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Hierarchies and co-occurrences among bird species visiting a feeder at an urban garden of Venezuela

Jerarquías y coincidencia entre especies de aves visitantes de un comedero en un jardín urbano de Venezuela

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ABSTRACT

Compared to the vast literature that has been generated in developed countries, research on birds that attend feeders in private gardens in the Neotropic are very scarce. This article analyzes the interactions among birds visiting a feeder in a private garden in the city of Guanare, Venezuela. Bird activities were recorded in 336 videos for an effective recording time (ERT) of 51.82 h, equally distributed between the dry and rainy seasons. Twenty species visited the feeder with the Blue-gray Tanager (*Thraupis episcopus*) representing 40.3% of visits. Bird visits during the rainy season (3,975) were 59.5% higher than those of the dry season (2,493). Taking the two seasons together, the feeder remained without birds 45.5% of the ERT and of the 28.25 hours in which at least one bird was present, 80.2% was occupied by solitary individuals. Solitary individuals of *Cacicus cela*, *Turdus leucomelas*, *T. nudigenis* and *Mimus gilvus* amounted to 50.5% of the time the feeder was in use; these species also showed a high percentage of exclusive occupancy of the feeder (%Exc, not shared with other species) reaching to 96.6% in the case of *M. gilvus*. The hierarchy of the species in their access to the feeder was positively correlated with their size (Spearman's rank, r = 0.87). Relatively large species (≥ 54g) won interspecific interactions in proportions above the expected by chance. Of 55 possible pairings of species co-occurrences at the feeder, 7.3% had positive associations, 30.9% negative associations, and 61.8% random associations. Negative associations always involved at least one large species, whereas there were not negative associations between pairs of small bird species. The size of the species is a determining factor in structuring the assemblage of birds visiting the feeder.

Key words: birds, co-occurrences, feeder, hierarchies, urban garden.

RESUMEN

Comparado con la vasta literature que se ha generado en países desarrollados, las investigaciones en el Neotrópico sobre aves que visitan comederos en jardines privados son escasas. En este artículo se analizan las interacciones entre aves que visitan un comedero abastecido con frutas en un jardín privado de la ciudad de Guanare, Venezuela. Las actividades de las aves fueron registradas en 336 videos con un tiempo efectivo de grabación (TEG) de 51,82 h, repartido equitativamente entre las estaciones seca y lluviosa. Veinte especies de aves visitaron el comedero, con el Azulejo (*Thraupis episcopus*) como la más frecuente (40,3% de las visitas). El número de visitas durante la estación lluviosa (3.975) fue 59,5% mayor que las de la estación seca (2.493). Tomando las dos estaciones en conjunto, el comedero permaneció sin aves presentes 45,5% del TGE. De las 28,25 horas en las cuales al menos un ave estuvo presente en el comedero, 80,2% correspondió a individuos solitarios. La ocupación por individuos solitarios de cuatro de las especies de mayor tamaño (*Cacicus cela*, *Turdus leucomelas*, *T. nudigenis* and *Mimus gilvus*) representó 50,5% del tiempo de uso del comedero. La Paraulata Llanera (*M. gilvus)* mostró un porcentaje de uso en exclusividad del comedero (%Exc) de 96,6. Hubo una correlación positiva entre la posición jerárquica de las especies y sus tamaños (Spearman, r = 0,87). Las especies relativamente grandes (≥ 54g) desplazaron a individuos de especies distintas a las suyas en proporciones superiores a las esperadas al azar. De los 55 pares de especies que podrían coincidir en el uso de comedero, 7,3% mostraron asociaciones positivas, 30,9% asociaciones negativas y 61,8% asociaciones al azar. Las asociaciones negativas entre pares de especies involucraron al menos una especie grande y no hubo asociaciones negativas entre especies pequeñas. El tamaño de las especies es un factor determinante en la estructuración del ensamblaje de aves que visitan el comedero.

Palabras clave: aves, coincidencias, comedero, jardín urbano, jerarquías.

INTRODUCTION

The urbanization process advances unstoppably on a global scale (Grimm *et al*. 2008, Cohen 2015, United Nations 2019) bringing drastic changes in the characteristics of the affected lands and makes them less hospitable for most of the species that occupied the former undisturbed areas or, on the contrary, creates favorable conditions for species adaptable to the new ecosystems (Chace & Walsh 2004, Shochat *et al*. 2006, Faeth *et al*. 2011, Belaire *et al*. 2014). People living in cities have few opportunities to observe "wild" animals other than those capable of occupying public green areas and private gardens. One way to increase the possibilities of observing these animals in their own houses is by providing resources that attract them. The most common of these attractants are birdfeeders (Goddard *et al*. 2009, Tryjanowski *et al*. 2015, Cox & Gaston 2018).

Compared to the vast literature that has been generated in developed countries, research on birds that attend feeders in private gardens in the tropics and in Latin America in particular are very scarce (Echeverría & Vasallo 2008), and in the case of Venezuela, there is just a handful of studies on this subject (Levin *et al*. 2000, Sainz-Borgo & Levin 2012, Seijas & Seijas-Falkenhagen 2020a, Seijas 2021).

