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RESEARCH ARTICLE

Feeding behavior by hummingbirds (Aves: Trochilidae) in artificial food patches in an Atlantic Forest remnant in southeastern Brazil

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ABSTRACT. During flight, hummingbirds achieve the maximum aerobic metabolism rates within vertebrates. To meet such demands, these birds have to take in as much energy as possible, using strategies such as selecting the best food resources and adopting behaviors that allow the greatest energy gains. We tested whether hummingbirds choose sources that have higher sugar concentrations, and investigated their behaviors near and at food resources. The study was conducted at Atlantic forest remnant in Brazil, between June and December 2012. Four patches were provided with artificial feeders, containing sucrose solutions at concentrations of 5%, 15%, 25% and 35% weight/volume. Hummingbird behaviors were recorded using the ad libitum method with continuous recording of behaviors. The following species were observed: the Brazilian ruby *Clytolaema rubricauda* (Boddaert, 1783), Violet-capped woodnymph *Thalurania glaucopis* (Gmelin, 1788), Scale-throated hermit *Phaethornis eurynome* (Lesson, 1832), White-throated hummingbird *Leucochloris albicollis* (Vieillot, 1818), Versicoloured emerald *Amazilia versicolor* (Vieillot, 1818), Glittering-bellied emerald *Chlorostilbon lucidus* (Shaw, 1812) and other *Phaethornis* spp. *C. rubricauda*, *P. eurynome* and *Phaethornis* spp. visited the 35%-sucrose feeders more often, while the *T. glaucopis* visited the 25%-sucrose feeders more often. *L. albicollis* and *A. versicolor* visited more often solutions with sugar concentration of 15%. *C. lucidus* visited all patches equally. Three behavioral strategies were observed: 1) *C. rubricauda* and *T. glaucopis* exhibited interspecific and intraspecific dominance; 2) the remaining species exhibited subordinance to the dominant hummingbirds, and 3) *P. eurynome* and *Phaethornis* spp. adopted a hide-and-wait strategy to the dominant hummingbird species. The frequency of aggressive behaviors was correlated with the time the hummingbird spent feeding, and bird size. Our results showed that hummingbirds can adopt different strategies to enhance food acquisition; that more aggressive species feeding more than less aggressive species; and that the birds, especially if they were dominant species, visited high quality food resources more often.

KEY WORDS. Behavioral strategies, dominance, food resources, subordination, trapline.

INTRODUCTION

Hummingbirds are specialized birds that consume predominantly nectar, but can also consume small arthropods (Cotton 2007). Individual hummingbirds have been recorded foraging in more than 200 flowers per day in a single plant (Snow and Snow 1986, Sick 1997, Ortiz-Pulido et al. 2012). They reach the highest aerobic metabolic rates among vertebrates during flight, which explains these voracious appetites (Suarez et al. 1990).

The net energy concept postulates that energetic costs during foraging must be lower than energy intake during foraging (Heinrich 1975). In order to obtain the necessary amount of energy, hummingbirds can select and protect the richest food patches available at an area (Loss and Silva 2005). Normally, sugar concentrations in the nectar of the flowers visited by hummingbirds vary between 20–25% (Roberts 1996), and experimental manipulations revealed that hummingbirds prefer sugar concentrations higher than 35% (Tamm and Gass 1986, Roberts 1996, López-Calleja et al. 1997). However, this preference was observed only when the nectar was collected during repeated licking (Kingsolver and Daniel 1983). Thus, in experiments with artificial flowers (hummingbird feeders), it is expected that hummingbirds forage more in feeders that had

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higher sucrose concentration, since energy intake is greater in these feeders and the volume of nectar is large enough to permit repeated licking cycles.

Three behavioral strategies can be adopted by hummingbirds when foraging: (A) dominance/territoriality, when an individual defends a territory containing food resources and excludes competitors from the resource (Feisinger 1976, Feisinger and Colwell 1978, Stiles 1978, Cotton 1998), and (B) intruder/subordinance, when an individual forages in defended patches until it is expelled by the territorial hummingbird (Feisinger and Colwell 1978, Stiles 1978, Barbosa-Filho and Araújo 2013). A third strategy is known as trapline foraging (C), when an individual repeatedly visits a set of plants in routes through different patches, exploiting resources without displaying any territorial behavior (Feisinger and Colwell 1978, Rios et al. 2010, Tello-Ramos et al. 2015). A trapliner hummingbird can either be expelled by territorialists when foraging in one food resource, or it can simply ignore the presence of the territorial individuals by moving across different territories (Feisinger and Colwell 1978, Garrisson and Gass 1999). Thus, a trapliner individual also can eventually act as a subordinate one, performing strategy B, yet an individual that acts according to strategy B may not necessarily adopt a traplining strategy.

