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Territorial behaviour and dominance hierarchy of *Anthracothorax nigricollis* Vieillot 1817 (Aves: Trochilidae) on food resources

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RESUMO: Comportamento territorial e hierarquia de dominância de *Anthracothorax nigricollis* Vieillot 1817 (Aves: Trochilidae) em recursos alimentares. Espécies dominantes são aquelas que delimitam e defendem territórios de outros indivíduos da mesma ou de outra espécie. Subordinadas são aquelas que utilizam de maneira furtiva e sorrateira fontes de néctar de outros indivíduos. Para descrever o comportamento de *Anthracothorax nigricollis* o presente trabalho teve como objetivos: descrever as interações agressivas, definir a hierarquia de dominância na área de estudo, investigar se ocorre partilha de recursos durante as visitas e comparar seu comportamento em estratos vegetativos diferentes. As espécies observadas em interação com *Anthracothorax nigricollis* Vieillot 1817 foram *Phaethornis pretrei* Lesson and Delattre 1839, *Thalurania furcata* Gmelin 1788 e *Polytmus guainumbi* Pallas 1764. Foram identificados e descritos nove atos comportamentais agrupados em quatro categorias. A espécie dominante é *A. nigricollis* com (0.9) dos ataques, seguida de *T. furcata* com (0.07) e *P. pretrei* (0.03). A partilha de recurso foi observada apenas no estrato arbustivo, em *C. surinamensis*, na qual houve partilha intraespecífica e interespecífica, sendo que *A. nigricollis* tolera mais *T. furcata* (0.27) e *P. pretrei* (0.55) do que *A. nigricollis* (0.18). A frequência de ocorrência dos comportamentos expressos por *A. nigricollis* nos três estratos vegetativos diferiram significativamente.

PALAVRAS-CHAVE: beija-flor, etograma, partilha de recurso, agressividade.

ABSTRACT: Dominant species are those which delimit and defend territories from other individuals of the same or different species. Subordinate species are those which, furtive and sneakily, use sources of nectar from other individuals. This study aimed to describe the aggressive interactions between species of hummingbirds, define which species are dominant and which are subordinate, investigate if the sharing of resources occurs during the visits, and compare the behaviour of the dominant species in different strata (tree, arbustive and herbaceous). The species observed interacting with *Anthracothorax nigricollis* Vieillot 1817 were *Phaethornis pretrei* Lesson and Delattre 1839, *Thalurania furcata* Gmelin 1788, and *Polytmus guainumbi* Pallas 1764. Nine behavioural acts grouped into four categories were identified and described. The dominant species is *A. nigricollis* (with 0.9 of the attacks), followed by *T. furcata* (with 0.07) and *P. pretrei* (with 0.03). The resource sharing was seen only in the shrub layer, in *C. surinamensis*, in which there was intraspecific and interspecific sharing. *A. nigricollis* showed higher interspecific toleration, *T. furcata* (0.27) and *P. pretrei* (0.55) than intraspecific *A. nigricollis* (0.18). The frequency of occurrence of behaviours expressed by *A. nigricollis* in the three vegetation strata differed significantly.

KEY-WORDS: hummingbirds, ethogram, resource sharing, aggression.

Hummingbirds (Trochilidae) make up one of the largest groups in the class with about 320 described species, 80 of which are found in Brazil. They are birds with high metabolism, consuming a daily average of up to eight times their own weight through a diet largely consisting of sugar. The beak and tongue of the hummingbird act as a pump, sucking nectar from a flower during flight (Sick 1997). In addition, it preys on insects and spiders that guarantee the proteins it needs for growth and development (Antunes 2003).

Competition is the use or dispute of a resource by two or more individuals. This may lead to territoriality when an individual delimits and defends an area containing a resource (territory) against the entrance of others. Competition is not expressed necessarily with aggression or threat, but may frequently be the cause of such behaviours (Brown 1964).

Although competition for resources is usually more intense within species, individuals from different species with similar ecological needs also compete, sometimes

through the defence of interspecific territories (Krebs and Davies 1996).

