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Nutrients in fruits as determinants of resource tracking by birds

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Fruit pulp is an important source of nutrients for many bird species. Fruit-eating birds use a variety of strategies to cope with changes in the availability of fruits, exhibiting a remarkable ability to track resources. We assessed the role of nutrient availability in the fruiting environment as a factor driving resource tracking by fruit-eating birds. Fruit consumption by the four most common frugivorous species in a 6-ha plot in the Southern Yungas montane forest of Argentina was assessed. We determined the content of selected nutrients (soluble carbohydrates, proteins, phenols, ascorbic acid and essential minerals) in 22 fruiting plant species eaten by birds, and measured fruit–frugivore interactions and the availability of nutrients and dry fruit pulp mass over 2 years. There was strong temporal covariation in the availability of the selected nutrients in fruits across the study period. Similarly, the availability of nutrients in the fruiting environment covaried with pulp mass. Fruit consumption by the four commonest bird species and the abundance of most species were positively associated with nutrient availability and dry pulp mass. Nutrient availability was a good predictor of temporal fruit tracking by three of the four commonest frugivores. Despite large differences in particular nutrient concentrations in fruits, overall nutrient (and pulp) quantity in the fruiting environment played a greater role in fruit tracking than did the nutritional quality of individual fruits. While overall nutrient availability (i.e. across fruit) and total pulp mass were important determinants of fruit tracking, we suggest that plant species-specific differences in fruit nutrient concentration may be important in short-term foraging decisions involved in fruit choice and nutritional balance of birds.

Keywords: Andean montane forest, food availability, foraging strategies, frugivores, fruit nutrient availability, fruit tracking, Neotropics.

Animals have evolved ways to cope with fluctuations in food availability at multiple scales. Through the ability to track resources, the abundance of consumers is distributed such that it matches variation in resource availability in space and time, thus enhancing the efficiency of food exploitation by consumers. This behaviour has been reported in many taxa including arthropods (e.g. Rowe & Richardson 2001, Cartar 2009), birds (e.g. Feinsinger 1980, Loiselle & Blake 1991, Blendinger & Ojeda 2001) and mammals (e.g. Guitián & Munilla 2010, Searle *et al.* 2010), and encompasses diverse trophic groups such as marine and terrestrial predators (Korpimaki 1994, Fauchald *et al.* 2000, Mauritzen *et al.* 2001), herbivores (Searle *et al.* 2010), granivores (Renton 2001, Boyes & Perrin 2010), nectarivores (Cartar 2004,

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Cotton 2007, Rothenwöhrer *et al.* 2011) and frugivores (Fleming 1992, Borgmann *et al.* 2004, Guitián & Munilla 2010). Animals may track resources with nomadic movements in unpredictable environments (Korpimaki 1994, Dean 1997) or migrate between seasonal ranges when resources vary predictably (Levey & Stiles 1992, Mauritzen *et al.* 2001). Over shorter time periods and distances, adjustments in animal abundance linked to changing patterns of resource availability may reflect food search decisions made across and within habitat patches (García & Ortiz-Pulido 2004, Saracco *et al.* 2004, Boyes & Perrin 2010).

Some experimental and many observational studies have found strong empirical evidence of matching patterns in the abundances of fruit-eating birds and fleshy fruits at various spatiotemporal scales (Rey 1995, Borgmann *et al.* 2004, Burns 2004, Tellería *et al.* 2008, Blendinger *et al.* 2012, 2015). Frugivores may track fruits to increase their resource intake, selecting food on the basis of fruit quantity and quality (Loiselle & Blake 1991, Rey 1995, Vergara *et al.* 2010). Although fruit is the primary source of food for some bird species in tropical forests (Pryor *et al.* 2001, Snow 2004, Firth & Firth 2009), most fruit-eating birds consume (or temporally switch to) other food items such as insects, particularly in subtropical and temperate environments where seasonality is more pronounced and fruit availability becomes more variable or unpredictable (e.g. Izhaki & Safriel 1989, Levey & Karasov 1989, Carnicer *et al.* 2008). However, fleshy fruit pulp still represents an important source of nutrients and energy for many bird species, and can be nutritionally characterized by an excess of digestible energy relative to the protein content compared with other dietary items usually consumed by frugivores (Jordano 2000). Fruit pulp is usually rich in soluble carbohydrates but may also contain appreciable amounts of lipids, proteins, free amino acids, fibre and micronutrients such as vitamins and minerals (Johnson *et al.* 1985, Herrera 1987, Schaefer *et al.* 2003a).

Little is known about the role of the nutritional value of fruits on bird decisions during resource tracking. Peters *et al.* (2010) found that the energy available in fruit can have positive effects on the richness of fruit-eating bird assemblages. Boyes and Perrin (2010) proposed that Meyer's Parrot *Poicephalus meyeri*, a seed-predator, tracks fruits more on the basis of their abundance and detectability than in terms of protein and energy acquisition rates; for this species, minimizing energy expenditure could be a key factor in foraging decisions. In Andean subtropical forests, we have shown that differences across bird species in fruit-tracking behaviour are largely explained by species-specific responses to changes in fruit mass availability and by their reliance on a more frugivorous diet (Blendinger *et al.* 2012). Thus, we proposed that estimation of nutrient availability in fruits could be useful in understanding the drivers of foraging decisions that lead to fruit-tracking (Blendinger *et al.* 2012). Previous studies of fruit-tracking by birds typically analysed some measure of fruit mass or a surrogate of it (e.g. fruit abundance); however, fruit species can differ greatly in their nutrient composition and content (Herrera 1987, Corlett 1996). Moreover, fruit-eating species differ in their digestive efficiency and in the requirements of nutrients obtained from fruits (Witmer & Van Soest 1998, Levey & Martínez del Rio 2001), and are able to discriminate among fruits with only slight differences in nutrient concentration (Schaefer *et al.* 2003b, Wilson & Downs 2011).

Here we assessed whether temporal fruit tracking by fruit-eating bird species can be explained by the availability of selected fruit nutrients. Blendinger *et al.* (2012) showed that consumer abundance, frequency of consumption and resource availability must be considered together to demonstrate resource tracking. On the basis of a 2-year sampling of fruit–frugivore interactions and availability of fruit pulp-mass and key nutrients, we (1) analysed the covariation in temporal changes of nutrient availability, (2) assessed whether temporal variations in frugivore abundances and in the frequency of fruit consumption match changes in the availability of specific fruit nutrients or a combination thereof, (3) assessed whether changes in the availability of selected nutrients is a more accurate explanation of fruit-tracking behaviour than variations in pulp mass availability, and (4) evaluated whether the most important fruit-eating species respond to nutrient availability according to their degree of specialization on a fruit diet.

