UNIVERSIDADE FEDERAL DE SÃO CARLOS
CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E RECURSOS NATURAIS

RAISSA SEQUINI CAPELÃO

AVIAN USE OF HONEYDEW (HEMIPTERA: COCCOIDEA) IN THE ATLANTIC FOREST OF SOUTHEASTERN BRAZIL

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais, para obtenção do título de Mestre em Ecologia e Recursos Naturais.

Orientação: Prof. Dr. Augusto João Piratelli

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SUMMARY

O uso de honeydew por aves (Hemiptera: Coccoidea) na Mata Atlântica do sudeste do Brasil

Resumo Honeydew é uma solução de carboidrato produzida e secretada por cochonilhas (Hemiptera), que se alimentam do floema de plantas hospedeiras, removendo compostos nitrogenados para a síntese de proteínas. Neste estudo analisamos fatores que podem afetar a secreção de honeydew por cochonilhas (Stigmacoccus paranaenses) (Stigmaccocidae) em árvores de *Inga* Mill. e descrevemos seu uso como recurso alimentar por aves em área de Mata Atlântica no sudeste do Brasil. Realizamos 359 horas de observação em 25 árvores focais da primeira quinzena de setembro de 2016 à primeira quinzena de setembro de 2017. Registramos 25 espécies de aves alimentando-se de honeydew, totalizando 3.261 visitas. Dezesseis dessas espécies nunca haviam sido registradas alimentando-se deste recurso. A maioria das visitas ocorreu no período da manhã (7:00 às 8:00 horas) e nos meses de inverno, e as espécies mais frequentes foram cambacica (Coerebinae) e sanhaços (Thraupidae). Sanhaço-de-encontro-amarelo (Thraupidae) foi a espécie que mais ativamente defendeu o recurso, com 44% de todas as 759 interações agonísticas observadas. Verificamos uma variação sazonal na produção de honeydew, com pico no inverno e ausente no verão. O consumo de honeydew está intrinsecamente ligado à variação de sua disponibilidade, que é afetada negativamente pela temperatura. Encontramos evidências de partilha de recursos entre os consumidores de honeydew, que inclui não apenas aves, mas também vários artrópodes. Embora o honeydew possa ser um recurso oportunista sazonal, parece valer a pena ser defendido, devido à sua alta concentração de açúcar, composição e facilidade de acesso, levando a um trade-off positivo.

Palavras-chave: dieta de aves, Inga, partilha de recursos, cochonilhas, interações tróficas.

Avian use of honeydew (Hemiptera: Coccoidea) in the Atlantic forest of southeastern Brazil

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Avian use of honeydew (Hemiptera: Coccoidea) in the Atlantic forest of southeastern Brazil

Abstract Honeydew is a carbohydrate solution produced and secreted by scale insects (Hemiptera), which feed on the phloem of host plants, removing nitrogen compounds for protein synthesis. Here we analyzed factors that may affect scale insects (*Stigmacoccus paranaenses*) (Stigmaccocidae) secretion of honeydew on *Inga* trees, and described its use as a feeding resource by birds in a rain Atlantic forest area, in southeastern Brazil. We performed 359 hours of observation on 25 focal trees from the first fortnight September 2016 to fortnight September 2017. We recorded twenty-five bird species feeding on honeydew, totaling 3,261 visits. Sixteen of these species were never recorded feeding on honeydew before. Most of the visits occurred in the morning (7:00 am to 8:00 am) and in the winter months, and the most recorded species were Bananaquit (Coerebinae) and Tanagers (Thraupidae). Golden-chevroned Tanager (Thraupidae) was the species that most actively defended the resource, with 44% of all 759 observed agonistic interactions. We verified a seasonal variation in honeydew production, peaking in the austral winter time and absent in the summer. Honeydew consumption is intrinsically linked to variation in its availability, which is negatively affected by temperature. We found evidence of resource partitioning among honeydew consumers, which includes not only birds but several arthropods. Although honeydew may be a seasonal opportunistic resource, it seems to be highly worth defending, because of its high sugar concentration, composition, and its easy-access, leading to a positive trade-off.

Key words: birds diet, *Inga*, resource partitioning, scale insects, trophic interactions.

INTRODUCTION

Research on ecological niches has grown in recent decades as ecologists have been focused on examining the relationship between biodiversity and resource use across communities (Hooper *et al*. 2005, Northfield *et al*. 2010). These studies have been mostly found across a wide range of community types and trophic levels; the more species, the more resource use (Finke & Snyder 2008). This trend is generally linked to complementary patterns of resource utilization among species, such as resource partitioning (Northfield *et al*. 2010). Resource-partitioning analyzes are a central part of community structure studies (Cody & Diamond 1975; Paine *et al*. 1981). They may clarify the limits at which interspecific competition influences the number of species that can coexist in a stable way (Schoener 1974).

Resource partitioning is an expected consequence of present and past competition (Paine *et al*. 1981). Traditionally, three dimensions of segregation of specific niches have been included in the n-dimensional niche theory: space, food and time (Alley 1982). The temporal dimension can be related to variation in the use of resources across seasons or throughout a day (Vila & Rodrigues-Teijeiro 1992). This segregation may be linked to reducing the value of foraging by competitors, by decreasing food availability (Schoener 1974). In the space dimension, species can use the same food resource foraging at different heights (e.g. in the same tree) (MacArthur 1958; Wilson 2010).

Honeydew is a carbohydrate solution produced and secreted by many Hemiptera, including scale insects (superfamily Coccoidea), like *Stigmacoccus paranaenses*. It is rich in carbohydrates of photosynthetic derivatives, and low concentrations of proteins (Grant & Beggs 1989; Dungan & Kelly 2003). These insects insert their stylets into the phloem cells of host plants for sap-sucking. They ingest more carbohydrates than they can assimilate or use, and secreting excess sugar through waxy anal tubes (Dungan & Kelly 2003). This excess (honeydew) is excreted in the form of sugary droplets that may contaminate the individual or serve as a medium growth of facultative saprophagous fungi, which form black-colored colonies (Latta *et al*. 2001).

As a high carbohydrate component, honeydew can be considered a liable food resource to be partitioned by many consumers (REFER?), and it may be a central component in the diet of nectarivorous and frugivorous birds, mainly along periods when flowers and fruits are not abundant (Feinsinger 1976; MacNally & Timewell 2005; Gamper & Koptur 2010). However, most papers on honeydew consumption are focused only on the mutualistic relationship between ants and Hemiptera (e.g. Way 1963; Bach 1991; Gullan 1997; Latta 2001). Few studies on the use of honeydew by birds have been conducted in Australia (Paton 1980), New Zealand (Beggs & Wardle 2006), Costa Rica (Jiron & Salas 1975), Colombia (Koster & Stoewesand 1973), Dominican Republic (Latta *et al*. 2001) and Mexico (Gamper & Koptur 2010; Lara *et al*. 2011). In Brazil, avian use of honeydew has been poorly documented; with a prevalence of association of scales insects with *Mimosa scabrella* (Fabacea) trees (Teixeira & Azevedo 2013).

