of foraging behavior and fecal sample analyses, which allow for the counting of the number of ingested items (Loiselle and Blake 1990, Fuentes 1994, Yoshikawa and Osada 2015). While both methods provide information about food resources used by birds, they also exhibit methodological limitations (Duffy and Jackson 1986). Direct observation does not reveal the proportion of digested and assimilated consumed food, with the risk of overestimating the consumption of conspicuous and easily identified resources (Duffy and Jackson 1986, Pearson et al. 2003, Caut et al. 2008, Sánchez et al. 2008). On the other hand, the analysis of fecal samples can be affected by digestion processes which hinder the identification of certain remains, leading to an underestimation of the intake of easily digestible foods (Rosenberg and Cooper 1990). Moreover, items counted by any of these methods does not allow for the estimation of the contribution of different dietary items in terms of mass, energy, or nutrients. Also, while the number of items ingested by a bird tends to overestimate the presence of small and numerous items (Hyslop 1980), this bias can be minimized using measures of volume and mass of ingested resources (Duffy and Jackson 1986, Kazantzidis and Goutner 2005). The amount of ingested mass is a more accurate measure of the crude energy and nutrients provided by a given food source.

In studies of fruit-eating birds, resource consumption is usually measured as percent occurrence in diet samples, and as counts (frequency) of ingested items. From these studies, it becomes clear that the estimation of the importance of fruits and arthropods in the diet varies largely between

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TABLE 1. Name and location of sampling sites, and summary of the sampling effort and sampling success in terms of quantity of food consumed per site. Total fruit and arthropod ingested per site by the four target bird species combined is expressed both as number of items consumed and their equivalent in mg of dry mass.

Sampling site	Geographical coordinates	Elevation (m a.s.l.)	Sampling effort (hr)	Total food ingested (number; mg dry mass)	
				Fruit	Arthropod
Anta Yacu	26° 46′ 57.40″ S, 65° 20′ 43.62″ W	995	45	256; 51,926	85; 159.75
Mundo Nuevo	26° 51′ 14.94″ S, 65° 21′ 11.27″ W	680	48	81; 27,585	55; 156.98
Potrero de las Tablas	26° 53′ 56.69″ S, 65° 23′ 47.18″ W	1,049	47	153; 35,984	37; 115.94
Puerta del Cielo	26° 45′ 43.16″ S, 65° 19′ 59.34″ W	976	45	228; 44,096	91; 497.50
Río Las Cañas	26° 46′ 28.52″ S, 65° 20′ 3.66″ W	805	48	276; 65,132	68; 224.94

and within methods used to quantify foraging behavior (Naoki 2003). In a few cases, researchers use alternative approaches, such as volumetric measurements (e.g., the volume of fruit and insect remains in fecal samples; Herrera 1984, Fuentes 1994), and more recently, stable-isotope analysis, to quantify the use of insects and fruits as sources of assimilated energy and nutrients (Herrera M. et al. 2005, 2009; Fair et al. 2013). Although the need for analyzing diet data in more than one form has been largely recognized (Rosenberg and Cooper 1990), to our knowledge, comparative studies of methods for measuring the contribution of different food sources in the diet of fruit-eating birds have not been carried out to date (but see Naoki 2003).

In this study, we (1) describe the diet of four frugivorous-insectivorous bird species, and (2) evaluate two methods for measuring their consumption of fruits and arthropods: number of ingested items and ingested dry mass. Our study aims to provide a deeper understanding of the importance of fruits and arthropods in the diet of fruit-eating bird species.