METHODS

Study site

We conducted this survey in Parque Sierra de San Javier, Tucumán, northwest Argentina, in subtropical Andean mountain forests known as the Southern Yungas. Climate is subtropical, with dry winters from May to September and wet summers from November to March. Average annual rainfall varies between 1300 and 1500 mm across the mountain range and the average annual temperature is 18 °C (Hunzinger 1997). The study site (26°30′S, 65°40′W, 970 m asl) was located in the elevational belt of vegetation known as 'Selva Montana', or lower montane forest. Vegetation features included emergent trees 25–30 m in height of *Cinnamomum porphyrium* (Lauraceae) and *Blepharocalyx salicifolius* (Myrtaceae); an upper canopy layer composed mainly of *Parapiptadenia excelsa* (Fabaceae), *Myrcianthes pungens* (Myrtaceae), *Pisonia zapallo* (Nyctaginaceae) and *Terminalia triflora* (Combretaceae); a lower canopy dominated by 5- to 12-m-high small trees of *Piper tucumanum* (Piperaceae), *Eugenia uniflora* (Myrtaceae), *Allophylus edulis* (Sapindaceae) and *Solanum riparium* (Solanaceae); and a dense understorey dominated by the shrub *Psychotria carthagenensis* (Rubiaceae). Typical vines and epiphytes included *Cissus striata* (Vitaceae), *Celtis iguanaea* (Celtidaceae), *Aechmea distichantha* (Bromeliaceae) and *Rhipsalis floccosa* (Cactaceae). Fieldwork was carried out in a 200 × 300-m plot, split in a grid of 150 cells of 20 × 20 m each; individual cells were the sampling units for all counts of both fruits and frugivores.

Bird counts

Field methods used to count birds, fruits and fruit consumption are explained in detail in Blendinger *et al.* (2012); here we present a summary of those methods. We sampled the abundance and foraging behaviour of the four most numerous frugivorous birds in the area, bi-monthly from September 2008 to August 2010, a total of 12 sampling periods. These species were Rufous-bellied Thrush *Turdus rufiventris* (Turdidae), Sayaca Tanager *Thraupis sayaca* (Thraupidae), Common Bush-Tanager *Chlorospingus ophthalmicus* (Emberizidae) and Golden-rumped Euphonia *Euphonia cyanocephala* (Fringillidae). Combined, they accounted for most fruit consumption events (83% of all records). Bird counts began at sunrise and were completed within 4 h. During three sampling days, five observers each traversed a block of 10 × 2 contiguous 20 × 20-m cells, walking slowly and recording all fruit-eating birds and their fruit-consumption behaviour for 20 min per cell, in all a 50-h sample per period. In each cell, we recorded all target bird species seen or heard. The small size of the sampling unit allowed us to obtain highly precise data on bird presence in the cell, beyond temporal and between-species differences in detectability. The location and displacement of individual birds were followed as far as possible while remaining within the cell, which gave us a comparative measure of plot use intensity (hereafter bird abundance) rather than an estimate of frugivore density. Thus, the number of birds recorded in the cell was used as the measure of cell use intensity. We also recorded every event of fruit consumption that we were able to detect, noting the species of frugivore and fruit consumed. An event of fruit consumption was defined as a visit of a fruit-eating bird to a plant in which the bird was either directly observed eating fruits or noted entering in a part of the plant with ripe fruits and remaining in there for a length of time consistent with fruit consumption. For each species, we reported a single value of both bird abundance and fruit consumption per sampling period, obtained by adding up all observations recorded in the 150 cells.

Fruit availability

During each field sampling period, we counted the abundance of ripe fruits of all bird-dispersed plants (trees, shrubs, vines and epiphytes) in each of the 150 grid cells. For the analyses, fruit abundance was expressed as dry pulp mass of ripe fruits, calculated for each species as the number of ripe fruits recorded multiplied by the mean dry pulp mass in grams of collected fresh ripe fruits. Fruit availability for each bird species was estimated as the total dry mass per sampling period of fruit species that the bird species consumed through the entire study. We excluded fruits that were consumed sporadically, defined as those fruit species that met all the following three criteria: (1) the fruit species represented < 5% in dry mass of the frugivorous diet of the focal species; (2) it was part of the upper quartile of fruit abundance during the periods in which it was consumed; (3) it was not a selected species in any of the sampling periods during which it was consumed by the focal frugivore. We defined selection based on the proportion of consumption divided by the proportion of abundance of a given fruit species in a sampling period; selection ratio < 1 indicated non-selection.

For each species, seeds were removed from collected ripe fruits and the fresh pulp samples were pooled. Dry pulp mass was calculated as the mean fresh-fruit weight minus mean seed weight and water content of the pulp. Water content was calculated as the weight difference before and after heating weighed fresh pulp in an oven at 60 °C for 4 days (the time after which no mass change was detectable to the nearest 0.1 mg). The content of each nutrient per fruit was calculated as the average dry pulp mass multiplied by the mean nutrient concentration (see below). In the three genera in which two species were consumed (Table S1), we only had nutrient data on the most frequent species (i.e. *Urera caracasana*, *Phoradendron falcifrons* and *Cestrum strigillatum*); thus, we estimated nutrient content of the species without nutritional data (i.e. *Urera baccifera*, *Phoradendron tucumanense* and *Cestrum lorentzianum*) using values from the other congener sampled. We assumed that variation between closely related species should be lower than among more distantly related species. Even if this assumption were not correct, the variability in nutrient content caused by such an assumption would probably be minimal, given that the three species without nutritional information jointly accounted for 0.6% of the total dry pulp mass produced during the study period.

Nutrient composition

Determination of sugar, protein and total polyphenol contents was carried out on aqueous extracts of fresh seedless fruits.

Sugars

The phenol–sulphuric acid method (Dubois *et al.* 1956) was used to determine total neutral sugars. Aliquots (0.8 mL) of different extract dilutions were taken and 0.04 mL of 80% phenol and 2 mL H_2SO_4 were added. After a 20-min period of incubation at 100 °C, absorbance at 490 nm was measured in a UV-visible Beckman-DU-650 spectrophotometer. Results were expressed as grams of glucose per 100 g dry weight. Reducing sugars were measured using the Somogyi–Nelson method. Aliquots (0.1 mL) of different extract dilutions were taken and 0.5 mL of copper tartrate reagent (Somogyi 1945) was added. The solution was heated at 100 °C for 15 min and 0.5 mL of arsenomolybolic acid reagent (Nelson 1944) was added. Absorbance was measured at 520 nm. Results were expressed as grams of glucose per 100 g dry weight.

Proteins

Soluble protein concentration was determined by the method of Bradford (1976) using bovine serum albumin (BSA) as standard. Aliquots (0.1 mL) of different extract dilutions were taken and 5 mL of dye solution (Coomassie Brilliant Blue G 250) was added. After 5 min at room temperature the absorbance was measured at 595 nm. Results were expressed as milligrams of BSA per 100 g dry weight.

Total polyphenols

Total polyphenols were determined using Folin–Ciocalteu's reagent (Singleton *et al.* 1999). The reaction mixture contained 20 μL of each preparation, 2 mL of distilled water, 200 μL of Folin–Ciocalteu reagent and 800 μL of sodium carbonate (15.9% w/v). Absorbance was measured at 765 nm. Results were expressed as milligrams of gallic acid equivalents per 100 g dry weight (mg GAE per 100 g dry weight).