From a conservation point of view, birdfeeders can have favorable or unfavorable effects (Galbraith *et al*. 2017, McBurney *et al*. 2018, Deguines *et al*. 2020). Among the unfavorable effects, it has been pointed out that feeders can facilitate the transmission of diseases and the proliferation of unwanted species; they also may contribute in the malnutrition of birds due to the provision of inappropriate food (Dunkley & Cattet 2003, Ishigame & Baxter 2007, Orros *et al*. 2015). Birdfeeders have been identified as responsible for exerting an important effect on the structuring of bird communities and to influence several aspects of bird ecologies, such as reduction of foraging time, increase in body condition, changes in survival and reproductive rates, changes abundance or density of species, among others (Galbraith *et al*. 2015, Møller *et al*. 2015, Tryjanowski *et al*. 2016). So, the use of feeders for conservation purposes should be based on well-conducted research (Fuller *et al*. 2008).

There are many factors that could intervene in structuring the assemblage of birds that visit a feeder, such as the species pool in the region, the seasonal changes in their respective abundances, the changes in nutritional requirements and in the behavior of birds in relation to their reproductive phenology, or the feeder location with respect to surrounding plant cover (Horn *et al*. 2002), but perhaps the most important factors are the preferences of the different bird species for the food that is offered in the feeder and the hierarchies that are stablished among them when accessing the food (Robb *et al*. 2008, Wojczulanis-Jakubas *et al*. 2015, Le Louarn *et al*. 2016, Deguines *et al*. 2020).

In this paper, I analize the interactions among birds visiting a feeder provided with fruits in a private garden in Guanare, Venezuela. The research is based on a data set greater than the one used in previous studies in the same garden (Seijas & Seijas-Falkenhagen 2020a, Seijas 2021) but with an emphasis on the role that inter and intra-specific relationships play in defining the pattern of use of the feeder and on the associations (or lack of them) between the different bird species.

MATERIALS AND METHODS

The study was carried out in a private garden on the outskirts of the city of Guanare, Portuguesa state, Venezuela. The birdfeeder consisted of a square cement block (40cm x 40cm and 5cm thick) placed at ground level. On it, pieces of fruit were placed and covered with a grid (5x5) of plastic-coated wires whose function was to prevent the birds from taking out or turning over the food, but which also served as perch for the birds. More details on the garden and feeder features can be found in Seijas & Seijas-Falkenhagen (2020a, b).

The activities of the birds were recorded on video with a cell phone placed on a tripod at a height of 30 cm and 1m away from the feeder. The recordings were made during days separated at irregular intervals of both the dry season (from December 14, 2019 to May 17, 2020) and the rainy season (from May 20, 2020 to October 13, 2020). The birdfeeder was provided with pieces of up to four fruit types, selected from banana, plantain, papaya, mango and avocado. Each combination of fruits was set as a trial to determine the feeding preferences of the different bird species. Detailed analyses of these preferences will not be attempted in this paper but partial results of some of these trials were discussed in Seijas & Seijas-Falkenhagen (2020a) and Seijas (2021).

Two to six sessions of variable duration (from 4 to 14min) were recorded during sampling days. The food was supplied ad libitum, as the birds never fully consumed it in the period from the start of the first recording session to the end of the last. All recordings were carried out during the early hours of the morning, but in the first 38 days of recording (between December 14, 2019 and April 20, 2020) the first session began 15 minutes before sunrise. As the rainy season approached, the cloudy sky made those minutes before dawn very dark. For that reason, beginning on April 25 2020, the first recording session of the day began at sunrise. The effective recording time (ERT) was taken as the duration of each video minus 30 seconds, considering that the behavior of the birds in the first 15 and last 15 seconds of each session could be conditioned by the presence of the researcher placing and removing the cell phone from the tripod where it was located.

For each bird visiting the feeder the following information was taken: Species, time of arrival and departure, interaction with other birds (in solitary, time shared with individuals of its own or other species). When a bird left the feeder, it was determined whether it was displaced by another bird or left it for reasons that are not relevant for this investigation. The individual who displaced another one from the feeder was taken as the winner and the displaced one as the loser, regardless of whether the displacement involved some physical contact or just intimidation (Wallace & Temple 1987).

Data were uploaded to an Excel spreadsheet designed to calculate the duration of each visit, time shared with other individuals, number of individuals (and species) sharing their visits, and time that the feeder was not in use (no birds present). The values and variables calculated from the data are defined in Table 1.

To evaluate the intensity of the intra and interspecific interactions, the quotient T_i/T was taken as the expected proportion of time that individuals of each species should spend at the feeder in solitary or sharing both with individuals of its own or other species if these possibilities were dictated by chance. That expected proportion was then substracted from the observed proportions $Solitary_i$/All solitaries, $Share\text{-}own_i$ /All sharing own, and $Share\text{-}others_i$ /All sharing others. To facilitate comparisons, the deviation from expected were expressed as Z-scores that were calculated substracting the mean of each set of differences and then dividing the results by their corresponding standard deviation (McClave and Dietrich 1994). The Z-score represents the distance between a given difference (expressed in standard deviation units) and zero, the expected value. The same procedure was followed to analyze the differences in the proportions of negative interactions between individuals of the same species ($Win\text{-}own_i$/All own) or other species ($W\text{-}others_i$/All-others) in relation to the expected proportion V_i/VT. For these analyses, pro-

Table 1. Names and definitions of values and variables used in the analyses. All values calculated taking into account the entire study.