METHODS

Study Area.—The study was conducted in Southern Yungas forests (Brown et al. 2001) at San Javier and Yerba Huasi mountain ranges in Tucumán province, Argentina. We sampled five sites representative of the diversity of vegetation phenology and composition of the lower montane forest in the area, distributed from 600–1100 m a.s.l. (Table 1). This altitudinal belt of vegetation is characterized by the dominance of perennial tree species: the forest canopy is dominated by *Ocotea porphyria*, *Blepharocalyx salicifolius*, *Terminalia triflora*, *Pisonia zapallo*, and *Parapiptadenia excelsa*. Typical treelet species are *Piper tucumanum*, *Eugenia uniflora*, *Allophylus edulis*, *Urera baccifera*, and *Solanum riparium*; vines and epiphytes are also common (Grau et al. 2010). Climate is subtropical, with dry winters (May–Sept) and wet summers (Nov–Mar). Average annual rainfall is ~1,300 mm and average annual temperature is 19°C (Minetti et al. 2005). The study was conducted from November to December 2012, during the peak breeding season for fruit-eating songbirds in the lower montane forest (Auer et al. 1997, Capllonch et al. 2008, Lomáscolo et al. 2010, Blendinger et al. 2015b).

Studied Species.—We studied the foraging behavior of four frugivorous-insectivorous species belonging to the core of the most common fruit-eating species in the study area (Blendinger et al. 2015b, Ruggera et al. 2016): the Rufous-bellied Thrush (Turdidae: *Turdus rufiventris*; Fig. 1A), the Slaty Thrush (Turdidae: *Turdus nigriceps*; Fig. 1B), the Sayaca Tanager (Thraupidae: *Thraupis sayaca*; Fig. 1C), and the Common Bush Tanager (Emberizidae: *Chlorospingus flavopectus* (previously *C.ophthalmicus*; Fig. 1D). According to previous diet studies based on the count of ingested items, these four bird species eat fruit and arthropods but exhibit different levels of specialization in the consumption of fruits in Southern Yungas forests (Giannini 1999, Rougès and Blake 2001, Rougès 2003). Common Bush Tanagers are mostly insectivorous and shift opportunistically towards a more frugivorous diet (Blendinger et al. 2012, 2016; see also Valburg [2002] for a study in Costa Rica), while the other three species regularly consume fruits during the

FIG. 1. Frugivorous-insectivorous bird species included in this study: (A) Rufous-bellied Thrush, (B) Slaty Thrush, (C) Sayaca Tanager, and (D) Common Bush Tanager. Photos: Rodrigo Aráoz.

year. Rufous-bellied Thrushes and the Slaty Thrushes consume varying amounts of both types of food, whose relative importance varies seasonally and regionally, with increasing fruit consumption during the wet summer season (Giannini 1999, Rougès 2003). Finally, Sayaca Tanagers display local movements to track changes in fruit availability, and they are the most specialized in fruit consumption of the four species (Rougès 2003, Blendinger et al. 2012).

Foraging Behavior.—One observer (MGN) visited each site between November and December, sampling up to 45 hrs to record the foraging behavior of birds. Samplings began at sunrise and continued for the next 10 hrs, with an hour break at noon. In some days, sampling was interrupted because of bad weather. At each site, the observer walked through an area of ~1.5 ha to record the foraging behavior of birds. When detecting an individual, all events of arthropod and fruit consumption were recorded until the bird was out of sight. Although data from successive records of the same individual are not statistically independent, the inclusion of all records is ecologically relevant for assessing which fraction of the diet corresponds to fruits and arthropods. Moreover, the use of single observations to quantify bird foraging behavior may be misleading when very different food types (such as arthropods and fruits) are involved (Naoki 2003).

We considered an event of fruit consumption when a bird visited a plant and consumed fruits, and we recorded the number of ingested fruits. In a few cases, this could not be achieved because of reduced visibility, in which case we used a conservative approach and considered the consumption to be equal to one fruit to avoid overestimation. We considered every observation of a bird eating an individual arthropod as an event of arthropod consumption, including observations of birds in attack and subsequently staying in the place to consume the prey, which was interpreted as a successful attack. Captured arthropods were visually ranked by size in three broad categories: <1 cm, 1–2 cm, and >2 cm; in the few cases when we could not see the size of the prey, we assigned it to the smaller category. Since the sampling period closely matched the peak of the breeding season, we discarded foraging events (of both frugivory and insectivory) in which the bird flew away with food in its beak. We assumed in those instances that the bird was going to feed nestlings.