It is through the defence of such territories that the aggressive interactions between hummingbirds occur. According to Huntingford and Chellappa (2006); and Camfield (2006) aggression may include a number of behaviours, from attacks and fights to threat and submission. This was observed by Anjos *et al.* (2003) in *Anthracothorax nigricollis*.

Dominant species are those that delimit and defend territories from individuals of the same or different species. Subordinate species are those who take resources such as nectar surreptitiously from another individual's territory and, when detected, are expelled from the territory (Stiles 1978). Rather than chasing intruders, subordinate species invest time and energy in less energetic or recently available resources (Gill 1988).

Piratelli (1993) showed that hummingbird territoriality may be explained by simultaneous visitations to a plant, which give rise to direct competition of this resource.

In their study, Loss and Silva (2005) affirm that territory defence in hummingbird is directly related to their weight. They suggest that smaller birds spend more energy on foraging and less energy on defence. This hypothesis was confirmed by Antunes (2003). Hainsworth and Wolf (1972) agree that size and territoriality are related, but argue that less energy is expended during foraging by smaller hummingbirds compared to their larger counterparts. They also affirm that the larger hummingbirds compensate for their little efficiency in foraging by dominating over costly resources, through the functional relation between large size and aggressive success.

According to Temeles *et al.* (2004), male *Eulampis jugularis*, spend significantly less time defending a territory when the availability of resources is scarce, restricting the use of aggression depending on the costs and benefits.

Proper management of hummingbird species depends on understanding its use of habitat and behaviour. Thus, this research aims to understand and describe the territorial behaviour of *Anthracothorax nigricollis* and its agonistic interactions, define a dominance hierarchy in the study area, investigate the sharing of resources, and compare the behaviour in different vegetal strata.

above sea level. The weather is tropical humid megathermic (Aw), according to the Köppen classification, with mean yearly temperature of 24.4°C, 1,500 mm of rainfall and relative humidity of 70-80% (R. Dallacort, *com. pess.*, 2008).

Data collection

Preliminary observations were performed by the *ad libitum* (all occurrences) method (Martin and Bateson, 2007) to build an ethogram focusing on the territorial behaviour of the studied species.

Quantification of the behaviours was accomplished by direct observation with sequence sampling (*sensu* Altman 1974). Between October 2007 and February 2008, observations were made in three different vegetation strata. Arboreal stratus observations were taken on *Inga edulis* Mart., and shrubby stratus on *Calliandra surinamensis* Benth, both of which belong to the Mimosaceae family. Herbaceous stratus observations were performed on a bush of 54 m² of *Leonotis nepetaefolia* (L.) W. T. Aiton belonging to family Lamiaceae. The observation time in each resource varied according to the flowering time of each plant totalling 87 h of sampling effort (27 h in *I. edulis*, 39 h in *C. surinamensis* and 21 h in *L. nepetaefolia*). For *I. edulis* and *C. surinamensis*, observations occurred between 6:00 and 9:00. For *L. nepetaefolia* observations occurred between 15:00 and 18:00, because this plant was more visited in the afternoon.

For each hummingbird visit, the following were recorded: the hour and the time spent at the flower, the visiting species, how many flowers it visited, and its behaviour according to the ethogram. When there were aggressive interactions the species involved were noted, as well as the kind of interaction. Dominance hierarchy followed the description by Stiles (1978).

A visit was defined as the arrival of a hummingbird at a resource plant, whether it was for feeding or only for sitting. Sharing occurred when two individuals were sitting and/or feeding on the same plant at the same time, or when they interacted and both remained at the resource.

Data analysis

Results were described by the mean value \pm standard deviation.

G-test was calculated using software BioEstat to compare the behaviours of *A. nigricollis* in different strata (tree, arbustive and herbal), with the following hypotheses: H_0 = territorial behavior of *A. nigricollis* is independent of vegetative stratum, H_1 = territorial behavior of *A. nigricollis* is associated with the vegetative stratum. The significance level used was $\alpha = 0.01$.