Typical behaviors exhibited by territorial hummingbirds are "perching near the food resource" (Loss and Silva 2005, Longo and Fischer 2006), inter- and intraspecific attacks (Loss and Silva 2005), and intense vocalizations and visual displays (Mendonça and dos Anjos 2006). Since the energetic cost of defending a territory can be up to three times higher than the cost of non-aggressively foraging (Gill and Wolf 1975), it is expected that individuals will engage in resource defense only when the fitness benefits of territoriality outweigh its costs (Brown 1964). Territorial individuals commonly have access to more food than subordinate ones (Justino 2009, Rios et al. 2010), and the intensity of the defense should increase with the quality of the defended resource (Justino et al. 2012). Hummingbirds, for example, defend clumped flowers rich in nectar more aggressively than scattered flowers (Temeles et al. 2005). Moreover, body size affects territoriality in hummingbirds, with medium to larger size species exhibiting more territoriality than smaller ones (Feisinger and Colwell 1978, Abrahamczyk and Kessler 2014).

The aim of this study was to evaluate the feeding behavior of hummingbirds in artificial food patches at an Atlantic Forest fragment in Brazil. We described the behavior exhibited by the hummingbirds in the food patches and identified the sugar concentration most visited by the birds. We hypothesized that: 1) most feeding visits would be to the feeders that have 35% sugar-concentration, since this food resource provides more energy to the birds (Tamm and Gass 1986, Roberts 1996); 2) larger and heavier hummingbirds will defend the feeders from smaller and lighter birds, since body size determines dominance in hummingbirds (Antunes 2003, Araújo-Silva and Bessa 2010); 3) smaller hummingbirds will exhibit subordination behaviors and bigger hummingbirds will exhibit dominance behaviors; and (4) the frequency of aggression behaviors exhibited by the hummingbirds will be correlated with the time spent feeding on the feeders, since dominant birds will have more access to the feeders due to their greater aggressiveness.

MATERIAL AND METHODS

The study was conducted in the Itacolomi State Park, in the city of Ouro Preto, Minas Gerais, southeastern Brazil (20°23'S, 43°30'W), in an Atlantic Forest remnant, from June to December 2012. Four artificial food patches, distant linearly 1.5-2.5 m from each other in a 6 m^2 area, were constructed in the core of the forest fragment (70m distant from the forest edges), each containing five artificial hummingbird feeders (200 ml plastic feeders Mr Pet®, with three red plastic flowers with short corollas) filled with a sugar-water solution of 5, 15, 25 or 35%. Nectar sugar concentration was computed diluting commercial sucrose in filtered water; e.g., in 35% sugar concentration, 350 g of sucrose was diluted in 750 ml of filtered water. Each food patch contained feeders filled with only one concentration, which remained available all day long. The solution was replaced each morning after the feeders were cleaned.

Behavioral recording sessions occurred continuously from 07:00 to 10:00 a.m. and from 02:00 to 05:00 p.m. each day, totaling 325 hours of observation (54 non-consecutive days in total). The birds were observed at a distance of 10m, using a 10x50 (Nikon TX Extreme) binocular. Hummingbirds were observed ad libitum with continuous recording of behaviors (Altmann 1974), and the birds were identified according to Sigrist (2009). We focused on both territorial and subordinate hummingbirds, recording all behaviors during the entire observation period. Since no hummingbirds were captured and marked, to avoid pseudoreplication, we only collected data on the same hummingbird species after intervals of 30 minutes, counting from the time the individual of that species left, or when two or more individuals of the same species were feeding at the same time on the food patch (we recorded behaviors of more than 10 ± 6 individuals feeding at the same time on the food patch). We evaluated the time spent in each food patch and the behavior exhibited by the hummingbirds in each food patch. An ethogram was built based on 100h of pilot observations and information from the scientific literature (Barçante and Mahecha 2004, Loss and Silva 2005, Toledo and Moreira 2008, Araújo-Silva and Bessa 2010) (Table 1).

Friedman's non-parametric ANOVA with Dunn's post-hoc tests were used to evaluate if the hummingbird species differed in the frequency of the behaviors they exhibited. Both frequency of behaviors and the time spent in the behavior were used in the analyses of the "feeding", "alert" and "vocalizing" behaviors; only the number of observations was used in the analysis of the other behaviors evaluated. Time spent feeding was used to evaluate sugar concentrations most visited by each

Table 1. Ethogram for the hummingbirds recorded at the Itacolomi State Park, Ouro Preto, Minas Gerais, Brazil.