Ingested Food Mass Estimation.—Food dry mass allows the comparison of ingested fruits and arthropods based on the matter provided to birds. We used the initial observational data to derive the dry mass provided by each ingested item. To calculate the dry pulp mass of each fruit consumed, we first estimated the mass of the fresh pulp at the species level, as the difference between the average mass of fresh fruit minus the average mass of seeds. We then estimated the dry mass of the pulp as the difference before and after heating the fresh pulp in an oven at 60°C for 4 days (Blendinger et al. 2015a). The dry mass of each arthropod was estimated using a power function with the length of the consumed arthropod: $y = a(x)^b$, using the mean of each size category (i.e., 0.5 cm, 1.5 cm, and 2.5 cm for the largest category) as x values. Function parameters were derived from values estimated for tropical arthropods by Gruner (2003), with $a = 0.034$ and $b = 2.191$.

Statistical Analyses.—We used the number and dry mass of ingested items in all analyses. ANOVA tests were used to analyze variations in the mean consumption of fruits and arthropods, and in the mean consumption of arthropod size categories among bird species. When obtaining significant differences, we conducted multiple pairwise comparisons a posteriori using Tukey HSD. Whenever necessary, we transformed consumption variables with the function $\log 10 + 1$ to improve the normality of residuals and the

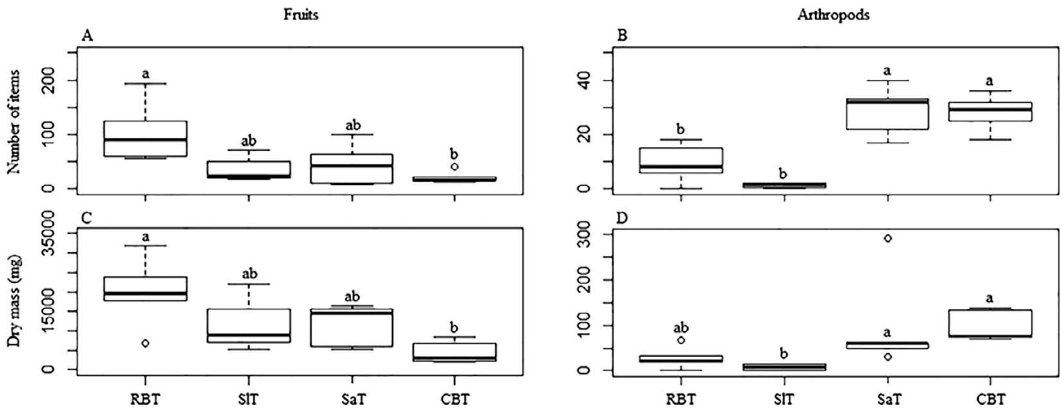

FIG. 2. Boxplots (with median, quartiles, percentiles, and extreme values) of the number of fruits (A) and arthropods (B); and the dry mass of fruit pulp (C) and arthropods (D) ingested by four bird species in Southern Yungas forests. Foraging records were gathered in ~1.5 ha and 45 hrs of observation per site; n = five sites. Different letters indicate significant differences ($P < 0.05$). RBT: Rufous-bellied Thrush, SlT: Slaty Thrush, SaT: Sayaca Tanager, CBT: Common Bush Tanager.

homogeneity of variances. When parametric assumptions were not met, even after variable transformation, we used the non-parametric Kruskal-Wallis test.

We defined the proportion of fruit in the diet as the ratio fruit / (fruits + arthropods). We then used the Kruskal-Wallis test to analyze the variation in the average proportion of fruit among bird species. Student's *t*-test for paired samples was used to analyze differences between food consumption methods (i.e., number of items consumed and ingested dry mass) for each bird species. All analyses were performed with R software (R Core Team 2015).

RESULTS

We recorded the consumption of 994 fruits and 336 arthropods, in over 472 independent feeding events (fruit: 301; arthropod: 171), equivalent to 224,723 mg of dry pulp and 1,155 mg of arthropod dry matter (Table S1).