The "Convergence Hypothesis" (Greenberg *et al*. 1993) explains the unique and uneven geographical distribution of the phenomenon of avian use of honeydew worldwide. It has been suggested that common regional climatic conditions have resulted in the few known cases of foraging of honeydew by birds. Habitats such as temperate forests and mild climate, contribute to the absence of ants consuming this resource, thus promoting greater use by birds.

Ten bird species were recorded feeding on honeydew in the south state of Santa Catarina, associated mostly with bracating trees (*Mimosa scabrella* Benth), including two species of hummingbirds (Reichholf & Reichholf 1973, Sick 1988). Another eight new species were registered in association with *Pseudopiptadenia leptostachya* (Fabacea) in the southeastern state of Minas Gerais, emphasizing description of behavioral maneuvers and resource defense (Teixeira & Azevedo 2013).

Here we describe the use of honeydew by birds in an Atlantic Forest in south-eastern Brazil, by observing visitation patterns on scale infested trees. Based on the premise that honeydew is a highly-disputed resource, we predict that there would be a spatiotemporal segregation among birds consuming this resource. We also looked for climatic and ecological variables that is likely to influence this consumption by birds and evaluate the space-temporal viability of honeydew. Additionally, we discuss the "Convergence hypothesis" in the context of the Atlantic Forest.

METHODS

Study area

The study was carried out in Carlos Botelho State Park (from now CBSP) (24° 06' 55''- 24° 14' 41'' S and 47° 47'18''- 48° 07' 17'' W), a protected area having 37,644 ha, including a steep mountainous terrain, with altitudes between 30 and 1,000 m a.s.l. (Lima *et al*. 2011; Antunes *et al*. 2013). The average annual temperature varies between 18 and 20°C and rainfall between 1500 and 2200 mm (São Paulo 2008). The predominant vegetation in CBSP is the rain forest, varying along the altitudinal gradient between dense lowland (0 - 50 m), dense sub montane (51 - 500 m) and montane (501 - 1,000 m) (Kronka *et al*. 2005).

The scale-insect *Stigmacoccus paranaenses* (Stigmacoccidae)

Adult females and cysts of scale insect were collected and identified as *Stigmacoccus paranaenses.* This species was already been recorded in Brazil in the southern states of Parana, Santa Catarina and Rio Grande do Sul, in *Inga* spp., *Schizolobium excelsum* (Fabaceae) and *Mimosa scabrella* (Mimosaceae) (Wolff *et all.* 2015). In this study, we describe the first record of *S. paranaenses* for the state of São Paulo (São Miguel Arcanjo), expanding the species distribution area. Tree species previously observed with these scale insects infestation in CBSP was *Inga vera*; *Inga sessilis* and *Inga edulis* (Fabacea) found mainly in areas near forest edges, surroundings of pounds and close to the facilities of the protected area. To verify which individuals were infested, we observed the presence of black spots on the trunk and branches, typical of a fungal colony, and white hair-like anal tubes (Fig. 1).

Dispersal of scale insects in each tree was quantified in two zones (1 = trunk, 2 = branches), based on a 6-point scale (0 = no anal tubes, 1 = 0-20% of branches and trunk with anal tubes, 3 = 41 -60% of branches and trunks with anal tubes, 4 = 61-80% of branches and trunk with anal tubes, 5 = 81-100% of branches and trunk with anal tubes).

Honeydew

Honeydew volume can vary over time and influences subsequent foraging events (Greenberg *et al*. 1993). Honeydew production patterns were monitored from 6:00 am to 6:00 pm, at 15-day intervals, from the first fortnight September 2016 to first fortnight September 2017.

We selected five anal tubes and collected secreted droplets through capillary tubes (5 µl) (Lara *et al*. 2011) at 6 am, 10 am, 2 pm and 6 pm. Next, we calculated the mean volume and estimated the mean sugar concentration through the Brix scale (Lara *et al*. 2011), using a portable optical refractometer, model Instrutherm RT-280.

Birds

To quantify the use of honeydew by birds, we performed focal observations throughout the day (6 am - 6 pm, uninterrupted) for two consecutive days at 15 - day intervals over the same period, totaling 359 hours of observation. For each visit to honeydew (bird probing an anal tube), we recorded: species identity, number of individuals, time of day, total time on the tree and total time feeding of honeydew. Nomenclature for bird species followed HBW and BirdLife International Illustrated Checklist of the Birds of the World (from Hoyo & Collar 2017) and diet classification followed Wilman (2014) (Fig. 2). Scale insects were observed infesting only trunks and branches, yet birds feeding on the foliage and using a more aggressive and abrupt behavior was assumed as foraging on arthropods, and therefore, was not recorded. Birds were not individually banded; thus, more than one visit may have been done by the same individual.

We recorded the following behaviors during the visits: bird consuming honeydew, consuming another resource, resting, cleaning feathers, inter and intraspecific interactions. Records of agonistic interactions allowed us to describe conditions under which the resource is defended. Honeydew feeding rates by birds were obtained by counting the number of drops collected in the anal tubes during a single visit.

Temporal differences in the use of honeydew by birds were compared along the day and throughout the year. The number of visits for each species and the total amount was compared along the day, by differences in foraging between morning and afternoon. We monthly compared the consumption rates for each species to detect temporal differences in resource use. We verified spatial differences in honeydew consumption by a visual division of the tree into "central area" (trunk) and "peripheral area" (all branches of the tree). In the central area, we divided the trunk in three zones: “low” (0-33.3% of the trunk); “middle” (33.4-66.7% of the trunk) and "high" (66.8-100% of the trunk). At each visit, we recorded where each species was feeding. All direct visual observations were made 5 meters from the focal tree, using binoculars and photographic documentation.

Factors that may influence honeydew consumption by birds

To identify other factors that may influence honeydew consumption by birds, we estimated the total number of flowers and fruits in trees within a radius of 15 meters of the focal tree, including the *Inga* trees themselves. We carried out this observation based on the premise that during a period of low flowering and fruiting, demand of honeydew by birds increases (Feinsinger 1976; MacNally & Timewell 2005; Gamper & Koptur 2010).