Abbreviation	Behavior	Description
FEE	Feeding	Hummingbird feeds in the artificial feeder, hovering or perched.
EXP	Expelling*	Hummingbird 1 expels hummingbird 2, pursuing it for long or small distances.
FLE	Fleeing**	Hummingbird 1 flees from hummingbird 2, who expelled it.
FIG	Fighting*	Hummingbirds fight using their beak.
FRI	Frightening*	Hummingbird 1 frightens hummingbird 2 simply due to its appearance in the area.
FRIED	Frightened**	Hummingbird 2 was frightened by hummingbird 1 simply due to its appearance in the area.
EXA	Expel attempt*	Hummingbird 1 tries to expel hummingbird 2, but hummingbird 2 continues to feed without caring about the presence of hummingbird 1.
IMP	Impassive	Hummingbird 2 behaves normally when hummingbird 1 tries to expel it from the feeders.
PRS	Persecution with only one individual identified*	Hummingbird 1 pursue hummingbird 2, but only one individual is identified.
AL	Alert*	Hummingbird perched, observing the food patches.
VOC	Vocalizing*	Hummingbird vocalizes in or near the food patches.

*Aggressive behaviors, **Subordinate behaviors.

Table 2. Average lengths (with tails and bills included) and weights of the hummingbird species recorded at Itacolomi State Park, Ouro Preto, according to Sick (1997) and Dunning-Junior (2008).

Species	Mean length (cm)	Mean weight (g)	Social status in this study
Amazilia versicolor	8.5	4.1	Subordinate
Chlorostilbon lucidus	8.5	2.5	Subordinate
Clytolaema rubricauda	12.0	7.9	Dominant
Leucochloris albicollis	10.5	6.3	Subordinate
Phaethornis eurynome	15.5	5.3	Subordinate
Phaethornis spp.	15.5	5.3	Subordinate
Thalurania glaucopis	11.1	4.8	Dominant

hummingbird species. The frequency of aggression behaviors recorded were summed ("expelling", "fighting", "frightening", "expel attempt", "alert" and "vocalizing") and correlated with the time spent feeding on all sugar concentrations (5-35%) and with hummingbird sizes and weights – according to Sick 1997 (Table 2) – using a Spearman's correlation test (Zar 1999). When an individual expelled or frightened another, he was considered the winner of the agonistic encounter. The individual that was expelled or frightened was considered the loser of the agonistic encounter. The sizes and weights of hummingbird species as defined by Sick (1997) were used in this study. All tests were conducted using the software Minitab v.16, at a confidence level of 95%.

RESULTS

Six species of hummingbirds of were recorded visiting the feeders during the study: Brazilian ruby *Clytolaema rubricauda* (Boddaert, 1783), Violet-capped woodnymph *Thalurania glaucopis* (Gmelin, 1788), Scale-throated hermit *Phaethornis eurynome* (Lesson, 1832), White-throated hummingbird *Leucochloris albicollis* (Vieillot, 1818), Versicoloured emerald *Amazilia versicolor* (Vieillot, 1818), Glittering-bellied emerald *Chlorostilbon lucidus* (Shaw, 1812) and an unidentified species of *Phaethornis* spp. [four species of *Phaethornis* Swainson, 1827 occur in the Itacolomi State Park: *P. eurynome*, *P. pretrei* (Lesson & Delattre, 1839), *P. squalidus* (Temminck, 1822) and *P. ruber* (Linnaeus, 1758) (Ribon 2006); data of more than one *Phaethornis* species could be computed in the results of *Phaethornis* spp., excluding *P. eurynome*, which results were analyzed separately].

The most-visited feeders were those containing a solution of 35% sugar, and the least-visited feeders were those containing a solution of 5% sugar; the frequency of visitations differed between the feeders ($F = 177.380$, d.f. = 3, $p < 0.001$, $n = 94$).

Clytolaema rubricauda, *P. eurynome* and *Phaethornis* spp. visited the feeders with sugar solution of 35% more often (*C. rubricauda*: $F = 164.5$, d.f. = 3, $p < 0.001$, $n = 4568$; *P. eurynome*: $F = 41.7$, d.f. = 3, $P < 0.001$, $n = 409$; *Phaethornis* sp.: $F = 9.6$, d.f. = 3, $p = 0.023$, $n = 71$). *Thalurania glaucopis* visited more often the feeders containing a sugar solution of 25% ($F = 154.6$, d.f. = 3, $p < 0.001$, $n = 5992$). *L. albicollis* and *A. versicolor* visited the feeders containing a sugar solution of 15% more often (*L. albicollis*: $F = 28.81$, d.f. = 3, $p < 0.001$, $n = 97$; *A. versicolor*: $F = 19.93$, d.f. = 3, $p < 0.001$, $n = 15$). *Chlorostilbon lucidus* was the species that less frequently visited the food patches, and no differences were found between the number of visits in each food patch ($F = 3.67$, d.f. = 3, $p = 0.34$, $n = 3$, Fig. 1).