MATERIAL AND METHODS

Study area

This work was conducted at the border of a fragment of a riparian forest close to Universidade do Estado de Mato Grosso – UNEMAT, *campus* of Tangará da Serra, placed at 14°38'48.39"S of latitude and 57°26'06.51"W of longitude with average height of 320 m

RESULTS

Description of the aggressive interactions

Nine behavioural acts were described and grouped into four categories (resting, resource guarding, indirect aggression, direct aggression; Table 1):

Resting:

- Sitting rest: between visits, the hummingbird sits on twigs at a height between 0.5 and 2 m. the individual often uses this time to clean the beak and feathers.

Resource guarding:

- Sentinel: the hummingbird sits within 10 m of the nectar resource, on the tip of a twig, singing or in silence, while searching for other birds by moving its head from right to left for as long as 14 minutes (Figure 1a);
- Forage singing: during the visits, the individual feeds on the nectar touching the corolla tube. In the interval between visiting two flowers it repeatedly sings loud, with tweets-“tim, tim, tim, tim”, or a short and acute call named “chirp”-“tcheam, tcheam, tcheam, tcheam”. Generally, calls occur when there is another individual nearby.

Indirect aggression:

- Aggressive call: during the interactions, the individual that attacks generally emits the chirp call, very much the same as when foraging.
- Frontal darting: the target of the aggression is sitting or flying, and the other darts in front of it at a mean distance of 10 to 30 cm and from 5 to 3 m above the ground, attempting to force the target to move from the territory (Figure 1b);
- Circular darting: the individuals dart in circles, one in front of the other, in a vertical position, with opened tails, from 1 to 7 m above the ground. This behavior generally culminates in chase (Figure 1c);

- Straight chase: an individual chases the other away from its territory with the body in the horizontal position, with a closed tail, flying in a straight line, and generally chirping. This occurs from approximately 2 to 7 m above the ground, with a distance of 0.10 to 3 m between the individuals (Figure 1d);
- Chasing in alternating directions: an individual chases the other from its territory with its body in the diagonal position, closed tail and flying in alternating directions. Generally emitting the chirp call between 1 and 7 m above the ground, with a distance as close as 10 cm between them (Figure 1e);

Direct aggression:

- Peck: they happen when the opponents enter in physical contact, combating each other with their beaks. It may possibly occur during chase.

During the sessions, the most frequent behaviour used by *A. nigricollis* was of “Sentinel” and the least frequent was “peck”. Within the indirect aggression category the most frequent behaviour was “straight chase” and the least frequent was “Circular darting” (Table 1).

Dominance hierarchy within the species

In the study area, four species of hummingbirds were observed: *Phaetornis pretrei*, *Anthracothorax nigricollis*, *Thalurania furcata*, and *Polytmus guainumbi*. *A. nigricollis* was considered the dominant followed by subordinate *T. furcata* and *P. pretrei* (Figure 2). *P. guainumbi* was observed less frequently and in only one resource. During the observation period no aggressive behaviour was recorded for this species, thus it was not accounted in the analysis of dominance hierarchy.

A. nigricollis showed the greatest frequency of aggressive attacks (Figure 2) and the sentinel behaviour was the most frequent within the resource guarding category (Table 1). *A. nigricollis* presented as much intraspecific (n = 46) as interspecific interaction (n = 34) (Table 2).

TABLE 1: Relative frequency of the observed acts of aggressive behaviour for *Anthracothorax nigricollis*.

Behavioural category	Behavioural act	Relative frequency
Rest	Sitting rest	0.04
Resource guarding	Sentinel	0.52
	Forage singing	0.14
Indirect aggression	Aggressive call	0.11
	Frontal darting	0.02
	Circular darting	0.01
	Straight chasing	0.09
	Chasing in alternate directions	0.06
Direct aggression	Peck	0.004

TABLE 2: Number of aggressive interactions registered for the observed species among *Anthracothorax nigricollis*, *Thalurania furcata* and *Phaethornis pretrei*. It is not possible to externally identify the sex of *P. pretrei*.