Ascorbic acid

Ascorbic acid was determined according to the method of Klein and Perry (1982). A fine powder of sample was extracted with metaphosphoric acid (1%) for 45 min at room temperature and filtered through Whatman No. 4 filter paper. The filtrate (1 mL) was mixed with 2,6-dichloroindophenol (9 mL) and the absorbance was measured within 30 min at 515 nm against a blank. Concentration of ascorbic acid was calculated on the basis of the calibration curve of authentic L-ascorbic acid (0.006–0.1 mg/mL), and the results were expressed as milligrams of ascorbic acid per 100 g of dry weight.

Minerals

Once weighed (0.20 g), the lyophilized samples were mixed with sub-boiling HNO_3 (8 mL) in a quartz glass and maintained for 45 min in a microwave oven at 280 °C and 75 bar. Then, Milli Q water was added until a volume of 25 mL was reached and the disintegrated material was filtered through a 0.45-μm filter. The Na, K, Ca, Fe, Mg and P levels of these solutions were determined by inductively coupled plasma mass spectrometry

(ICP-MS). The results were expressed as milligrams per 100 g of dry weight.

For each bird species and sampling period, we calculated an index of nutritional reward (C) of fruit pulp based on fruit availability to that frugivore:

$$C = \sum (f_i * \sum p_{ij})$$

where f_i is the proportion of dry fruit mass of the ith species relative to the total dry fruit mass available in the sampling period, and p_{ij} is the proportion of nutrient concentration belonging to the jth nutrient of the ith fruit species, relative to the maximum value of j recorded in fruit species consumed by the frugivore of interest. This index combines the concentration and amount of nutrients per fruit and is an expression of the nutritional quality of fruits available for each species of fruit-eating birds in a given sampling period. To explore the relations between fruit quality, fruit quantity and fruit consumption per bird species across sampling periods, we plotted the index of nutritional reward (C) of fruit pulp, the availability of dry pulp mass and fruit consumption values.

Statistical analysis

We used a principal component analysis (PCA) to explore the interspecific variation in mean concentration of nutrients of fruits consumed by birds. All fruit variables were expressed in milligrams per 100 g of dry weight and were $\log_{10}$-transformed before analysis. To analyse the covariation in availability of different nutrients to each frugivorous species across the study period, we conducted pairwise Pearson correlations. Alpha for significance was set to 0.0045 (conventional $\alpha = 0.05$ divided by the number of variables compared, a compromise between conventional alpha and the strict Bonferroni-corrected value) to correct for multiple testing.

In a previous contribution (Blendinger *et al.* 2012), we showed the absence of temporal autocorrelation between successive sampling periods in the abundance of fruit-eating birds and in the frequency of fruit consumption. Thus, we conducted simple linear regressions to assess the importance of single fruit variables (nutrients and pulp mass) on frugivore abundances and frequency of fruit consumption ($n = 12$ sampling periods). Because of the strong collinearity found between variables, we use a bird species-specific PCA to reduce the multiple dimensions of nutrient availability for each bird species. All frugivore and fruit variables were $\log_{10}$-transformed to meet the assumptions of normality and homoscedasticity. Additionally, to explore whether the patterns observed could be due to specific fruit species rather than all fruit species consumed, we conducted linear regressions to determine the importance of dry pulp mass for those species most consumed by each frugivore (Table S1) to explain the abundance and fruit consumption frequency of particular frugivorous species.

To assess the role of nutrients and pulp mass as potential drivers of fruit-tracking behaviour, we used general linear models. We included composite nutrient variables (PCs: principal components; see above) and dry pulp mass (estimated as the sum of total mass across available species) as explanatory variables of frugivore abundances and frequency of fruit consumption. Model selection was based on the Akaike information criterion adjusted for small sample size (AICc), assuming that models with differences in AICc values of two or less (ΔAICc < 2) have a similar level of empirical support. We further checked competitive models for uninformative parameters, which is when variables with poor explanatory power are added to an otherwise good model (Arnold 2010). Uninformative parameters can be detected by inspecting whether models with additional parameters have very similar values of the maximized log-likelihood as the best model, and these models were not considered competitive (Arnold 2010). Furthermore, Akaike weights were used to determine which competitive models could be judged the best model. Statistical analyses were performed with INFOSTAT software version 2012 (Di Rienzo *et al.* 2008), except general linear models, which were performed using R 2.15 (R Core Team 2013) with the *stats* package and modifications following Bolker (2008).

RESULTS

All four fruit-eating species were present in each of the 12 sampling periods, except Golden-rumped Euphonia, which was absent in one period (April 2010). Fruits were available for all species in every sampling period, except for Golden-rumped Euphonia, for which fruits were available in only nine sampling periods. Fruit consumption was observed in all 12 sampling periods by Sayaca Tanager ($n = 470$ events), 11 periods by both Rufous-bellied Thrush ($n = 431$) and Common

Bush-Tanager (n = 127), and in six periods by Golden-rumped Euphonia (n = 75).

The four bird species collectively consumed 21 fruit species of 18 genera (Table S1). The first four principal components (eigenvalues > 1) together explained 76.82% (Fig. 1) of the total variation of nutrient concentrations in fruits. Consumed fruit species differed strongly in their nutrient content. The most different fruit species along the first three principal components (PC1–3, Fig. 1) were *Blepharocalix salicifolium*, *Rhipsalis floccosa*, *Celtis iguanaea*, *Urera caracasana*, *Allophylus edulis* and *Zanthoxylum coco*, none of which was quantitatively important in the diet of our four principal fruit-eating species (Table S1). Moreover, *Phoradendron falcifrons* and *Psychotria carthagenensis*, the most frequently consumed fruits by any fruit-eating species (Table S1), were not clearly differentiated from the remaining fruit species in any of the first three PCs. These two fruit species exhibited average nutritional values among the fruits eaten by birds.

Covariation in nutrient availability

Availability of different nutrients in fruits eaten by each of the four frugivores varied similarly across the study period (Fig. 2). For each species of bird, variables of nutrient availability were highly and positively correlated in most cases (214 out of 220 comparisons; $r \geq 0.57$, $P < 0.05$), even after a correction for multiple tests (192 of 220 comparisons; Table S2). However, temporal variation in some nutrients was less pronounced for some birds. For instance, calcium and ascorbic acid varied much less than magnesium for the Rufous-bellied Thrush (Fig. 2), perhaps due to the reliance of this bird on fruits with rather average nutrient concentration (such as *P. carthagenensis*) during the winter. By contrast, ascorbic acid exhibited the greatest variation of all nutrients, with the lowest availability values for the other three bird species (Fig. 2). According to this analysis, the Golden-rumped Euphonia faced an absolute lack of the sampled nutrients at the end of each summer, right after the breeding season.