Clytolaema rubricauda won most of the aggressive encounters with other hummingbird species, both in total and in each different sugar solution concentrations, followed by *T. glaucopis* (Table 3). No other species won aggressive encounters (Table 3).

Aggressive behaviors ("expelling", "fighting", and "expel attempt") were exhibited by *C. rubricauda*, *T. glaucopis*, *P. eurynome* and *L. albicollis*. Among the aggressive behaviors, *P. eurynome* and *L. albicollis* exhibited only "expel attempts" against other hummingbirds (Table 4). The other species did not exhibit aggressive behaviors, but displayed subordinate behaviors (Table 4).

Clytolaema rubricauda and *T. glaucopis* behaved similarly, being the most aggressive species observed (Table 4). The behavior "frightened" differed between these species, with *T. glaucopis* being frightened more often (Table 4). The behaviors "expelling" and "fighting" were only exhibited by these species, and *C. rubricauda* expelled more and fought less than *T. glaucopis* (Table 4). *Amazilia versicolor*, *C. lucidus*, *L. albicollis*, *P. eurynome*

Table 3. The outcomes of aggressive encounters between different hummingbird species in relation to different sugar solution.

Winners	Losers						
	Aggressive winning percentages between species						
	A. versicolor	*C. lucidus*	*C. rubricauda*	*L. albicollis*	*P. eurynome*	*Phaethornis* sp.	*T. glaucopis*
C. rubricauda	–	–	–	100.00% (12)	100.00% (44)	100.00% (9)	87.66% (334)
T. glaucopis	100.00% (1)	100.00% (1)	12.34% (47)	100.00% (20)	100.00% (43)	100.00% (10)	–
	Aggressive winning percentages between species in 5% patch						
	A. versicolor	*C. lucidus*	*C. rubricauda*	*L. albicollis*	*P. eurynome*	*Phaethornis* sp.	*T. glaucopis*
C. rubricauda	–	–	–	–	–	–	100.00% (7)
T. glaucopis	100.00% (1)	–	–	–	–	–	–
	Aggressive winning percentages between species in 15% patch						
	A. versicolor	*C. lucidus*	*C. rubricauda*	*L. albicollis*	*P. eurynome*	*Phaethornis* sp.	*T. glaucopis*
C. rubricauda	–	–	–	100.00% (2)	100.00% (3)	–	89.39% (59)
T. glaucopis	–	–	10.61% (7)	100.00% (5)	100.00% (4)	100.00% (1)	–
	Aggressive winning percentages between species in 25% patch						
	A. versicolor	*C. lucidus*	*C. rubricauda*	*L. albicollis*	*P. eurynome*	*Phaethornis* sp.	*T. glaucopis*
C. rubricauda	–	–	–	100.00% (2)	100.00% (9)	100.00% (3)	87.59% (120)
T. glaucopis	–	100.00% (1)	12.41% (17)	100.00% (5)	100.00% (3)	100.00% (3)	–
	Aggressive winning percentages between species in 35% patch						
	A. versicolor	*C. lucidus*	*C. rubricauda*	*L. albicollis*	*P. eurynome*	*Phaethornis* sp.	*T. glaucopis*
C. rubricauda	–	–	–	100.00% (3)	100.00% (27)	100.00% (6)	88.55% (116)
T. glaucopis	–	–	11.45% (15)	100.00% (7)	100.00% (35)	100.00% (4)	–