Symbol	Definition
T_i	Time spent at the feeder by all individuals of the i_{th} species.
T	Time spent at the feeder by all visitors (ΣT_i)
$Solitary_i$	Time spent by solitary individuals of the i_{th} species
$ShareOwn_i$	Time shared by the i_{th} species only with conespecifics.
$ShareOthers_i$	Time shared by the i_{th} species with individuals of other species
$\%Exc_i$	Percentage of time the i_{th} species spent at the feeder without sharing it with individuals of other species: $(Solitary_i + ShareOwn_i)/T_i)*100$.
V_i	Number of visits of the i_{th} species
VT	Total number of visits to the feeder (ΣV_i)
All-own	Number of times that visiting birds were displaced by individuals of their own species
All-others	Number of times that visiting birds of a certain species was displaced exclusively by individuals of species other than their own.
$W\text{-}own_i$	Number of interactions won by the i_{th} species to individuals of its own species
$W\text{-}others_i$	Number of interactions won by the i_{th} species to individuals of other species

portions were arcsine squareroot transformed to stabilize variances and normalize values.

A Winner-loser dominance matrix (Levin *et al*. 2000, Seijas & Seijas-Falkenhagen 2020a) was used to calculate the percentage of interactions with individuals of other species a particular species won (%W). The Hierarchy (H) of a species was determined counting the the number of other species it displaced from the feeder in the majority of their interactions. The hierarchies of the species were correlated with their weight and their %Exc_i. Statistical analyzes were performed with Past 4.02 (Hammer *et al*. 2001).

To evaluate the degree of association (positive, negative or none) between species pairs co-occuring at the feeder, a subset of the visits were selected. This was done by taking in each recording session the fifth individual reaching the feeder, and then the following individuals separated by ten positions in their order of arrival (5, 15, 25, 35, etc). This guarantees that each selected visit did not overlap with the previous or subsequent selected one, since a preliminary analysis of the data showed that rarely does a bird share with 10 or more individuals during a visit (that only occurred in 0.49% of the total visits to the feeder). Visits of five or less seconds, and individuals that remained with the focal individual for such short period of time were also discarded, because in many cases stays at the feeder for such a short duration can hardly qualify as "time-sharing", since the displacement of one individual by another does not occur instantaneously, but there may be some intimidations, threats or even fights, which can take a few seconds to end up with the abandonment of the feeder of one of the individuals involved. The selected visits (N) allowed determining which species shares the feeder. To evaluate whether there were positive, negative or random association between the different pairs of species co-occurring at the feeder, the probabilistic model described by Veech (2013, 2014) was used. Said model uses presence/absence data to calculate expected frequencies of occurrences between species pairs if they were distributed independently of each other across the selected visits. That model is expressed mathematically as:

$$\boldsymbol{P_j = \frac{C(N, j) \times C(N - j, N_2 - j,) \times C(N - N_2, N_1 - j)}{C(N, N_2) \times C(N, N_1)}}$$

where N is the number of selected visits; N_1 and N_2 are the number of times species 1 and 2 appear in N, respectively; j is the number of visits where the same species appear sharing the feeder; $C(N, j)$ is the number of possible combinations in which two species could appear simultaneously J times in the N selected visits; $C(N - j, N_2 - j)$ is the number of possibilities of locating species 1 among the remaining places where species 2 is not present; $C(N - N_2, N_1 - j)$ is the number of ways in which species 2 could be located among those that do not have species 1. The denominator represents all the possible combinations in which species 1 and 2 can be arranged in the N selected visits, without taking j into account. The numerator is a subset of the numerator and therefore the quotient P_j is always < 1 and represents the probability that a given combination of two species will appear sharing *j* times when N visits are selected. More details and discussions about this model, its meaning and its applicability can be read in Arita (2016). Griffith *et al*. (2016) show a simplified version of the model.

The birds visiting the feeder were not tagged, so with the exception of a few individuals that have peculiar characteristics that distinguish them, it was not possible to individualize the visits. However, based on observations made over the years (Seijas & Seijas-Falkenhagen 2020b) it can be stated that the most abundant species in the garden is the Saffon Finch (*Sicalis flaveola*) whose numbers in the lawn of the garden can sometimes exceed several dozens. Around 20 Yellow-rumped Cacique (*Cacicus cela*) are in and out of the garden every day. The number of Blue-gray tanagers (*Thraupis episcopus*) that daily visit the feeder has been estimated between 20 and 30. In the case of thrushes (*Turdus leucomelas* and *T. nudigenis*) it is possible to observe a maximum of 5-6 individuals foraging in the garden along the day. Some species go down to the feeder in what appear to be small family groups (*Ramphocelus carbo*, *Mimus gilvus*, *Euphonia laniirostris*, *Campylorhynchus nuchalis*, *Icterus nigrogularis*). Other species (*Stilpnia cayana*, *Thraupis palmarum*, *Saltator coerulescens*, and occasionally *Melanerpes rubricapillus*) often descend in pairs. Other birds were sporadic visitors.