Tracking of fruit nutrients

In the bird-specific PCAs of fruit nutrients available in fruits, the first PC explained a substantial amount of the total variation for all bird species (> 80%; Table 1). Only the first PCs were significantly related to frugivore response variables (see below); the relative contributions of each nutrient

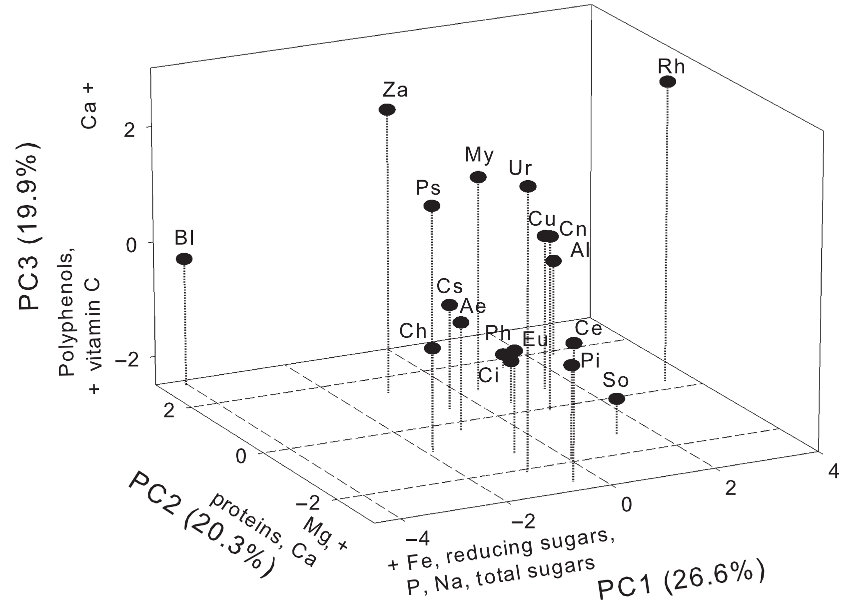

Figure 1. PCA plot showing the variation in nutrient concentrations of fruit species consumed by four frugivorous birds in the Yungas forest of northwest Argentina. Ae, *Aechmea distichantha*; Al, *Allophylus edulis*; Bl, *Blepharocalix salicifolium*; Ce, *Celtis iguanaea*; Cs, *Cestrum strigilatum*; Ch, *Chamissoa altissima*; Ci, *Cissus striata*; Cn, *Cinnamomum porphyrium*; Cu, *Cupania vernalis*; Eu, *Eugenia uniflora*; My, *Myrsine laetevirens*; Ph, *Phoradendron* spp.; Pi, *Piper tucumanum*; Ps, *Psychotria carthagenensis*; Rh, *Rhipsalis floccosa*; So, *Solanum riparium*; Ur, *Urera caracasana*; Za, *Zanthoxylum coco*.

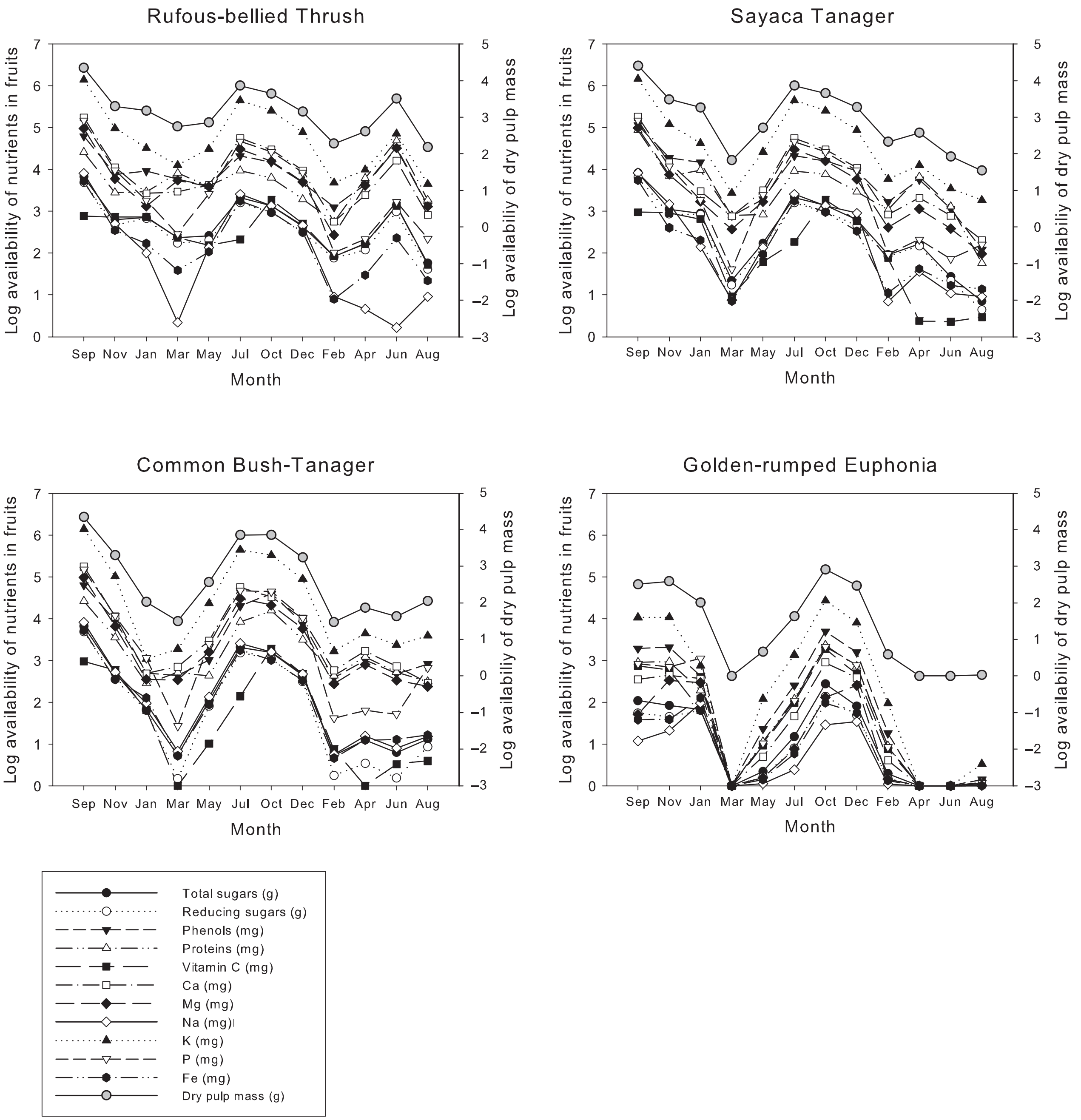

Figure 2. Temporal variation in fruit nutrients (in milligrams) available to four frugivorous bird species recorded bimonthly in a 6-ha plot in the Yungas forest, northwest Argentina. The availability of dry pulp mass (in grams) is shown on the second *y*-axis.

to the variance of PC1s are given in Table 1. In all bird species, PC1 was highly correlated with dry pulp mass ($r > 0.90$, $P < 0.001$).

Rufous-bellied Thrush

Fruit consumption was significantly associated with PC1, and the relation with bird abundance was marginally significant (Fig. 3). Three single nutritional variables showed a relation slightly stronger than PC1 with fruit consumption (Fe, P, K) and bird abundance (Fe, Mg, Ca) (Tables 2 and 3). The availability of dry pulp mass explained part of the variation in the frequency of fruit consumption, but not of bird abundance (Tables 2 and 3).

Table 1. Relative contributions to the first principal component (PC1) of fruit nutrient variables available for four fruit-eating bird species across the study period. The percentage of variance explained by PC1 is given in parentheses.