Defending species		Attacking species			Total
		<i>A. nigricollis</i>	<i>A. nigricollis</i>	<i>T. furcata</i>	
		♂	♀	♂	
<i>A. nigricollis</i>	♂	31	0	0	31
	♀	13	2	1	16
	♂	10	1	1	12
	♀	6	0	4	13
	<i>P. pretrei</i>	15	2	0	17
Total		75	5	6	89

Although *T. furcata* and *P. pretrei* were observed defending a territory, they were considered subordinate, because they were banished from territories by *A. nigricollis* (Table 2). Despite being considered subordinate of *A. nigricollis*, *T. furcata* (male) were observed defending territory from female of *A. nigricollis*. For *T. furcata*,

the observed interactions were intraspecific (n = 5) and interspecific (n = 1). *P. pretrei* was considered the lowest species in the dominance hierarchy (Figure 2). However, one was observed attacking a female *T. furcata*. *T. furcata*, in turn was observed using the traplining foraging strategy.

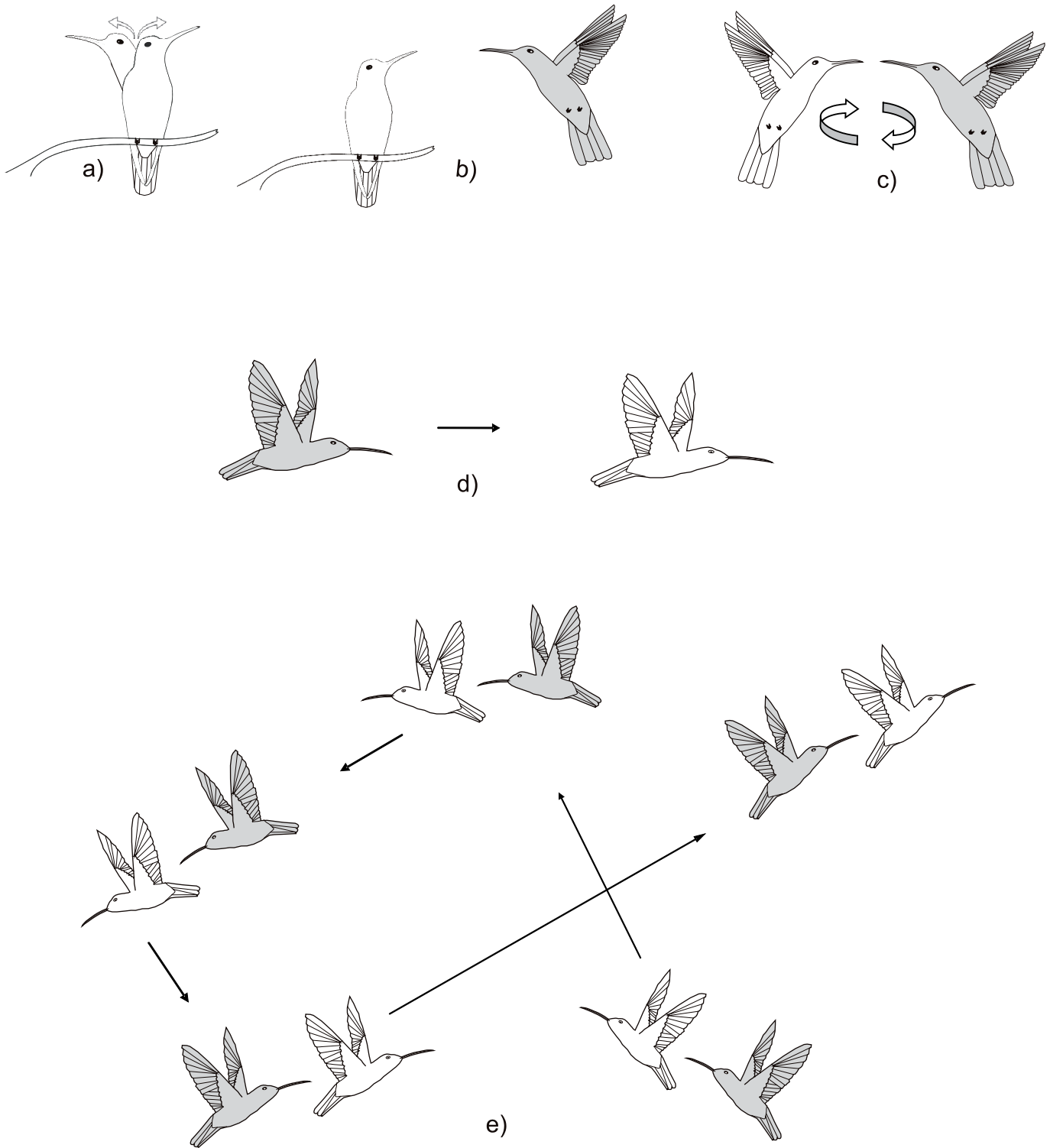


FIGURE 1: Behaviour depictions of the agonistic interactions observed for *Anthracothorax nigricollis*: Resource guarding: Sentinel (a). Indirect aggression: Frontal darting (b); Circular darting (c); Chasing straight (d); and Persecution in alternating directions (e).

Resource partitioning

Resource partitioning was observed only in arbustive stratus *C. surinamensis* between *A. nigricollis*, *T. furcata* and *P. pretrei* (Figure 3). As mentioned, *P. guainumbi* visited the resource seldom and it did not interact with other species. It was observed that intraspecific partitioning occurred more often than interspecific, particularly between *A. nigricollis* and the other species (Figure 2).

Comparison of the dominant species behaviour in different strata