Fruit Consumption.—Rufous-bellied Thrushes consumed 12 fruit species (mean ± SD = 4.20 ± 1.92 species per site), while Slaty Thrushes and Sayaca Tanagers consumed 9 (3.00 ± 2.34) and 15 species (5.20 ± 2.48) respectively, and Common Bush Tanagers consumed 10 species (3.60 ± 0.54) (Table S1). Mean fruit consumption differed significantly among bird species, both in terms of number of items (ANOVA, $F = 4.74$, d.f. = 3, $P = 0.016$) and in dry pulp mass ($F = 4.64$, d.f. = 3, $P = 0.017$). In both cases, consumption was significantly higher in Rufous-bellied Thrushes than in Common Bush Tanagers, while Slaty Thrushes and Sayaca Tanagers showed intermediate values (Fig. 2A, C).

Arthropod Consumption.—Average arthropod consumption differed significantly between bird species, both in number of items (Kruskal-Wallis, $X^2 = 13.39$, d.f. = 3, $P = 0.003$) and in dry mass (ANOVA, $F = 6.67$, d.f. = 3, $P = 0.004$). Arthropod consumption was significantly higher in Sayaca Tanagers and Common Bush Tanagers than in the two species of thrushes (Fig. 2B, D).

Since we recorded only five events of arthropod consumption by Slaty Thrushes, we did not make any inferences about arthropod size categories ingested by this species. Size categories of the arthropods consumed differed significantly in each bird species (Rufous-bellied Thrush: Kruskal-Wallis, $X^2 = 6.60$, d.f. = 2, $P = 0.036$; Sayaca Tanager: Kruskal-Wallis: $X^2 = 11.03$, d.f. = 2, $P = 0.004$; Common Bush Tanager: ANOVA, $F = 38.59$, d.f. = 2, $P < 0.001$). In all cases most of the prey were <1 cm (Fig. 3A). Among the three bird species, the consumption of arthropod dry mass was similar between size categories (all $P > 0.10$; Fig. 3B).

Proportion of Fruits and Arthropods in the Diet.—The average proportion of fruit in the diet was significantly different across the four species of birds, both in terms of number of items ingested (Kruskal-Wallis, $X^2 = 14.18$, d.f. = 3, $P = 0.002$)

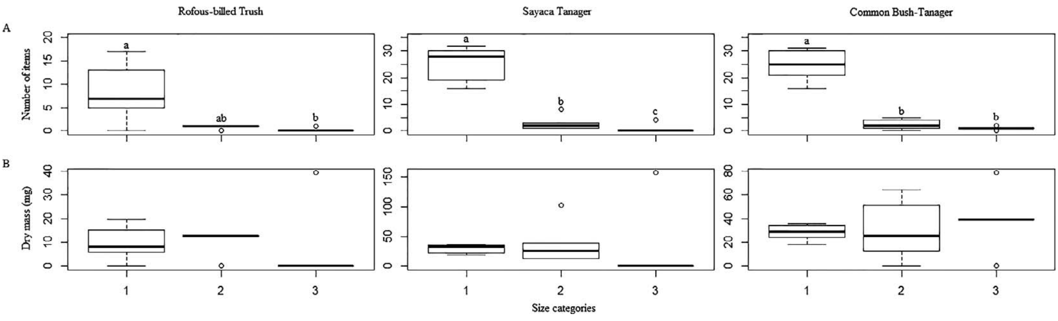

FIG. 3. Consumption of arthropods of three size categories (1: <1 cm; 2: 1–2 cm; 3: >2 cm) by three bird species in Southern Yungas forests, expressed in (A) number of ingested items and (B) ingested dry mass matter. Boxplots include the median, quartiles, percentiles, and extreme values. Different letters indicate significant differences ($P < 0.05$).

and in dry mass ($X^2 = 14.57$, d.f $= 3$, $P = 0.002$). In terms of item number, consumption was significantly higher in Rufous-bellied and the Slaty thrushes than in Sayaca Tanagers and Common Bush Tanagers (Fig. S1A). The mean proportion of pulp dry mass was significantly higher in both thrush species than in the other two bird species, and higher in Sayaca Tanagers than in Common Bush Tanagers (Fig. S1B).