We also sampled climatic variables as temperature (ºC), humidity (%), dew point (ºC), pressure (hPa), wind (m/s), radiation (KJ/m^2) and rainfall (mm) from the São Miguel Arcanjo Automatic Surface Observation Weather Station, opened on 08/16/2006, located at latitude -23.852022º, longitude -48.164817º, at 676 meters altitude, available on the National Institute of Meteorology (INMET) website. We computed these variables every 15 days, from 6 am to 6 pm (during the study period) to verify whether these climatic variables influence the production and consequently the consumption of honeydew by birds.

Arthropods feeding on honeydew

Several Hymenoptera, such as ants, bees, and wasps, have honeydew as an key component in their diets (Latta *et al*. 2001). We carried out observation on honeydew consumer insects to verify whether their presence influences bird foraging events, based on the assumption that birds may compete with these insects, resulting in temporal foraging segregation. To verify which insects feed on honeydew and whether there would be a temporal segregation between them and birds, we performed observations three-times a day (7 am, 12 pm and 5 pm), at 15-day intervals, totaling 44 observation hours. We recorded insect species and the number of foraging individuals. We collected one individual of each insect species feeding on honeydew, which were later preserved in liquid medium (70% alcohol) for further identification.

Data analysis

We used One-way ANOVA to test differences in honeydew production (temperature and volume) throughout the day (among 6 a.m., 10 a.m., 14 a.m. and 18 a.m) and throughout the year (study period) and to test temporal differences in honeydew consumption between birds and arthropods (total number of visits per hour from each group). Temporal-spatial differences in bird honeydew consumption were obtained by comparing the total number of visits for each species between morning and afternoon (temporal differences) and between central and peripheral area of the tree (spatial differences) among bird species were verified using *t*-test (one sample).

The Pearson correlation coefficient was used to verify the independence among the variables likely to influence honeydew consumption by birds; bird richness, honeydew volume (µl) honeydew sugar concentration (brix), air temperature (°C), air humidity (%), dew point (°C); pressure (hPa), wind (m/s), radiation (kJ/m²), rainfall (mm), number of fruits, number of flowers, degree of infestation of cochineal (1-6 scale), tubules with honeydew (%), mean and number of honeydew-consuming arthropods. (Appendix S1). We selected for subsequent analyzes those with values greater than 0.8. Next we performed ANOVA to verify the significant variables influencing the consumption of honeydew by birds.

We detected relationships between the predictor variables (those selected by ANOVA) and the number of visits through the redundancy analysis (RDA), a multiple linear regression, followed by a main component analysis (PCA) of the adjusted values table, in which the response variable is a (y) of the number of bird visits to the honeydew that is explained by a matrix (x) of predictor variables (Boccard *et al*. 2011). The analyzes were performed in the software R version 3.4.2 (R Development Core Team 2017).

RESULTS

Scale-insects, *Stigmacoccus paranaenses*

Twenty-five (29.4%) of 85 observed trees in surroundings of pounds and CBSP facilities were infected. Eleven individuals were identified as *Inga vera*; five as *Inga sessilis;* four as *Inga edulis* and four could not be identified at the species level.

Honeydew

We found a not by chance variation in the monthly mean volume (µL) of honeydew (F = 7.25, $P \leq 0.001$), peaking in September and absent from November to February (Fig. 3A). The mean sugar concentration also varied significantly during the studied period (F = 34.13, $P \leq 0.001$); the highest reading was measured in September and April 2017 and the lowest in August 2017 (Fig. 3B).

Mean honeydew volume has significantly varied along a day ($F=9.25$, $P\leq 0.001$) (Fig. 4A); the lowest value was measured at dawn (6 am) and the lower, at 2 pm. However, the sugar concentration did not change significantly (F = 2.68, P = 0.987) (Fig. 4B).

Birds

We recorded 25 bird species foraging on honeydew, totaling 3,261 foraging events (Table 1) The Bananaquit (*Coereba flaveola*) was the species with the highest number of visits (n = 1,042). Eleven frugivores / nectarivores accounted for 44% of visits, followed by eight insectivores (32%) and six omnivores (24%). (Appendix S2).

Of the 25-recorded species in this study, 16 were not previously reported as honeydew consumers.

Among the most frequent visitors, those who foraged more quickly were Bananaquit 39.1 anal tubes/min); Violet-capped Woodnymph (*Thalurania glaucopis)*) (35 anal tubes/min) e Golden-chevroned Tanager (*Thraupis ornata)* (29.7 anal tubes/min). Golden-chevroned Tanager had the highest average time foraging on honeydew (13.82 min / per visit) resulting in higher numbers of total filaments visited (137,546 anal tubes, ~ 40% of all visits).

Monthly total visits of birds varied significantly (t = 3.033, P = 0.010), with July (936 visits), June (596 visits) and August 2017 (542 visits) with highest number of visits. No visits were recorded between November and February. The total number of visits also had a not by chance variation throughout the day (t = 10.56, $P \leq 0.05$). The highest number of visits (n = 439) was recorded in in-between 7:00 am and 7:59 pm, and the lowest, from 5:00 pm to 6:00 pm (121 visits) (Appendix S4).

We detected significant temporal differences in frequency of visits for six species, with higher amount in the morning for Golden-chevroned Tanager (t = 4.173, P = 0.001), Sayaca Tanager (t = 3.605, P = 0.004), Violet-capped Woodnymph (t = 3, P = 0.013), Tropical Parula (t = 2.4886, P = 0.032), Green-headed Tanager (t = 2.373, P = 0.041) and Red-necked Tanager (t = 2.271, P = 0.046). Seasonal differences in the number of monthly visits were verified for Bananaquit (t = 3.407, P = 0.005), Blue Dacnis (t = 2.656, P = 0.020), Rufous-headed Tanager (t = 2.869, P = 0.141), Tropical Parula (t = 2.377, P = 0.034) and Violet-capped Woodnymph (t = 2.665, P = 0.020). No significant spatial differences were found between bird species for both the vertical and horizontal planes.

We observed 759 agonistic behaviors, from which 64.4% (n=489) were interspecific and 35.6% (n=270) intraspecific. Among the most active consumers of honeydew, Golden-chevroned Tanager was the most aggressive and dominant species (66.1% of all agonistic interactions; n=502), being excluded only by other individuals of same species (Appendix S3). We also observed one event of the Yellow-fronted Woodpecker (*Melanerpes flavifrons*) investing in a Golden-chevroned Tanager.