The relative frequency of occurrence of the behaviours presented by *A. nigricollis* in the three strata, *Inga edulis* (arboreal), *Calliandra surinamensis* (shrubby) and *Leonotis nepetaefolia* (herbaceous) differed significantly. The results show a statistically significant association between the behaviour of *A. nigricollis* and different strata of vegetation ($G = 213.2986$; d.f. = 18; $P < 0.0001$), accepting the alternative hypothesis that the behaviour is defined by the plant being defended. The behaviour of sitting rest occurred only in *C. surinamensis*. Sentinel happened more often in *I. edulis* and less often in *L. nepetaefolia*. *A. nigricollis* foraged singing more on *C. surinamensis* and less on *I. edulis*. However, the behaviours

forage singing, circular darting and peck only occurred on *I. edulis* (Figure 3).

DISCUSSION

Aggressive behaviour description

The sentinel behaviour was the most frequent for *Anthracothorax nigricollis* since it is the dominant species in the study area. According to Stiles (1978), this is one of the characteristic behaviours for dominant species. In accordance with Lorenz (1966), disputes between species consist of displays and, most of the time, they are ended without damages. Pecking was rare, while straight and alternated chasings were more frequent acts.

It is possible that circular darting was less frequent because it occurred only in *I. edulis* and only between males of *A. nigricollis*. This behaviour was exhibited before direct disputes for the territory (Krebs and Davies 1996).

Dominance hierarchy

Anthracothorax nigricollis was considered dominant (*sensu* Stiles, 1978). This species was also considered