RESULTS

Two-hundred and five videos were recorded during the 2019-2020 dry season and 131 during the 2020 rainy season. The average duration of the videos in the rainy season was longer, but the ERT was very similar between both seasons (25.90 and 25.92 hours, respectively). In each climatic season, the feeder had no birds present for a high percentage of the recordings time. These visitor-free lapses represented 51.0% of the ERT during the dry season and 40.0% during the rainy season (Table 2). However, in the dry season recording sessions that began 15 minutes before sunrise (N = 38), the feeder remained 59.5% of the time without birds, while in subsequent sessions recorded on the same days, that time was 49.2%; the differences are significant (Two-sample paired test, $t = 3.04$, $P = 0.014$).

Table 2. Time allocation at the feeder. Ert is the recording time minus 30 seconds per each session (see text).

Recording time category	Dry season sessions (205)		Rainy season sessions (131)	
	Hours	%	Hours	%
Total recording time	27.61		27.15	
Effective recording time (ERT)	25.90	100	25.92	100
Without birds	13.21	51.0	10.36	40.0
In use (birds present)	12.69	49.0	15.56	60.0
Solitary individuals	10.64	41.1	12.00	46.3
Shared by two or more birds	2.05	7.9	3.57	13.8

Taking both seasons together, 20 species of birds visited the feeder. Visits for the rainy season (3,975) were 59.5% greater than those of the dry season (2,493). There was also a similar difference (62.7%) in the accumulated time of the visits of all the birds (29.4h during the rainy season versus 18.1h during the dry one; Table 3). These differences are partially explained by the 38 sessions that started before sunrise in the dry season; if these sessions are excluded there was still a 1.46 fold diference in the number of visits per hour during the rainy season. The most noticeable difference in the number of visits between the two seasons were those of the Silver-beaked Tanager (*Ramphocelus carbo*, 288 more visits), the Thick-billed Euphonia (*Euphonia laniirostris,* 370 more visits) and the Blue-gray Tanager (714 more visits). The increase in the number of visits of these three species represented 92.6% of the difference between the two seasons. Despite these differences, there was a high correlation in the relative frequency of the species (V_i) in both seasons (Spearman Rank, n = 20, r = 0.753, P < 0.001). For most of the following statistical analyses birds with less than 30 visits to the feeder were not taken into account.

The Blue-gray Tanager was the bird with the highest number of visits (40.3%) but its time at the feeder was only 26.7% of the time (T) spent by all bird species. As occurred with all species, the %Exc of *T. episcopus* was higher during the dry season (71.1%) than during the rainy season (46.6%), with a combined %Exc = 55.2%. Large birds (≥54 g) in solitary amounted to 52.7% of the time that the feeder was in use, but almost half of that time (24.1%) was spent by the Pale-breasted Thrush (*Turdus leucomelas*) alone. The time spent at the feeder as solitary individuals by the Tropical Mockinbird (*Mimus* gilvus) was not as high as other large birds, but the time sharing in exclusivity with individuals of its own species was the highest (%Exc = 93.2).

Figure 1 depicts how much each of the 11 most common species departed from the expected proportion of time at the feeder as solitary, or sharing it with its own or other species. The patterns for three species deserve to be highlighted. The Pale-breasted Thrush showed the largest deviation above expected (Z = 1.91) when comparing solitary visitors. This species was also the one that shares the least with individuals of its own species (Z = -1.78) and showed an important deviation below expected when sharing with individuals of other species (Z = -1.49). The Mockingbird was the least prone to share with individuals

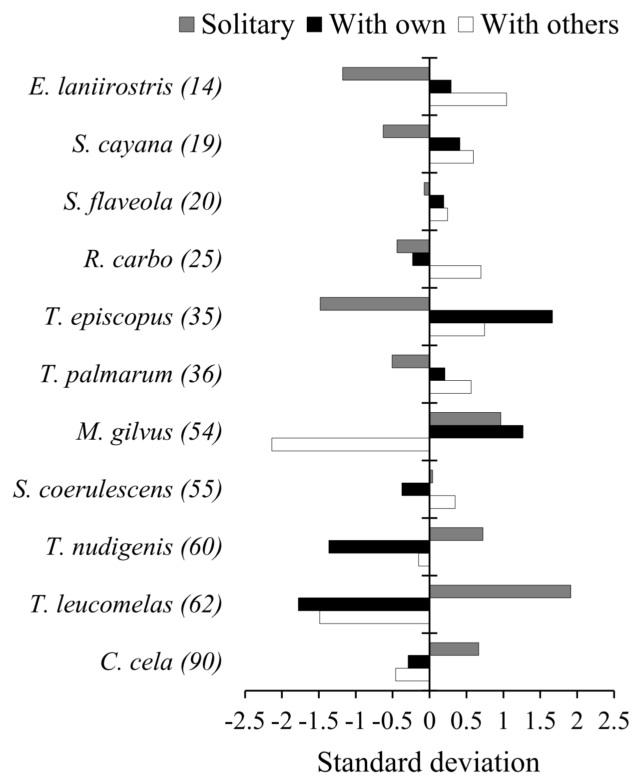

Figure 1. Differences (expressed as Z-scores) of observed minus expected proportions of time spent by birds as solitary individuals, or sharing the feeder with individuals of their own or other species in a private garden in Guanare, Venezuela. The mass (g) of each species is shown in parentheses.