Arthropods feeding on honeydew

We recorded ten Hymenoptera species feeding on honeydew, including four ants (Formicidae); two bees, European bee (*Apis mellifera)* (Apidae) and *Trigona* sp.(Apidae); four wasps *Polistes* sp. (Vespidae) and four Diptera, Tipulidae (*Brachyprema* sp.); Muscidae; Drosophilidae and Tachinidae. They totalized 4,149 visits. The species that most consumed the resource was *Trigona* sp., with 78.2% of visits (n = 3,244); followed by wasps, 11.9% (n = 494); ants, 5.3% (n = 222); European bee 2.4% (n = 100) and Diptera, 2.1% (n = 89). Day time difference in the number of visits was not significant (t = 1.545 P = 0.2623) and likewise, we found no temporal difference on honeydew foraging between arthropods and birds (F = 1,546 P= 0,282).

Factors that may influence honeydew consumption by birds

The RDA identified four explanatory variables that significantly influenced bird foraging to honeydew: honeydew volume (μL), temperature (°C), air humidity (%) and abundance of arthropods consuming honeydew, which accounted for approximately 90.5% of the data variation (Appendix S4). The first axis explained 72.5% of the variance and was influenced by the abundance of arthropods consumer and temperature. The second axis explains 18% of the data variation and was associated to honeydew volume and air humidity. The volume of honeydew (hd.mc) was the variable that most positively explained the number of visits (F = 11.03, P = 0.001), together with air humidity (F =2.7 P = 0.029) having most strongly influenced *Thraupis ornata* (Thor); *Thalurania glaucopis* (Thgl) *and Dacnis cayana* (Daca) (Fig. 5A). First fortnight September 2016, August, June and July were the months with the highest volume of honeydew and, thus, the highest number of visits (Fig. 5B). *Coereba flaveola* (Cofl); *Setophaga pitiayumi* (Sepi); and *Hemitrhaupis ruficapilla* (Heru) were more strongly affected by the abundance of honeydew consumer arthropods (arth.m) (F = 5.96, P = 0.004) (Fig. 5A), and this was higher in April, October, March, May, and September 2017. The volume of honeydew was negatively influenced by temperature (temp) (F = 3.61, P = 0.003), which has negatively affected the number of visits. In the months having higher temperatures (i.e., November, December, January and February), there were no visits due to absence of honeydew (Fig 5B).

DISCUSSION

Seasonality in honeydew production

Honeydew is an extremely seasonal resource, peaking in the winter months and absent in the austral summer. We noticed that climate conditions interfere with honeydew concentration. As the temperature increases throughout the day, air humidity decreases, the heat evaporates the honeydew droplets, making them thicker, increasing sugar concentration. Indeed, we recorded highest sugar concentration at 2 pm. In the meantime, at 6 am, air humidity dilutes the droplets, decreasing sugar concentration.

Lower temperatures lead to higher scale insect density and higher honeydew production (Sagata & Gibb 2016). Favorable temperatures may increase phloem flux by reducing seam viscosity, or by increasing plant pressure turgor (Thomas *et al*. 2004; Sagata & Gibb 2016). Elevated temperatures, over 29°C, impair the physiological functions, size and foraging behavior of sap-sucking insects (Sagata & Gibb 2016). The negative relation between hot temperatures and honeydew production brings a warning about global climate change. By the end of this century, higher temperatures could cause a decline in honeydew availability, resulting in adverse effects on trophic ecology and the ecological interactions of species that use this resource (Sagata & Gibb 2016).

One question that arises is concerning the negative impact that scale insects can exert on the host plants. Scale insects used only 1.8% of the net primary production of *Nothofagus solandri* (Nothofagaceae) trees in New Zealand, with no significant adverse effects on the host plant (Dungan & Kelly 2003). The production of honeydew by scale insects may have few effects on the growth and reproduction of host plants, because trees infested by scale insects have a higher photosynthetic rate to compensate the sucking of sap by these insects (Retuerto *et al*. 2004, Dungan *et al*. 2007).

Birds

Honeydew was consumed by several species, including not only nectarivores, but also insectivores and omnivores, suggesting that this resource is widely known and widespread in the community.

We found no temporal segregation between birds or insects in the daytime. Several bird species feeding on honeydew at the same time over a tree, may suggest that some species use the resource with greater intensity than others, reducing the competition, and allowing many species to explore at similar times (Vila & Rodrigues-Teijeiro 1992). Resource partition is a result of difference in the resource use, which allows the coexistence of different species, promoting biodiversity (e.g., Tilman 1982; Svenning 1999). We observed temporal segregation in bird feeding throughout the year, due to the extremely seasonal nature of the resource, a pattern also detected in Australia (Paton 1980), Mexico (Greenberg *et al*. 1993), Dominican Republic (Latta *et al*. 2001) and New Zealand (Gardner-Gee & Beggs 2013), suggesting a general pattern in seasonality.

We did not observe any birds preying on bees, wasps and other insects that were consuming honeydew. The winter months, when honeydew was available, were also the time having the highest visitation of these arthropods. Yet, although the RDA exposed a positive relationship between the number of visits of birds and arthropods, there was no real influence of these lasts on the consumption of honeydew by birds.

We stress that, when feeding on honeydew, birds only probed the drops, consuming honeydew without breaking the anal tube or causing any damage to the scale insects. Honeydew, secreted through long anal filaments, seems to be particularly suitable for birds to forage, as they produce relatively large droplets and are not easily collected by ants (Latta *et al*. 2001). Yet, these filaments allow several bird species feeding on this resource in less accessible areas over a tree (*e.g.* trunks). The evolutionary history of the long anal filament may be intrinsically related to the consumption of honeydew, since its secretion relatively far from the individual can avoid possible predation and mechanical damage to the scale insects (Greenberg *et al*. 1993).

Low winter flowering was expected, leading to a higher number of visits to honeydew (Feinsinger 1976; MacNally & Timewell 2005; Gamper & Koptur 2010). However, in CBSP the average number of flowers was high in July. This can be explained by the explosive flowering of the non-native *Rhododendron* sp (Ericaceae) in the surroundings of CBSP facilities in winter. Although many birds feed on the nectar of this plant, July was also the month having the highest visitation to honeydew. Thus even when nectar is available, honeydew is a viable food resource for birds, which may be explored not only when there are restrictions on nectar supply. Yet, as no bird species is exclusively dependent on this resource, honeydew may be a widely opportunistic resource.

We claim attention for the Greenish Tyrannulet (*Phyllomyias virescens*) (Tyrannidae), an altitudinal migrant, which migrates in small numbers to the countryside of the state of São Paulo in the winter (Antunes & Willis 2003). We recorded this species consuming honeydew in July. It is interesting to note how non-residents learn about the availability of this resource in the area. The theory of mixed species flocks suggests that the frequency of wing-bar flashes and calls may be important in initiating a bird flock (Greig-Smith 1976) and the cluster of species around the *Inga* trees may have drawn attention of this species to the honeydew sites.