The percentage of fruits in the diet was much more variable among species in terms of number of ingested items (from 41.9% in Common Bush Tanagers to 99.9% in Slaty Thrushes) than measured as ingested pulp dry mass (from 97.2% in Common Bush Tanagers to 99.9% in Slaty Thrushes) (Table 2). In three of the four species (Rufous-bellied Thrush, Sayaca Tanager, and Common Bush Tanager), the proportion of fruit in the diet differed significantly between the methods used to measure it (Table 2).

DISCUSSION

The comparison of two methods to quantify food consumption by birds allowed us to determine that, when the gross amount of ingested matter is considered, the proportion of arthropods in the diet of frugivorous-insectivorous species is much smaller than previously reported. These results contrast with those derived from more traditional methods based on the number of items consumed (Giannini 1999, Rougès and Blake 2001, Rougès 2003), and highlight the importance of more reliable measurements of the contribution of different types of food to characterize the diet of frugivorous-insectivorous bird species. Also, our results question the reliability of the current knowledge about the diet of these bird species derived from prey items counting.

The diet of fruit-eating birds of Southern Yungas forests has been studied in detail by Giannini (1999) and Rougès (2003) through the analysis of fecal samples. For the four species studied in this

TABLE 2. Frequency of fruits and arthropods in the diet of birds during the wet season in Southern Yungas forests. Student's *t*-test for paired samples between the proportion of fruit in number of items and dry matter for each bird species; significant values are highlighted in bold.

	Fruits (%)		Arthropods (%)		Number of items versus dry mass ingested	
Species	Number of items	Dry pulp (mg)	Number of items	Dry mass (mg)	*t*	*P*
Rufous-bellied Thrush	91.66	99.86	8.34	0.14	**2.92**	**0.04**
Slaty Thrush	96.28	99.94	3.72	0.06	2.44	0.09
Sayaca Tanager	52.05	99.14	47.95	0.86	**5.72**	**0.004**
Common Bush Tanager	41.91	97.19	58.09	2.81	**13.21**	**0.0001**

paper, both authors report a higher consumption of fruits by Sayaca Tanagers (77% and 70% respectively) than by Common Bush Tanagers (36% and ~8% respectively). The relative importance of fruits in the diet of the Rufous-bellied and the Slaty thrushes was much more variable between studies (Giannini 1999: 56% in the Rufous-bellied Thrush and 81% in the Slaty Thrush; Rougès 2003: ~15% in both species). These differences among studies are at least partially the consequence of the different criteria used to count arthropods versus fruit (more conservative in Giannini 1999). Overall, results in Giannini (1999) and Rougès (2003) are consistent with our own results based on the frequency of prey items consumed, and agree with that expected for frugivorous- insectivorous species in Turdinae (Collar 2016) and Thraupidae (Hilty and Bonan 2016). However, in terms of ingested food dry-mass, the four species studied here consumed fruit in a similar proportion, representing >95% of their diet. This finding challenges prior ideas claiming that fruit-eating species distribute in a gradient of fruit consumption specialization, and that animal origin food represents an important fraction of their diet during the breeding season.