Table 3. Number of visits and cumulative time spent by the different bird species at a feeder in a private garden in Guanare, Venezuela. Total times (at the bottom) expressed in hours. See definitions of variables in Table 1.

Species / (body mass, g)	Dry season (25.90h)					Rainy season (25.92h)				
	Cumulative time min)					Cumulative time (min)				
	V_i	T_i	$Solitary_i$	Own_i	$\%Exc_i$	V_i	T_i	$Solitary_i$	Own_i	$\%Exc_i$
Cacicus cela (90)	90	48.8	39.6	2.3	86.0	57	37.3	25.7	2.6	75.7
Coereba flaveola (9)	4	6.3	3.7	0.0	58.5	9	4.5	0.8	0.0	17.5
Campylorhynchus nuchalis (25)	38	13.0	8.5	3.0	87.7	34	9.4	5.5	1.0	68.7
Euphonia laniirostris (14)	75	29.1	13.3	1.2	49.6	445	230.7	41.2	41.6	35.9
Icterus nigrogularis (38)	-	-	-	-	-	62	33.3	10.3	2.6	38.9
Mimus gilvus (54)	255	198.9	120.8	71.3	96.6	207	200.4	141.5	38.7	89.9
Melanerpes rubricapillus (48)	25	17.2	9.3	0.0	53.8	31	21	8.6	0	40.9
Psarocolius decumanus (180)	3	2.0	2.0	0.0	100	-	-	-	-	-
Ramphocelus carbo (25)	10	6	2.0	0.7	45.3	298	111.7	32.5	8.4	36.6
Saltator coerulescens (55)	40	18.7	14.0	0.1	75.8	118	59	20.8	3.1	40.5
Sicalis flaveola (20)	79	41.5	20.7	5.3	62.7	53	35.5	9.9	5.7	43.9
Sporophila intermedia (12)	16	14.8	7.0	0.0	46.9	8	4	0.9	0.0	21.1
Stilpnia cayana (19)	186	80.6	28.5	20.2	60.4	223	92.9	19.6	11.9	33.9
Thraupis episcopus (35)	946	266.7	99.0	90.7	71.1	1660	492.9	120.3	109.3	46.6
Thraupis glaucocolpa (33)	3	1.9	0.2	0.0	12.3	-	-	-	-	-
Turdus leucomelas (62)	515	247.7	223.6	0.1	90.3	410	251.3	185.2	13.3	79.0
Turdus nudigenis (60)	107	45.4	33.7	0.0	74.2	237	129	85.9	0.8	67.2
Thraupis palmarum (36)	101	45.2	12.7	10.1	50.4	121	50	11.4	4.0	30.8
Tachyphonus rufus (33)	-	-	-	-	-	1	0.6	0.1	0	22.7
Icterus icterus (68)	-	-	-	-	-	1	0.3	0.3	0	100
Totals	2,493	18.1h	10.6h	3.4h	-	3,975	29.4h	12.0h	4.1h	-

of other species (Z = -2.14) and shared more than expected with individuals of its own species (Z = 1.27). Finally, the Blue-gray Tanager shared more than expected with individuals of its own species (Z = 1.67) and stayed as solitary less than expected (Z = -1.48).

There were 3,196 occasions in which a bird was displaced by another from the feeder. The winner-loser dominance matrix in Table 4 summarizes 2,536 of those events for the 14 species with the higher number of records. When interactions between individuals of the same species are excluded from the analysis, both the percentage of encounters won by each species (%W) and their hierarchical position (H) are positively correlated ($P < 0.001$) with their mass (Spearman´s rank $r = 0.84$ and 0.87, respectively). The size of the species also correlated positively with %Solitary (P <0.001, $r =< 0.001$) and %Exc (P = 0.02, r = 0.60).

Relatively large birds (≥ 54g) won interactions with individuals of other species in proportions above the expcted value; the Pale-breasted Thrush highlights among them with a Z-score of 2.05 (Fig. 2). Three species won their interactions with individuals of their own species above the expected proportion but only two of them are worth mentioning: the Pale-breasted Thrush (Z = 1.22) and, particularly, the Blue-gray Tanager (Z = 2.18). This Tanager won the lowest proportion of interactions with birds different to its own species (Z = -1.61) followed by the Thick-billed Euphonia (Z = -1.12). Finally, the Tropical Mockingbird (Z = -0.80) and the Burnished-buff Tanager (*Stilpnia cayana,* Z = -1.26) were the species with the least negative interactions with individuals of their own species.