The Convergence hypothesis

Greenberg *et al*. (1993) postulate that low ant density decreases resource competition by reducing standing crops and allowing honeydew levels enough to sustain birds. Indeed, the density of ants in this study was low, but visits of other honeydew consumer insects such as Diptera and Hemiptera were extremely high, sometimes even higher than bird's; yet, competition itself may not explain the development of bird-Hemiptera systems. The constituents of the phloem and, hence, the honeydew, may differ according to plant species, plant part infested, plant age or seasonally (Way 1963; Latta *et al*. 2001). These differences in honeydew chemistry may affect foraging by ants, and then by birds (Gullan 1997; Latta *et al*. 2001). No birds have visited honeydew produced by the scale insect *Coelostomidia wairoensis* (Coccoidea: Coelostomidiidae) in kanuka tree forests in New Zealand, even without ants (Gardner-Gee *et al*. 2013). This may be another suggestion that ant's presence is not the only factor that explains bird foraging patterns. In this case, the presence of *Vespula* (Vespidae) wasps was considered a feasible explanation.

We found evidences that honeydew is consumed by a broad range of birds and insects in a rain subtropical forest, even when nectar – a high energetic resource - is available, suggesting a resource partition among honeydew consumers. Although honeydew may be a seasonal opportunistic resource, it seems to be highly worth defending, because of high sugar concentration of its composition and its easy-access.

In the present study, we observed seasonality in honeydew production, which resulted in a peak of bird visitation to the resource in the winter months. The premise of a temporal segregation was confirmed for some bird's species, with greater use in the morning period, however, the premise of a spatial segregation was not confirmed. We detected a large number of agonistic behaviors among birds when foraging on honeydew, proving this to be a highly disputed resource. We verified a great use of honeydew by arthropods, mainly bees and wasps, refuting the "Convergence hypothesis" (Greenberg *et al*. 1993) with regard that competition for the resource is a limiting factor for the avian use of honeydew.

This work helped to clarify how the consumption of a highly energetic resource, which is honeydew, occurs in an Atlantic Forest area of Brazil, a region in which this interaction has been poorly documented. Data acquired in this study can build the knowledge base of this trophic interaction in the studied biome, and serve as a parameter for future studies in the region and for comparison with other areas around the world.

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TABLES

Table 1. Birds consumer of honeydew on *Inga* spp. in Carlos Botelho State Park, Brazil. Nomenclature of bird species followed Hoyo & Collar (2017). Diet based on Wilman (2014): I = insectivores, O = omnivores, F / N = frugivores / nectarivores; Body mass in grams, based on Wilman (2014); No visits = total number of visits to honeydew; Visits (%) = percentage of visits; Mean time = mean time foraging on honeydew in minutes; No tubes = total number of anal tubes visited; feeding rate = anal tubes visited / minute and Record: P = Previously registered in previous papers, N = New record.

Species	Family	Diet	Body mass	No visits	Visits (%)	Mean time	No tubes	Feed rate	Record
Dusky-throated Hermit (*Phaethornis squalidus*)	Trochilidae	F/N	3.4	1	0,03	0,41	2	60,48	N
Violet-capped Woodnymph (*Thalurania glaucopis*)	Trochilidae	F/N	4,8	778	23,86	0,94	25270	34,91	Teixeira *et al*. 2013
Sapphire-spangled Emerald (*Amazilia lactea*)	Trochilidae	F/N	4,6	3	0,09	0,41	75	60,48	Teixeira *et al*. 2013
Yellow-fronted Woodpecker (*Melanerpes flavifrons*)	Picidae	O	57,8	37	1,13	10,47	3190	20,71	N
Streaked Xenops (*Xenops rutilans*)	Xenopidae	I	11,2	1	0,03	2,00	10	5,00	N
White-browed Foliage-gleaner (*Anabacerthia amaurotis*)	Furnariidae	I	19,2	1	0,03	2,00	10	5,00	N
Greenish Tyrannulet (Phyllomyias virescens)	Tyrannidae	I	8,2	3	0,09	7,33	480	21,82	N
Sepia-capped Flycatcher (*Leptopogon amaurocephalus*)	Rhynchocyclidae	I	11,7	1	0,03	0,17	3	17,65	N
Greenish Schiffornis (Schiffornis virescens)	Tityridae	O	25,6	1	0,03	3,00	50	16,67	N
Bananaquit (*Coereba flaveola*)	Coerebinae	F/N	10	1042	31,95	4,40	1E+05	39,12	Teixeira *et al*. 2013
Tropical Parula (*Setophaga pitiayumi*)	Parulidae	I	6,82	82	2,51	4,37	13292	40,69	Sick 1988
Golden-crowned Warbler (*Basileuterus culicivorus*)	Parulidae	I	10,5	59	1,81	2,10	3126	26,58	N
Rufous-headed Tanager (*Hemithraupis ruficapilla*)	Thraupidae	I	11	29	0,89	3,08	2084	29,45	Teixeira *et al*. 2013
Blue Dacnis (*Dacnis cayana)*	Thraupidae	O	13	169	5,18	4,22	14165	28,68	Teixeira *et al*. 2013
Green-headed Tanager (*Tangara seledon*)	Thraupidae	F/N	18,7	213	6,53	4,39	12458	30,12	N
Red-necked Tanager (*Tangara cyanocephala*)	Thraupidae	F/N	18	42	1,29	5,07	2270	29,87	N
Brassy-breasted Tanager (*Tangara desmaresti*)	Thraupidae	F/N	20,4	1	0,03	6,00	180	30,00	N
Burnished-buff Tanager (*Tangara cayana*)	Thraupidae	F/N	18	17	0,52	3,33	1616	30,33	Teixeira *et al*. 2013
Sayaca Tanager (*Thraupis sayaca)*	Thraupidae	O	32,5	116	3,56	3,30	7886	30,24	Teixeira *et al*. 2013
Azure-shouldered Tanager (*Thraupis cyanoptera*)	Thraupidae	F/N	43,3	4	0,12	3,00	270	30,00	N
Golden-chevroned Tanager (*Thraupis ornata*)	Thraupidae	F/N	33	610	18,71	13,82	2E+05	29,71	N
Ruby-crowned Tanager (*Tachyphonus coronatus*)	Thraupidae	I	29,3	14	0,43	1,69	633	28,73	Sick 1988, Teixeira *et al*. 2013
Chestnut-bellied Euphonia	Fringillidae	F/N	14,4	4	0,12	0,40	27	16,67	N

(*Euphonia pectoralis*)										
Variable Oriole (*Icterus pyrrhopterus*)	Icteridae	O		8	0,25	4,83	780	26,90		N
Golden-winged Cacique (*Cacicus chrysopterus*)	Icteridae	O	36,2	25	0,77	7,80	3255	20,87		N