	Rufous-bellied Thrush (81.94%)	Sayaca Tanager (91.96%)	Common Bush-Tanager (93.56%)	Golden-rumped Euphonia (93.84%)
Total sugars	0.108	0.097	0.096	0.096
Reducing sugars	0.105	0.095	0.093	0.095
Polyphenols	0.100	0.092	0.093	0.093
Proteins	0.057	0.078	0.084	0.093
Ascorbic acid	0.063	0.071	0.079	0.089
Ca	0.108	0.096	0.090	0.096
Mg	0.092	0.096	0.094	0.087
Na	0.058	0.093	0.095	0.080
K	0.107	0.098	0.092	0.086
P	0.097	0.090	0.091	0.095
Fe	0.106	0.094	0.093	0.090

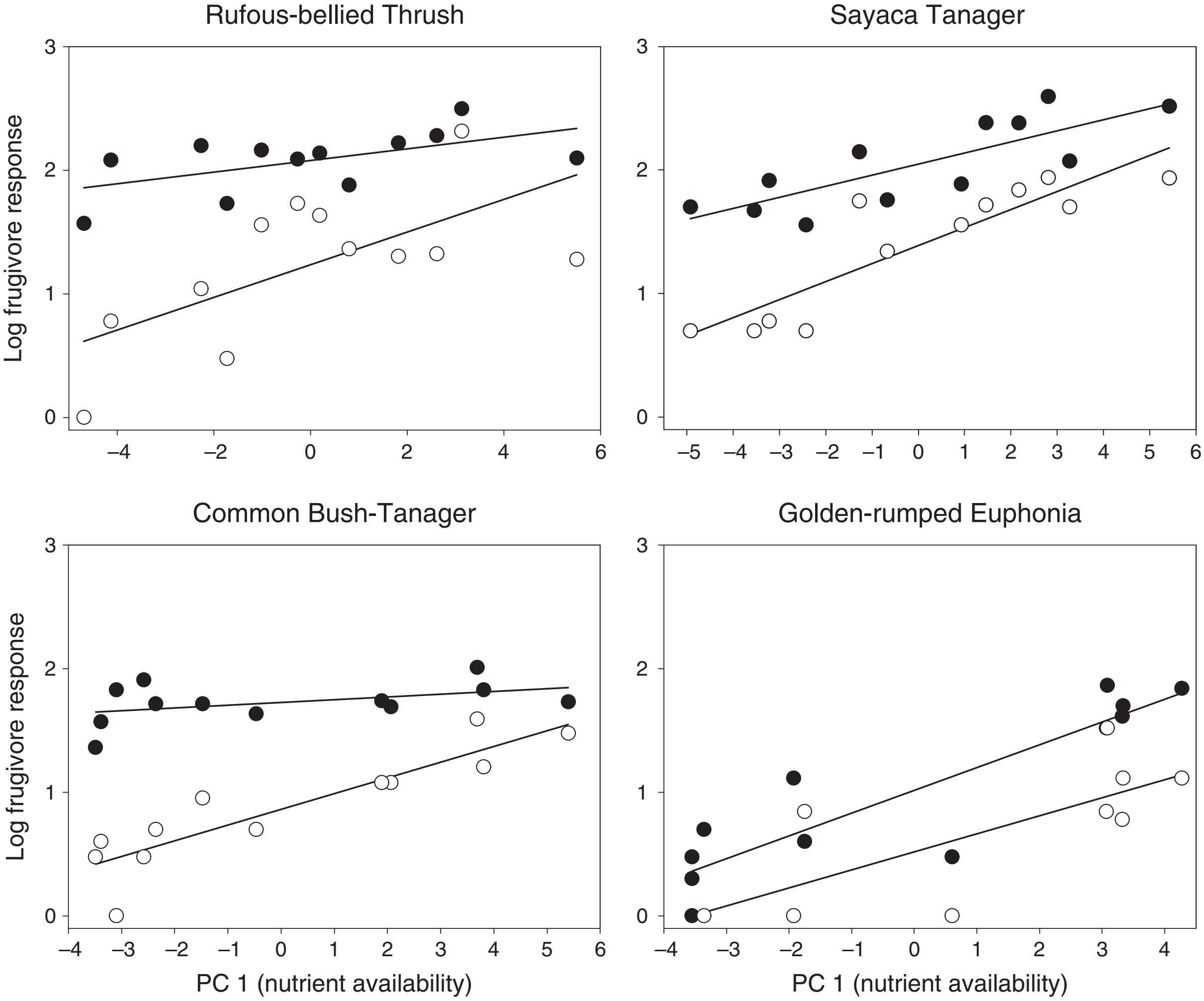

Figure 3. Linear regressions of fruit consumption (○) and bird abundance (●) of four species of frugivores on the availability of nutrients in fruits along 12 bimonthly sampling periods in a 6-ha plot in the Yungas forest, northwest Argentina (R^2 and *P*-values are given in Tables 2 and 3). PC1 (first principal component; > 80% of the variance explained in all cases) represents the main gradient of increase in availability of nutrients in fruits for each bird species.

Table 2. Linear regressions of fruit consumption on the availability of nutrients in fruits and dry pulp mass over a 2-year period, sampled bimonthly, in a 6-ha plot in the Yungas forest, northwest Argentina. The relation between fruit consumption with the first principal component (PC1, see Table 1) of a multivariate analysis of fruit nutrients available for each bird species is also included.

	Rufous-bellied Thrush (*n* = 12)		Sayaca Tanager (*n* = 12)		Common Bush-Tanager (*n* = 12)		Golden-rumped Euphonia (*n* = 9)	
	R^2	*P*	R^2	*P*	R^2	*P*	R^2	*P*
Single variables								
Total sugars	**0.39**[a]	0.03	**0.79**	0.0001	**0.83**	< 0.0001	**0.55**[a]	0.02
Reducing sugars	**0.39**[a]	0.03	**0.78**	0.0001	**0.83**	< 0.0001	**0.55**[a]	0.02
Polyphenols	0.31	0.06	**0.78**	0.0002	**0.72**	0.0005	**0.53**[a]	0.03
Proteins	0.13	0.25	**0.65**	0.001	**0.64**	0.002	**0.54**[a]	0.03
Ascorbic acid	0.18	0.17	**0.49**[a]	0.01	**0.64**	0.002	**0.54**[a]	0.03
Ca	**0.39**[a]	0.03	**0.73**	0.0004	**0.72**	0.0005	**0.53**[a]	0.03
Mg	0.29	0.07	**0.75**	0.0003	**0.76**	0.0002	**0.45**[a]	0.048
Na	**0.39**[a]	0.03	**0.80**	< 0.0001	**0.83**	< 0.0001	**0.45**[a]	0.048
K	**0.44**[a]	0.02	**0.77**	0.0002	**0.68**	0.0009	**0.51**[a]	0.03
P	**0.51**[a]	0.009	**0.73**	0.0004	**0.76**	0.0002	**0.53**[a]	0.03
Fe	**0.52**[a]	0.007	**0.77**	0.0002	**0.79**	0.0001	**0.52**[a]	0.03
Dry pulp mass	**0.41**[a]	0.03	**0.79**	0.0001	**0.77**	0.0002	**0.54**[a]	0.02
Composite variable								
PC1	**0.43**	0.02	**0.80**	< 0.0001	**0.80**	< 0.0001	**0.55**	0.02

Significant relationships are highlighted in bold.