For the analyses of co-occurrences, 518 visits were selected including 15 of the 20 species that went down to the feeder. The relative frequency of the species that ap-

Table 4. Winner-loser dominance matrix for species that visited the feeder in a private garden of Guanare, Venezuela. The diagonal (underlined) indicates the number of times that an individual was displaced by another of its own species. These last values were not included in the accounts of "wins" or "losses".

Winners	Losers														%W	H	Wg
	Cc	Mg	Tl	Sco	Mr	Tn	Cn	Rc	Te	Tp	In	Sca	Sf	El			
C. cela	27	20	36	3	4	7	4	1	44	10	2	9	2	7	97.4	13	90
M. gilvus	4	6	46	7	3	5	2	2	69	9	0	14	3	6	92.4	12	54
T. leucomelas	0	0	185	7	0	82	13	54	571	48	7	70	7	21	87.1	10	62
S. coerulescens	0	0	17	2	0	13	0	4	37	3	1	5	0	3	78.6	7	55
M. rubricapillus	0	0	15	0	0	3	0	3	6	1	0	1	0	2	77.5	7	48
T. nudigenis	0	0	1	0	1	6	2	12	90	5	4	6	1	16	50.9	7	60
C. nuchalis	0	0	8	0	1	4	0	0	4	0	0	4	2	0	51.1	5	25
R. carbo	0	0	2	0	0	0	0	3	26	3	0	3	2	9	36.9	5	25
T. episcopus	0	2	4	1	0	17	0	1	526	22	0	59	17	64	17.8	4	35
T. palmarum	0	0	0	0	0	2	0	0	14	2	0	6	1	3	24.3	3	36
I. nigrogularis	0	1	0	0	0	0	0	0	2	0	1	0	0	0	17.7	2	38
S. cayana	0	0	1	0	0	0	0	0	0	0	0	0	1	7	4.8	2	19
S. flaveola	0	0	0	0	0	0	1	0	0	0	0	0	8	1	5.1	1	20
E. laniirostris	0	0	0	0	0	0	0	0	0	0	0	0	1	23	0.7	0	14

%W: Percentage of encounters won to other species. H: Hierarchy. Wg: mass in grams (from Hilty 2003).

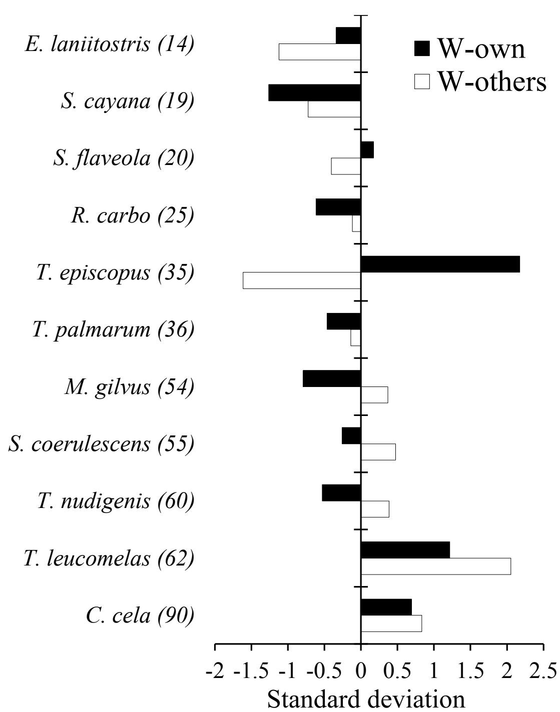

Figure 2. Differences (expressed as Z-scores) of observed minus expected proportions of interaction wons by birds to individuals of their own or other bird species in a private garden in Guanare, Venezuela. The size (grams) of each species is shown within parentheses.

pear in the selected group was highly correlated with the frequency of bird species in the total visits (Pearson r = 0.983). The 105 possibilities of different pairings and the number of times these pairings occurred in the selected sample appear in Table 5.

The analyses of co-occurrences showed discrepancies if the data came from the dry season (N = 203), the rainy season (N = 315), or the whole selected visits (N = 518). In the first case, two pairs of species showed positive associations: the Burnished-buff Tanager with the Thick-billed Euphonia (P = 0.012), and the Saffron-finch with the Palm Tanager (*Thraupis palmarum*) (P = 0.039) and five pairs showed negative associations, all of them involving the Pale-breasted Thrush and the Mockinbird. With the data from the rainy season there were three pairs of species with positive associations, all of them different from those of the dry season: the Red-crowned Woodpecker (*Melanerpes rubricapillus*) with *S. cayana* (P = 0.046) and also with the Yellow Oriole (*Icterus nigrolularis*) (P = 0.051), as well as *R. carbo* with *T. palmarum* (P = 0.036). The negative associations for the rainy season rose to 11, with the Mockinbird the Pale-breasted Thrush as the most frequently involved. Finally, with the joint data, there were 4 pairs of positive and 17 negative associations, among the former, that involving *R. carbo* with *T. palmarum* was

Table 5. The number of co-occurrences of individuals of different species at a feeder in a private garden in Guanare (Venezuela) is indicated where rows and colunms intercept. The underlined values show the number of times individuals of the same species shared the feeder.