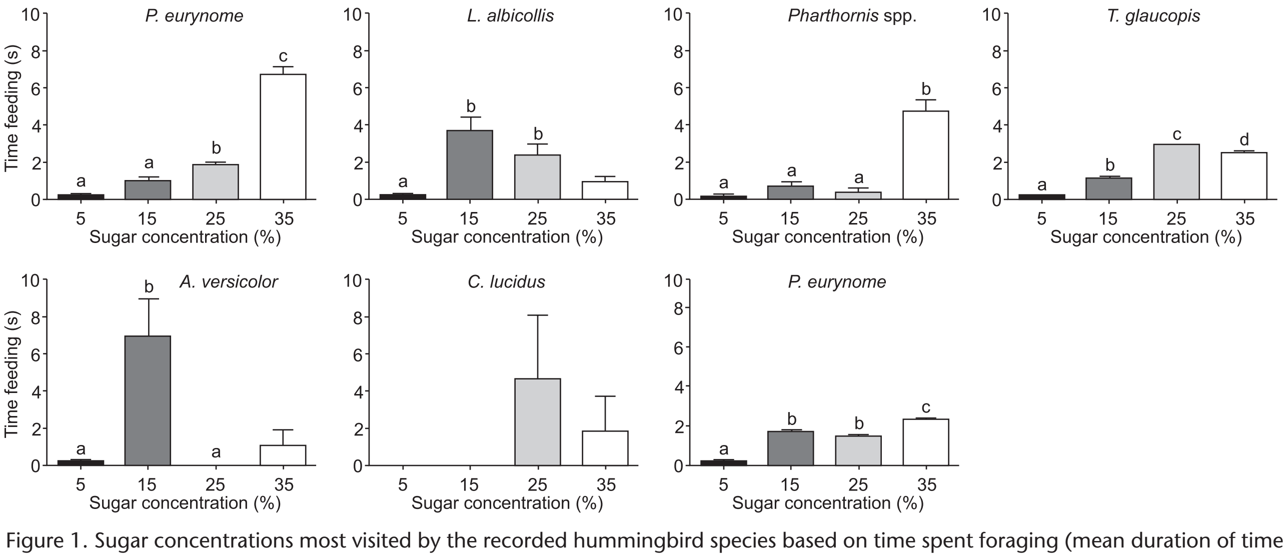


Figure 1. Sugar concentrations most visited by the recorded hummingbird species based on time spent foraging (mean duration of time spent foraging ± SD). Different letters represents statistical differences between sugar solutions as per the results of Dunn's post hoc tests (P-value < 0.05).

and *Phaethornis* spp. also behaved similarly, but these species expressed more subordinate than aggressive behaviors (Table 4).

Thalurania glaucopis got involved in the greatest number of pursuits in which only one bird was identified, and they also expressed more "expel attempts" (Table 4). *Clytolaema rubricauda* stood alert, vocalized, fought and expelled more times than any other species. Furthermore, it stood impassive when faced with the expel attempts of *T. glaucopis* (Table 4) more often than the other species. *Thalurania glaucopis* fed the most, both in terms of time spent feeding and frequency of feeding, followed by *C. rubricauda* and *P. eurynome*, (Tables 3, 4).

Time spent feeding was positively correlated with the expression of aggressive behaviors ($r = 0.86$, $p < 0.0001$) (Fig. 2). Two of the biggest hummingbirds, *C. rubricauda* and *T. glaucopis*,

Table 4. Behaviors (mean number of total recordings ± standard error) exhibited by the six hummingbird species visiting artificial flowers in an Atlantic Forest remnant of Brazil, from June to December 2012.

Behaviors	Species							F	P-value
	A. versicolor	*C. lucidus*	*C. rubricauda*	*L. albicollis*	*P. eurynome*	*Phaethornis* spp.	*T. glaucopis*		
FEE	0.16 ± 0.06 ^{a}	0.03 ± 0.02 ^{a}	48.45 ± 2.02 ^{b}	1.05 ± 0.27 ^{a}	4.44 ± 0.56 ^{c}	0.76 ± 0.16 ^{ac}	63.67 ± 3.71 ^{b}	383.09	< 0.001
EXP	–	–	16.49 ± 1.65 ^{a}	–	–	–	7.62 ± 0.70 ^{a}	325.66	< 0.001
FLE	0.02 ± 0.02 ^{a}	0.03 ± 0.02 ^{a}	9.60 ± 0.02 ^{b}	0.67 ± 0.19 ^{a}	1.26 ± 0.19 ^{a}	0.46 ± 0.10 ^{a}	12.13 ± 0.84 ^{b}	324.56	< 0.001
FIG	–	–	0.58 ± 0.10 ^{a}	–	–	–	2.04 ± 0.27 ^{a}	72.66	< 0.001
FRI	–	–	0.96 ± 0.13 ^{a}	0.01 ± 0.01 ^{b}	0.03 ± 0.09 ^{bc}	–	0.51 ± 0.10 ^{ac}	59.06	< 0.001
FRIED	0.02 ± 0.02 ^{a}	–	0.32 ± 0.08 ^{a}	0.32 ± 0.02 ^{a}	0.53 ± 0.17 ^{a}	0.32 ± 0.02 ^{a}	0.87 ± 0.12 ^{b}	47.68	< 0.001
EXA	–	–	0.03 ± 0.02 ^{ab}	0.01 ± 0.01 ^{a}	0.02 ± 0.02 ^{ab}	–	0.39 ± 0.07 ^{b}	17.00	0.01
IMP	–	–	0.36 ± 0.07 ^{a}	–	0.01 ± 0.01 ^{b}	–	0.11 ± 0.04 ^{ab}	17.19	0.01
PRS	–	0.01 ± 0.01 ^{a}	1.56 ± 0.33 ^{b}	–	0.01 ± 0.01 ^{a}	–	1.88 ± 0.30 ^{b}	77.11	< 0.001
AL	0.02 ± 0.02 ^{a}	0.03 ± 0.02 ^{a}	24.87 ± 1.84 ^{b}	0.34 ± 0.11 ^{a}	0.10 ± 0.05 ^{a}	0.02 ± 0.02 ^{a}	18.40 ± 1.31 ^{b}	341.38	< 0.001
VOC	0.10 ± 0.06 ^{a}	0.11 ± 0.04 ^{a}	2.44 ± 0.29 ^{b}	0.22 ± 0.06 ^{a}	0.14 ± 0.04 ^{a}	–	1.67 ± 0.28 ^{b}	138.76	< 0.001