[a]Non-significant after a correction for multiple tests (α = 0.0042).

Table 3. Linear regressions of bird abundance on the availability of nutrients in fruits and dry pulp mass over a 2-year period, sampled bimonthly, in a 6-ha plot in the Yungas forest, northwest Argentina. The relation between fruit consumption with the first principal component (PC1, see Table 1) of a multivariate analysis of fruit nutrients available for each bird species is also included.

	Rufous-bellied Thrush (*n* = 12)		Sayaca Tanager (*n* = 12)		Common Bush-Tanager (*n* = 12)		Golden-rumped Euphonia (*n* = 12)	
	R^2	*P*	R^2	*P*	R^2	*P*	R^2	*P*
Single variables								
Total sugars	0.26	0.09	**0.57**[a]	0.005	0.10	0.16	**0.79**	0.0001
Reducing sugars	0.23	0.11	**0.54**[a]	0.007	0.20	0.15	**0.79**	0.0001
Polyphenols	0.27	0.08	**0.60**	0.003	0.19	0.15	**0.77**	0.0002
Proteins	0.26	0.09	**0.52**[a]	0.009	0.13	0.26	**0.77**	0.0002
Ascorbic acid	0.09	0.34	**0.39**[a]	0.03	0.13	0.25	**0.76**	0.0002
Ca	0.33	0.05	**0.66**	0.001	0.11	0.28	**0.79**	0.0001
Mg	**0.36**[a]	0.04	**0.66**	0.001	0.14	0.23	**0.75**	0.0003
Na	0.18	0.18	**0.70**	0.0007	0.19	0.16	**0.72**	0.0005
K	0.29	0.07	**0.64**	0.002	0.17	0.18	**0.75**	0.0003
P	0.31	0.06	**0.61**	0.003	0.26	0.09	**0.78**	0.0001
Fe	**0.36**[a]	0.04	**0.65**	0.002	0.23	0.11	**0.77**	0.0002
Dry pulp mass	0.28	0.08	**0.60**	0.003	0.19	0.16	**0.78**	0.0001
Composite variable								
PC1	**0.32**[a]	0.05	**0.65**	0.002	0.22	0.13	**0.80**	< 0.0001

Significant relationships are highlighted in bold.

[a]Non-significant after a correction for multiple tests (α = 0.0042).

Sayaca Tanager

Fruit consumption and bird abundance were significantly associated with PC1 (Fig. 3). No single variable of nutritional content showed a stronger relation than PC1 to fruit consumption, but three variables (Na, Ca, Mg) showed a relation slightly stronger than PC1 with bird abundance (Tables 2 and 3). The availability of dry pulp mass explained much of the variation in both fruit consumption and bird abundance (Tables 2 and 3).

Common Bush-Tanager

PC1 explained part of the variation in fruit consumption, but none of bird abundance (Fig. 3). Four single nutritional variables (total sugars, reducing sugars, Na, Fe) showed a slightly stronger relation than PC1 with fruit consumption (Table 2). The availability of dry pulp mass explained much of the variation in the frequency of fruit consumption but bird abundance was not related to it (Tables 2 and 3).

Golden-rumped Euphonia

Fruit consumption and bird abundance were significantly associated with PC1 (Fig. 3). No single variable of nutritional content showed a stronger relation than PC1 with either fruit consumption or bird abundance (Tables 2 and 3). Dry pulp mass availability explained some of the variation in fruit consumption and much of the variation in bird abundance (Tables 2 and 3).

Plant species-specific regressions (Table S3) showed that, in general, the availability of dry pulp mass of the most consumed fruits had lower predictive values for frugivorous activity than the availability of total dry pulp mass. Among those species, *Phoradendron* spp. had pulp mass availability that was significantly related to the total fruit consumption of Sayaca Tanager, Common Bush-Tanager and Golden-rumped Euphonia (Table S3).

The best set of models of fruit consumption for each species always included models with a single variable of overall nutrients (PC1) or of dry pulp mass (Table 4). Among nearly equally good models, the model of nutrient availability (PC1) always had lower AICc values and greater Akaike weight values than the model of dry pulp mass, but only in Common Bush-Tanager was the Akaike weight of nutrients clearly greater (2.18 times) than that of pulp mass. Best models of fruit-eating bird abundances included PC1 in the four cases analysed, and dry pulp mass and PC1 + dry pulp mass were selected in three cases each (Table 4). In no cases was PC2 in the best set of models. Models that included PC2 did not show an important reduction in deviance or higher Akaike weights than those models that did not include it.

In all frugivorous species except the Rufous-bellied Thrush, which showed no clear pattern, the

Table 4. Models of (a) the abundance of fruit-eating bird species and (b) their frequency of fruit consumption in Yungas forests of northwest Argentina. Explanatory bird species-specific variables are the availability of dry pulp mass and the two-first principal components of a multivariate analysis on availability of particular nutrients in fruits (PC1, PC2).

	Rufous-bellied Thrush			Sayaca Tanager			Common Bush-Tanager			Golden-rumped Euphonia		
Model	ΔAICc	Deviance	*w*	ΔAICc	Deviance	*w*	ΔAICc	Deviance	*w*	ΔAICc	Deviance	*w*
(a) Bird abundance												
PC1	**0.00**	0.460	0.39	**1.75**	0.490	0.23	**0.44**	0.245	0.28	**0.00**	0.964	0.49
PC2	4.65	0.678	0.04	14.20	1.382	0.00	2.67	0.295	0.09	19.45	4.875	0.00
Pulp mass	**0.71**	0.488	0.27	3.10	0.548	0.12	**0.00**	0.236	0.34	**1.10**	1.057	0.28
PC1 + PC2	3.65	0.460	0.02	4.68	0.489	0.05	5.85	0.239	0.02	8.17	0.963	0.01
PC1 + pulp mass	**1.55**	0.386	0.18	**0.00**	0.312	0.55	**1.60**	0.199	0.15	3.55	14.675	0.08
PC2 + pulp mass	4.35	0.487	0.06	5.39	0.547	0.04	3.81	0.230	0.05	3.66	1.014	0.08
PC1 + PC2 + pulp mass	6.20	0.384	0.04	6.73	0.311	0.02	3.35	0.191	0.06	4.27	0.947	0.06
(b) Fruit consumption												
PC1	**0.00**	2.318	0.39	**0.00**	0.603	0.44	**0.00**	0.458	0.50	**0.00**	1.145	0.42
PC2	6.12	3.861	0.02	19.10	2.960	0.00	19.22	2.273	0.00	13.75	3.599	0.00
Pulp mass	**0.35**	2.388	0.33	**0.43**	0.624	0.35	**1.51**	0.520	0.23	**0.24**	1.167	0.37
PC1 + PC2	6.83	2.131	0.01	8.16	0.596	0.01	6.83	0.441	0.02	8.32	1.141	0.01
PC1 + pulp mass	3.49	2.284	0.07	3.62	0.600	0.07	2.56	0.418	0.14	3.66	1.144	0.07
PC2 + pulp mass	2.65	2.229	0.10	3.53	0.620	0.07	6.82	0.501	0.02	3.63	1.161	0.07
PC1 + PC2 + pulp mass	3.20	2.037	0.08	4.01	0.592	0.06	3.21	0.403	0.10	3.84	1.139	0.06

The best supported models are highlighted in bold.

rank of fruit consumption across the study period tended to increase with the amount of pulp mass available, but not with the nutritional reward of available fruit pulp (Fig. 4). This was particularly noticeable in the Common Bush-Tanager, which showed an inverse relation ($r = -0.59$, $P = 0.04$) between the amount of pulp available and its nutritional quality, and a clear increase in fruit consumption associated with pulp mass quantity.