Table 2. Number of total visits of the ten most frequent bird species to honeydew in different tree areas, in Carlos Botelho State Park Legend: Thgl= *Thalurania glaucopis;* Mefl= *Melanerpes flavifrons;* Cofl= *Coereba flaveola*; Sepi= *Setophaga pitiayumi*; Bacu= *Basileuterus culicivorus*; Heru= *Hemithraupis ruficapilla;* Daca= *Dacnis cayana;* Tase= *Tangara seledon;* Tacy= *Tangara cyanocephala*; Thsa= *Thraupis sayaca*; Thor= *Thraupis ornata*; Cach= *Cacicus chrysopterus.*

	Thgl	Mefl	Cofl	Sepi	Bacu	Heru	Daca	Tase	Tacy	Thsa	Thor	Cach
Peripheral area	291	16	760	78	17	23	111	69	12	75	365	18
Central Area	481	1	39	0	39	0	6	25	3	4	5	2
Low	253	1	24	0	36	0	2	13	2	0	1	0
Medium	167	0	10	0	3	0	0	10	0	2	4	2
High	61	0	5	0	0	0	4	2	1	2	0	0

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FIGURES

Fig. 1. Scale insect secreting honeydew (drop) through the waxy anal tube in Carlos Botelho State Park, southeastern Brazil. Fungi growing on the base of *Inga* spp. branches, giving it a blackened appearance. Photo by R. S. Capelão.

Fig 2. Bananaquit (*Coereba flaveola*) (left) and Yellow-fronted Woodpecker (*Melanerpes flavifrons*) foraging on honeydew. Photo by R. S. Capelão (left) and A. J. Piratelli (right) in Carlos Botelho State Park, southeastern Brazil.

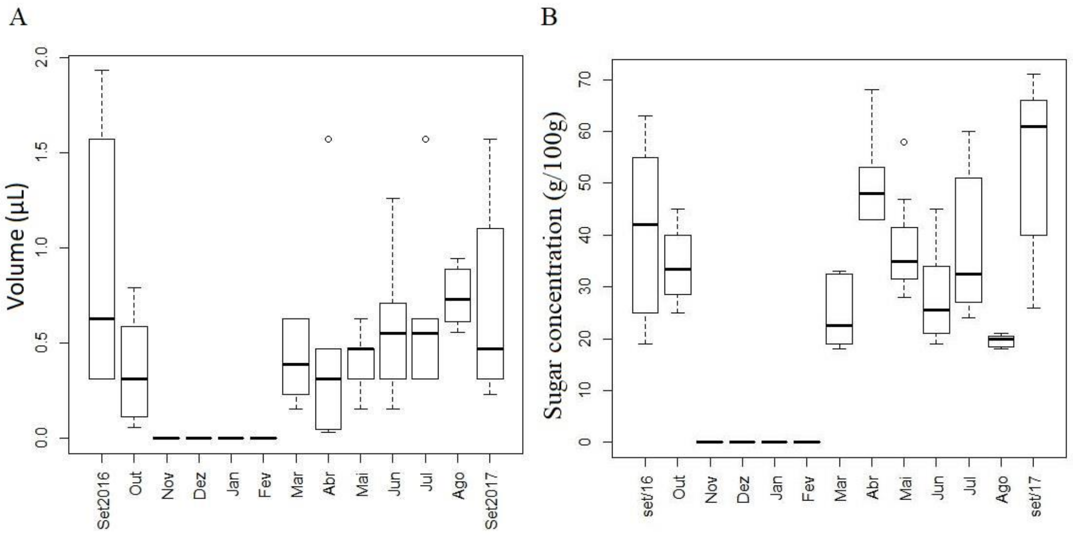

Fig. 3. (A) Median of honeydew volume (µL). (B) Median of sugar concentration (g/100g) of honeydew throughout the year (95% confidence limits) in Carlos Botelho State Park, southeastern Brazil

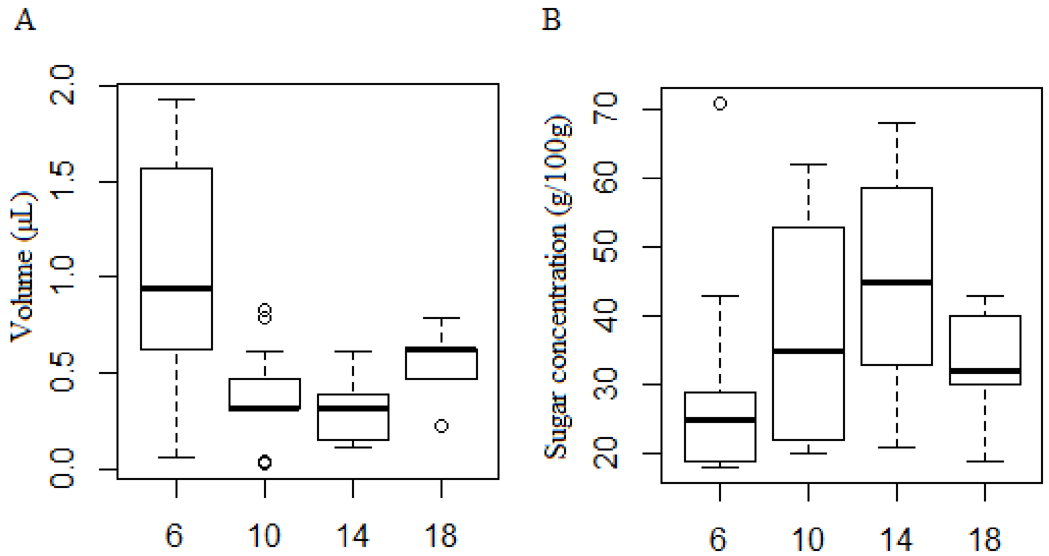

Fig. 4. (A) Median of honeydew volume (µL), (B) Median of honeydew sugar concentration (g/100g) between 6:00 a.m. to 6:00 p.m. (95% confidence limits).