F = Friedman's test; N = 326; df = 6. Superscript letters: Different letters mean statistical differences according to the Tukey's post hoc test. Behaviors: FEE = feeding; EXP = expelling; FLE = fleeing; FIG = fighting; FRI = frightening; FRIED = frightened; EXA = expel attempt; IMP = impassive; PRS = persecution with only one individual identified; AL = alert; VOC = vocalizing.

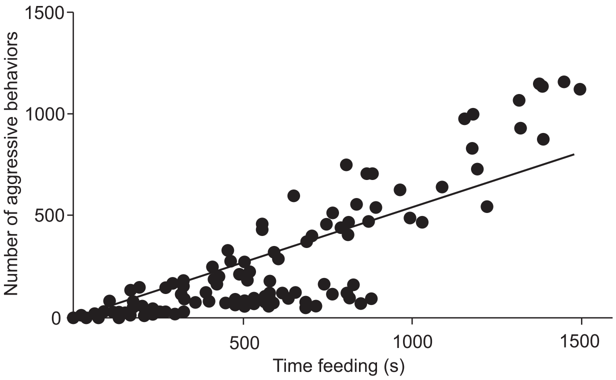


Figure 2. Positive correlation between the time spent feeding and the exhibition of aggressive behaviors by the hummingbirds. For this analysis, we included the time spent feeding by all hummingbird species in all sugar concentrations, and we summed the aggressive behaviors "expelling", "fighting", "frightening", "expel attempt", "alert" and "vocalizing".

expressed more aggressive behaviors than smaller species ($r = 0.24$, $p < 0.05$), but they also expressed more submission behaviors than smaller ones ($r = 0.17$, $p < 0.0001$) (Figs 3–4). The same results were found for hummingbird weight: two of the heaviest hummingbirds, *C. rubricauda* and *T. glaucopis*, expressed more aggressive ($r = 0.39$, $p < 0.001$), as well as submission ($r = 0.17$, $p < 0.001$) behaviors than lighter species (Figs 5–6).