DISCUSSION

Temporal adjustments in the abundance of fruit-eating birds were partially explained by the total amount of nutrients available in the fruiting environment, but not by changes in the nutritional reward provided by individual fruits. The availability of nutrients was a good predictor of temporal fruit tracking by three of our four focal fruit-eating bird species. However, changes in availability of nutrients in fruits closely matched changes in the overall amount of pulp available for each frugivorous species. Our study revealed strong differences in the relative importance of the quantity and quality of food as determinants of the trophic ecology of fruit-eating birds. Foraging animals are subject to a hierarchy of decisions whereby mechanisms such as the ability to track resources (e.g. Guitián & Munilla 2008, Blendinger *et al.* 2012) and the ability to switch seasonally between main

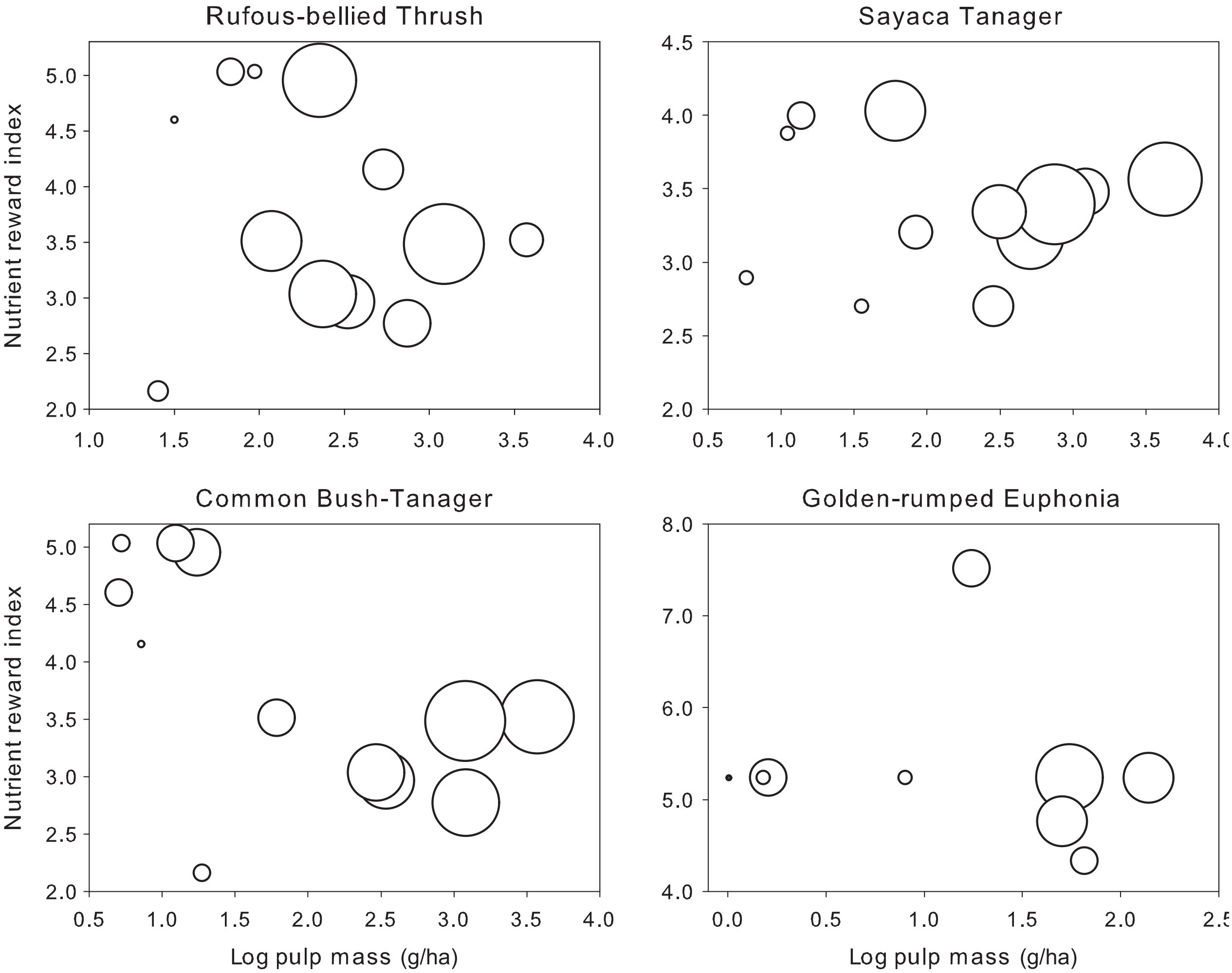

Figure 4. Relations among the availability of dry pulp mass, pulp nutrient reward and fruit consumption by four bird species. Fruit consumption is expressed in ranks from 1 to 12 ($n = 12$ sampling periods) to improve clarity; bubble size shows the rank of fruit consumption per sampling period across the whole study.

food types (Herrera *et al.* 2005, Carnicer *et al.* 2008) would primarily be regulated by the overall quantity of available fruits. Meanwhile, fruit nutritional rewards would influence the individual's short-term decisions, such as which fruit to select (e.g. Fuentes 1994, Witmer & Van Soest 1998, Bolser *et al.* 2013). Thus, nutrient content in fruits may play a more important role at a level hierarchically subordinate to overall resource quantity.

The fruit-tracking hypothesis states that birds adjust their abundances over time in response to changes in fruit availability (Rey 1995, Burns 2004). The nutritional approach applied in this study allowed us to achieve a better understanding of the fruit-tracking behaviour by birds, as compared with more conventional measures of fruit abundance. General trends in our study suggest that, from the perspective of fruit tracking, the detailed assessment of nutritional composition is just a little more informative than looking at fruit dry pulp mass (considered an accurate measure of fruit abundance; Blendinger *et al.* 2012). Moreover, in only one of eight cases was a model that combined dry pulp mass and nutrient availability more informative than models of individual variables.