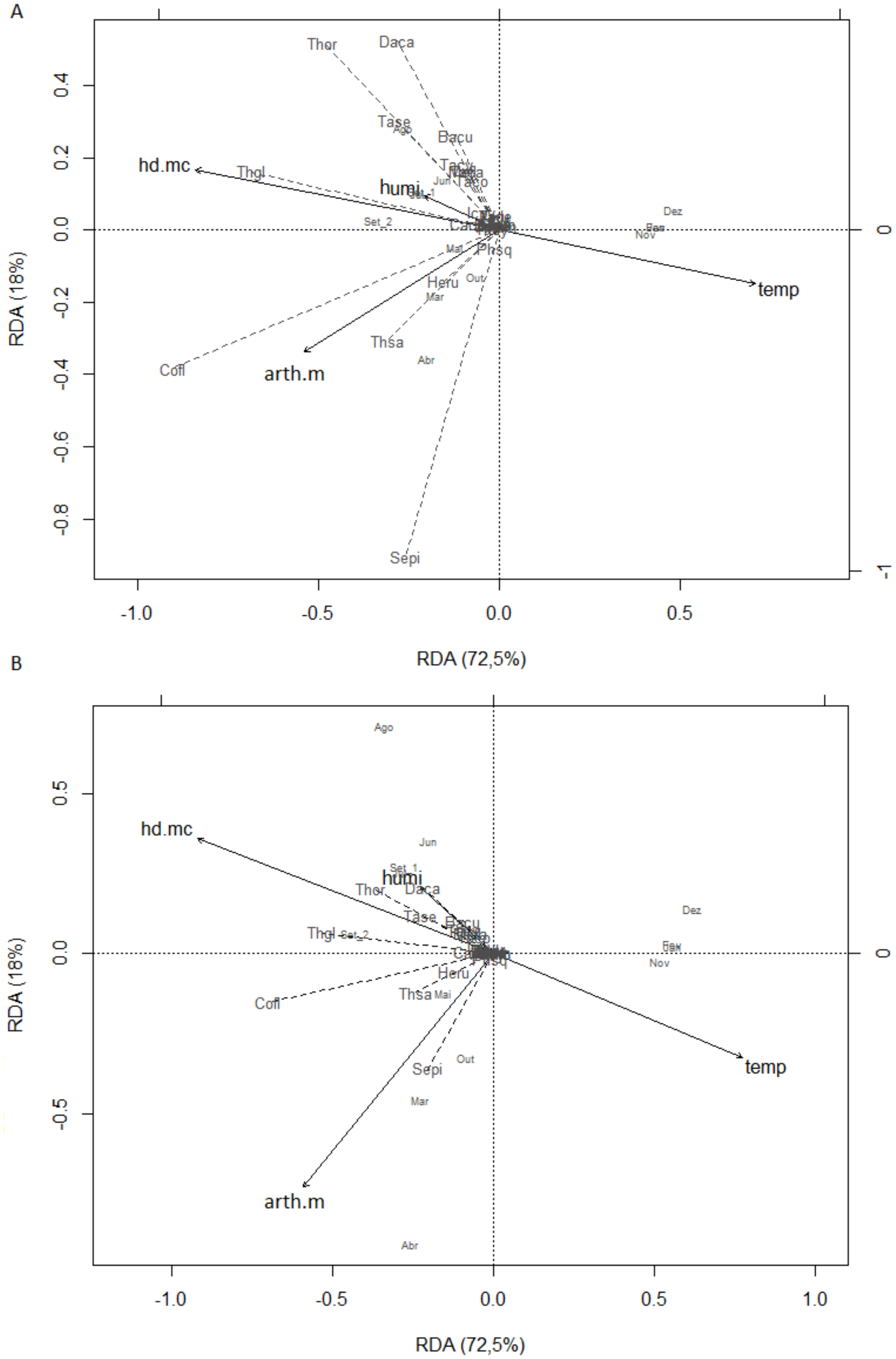

Fig. 5. Redundancy analysis (RDA) relating the influence of the variables on the number of bird visits to honeydew. (A) Focus on the composition of the bird species; (B) Focus on the monthly variation (sample units). Legend: hd.mc= honeydew volume (µL), humi= air humidity (%), arth.m= mean number of honeydew consumer arthropods and temp= temperature (°C).

SUPPLEMENTARY INFORMATION

Appendix S1. Variables affecting consumption of honeydew by birds in Carlos Botelho State Park, Brazil. Legend: visi.tt= total number of bird visits; rich=bird richness; hd.mc= mean honeydew volume (µL); brix= mean honeydew sugar concentration (g/100g); temp= mean temperature (ºC); humi= mean relative humidity (%); dew= dew point (ºC); hPa= pressure (hPa); wind (m/s); rad= radiation (KJ/m^2); rain (mm); fruit= number of fruits; flr= number of flowers; infest.m= mean scale insect infestation; tubes= mean percetage of anal tubes with honeydew*;* inse.m= mean number of honeydew consumer arthopods; arth.tt= total honeydew number of consumer arthopods.

Month	visi.tt	rich	hd.mc	brix	Temp	humi	dew	hPa	Wind	rad	rain	fruit	flr	infest.m	tubes	arth.m	arth.tt
Sep_1	485	12	0.954	41.36	15.9	581.9	7.54	942.5	1.924	1534.76	0.0049	256.78	186.24	5	100	39	351
Oct	67	5	0.386	34.25	24.9	75	19.11	937.1	2.11	960.37	0	245	425	2	10	193.3	1160
Nov	0	0	0	0	22.4	73.21	17.4	938.29	3.46	1622.69	1.3	200	100	1	0	0	0
Dec	0	0	0	0	25.1	78.08	20.34	930.71	3.2	1554.78	0.425	168.75	172.92	2	0	0	0
Jan	0	0	0	0	23.4	83.54	20.11	928.3	1.71	1551.73	0.5	297.5	190	3	0	0	0
Feb	0	0	0	0	23.4	78.58	18.52	929.24	0.59	1343.48	0	90	52.5	3.5	0	0	0
Mar	127	8	0.405	24.58	18.4	88.44	24.35	826	119.46	483.46	9.55	0	19	5	20	148	444
Apr	62	6	0.317	50.5	18.9	85.06	15.38	939.43	0.75	1467	0	3.33	19.33	5	38.9	203.3	610
May	205	12	0.393	38	13.9	76.55	52.23	604.81	343.21	1292	1058.1	150	20.5	5	40	42.5	255
Jun	596	16	0.57	28.12	15.8	85.34	12.27	944.5	1.87	2068.33	0	35	115	5	97.5	33.33	200
Jul	936	16	0.609	38.12	15.9	83.03	10.95	948.3	0.86	1616.25	0.025	19.62	541.1	5	100	63.67	382
Aug	542	14	0.747	19.57	14	85.64	11.53	947.13	3.83	787.29	0	20.45	588.09	5	94.5	7.2	36
Sep_2	241	14	0.691	54.17	19.5	77.26	12.72	941.63	1.03	1028.67	0	0	964	5	60	161.4	807