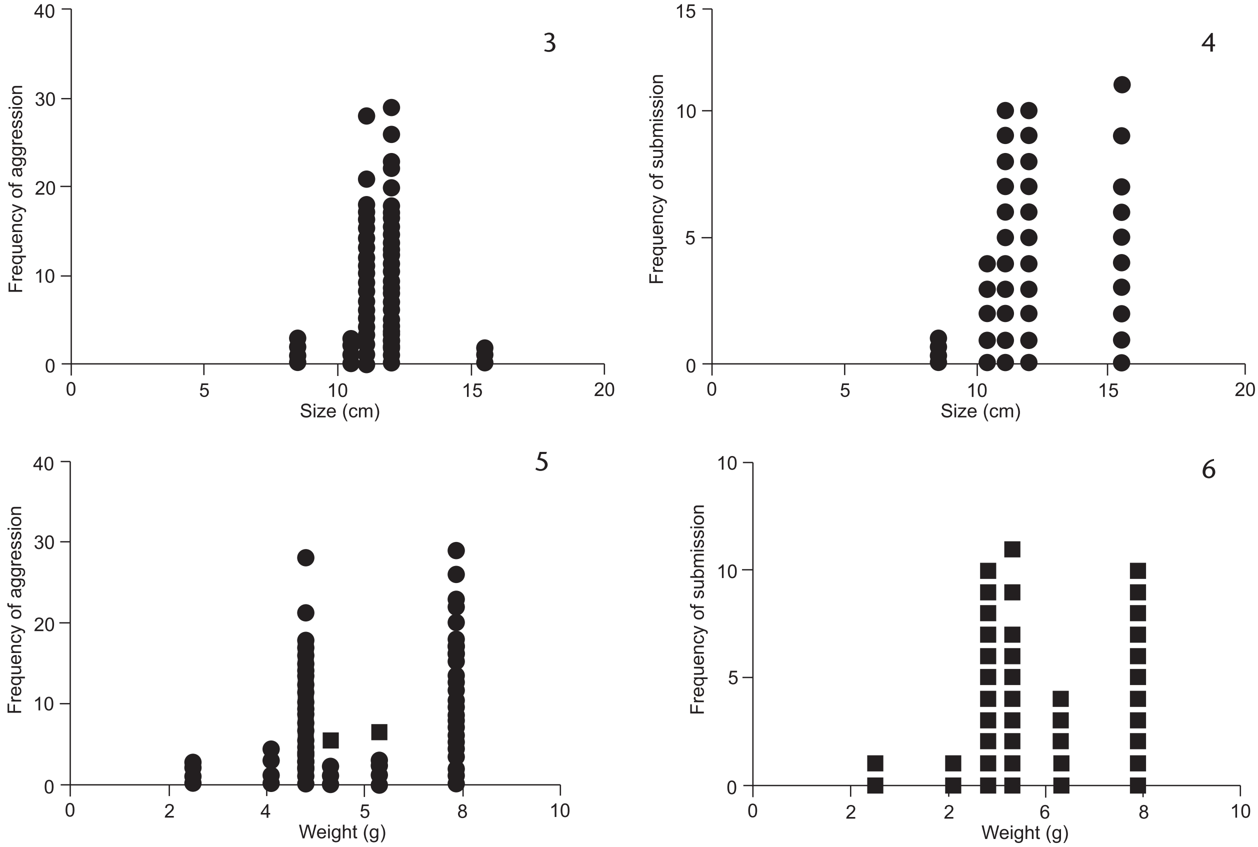
DISCUSSION

Clytolaema rubricauda and *T. glaucopis* were considered dominant hummingbirds in this study since they presented the greatest feeding frequencies and were the most aggressive. Besides, since they expressed the behaviors "alert", "expelling" and "vocalizing" more often than other species, they were also considered territorial. All other hummingbird species in our data fed less and expressed fewer aggressive behaviors, and were therefore considered subordinates.

Thalurania glaucopis and *C. rubricauda* also exhibited the "fleeing" behavior more often, due to the great number of pursuits within and between individuals of these two species. The frequency of aggressive behaviors exhibited by *A. versicolor*, *L. albicollis*, *P. eurynome* and *Phaethornis* spp. was statistically lower than by *T. glaucopis* and *C. rubricauda*; the former species were expelled from the feeders by the latter dominant species, therefore feeding less in the artificial patches. Dominant species limit the access of subordinate species to food sources (Stiles 1978, Roussau et al. 2014) when defending a territory, but only if the energy gain is higher than the energy loss (Heinrich 1975). The artificial food patches created in this study, especially those with 35% sugar concentration, had enough energy to warrant the expression of territorial behaviors. These behaviors allowed the dominant species to have more access to food resources than the subordinate species. More aggressive and territorial hummingbirds spent more time feeding in the artificial flowers in this study than the less aggressive and subordinate species, confirming our hypothesis.

One of the factors determining aggressive behavior in hummingbirds is body size; the bigger and heavier the hummingbird is, the more dominant it is (Antunes 2003, Loss and Silva 2005, Mendonça and dos Anjos 2006, Rodrigues et al. 2009). In this study, small and light hummingbird species were expelled from the food patches by the bigger and heavier species, except for *Phaethornis* spp. and *P. eurynome* (Sick 1997), which were expelled the most from the food patches, even though they are the biggest recorded in the study area.