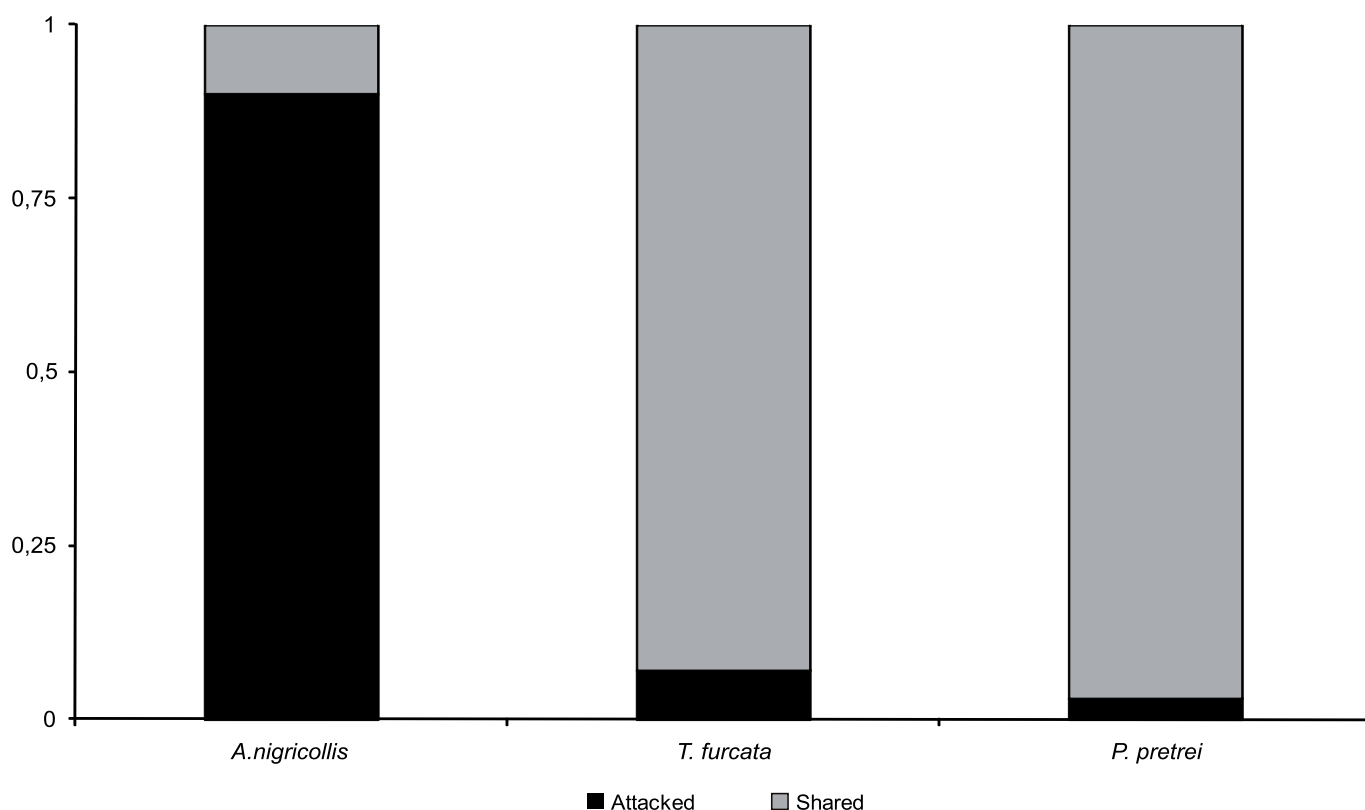


FIGURE 2: *Anthracothorax nigricollis* is more aggressive towards conspecifics. Relative frequency of aggressive attacks (black columns) and resource sharing (gray columns) of *A. nigricollis* with their conspecifics, with *Thalurania furcata* or with *Phaethornis pretrei*.

dominant in relation to *Hylocharis chrysura* by Mendonça and Anjos (2006). In his study, Antunes (2003) observed that *A. nigricollis* had few visits and, when it did, it was submissive to *Melanotrochilus fuscus*, which, thus, was dominant. Anjos *et al.* (2003) related the low number of aggressive interactions in *A. nigricollis* to the abundant supply of food in the study area. For *Selasphorus rufus*, Camfield (2006) observed that the intensity of the territory defence increased with the quality of the resource. The same was observed by Temeles *et al.* (2004) for *Eulampis jugularis*. Therefore, we suggest that what may have driven the high frequency of aggressive attacks in *A. nigricollis* were the few flowering plants in the period of observation.

Thalurania furcata presented both intra and inter-specific territoriality, with the biggest number of attacks against female individuals of its species. The same was observed by Abreu and Vieira (2004) in *T. glaucopsis*. Coelho and Barbosa (2004) observed females of *T. furcata* defending territory from *Phaethornis pretrei*, which was not seen in the present work. Castro and Araújo (2004) observed male and female individuals of *T. glaucopsis* sitting close to the resource between visits and defending territory. Passos and Sazima (1995) also observed territory defence by *T. glaucopsis*, although it was against *Phaethornis eurynome* and *P. squalidus*.