C. cel	*C. nuc*	*E. lan*	*I. nig*	*M. gil*	*M. rub*	*R. car*	*S. coe*	*S. fla*	*S. int*	*S. cay*	*T. epi*	*T. leu*	*T. nud*	*T. pal*	
23	0	0	1	1	1	1	0	0	0	1	5	2	0	0	*C. cel*
	7	0	0	0	0	0	0	0	0	0	1	0	1	0	*C. nuc*
		90	0	0	3	12	10	9	0	17	57	12	12	11	*E. lan*
			12	2	1	1	1	0	0	1	4	0	0	0	*I. nig*
				56	0	0	0	0	0	3	5	0	1	2	*M. gil*
					13	2	0	1	0	4	9	2	0	0	*M. rub*
						48	6	1	0	7	27	8	4	8	*R. car*
							32	3	0	6	17	2	0	0	*S. coe*
								31	4	4	12	5	2	5	*S. fla*
									6	0	1	2	0	1	*S. int*
										74	39	11	3	8	*S. cay*
											260	26	23	25	*T. epi*
												119	2	1	*T. leu*
													42	3	*T. nud*
														46	*T. pal*

maintained. In all cases, negative associations involved pairs of a large species (≥ 54g) with a small one (≤ 48 g) or pairs of large species. That is, there were no negative associations between small species.

Considering only the 11 species with the highest number of occurrences in the 518 selected records (Table 5), five of the ten possible pairs among the large species showed negative associations (Fig. 3). In contrast, all 15 possible pairs between the smallest species (upper left corner) showed neutral or positive associations. The Tropical Mockingbird and the Pale-breasted Thrush were the species with the highest number of negative associations with other species (8 and 7, respectively). Globally, the species pairs included in figure 3 show 7.3% positive associations; 30.9% negative associations and 61.8% random associations.

The Thick-billed Euphonia was the bird with highest number of positive associations (three), two of them with relatively large species such as the Grayish Saltator (*Saltator coerulescens*) and the Bare-eyed Thrush (*Turdus nudigenis*). This last species (the third largest bird) did not show a negative association with any of the small species. A species pair not included in the figure but that showed a significant positive association was that of the Saffron-finch and the Gray seedeater (*Sporophila intermedia*) ($P < 0.001$).

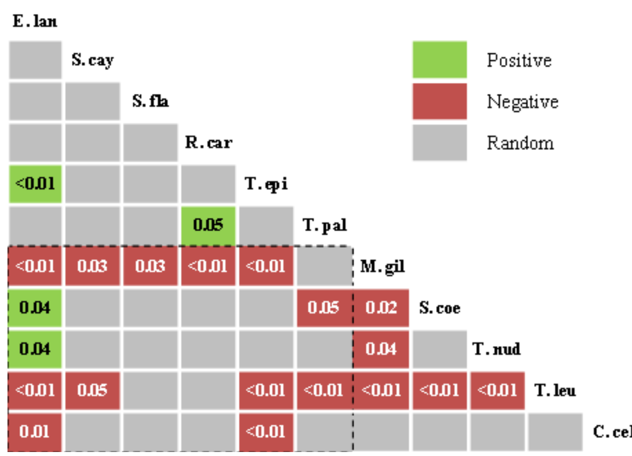

Figure 3. Association between species pairs at a birdfeeder in a private garden in Guanare, Venezuela. The abbreviated scientific names of the birds indicate both rows and columns. The species are ordered according to their size with the smallest (*Euphonia laniirostris*) in the upper left corner and the larger (*Cacicus cela*) in the lower right corner. The numbers inside the red or green boxes indicate the P values calculated according to the probabilistic model of co-occurrences (Veech 2013). Boxes included in the square delimited by a broken line represent interrelationships between small species (≤ 48g) and large ones (≥ 54g). Boxes above that rectangle represent interrelationships between small species and those to the right represent interrelationships between large species.

DISCUSSION

Although the time spent videoing bird activities during dry or rainy seasons was nearly the same, during the dry season there was a lower number of visits to the feeder. Not all species changed the frequency of their visits in the same proportion and three of them (*R. carbo*, *E. laniirostris* and *T. episcopus*) accounted for almost 93% on the increase in numbers of visits between the two seasons. These differences are probably related to changes in the phenology of birds and fruiting plants alike. Although there is no detailed information available on the reproductive biology of the first two species, according to Hilty (2003) they reproduce mostly during the dry season, and maybe the time devoted to nesting and raising chicks (and looking for other food types, for example) keeps them partially away from the feeder. On the other hand, the Blue-gray Tanager reduced drastically its number of visits from late January to early March 2020, which coincided with the copious fruiting of a *Chrysophillum sp* tree just 20 meters from the feeder, where individuals of all bird species that visited the feeder were observed eating its fruits, and the most numerous of them belonged to *T. episcopus* (Seijas & Seijas-Falkenhagen 2020b).