Appendix S2. Visits to honeydew for each month from the first half of September 2016 (Sep_1) to the first half of September 2017 (Sep_2) for the 25 species registered. Legend: M=Month; Phsq= *Phaethornis squalidus;* Thgl= *Thalurania glaucopis;* Amla = *Amazilia lactea*; Mefl= *Melanerpes flavifrons;* Xeru= *Xenops rutilans;* Anam= *Anabacerthia amaurotis;* Phvi= *Phyllomyias virescens*; Leam= *Leptopogon amaurocephalus*; Scvi= *Schiffornis virescens;* Cofl= *Coereba flaveola;* Sepi= *Setophaga pitiayumi;* Bacu= *Basileuterus culicivorus;* Heu= *Hemithraupis ruficapilla;* Daca= *Dacnis cayana;* Tase= *Tangara seledon;* Tacy= *Tangara cyanocephala*; Tade= *Tangara desmaresti;* Taca= *Tangara cayana;* Thsa= *Thraupis sayaca;* Thcy= *Thraupis cyanoptera;* Thor= *Thraupis ornata;* Taco= *Tachyphonus coronatus;* Eupe= *Euphonia pectoralis;* Icpy= *Icterus pyrrhopterus;* Cach= *Cacicus chrysopterus.*

M.	Phsq	Thgl	Amla	Mefl	Xeru	Anam	Phvi	Leam	Scvi	Cofl	Sepi	Bacu	Heru	Daca	Tase	Tacy	Tade	Taca	Thsa	Thcy	Thor	Taco	Eupe	Icpy	Cach
Sep_1	0	66	0	11	0	0	0	0	0	133	5	0	10	21	31	0	0	6	41	0	142	0	0	6	13
Oct	0	11	0	0	0	0	0	0	0	45	1	0	2	0	0	0	0	0	2	0	6	0	0	0	0
Nov	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dec	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jan	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Feb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mar	1	15	0	0	0	0	0	0	0	44	30	0	2	0	0	0	0	0	24	0	9	0	0	0	2
Apr	0	10	0	0	0	0	0	0	0	25	21	0	1	0	3	0	0	0	2	0	0	0	0	0	0
May	0	39	0	0	0	0	0	0	0	82	6	3	4	10	17	12	0	0	15	2	13	0	2	0	0
Jun	0	125	0	17	0	0	0	1	1	157	4	14	1	34	95	14	0	1	6	0	122	2	2	0	0
Jul	0	289	3	5	0	1	3	0	0	273	14	27	2	31	5	0	0	0	8	2	259	5	0	0	9
Aug	0	171	0	0	1	0	0	0	0	170	1	14	5	54	59	12	1	6	5	0	39	4	0	0	0
Sep_2	0	52	0	4	0	0	0	0	0	113	0	1	2	19	3	4	0	4	13	0	20	3	0	2	1

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Appendix S3. Number of agonistic behaviors among the 25 consuming species of honeydew in the Carlos Botelho State Park, Brazil. Legend: Ags. = aggressors; Beat.= beaten; U.s.= unidentified species; Phsq= *Phaethornis squalidus;* Thgl= *Thalurania glaucopis;* Amla = *Amazilia lactea*; Mefl= *Melanerpes flavifrons;* Xeru= *Xenops rutilans;* Anam= *Anabacerthia amaurotis;* Phvi= *Phyllomyias virescens*; Leam= *Leptopogon amaurocephalus*; Scvi= *Schiffornis virescens;* Cofl= *Coereba flaveola;* Sepi= *Setophaga pitiayumi;* Bacu= *Basileuterus culicivorus;* Heu= *Hemithraupis ruficapilla;* Daca= *Dacnis cayana;* Tase= *Tangara seledon;* Tacy= *Tangara cyanocephala*; Tade= *Tangara desmaresti;* Taca= *Tangara cayana;* Thsa= *Thraupis sayaca;* Thcy= *Thraupis cyanoptera;* Thor= *Thraupis ornata;* Taco= *Tachyphonus coronatus;* Eupe= *Euphonia pectoralis;* Icpy= *Icterus pyrrhopterus;* Cach= *Cacicus chrysopterus.*

Beat	Phsq	Thgl	Amla	Mefla	Xeru	Anam	Phvi	Leam	Scvi	Cofl	Sepi	Bacu	Heru	Daca	Tase	Tacy	Tade	Taca	Thsa	Thcy	Thor	Taco	Eupe	Icpy	Cach
Ags																									
Phsq	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thgl	0	82	1	0	0	0	0	0	0	5	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0
Amla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mefla	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Xeru	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anam	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phvi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leam	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scvi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cofl	0	30	0	0	0	0	0	0	0	100	6	4	0	0	0	0	0	0	0	0	0	0	0	0	0
Sepi	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bacu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heru	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Daca	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Tase	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0
Tacy	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tade	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Taca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thsa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Thcy	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Thor	0	73	0	1	0	1	0	1	0	215	12	10	1	15	44	2	0	1	43	0	43	10	1	1	1
Taco	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eupe	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Icpy	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cach	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

Appendix S4. Forward selection of the factors that may influence honeydew consumption by birds. Total, unconstrained and constrained inertia explained by Redundancy Analysis (RDA) performed between birds visits to honeydew and the significant variables selected in the forward selection. Significance of the whole model is provided. R2 = coefficient of multiple determination; Cum = cumulated; Adj = adjusted takes into consideration the number of degrees of freedom. Variables: hd.mc= honeydew volume (µL); arth.m= mean number of honeydew consumer arthropods, temp= temperature (°C), humi= air humudity (%), rainfall (mm), hpa (Pressure), flr = number of flowers, brix= mean honeydew sugar concentration (g/100g), fruit = number of fruits, infest.m= mean scale insect infestation.

Forward selection	Order	R2	R2Cum	AdjR2Cum	*F*	*P*
hd.mc	1	0.501	0.501	0.455	11.030	0.001
arth.m	10	0.187	0.687	0.625	5.962	0.004
Temp	3	0.090	0.777	0.702	3.616	0.003
Humi	4	0.056	0.833	0.750	2.706	0.029
Rainfall	6	0,037	0.870	0.777	1.990	0.102
hPa	5	0.033	0.903	0.807	2.057	0.194
Flr	8	0.027	0.931	0.834	1.971	0.174
Brix	2	0.017	0.948	0.843	1.284	0.343
Fruit	7	0.009	0.957	0.826	0.629	0.570
infest.m	9	0.004	0.960	0.762	0.190	0.807
RDA model	Inertia	Proportion	Rank			
Total	0.310	1.000				
Constrained	0.259	0.833	4			
Unconstrained	0.052	0.167	7			
significance	*Df*	Var	*F*	N.Perm	Pr(>F)	
Model	4	0.258	9.994	999	0.001	
Residual	8	0.051				