Coelho and Barbosa (2003, 2004) observed *Thalurania furcata* using the traplining strategy, which only occurred with the females of this species in the present study. We suggest that, although it showed territory defence, *T. furcata* is a subordinated species of *A. nigricollis* because it presented less aggressive attacks in comparison.

P. pretrei only defended territory from female *T. furcata*. Machado *et al.* (2007) observed territory defence between *P. pretrei*, *Colibri serrirostris* and *Chlorostilbon lucidus*. Although it attacked both the species, *P. pretrei* was considered subordinated for showing a minor total number of attacks. These authors also observed intraspecific interaction in *P. pretrei*, which was not observed here.

P. pretrei was observed by Coelho and Barbosa (2003, 2004), Consolaro *et al.* (2005), Machado *et al.* (2007), using the traplining strategy. Castro and Araújo (2004) observed the same for *P. ruber*, which was considered as a territory parasite of other species by these authors. *P. ruber* was also considered by Machado and Semir (2006) a territory parasite of *P. eurynome*, which, despite being a trapliner, showed territorialism when suitable, as during the flowering period of *Vriesea altodaserrae* L.B.Sm. Traplining foraging was observed for *P. pretrei* in this study.

P. pretrei was considered the most subordinate species since it presented the minor frequency of attacks in

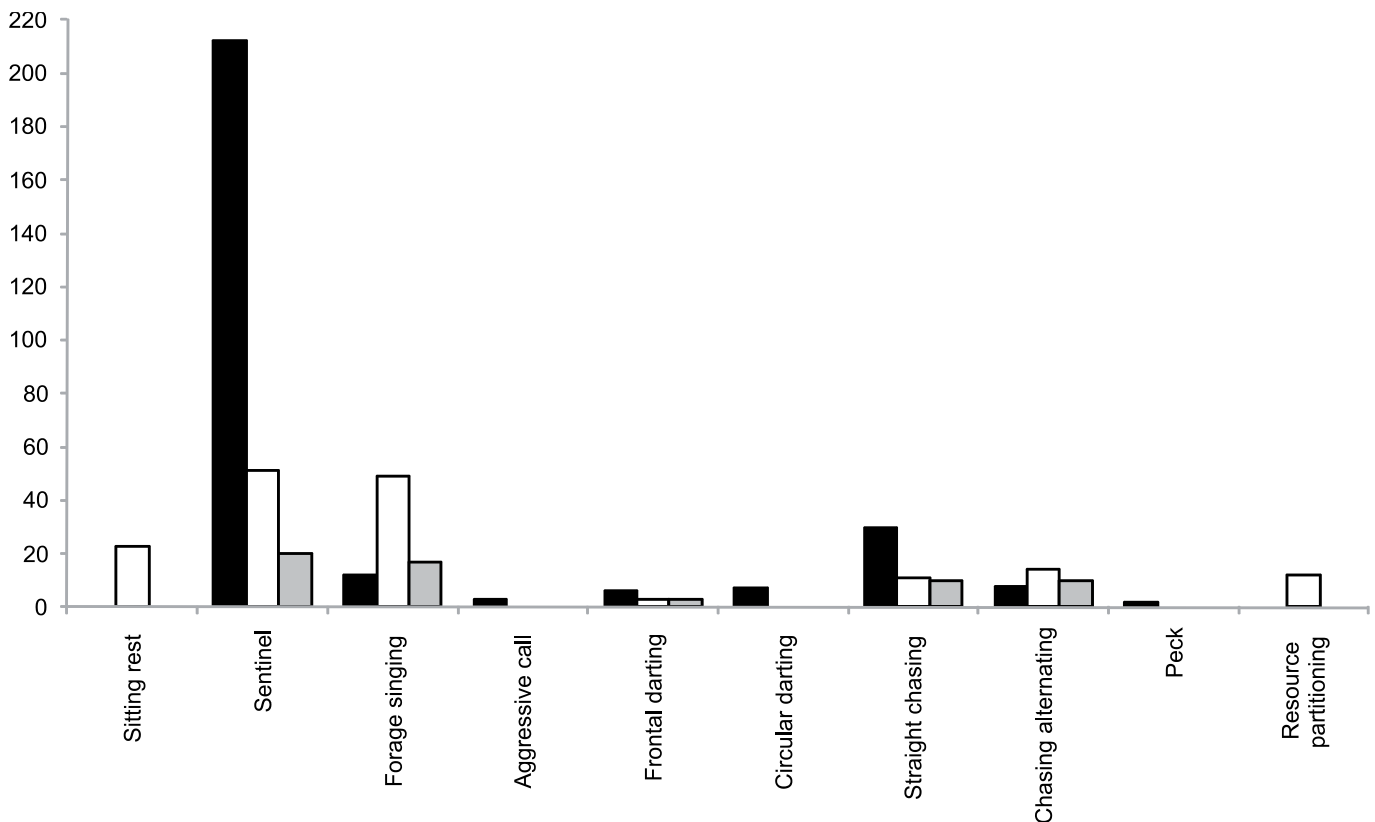


FIGURE 3: *Anthracothorax nigricollis* behaviour differ in trees, shrubs and herbs. Comparison of behavioral acts expressed by *Anthracothorax nigricollis* in three different strata: black column *I. edulis* (tree), white column *C. surinamensis* (shrub) and gray column *L. nepetaefolia* (herbs).

comparison to *A. nigricollis* and *T. furcata*. That it defended resources in *L. nepetaefolia* may be explained by the resource being rich in nectar, thus inducing territory defence behaviour, as suggested by Machado and Semir (2006) for *P. eurynome*.

Resource partitioning

Resource partitioning happened only in *Calliandra surinamensis* and with a relatively low frequency (0.13) in relation to aggressive meetings between the species. We suggest that during the observation period, there were few flowering plants, causing more aggressive meetings and low resource partitioning.