Food dry mass is a more reliable estimator of the bulk source of nutrients and energy gained by birds than frequency or percent occurrence of ingested items. Gravimetric measurements can be easily derived in estimations of crude nutritional and energy contribution of different dietary items (Duffy and Jackson 1986, Rosenberg and Cooper 1990), which cannot be achieved with the number or frequency of prey items. While these estimations do not allow knowing how much of each food type is assimilated—for which isotopic analyses are a more appropriate method—it is evident that these four species meet most of their energy and nutrient requirements during the breeding season from fruit pulp. Fruit pulp is particularly rich in water and soluble carbohydrates or lipids, and contains other compounds such as free amino acids, fiber, vitamins, anthocyanins, and minerals (Johnson et al. 1985, Jordano 2000, Schaefer et al. 2003, Blendinger et al. 2015a). Pulp is thus an important source of nutrients and energy, and is nutritionally characterized by an excess of digestible energy compared to arthropods but is lower in protein content. The average protein concentration in dry mass is almost 10 times smaller in fruit pulp than in insects (Hilty and Bonan 2016), for which it is expected that arthropods become the main source of protein and a key resource for fruit-eating birds. Thus, it is widely accepted that most fruit-eating birds must complement their diet with arthropods to fulfill their protein requirements for growth and reproduction (Bosque and Pacheco 2000, Herrera M. et al. 2005, Hilty and Bonan 2016). However, in this study, fruit-eating birds did not obtain important fractions of protein from arthropods, since they accounted for <5% of total dry matter ingested. Similarly, Herrera M. et al. (2009) used isotopic data to determine that the Yellow-throated Euphonias (*Euphonia hirundinacea*) rely predominantly on fruits as a source of assimilated nitrogen to suggest that ingested biomass is mostly of plant origin. Future studies assessing the relative contribution of protein and other animal origin nutrients in the diet of fruit-eating birds are needed to more accurately determine the importance of arthropods as a complement of fruit in the diet of birds of the Southern Yungas forests.

The combination of methods used in this study (i.e., direct observation of foraging behavior and calculation of ingested dry mass) is not free from possible sampling biases. One possible source of bias might be the difficulty of distinguishing the consumption of arthropods in the field, particularly in the case of the smaller ones. However, the bias involved should be low, since the contribution of each small arthropod to the dry mass ingested is negligible. Furthermore, the frequency of arthropods in the diet falls within the range of values reported in literature for these bird species (Valburg 1992, Giannini 1999, Rougès and Blake 2001, Manhães 2003, Rougès 2003, Gasperin and Pizo 2009). Another source of bias might derive from the fact that our estimations of the dry mass of each eaten fruit were derived from the mean dry mass of the pulp of the whole fruit. In this sense, we may have overestimated pulp consumption by Sayaca Tanagers and Common Bush Tanagers because of their particular fruit-handling behavior: these species are pulp-mashers, crushing the fruit during mandibulation, swallowing the juice and pulp, and discarding the seeds that usually remain attached to some pulp. While Sayaca Tanagers swallow whole small fruits and mash larger ones, Common Bush Tanagers typically mash all the fruits they consume. Despite this potential methodological limitation, it is very likely that the influence of this behavior is minor and does not modify the main trends found.

Conclusions.—We show that the joint consideration of frequency of ingested items and item dry mass is a much more appropriate approach than methods based solely on item counting, for dietary studies aiming at determining the contribution of various prey items of frugivorous-insectivorous birds. This avoids the overestimation of small and numerous resources which contribute comparatively little to the total energy and nutrients ingested (in this case, mostly arthropods). Recently, Davies and Pineda Munoz (2016) pointed out that failing to explicitly consider the different temporal scales of dietary proxies and the variability of the diet can lead to incongruence in diet inferences. Fecal sample analysis and direct observation were considered as reliable methods to provide estimates of the relative importance of broad food categories in small birds (e.g., Rosenberg and Cooper 1990, Gasperin and Pizo 2009). However, we found that these methods might seriously distort biological patterns of food consumption by fruit-eating birds if uncoupled to gravimetric estimations of ingested food. Our study suggests that the contribution of fruits to meet the daily requirements of nutrients and energy in certain birds traditionally considered as frugivores-insectivores might be higher than that reported. In subtropical Southern Yungas forests, at least during the wet season, this applies even to the Common Bush Tanager, which has been considered mostly an insectivorous species (Rougès 2003); and for the Rufous-bellied and Slaty thrushes, which belong to a taxon for which fruits have been proposed to represent a negligible contribution to the diet (Collar 2016).

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