Justino (2009) and Rios et al. (2010) found that individuals of *Phaethornis* explored less the food resources they were studying



Figures 3–6. Positive correlation between size (cm) and the exhibition of aggressive (3) and submissive (4) behaviors by the hummingbirds. Positive correlation between weight (g) and the exhibition of aggressive (5) and submissive (6) behaviors by the hummingbirds. For both analysis, we included aggressive and submissive behaviors exhibited by all hummingbird species in all sugar concentrations, and we summed the aggressive behaviors "expelling", "fighting", "frightening", "expel attempt", "alert" and "vocalizing", and the submissive behaviors "fleeing" and "frightened".

than other hummingbird genera. This genus is known to use the trapline strategy for food acquisition, where routes are followed with no defined territories (Feisinger and Colwell 1978, Gill 1988, Garrisson and Gass 1999 Temeles et al. 2006, Rios et al. 2010). In this study, *Phaethornis* hummingbirds avoided confrontations with territorial species, hiding whenever dominant individuals arrived in the area. This could explain the low number of species of this genus recorded feeding in this and other studies, even though they are bigger than the dominant species recorded here. It is interesting to observe that even in our limited sample size, the Phaetornithinae in this study showed a preference for the richest sugar solution (35%); their large size probably provided some protection against the dominant species *C. rubricauda* and *T. glaucopis*. They were recorded being frightened many times by the dominant species, but instead of flying away, they hid in the shrubs, remained quiet, and returned to the feeder soon after the dominant species left the area. To the best of our knowledge, this hide-and-wait strategy had never being recorded for Phaethornithinae before. Thus, our hypothesis of bigger and heavier hummingbirds being the most aggressive were partially corroborated, since not only size seemed to be related to aggressive behavior and time spent feeding, but also the behavioral strategy adopted by the hummingbird, with bigger territorial hummingbirds and bigger trapliners feeding more than smaller submissive ones.

Hummingbirds often show food preferences (Heinrich 1975, Loss and Silva 2005), but not all species do. In this study, five out of seven species fed more on the 25-35% sucrose feeders, showing that hummingbirds prefer the most energy-dense solutions. Barçante and Mahecha (2004) analyzed the interactions between two species in areas with food resources available, and found that the dominant species selected the resources according to their quantity and quality, while the subordinate species chose resources according to the presence or absence of the dominant species, preferring less rich resources that were not guarded. Stiles

(1978) described the same behavior, i.e., subordinate species wait for the dominant to leave the area before feeding, or they sneak in to feed until they are expelled by the dominants; such strategies were also observed in the present study. The fact that *C. lucidus* did not have a preference for a certain sugar concentration, and the great amount of time *A. versicolor* and *L. albicollis* spent feeding at the 15% sugar concentration feeders were probably due to the influence of the dominants, which forced the subordinates to feed on less concentrated sugar solutions or to wait until the dominants were absent before feeding on the richest sucrose feeders. The subordinate species would probably show a preference for the more profitable resource (35% sucrose feeders) if the dominant species were absent, but this hypothesis needs to be tested. The influence of the dominant hummingbirds on the feeding behavior of the submissive hummingbirds was demonstrated by Pimm et al. (1985). Thus, our hypothesis of preference for the richest sugar solution feeders was corroborated, but dominance and subordination of each species were important in the sugar solution choices of hummingbirds.

Van-Sluys and Stotz (1995) proposed that dominant hummingbirds have difficulties defending all resources within large territories, which gives subordinate species a chance to feed there occasionally. In this study, all feeders were located in a 6 m^2 area. Clearly, 6 m^2 is not a big area, but facing a virtually infinite food resource, many individuals visited the area at the same time, which made it difficult for the dominant hummingbirds to expel all subordinates. While the dominant was chasing a subordinate, other subordinates would take advantage and feed on the momentarily available food resource, which can explain the visits of subordinate individuals. Even with so many intruders, dominant hummingbirds did not abandon their aggressive behaviors, showing that the artificial food patches were an important energy resource at that time. It is important to state that the presence of the feeders, an unlimited resource of carbohydrates, may have increased the abundance of the hummingbirds in the area, as observed by Sonne et al. (2016) in their study, and that this increase may have influenced the expression of dominant and/or subordinate behaviors by the hummingbirds; larger numbers of hummingbirds around the richest sugar concentration feeders may have led to difficulties in defending the food resource by the dominant individuals.

In conclusion, all three behavioral strategies related to food resources were recorded for this area of Atlantic Forest. *Clytolaema rubricauda* and *T. glaucopis* were the dominant species; *A. versicolor*, *C. lucidus*, and *L. albicollis* are the subordinate species, and *P. eurynome* and *Phaethornis* spp. are the species that used the trapline strategy or acted as subordinate species with an evasive strategy to avoid confrontations with the dominants. The richest sugar solutions, with 25% and 35% sugar concentration, were most visited by the dominant species and by Phaetornithinae species; subordinate species visited less rich food patches. Finally, aggression was directly linked to the time that a hummingbird spent feeding; the more aggressive it was, the more it fed.

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