Comparing the resource partitioning by *A. nigricollis* with *A. nigricollis*, *T. furcata* and *P. pretrei*, and the number of aggressive meetings, it was observed that *A. nigricollis* is more tolerant to other species than its own. The same was observed by Antunes (2003) in which *Melanotrochilus fuscus*, *Eupetomena macroura*, *Aphantochroa cirrhochloris* and *Amazilia lactea*, species considered by this author as dominant, applied a greater number of interspecific aggressive interactions. This is possibly due to the intense intraspecific dispute for territories between dominant individuals. Since these are about the same size and have similar abilities, they often end up in direct aggression. Moreover, the niche overlap between individuals of the same species is bigger than between individuals of related species. Between individuals of different species these interactions diminish. The presence of a dominant individual on a given resource can more easily drive invaders of a different species away, as a subordinate gives up the fight once it recognizes the rank position of the opponent (Krebs and Davies 1996).

Comparison of the dominant species' behaviour in different strata

The behaviours circular darting, peck and forage singing had only occurred in *I. edulis*. In this resource the interactions had occurred between *A. nigricollis* males. When there was an individual close to the resource, the foraging one sent the chirp signal to announce its presence. Then, they would dart in circles as a display before direct aggression (Krebs and Davies 1996). When neither opponent gave up, the individuals began direct aggression. The significant difference in the behavioural acts presented by *A. nigricollis* in the three vegetative strata can be explained by the resources being used for distinct purposes, *I. edulis* for guarding, *C. surinamensis* as food source, resting and guarding; and *L. nepetaefolia* a herbaceous only for feeding.

CONCLUSION

- Nine behavioural acts were described and grouped into four distinct categories;
- *Anthracothorax nigricollis* was considered the dominant species in the study area followed by *Thalurnia furcata* and *Phaetornis pretrei*;
- Resource partitioning occurred during the visits, but this was rare in relation to the aggressive meeting due to food scarcity in the area;
- *Anthracothorax nigricollis* differs in its behaviour in the three plant strata. This probably happens because it uses these species for different purposes as resting, guarding resources and feeding.

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