There was a clear hierarchy among the birds accesing the feeder, which was essentially determined by the size of the species: the largest ones dominated the smallest, as has been observed in many other studies in birdfeeders (Wojczulanis-Jakubas *et al*. 2015, Galbraith *et al*. 2017, Deguines *et al*. 2020, among others). A notorious discrepancy in this aspect was offered by the Bared-eyed Thrush, a bird with a hierarchical position below what would be expected according to its weight (60 gr). This contrasts with the comments on Verea *et al*. (2016) who pointed out that *T. nudigenis* dominates over several species, including *T. leucomelas*, something that occurred only once in the 83 confrontations between these species recorded in the present study. The Bared-eyed Thrush shares very little with individuals of its own species, an indication of strong intra-specific antagonistic relationships, but compared to *T. leucomelas* it shares a little more with species smaller than itself.

A high fraction of the time that the feeder was in use (with birds present) it was mostly occupied by solitary individuals of some of the largest species, highlighting among them the Pale-breasted Thrush and the Tropical Mockingbird. These two species dominated the feeder by excluding other species, particularly the smaller ones.

Larger species (≥54g) displaced individuals of other species more frequently than expected by chance. That difference was particularly high in the case of the Pale-breasted Thrush. This species totaled a number of interactions won greater than its number of visits. This means that in some visits it displaced more than one individual at a time. Most of these antagonistic interactions (17.4%) were against individuals of its own species. Verea *et al*. (2016) point out that *T. leucomelas* can form groups of up to eight individuals, but it seems that these groups are not very cohesive. This thrush is a very territorial species and in the reproductive season fights occur (presumably between males) that can lead to the death of one of the contenders (Seijas & Seijas-Falkenhagen 2020b). The Tropical Mockingbird showed a much lower number of antagonistic encounters with other species than the Pale-breasted Thrush, but the confrontations between these two species were overwhelmingly won by *M. gilvus* (49 to zero). The dominance that the Mockinbird exerts over the feeder occurs even when it is not occupying it. One or more Mokingbirds remain vigilant in the vicinity of the feeder and attack other birds that approach it, which was not always registered in the videos.

Most small birds (<54g) displaced individuals of other species less than expected by chance; that is, they used the feeder sharing it with individuals of their own species or with individuals of other relatively small species. This can be interpreted as a response of the small species to the monolopy of the feeder by the larger species; that is, they need to share with other species the relative little time that larger birds leave them available. One exception to this pattern is offered by the Blue-gray Tanager that interacted negatively much more than expected with individuals of its own species and much less than expected with individuals of other species. The fact that *T. episcopus* shares a high proportion of its time at the feeder with individuals of its own species is probably a consequence of its abundance, with more than 40% of the total visits. However, it seems to be a very tolerant species toward individuals of other species.

According to the co-occurrences analyses, it is clear that larger species associate negatively among them and with the relatively smaller species. Although the smaller species were limited to use the feeder only a small part of the time, the positive associations between them were rather rare. Overall, the percentages of positive, negative and random associations found in this study are very similar to those quantified by Galbraith *et al*. (2017) in birdfeeders in Auckland, New Zealand: 7.3% vs 8.3%, 30.9% vs 27.8%, and 61.8% vs 63.9%, respectively.

The positive association between the Silver-beaked Tanager and the Palm Tanager is probably a fortuitous event. The first species of this pair visited the feeder very few times in the dry season, but there was a considerably increased in its number of visits during the rainy season, so the positive association is produced by their co-occurrences in that season. As has been mentioned by Blanchet *et al.* (2020), co-occurrence is not evidence of ecological interactions, although these authors were referring to association of species in natural communities. Co-occurrences can occur due to various causes, such as coincidences in their biological cycles and visits to the feeder at the same stages of their cycles (whatever these are) or also because the species share the preferences for the type of fruit offered. A clear example of the latter case is the positive association between the Saffron Finch and the Gray Seedeater; both species only visited the feeder on the occasions that mango was offered (Seijas & Seijas-Falkenhagen 2020a, Seijas 2021). The Thick-billed Euphonia was the species with the highest number of positive associations, including two with relatively large species (*S. coerulescens* and *T. nudigenis*). This bird is the smallest among the birds that visited the feeder. Perhaps due to its small size it is not seen as serius contender to care about by other birds, which tolerate its presence at the feeder.

All species that visited the feeder during this study are native. That is probably a consequence of the exclusive use of fruits as attractants. If other types of food had been used, such as grains (corn, rice, sunflower) or cooked food (pasta, cooked rice, bread) surely other species would have appeared, as I have observed in some birdfeeders in the city. These species include the exotic domestic pigeon (*Columba livia*) and other species that, although not exotic, are very synanthropic and uninteresting from a conservation point of view, such as the Carib Grackle (*Quiscalus lugubris*) and several small pigeons such as the Eared Dove (*Zenaida auriculata*), the Scale Dove (*Columbina squammata*) and the Ruddy Dove (*Columbina talpacoti*). Likewise, the presence of a granivore such as Saffron Finch should have been much more noticeable, as it is the most synanthropic species in Guanare (Seijas *et al*. 2011).

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