Life history attributes of fruit-eating species and the strength of competing mechanisms relevant to resource tracking could determine species-specific responses to changes in availability of nutrient in fruit. We found that the most frequent fruit-eating bird species in our study site did not respond in the same way to temporal changes in nutrient availability. On the one hand, those species with a more frugivorous diet (i.e. Rufous-bellied Thrush, Sayaca Tanager and Golden-rumped Euphonia; Blendinger *et al.* 2012, M.G. Názaro & P.G. Blendinger unpubl. data) tracked temporal changes in nutrient availability. On the other hand, the abundance of the less frugivorous species (Common Bush-Tanager) did not change but fruit consumption did, in relation to nutrient availability, suggesting a switch from a less to a more frugivorous diet during periods of increased fruit-nutrient availability. In a previous study, we have shown that the abundance of fruit-eating birds and fruit consumption should covary with fruit availability for these changes to be attributed to resource tracking, as factors other than fruits may influence local bird abundance, and changes in the frequency of fruit consumption may reflect temporal shifts between alternative resources (Blendinger *et al.* 2012). The period of greatest fruit availability and fruit consumption for the Common Bush-Tanager was from July to December, partially overlapping the annual peak of arthropod activity (November to December) reported for the lower montane forest (Rougès 2003), suggesting that nutrient acquisition from fruits by this species is dependent on the availability of fruit rather than being a by-product of the shortage of arthropods.

The available fruit pulp mass of highly consumed species was, in some cases, a good predictor of fruit tracking. This is rather surprising because the correlation between bird abundance with abundance of a single fruit species may appear too simple to allow detection of bird–fruit covariation given the complexity of food preferences in fruit-eating birds (Levey & Benkman 1999, Blendinger *et al.* 2012). The mistletoe *Phoradendron* spp. stands out as a species that offered pulp in quantities that could predict its consumption by Sayaca Tanager, Common Bush Tanager and Golden-rumped Euphonia. This may reflect hidden aspects of resource tracking in line with theoretical results that suggest that food complexity (e.g. nutritional variation) may not translate directly into axes of actual resource use; specifically, that the resolution of the resource use axis may be coarser than the actual complexity of the resources (see Orlando *et al.* 2009). Except for the Golden-rumped Euphonia, the other bird species consume fruits in a rather generalist fashion (Giannini 1999) and so they were not expected to respond to particular fruit species. It is interesting that *Phoradendron* spp. exhibited average nutritional composition, suggesting that nutrient combinations in a single fruit species of this type may meet the needs of almost any frugivore.

Birds can regulate their diet preferences to satisfy physiological needs, and frugivores are able to discriminate very small differences (1–10%) in the concentration of some nutrients (Schaefer *et al.* 2003b, Catoni *et al.* 2011, Wilson & Downs 2011). This is in line with the observation that certain nutrients better matched the temporal changes in fruit-eating birds than pulp mass. For example, the availabilities of mineral ions such as phosphorus and iron, both essential micronutrients, were the best predictors of fruit consumption by the Rufous-bellied Thrush. Similarly, sugars were better predictors of the frequency of fruit consumption than was pulp mass for all species except the Rufous-bellied Thrush (Table S1). Frugivorous birds might track sugar availability because a diet based on sugar-rich fruits results in fast rates of digestion and high rates of energy intake (Lepczyk *et al.* 2000, Levey & Martínez del Rio 2001). Polyphenols, and to a lesser extent ascorbic acid, were also strongly related to changes in frequency of fruit consumption and bird abundance of Sayaca Tanager, Common Bush-Tanager and Golden-rumped Euphonia. Our measure of total polyphenols includes anthocyanins as well as other substances such as tannins, which are usually related to defensive function against pathogens and herbivores (Cazetta *et al.* 2008, Schaefer *et al.* 2008). Moreover, anthocyanins and ascorbic acid are important micronutrients as the most frequent anti-oxidant compounds in fleshy fruits, scavenging oxidative stress brought about by reactive oxygen species (Catoni *et al.* 2008, Zampini *et al.* 2011).

Nutrient requirements of birds shift temporally, linked to specific annual life-cycle stages such as breeding, moulting and self-maintenance. For example, an increased demand for calcium occurs during the breeding season to meet eggshell formation and the fast skeletal growth of nestlings (Graveland & Berends 1997, Bureš & Weidinger 2003). An increase in phosphorus demand could also occur during the breeding season, as there is a nutritional role of phosphorus in eggshell formation and bone calcification. In the Southern Yungas forest, protein-rich fruits may be more important in the diet during cold periods when arthropods become less active (Rougès 2003), given that most frugivorous birds derive dietary protein from a mixture of fruits and insects (Levey & Karasov 1992, Herrera *et al.* 2005). The lack of high consumption of calcium and phosphorous in summer and proteins in winter in this study may be explained by the marked temporal covariation in availability of nutrients in fruits, which also prevented the assessment of additive effects of different types of nutrients and their interaction across the study period. However, this temporal covariation was a consequence of the dynamics of overall fruit quantity as the main source of change in the availability of nutrients, beyond interspecific differences in nutrient concentration. Thus, nutrient-based fruit tracking is unlikely to be primarily affected by trade-offs involving different bird life-stage requirements throughout the year.

Frugivorous–insectivorous bird species may use different foraging strategies to adjust their nutritional demands to available resources. Because gut processing time and some digestive pathways for nutrients differ between foods of animal and fruit origin (Levey & Karasov 1989, Afik & Karasov 1995, Whelan *et al.* 2000, Levey & Martínez del Rio 2001, Herrera *et al.* 2005), resource tracking and switching behaviour between major food types may reflect deeper interspecific differences in their physiological abilities. We might expect that bird species that track nutrients in fruits throughout the year would be less able to modulate nutrient transport and gut retention time and to undergo changes in gut morphology in response to changes in diet composition, than species that undergo seasonal switch between arthropods and fruits. Inclusion of digestive physiology in studies of the foraging ecology of birds will be an important research avenue to understand why some species track resources and others do not.

In summary, the temporal variation in the amount of nutrients available in the fruiting environment was much more dependent on the amount of fruit pulp produced than on fruit species composition. We conclude that fruit quantity, in terms of either amount of nutrients or amount of pulp, but not the nutritional quality of fruits, is relevant to explain fruit tracking by birds. Even so, the amount of nutrients explained tracking of food by fruit-eating birds better than the amount of pulp available, suggesting that birds not only respond to the abundance of resources but also select fruits based on their nutritional content. These findings also have important practical connotations for future studies of food tracking. Pulp mass was almost as reliable as nutrients as an indicator of the local availability of fruits for frugivorous birds, and certainly more detectable for a foraging bird than any subtle difference in nutrient concentration. For this reason and because dry pulp mass is easier to obtain and more affordable than specific nutrients, we propose the use of dry pulp-mass availability as a reliable measure of resource tracking in future comparative studies. Although the strong covariation of nutrient availability and pulp mass did not allow us to discern whether birds track changes in availability of individual nutrients rather than total fruit availability, the former seems unlikely given that specific nutrient requirements vary in time according to bird life-cycle stages. While the overall nutrient availability (i.e. across fruit) and pulp mass was an important determinant of frugivore abundances and fruit consumption, the nutritional reward of fruits available in the forest environment does not appear to have a driving role in bird decisions of resource tracking. We propose that differences in nutritional quality of particular fruit species can be important in short-term foraging decisions involved in specific fruit choices and nutritional balance. This study provides the first assessment of the role of nutrient availability in the fruiting environment as a causal factor in resource tracking by seed dispersers.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Fruits consumed by birds across the entire study.

Table S2. Pairwise comparisons between availability of different nutrients in fruits that were not significantly correlated after a correction for multiple tests.

Table S3. Species-specific regressions between dry pulp mass availability of the most consumed fruit species and fruit-eating bird abundance and fruit consumption.