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## Research Article

# Evidence of Competition Between Two Canopy Ant Species: Is Aggressive Behavior Innate or Shaped by a Competitive Environment?

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Competition occurs in all ecological communities, although it has not always been experimentally tested as a structuring force in the distribution of species. We tested the hypothesis that the aggressiveness exhibited by *Camponotus rufipes* changes according to the pressures of a competitive environment. This is a dominant species in the montane forest of the Itacolomi State Park, Brazil, where *Camponotus sericeiventris* does not occur. Using bait traps in a field site where both species occur, (“Juiz de Fora” site) we showed that *C. sericeiventris* was able to remove *C. rufipes* workers at the same bait. In the laboratory, we used dyadic encounters to test workers from both species taken from colonies found in areas where both occur and where only *C. rufipes* was found. *Camponotus rufipes* from Itacolomi fought significantly less and was killed during the first few minutes in 60% of the events. On the other hand, the workers that co-existed with *C. sericeiventris* in the field were more aggressive, but less efficient fighters than the latter. This investigation demonstrated existence of competition between *C. rufipes* and *C. sericeiventris*, and also the lower aggressiveness of *C. rufipes* individuals that did not co-exist in the field with *C. sericeiventris*.

## 1. Introduction

The importance of competition for structuring ecological communities is a matter for debate, and it has been extensively researched in ant assemblages [1]. Exploitation and interference competition in ants involve mutual aggression, which can frequently be observed, often resulting in injuries, death, and the avoidance of one colony by another [1]. The more similar are the species' morphology and niche breadths, the stronger is the competition [2, 3]. Species co-existence is possible when there are diversified strategies for resource usage, namely, time partitioning, feeding-source differentiation, or nesting locations [1, 3]. On the other hand, competition causes hierarchical dominance amongst

the species through the use of aggression, food source exclusion, and different foraging strategies [4, 5]. Dominant ant species can influence the occurrence of other species and play a major role in ant assemblage structuring, in which they generate distribution patterns and a mosaic-like species co-existence, especially in forest canopies [6–9].

Territorial defence is related to dominance and occurs widely among canopy ant species in tropical rainforests [5]. Here, we observe the occurrence of a hierarchical competition that is based on their social organization and, ultimately, on foraging workers density. Hence, when a nonterritorial species encounter a territorial one, the former tends to run way from aggressive conflict, which may result in locally improbable species pairs [10, 11].

*Camponotus (Myrmothrix) rufipes* (Fabricius, 1775) is normally associated with ecotones between forests and open vegetation and is rarely found in great quantities in the canopy of lowland forests [12–18]. However, in the State Park of Itacolomi, a montane forest ecosystem in the borders between the Brazilian Cerrado and the Atlantic rainforest, this species is the most frequent member of this genus in the canopy [18]. In this particular forest the potential competitor, *Camponotus (Myrmepomis) sericeiventris* (Guérin-Ménéville, 1838), which has a similar body size and uses the same kinds of food and nesting sites, was absent, unlike in the other areas of Atlantic rainforest and in most other Neotropical arboreal ecosystems [19]. On the contrary of *C. rufipes*, the latter is mostly frequent and dominant in the upper canopy [19, 20].

The present work investigates the degree of *C. rufipes* aggressiveness in contrasting competitive environments by means of direct observation in field and laboratory. We tested the hypothesis that *C. rufipes* shows different behaviours depending on the nature of the competitive environment. The prediction is that levels of aggressiveness of *C. rufipes* vary in response to presence or absence of competition from *C. sericeiventris*.

## 2. Methods

**2.1. Field Experiments.** Observations were carried out at two locations in the Atlantic rainforest. The first was Itacolomi State Park (Itacolomi), Minas Gerais State (20°22'30''S and 43°32'30''W), between 1000–1300 metres above sea level, within an area of 7.543 hectares, and belonging to the Espinhaço Mountain Range, which has a tropical montane climate, with rainfall varying from 1000 to 1500 mm per year and the temperatures between 4°C and 33°C [21]; The second was the campus of the Federal University of Juiz de Fora (UFJF) (21°46'47''S and 43°22'24''W), at 818 metres above sea level, also with a well-defined rainy and dry seasons, an annual average temperature of 19.3°C, and a annual precipitation of 1500 mm [22]. Both species, *C. rufipes* and *C. sericeiventris*, were encountered at the UFJF campus, but only *C. rufipes* was found in Itacolomi.

At Itacolomi, three trees were selected because of the high foraging activity of previously observed *C. rufipes* ants [18]. At the UFJF Campus, three trees were also selected in a territorial border where both *C. rufipes* and *C. sericeiventris* coexisted: in two of the trees there was an intense foraging by *C. rufipes* ants, due to the existence of nests closer than 10 metres to their trunk; in the third, there was a *C. sericeiventris* nest. The experiments were conducted during the months of October and November 2007.

Observations were made on one tree per day, thus in 3 days all trees were observed. Afterwards, two new rounds of observations, following the same order, were executed. Hence, in 9 days all trees were observed three times, with 2 days intervals between each observation. As the experiment was conducted within a short and continuous time interval, no relevant change in weather conditions was noticed. On the trunks of each of these trees a paper towel with attractant bait made of sardines (10 g) and honey (1:1; g:g) was

placed. The behavioural recordings started with the arrival of the first *C. rufipes* ant in Itacolomi, whereas at the UFJF Campus it started when the first *C. rufipes* or *C. sericeiventris* appeared. From that moment on, we used the sequential sampling method [23]. For 4 hours, during five minutes at 10-minute intervals, all ant behaviours were recorded. These recordings include not only the behaviour of the two species in focus but also that of all the other species that appeared. Hence, this experiment was composed of six behavioural recordings per tree, constituting 18 repetitions, that provided 288 records. The observed behavioural acts were then divided into three categories: action, reaction, and nonaggressive.

Access to the tree crowns was achieved by tree-trunk climbing, either with or without a rope, and using safety equipment (see Ribeiro et al. [24]). Contingency tables were created to analyse species superiority in aggressiveness for both action and reaction types of behaviour. The analyses were done using Chi-square at a 5% significance level.

**2.2. Laboratory Experiments.** Experimental dyadic encounters were manipulated between *C. rufipes* and *C. sericeiventris* workers from different colonies collected in both Itacolomi and UFJF. Approximately 70 workers of *C. rufipes* from an Itacolomi colony were collected. Meanwhile, 50 workers of this species, along with 50 workers of *C. sericeiventris*, were collected from UFJF in an area where they coexisted. These collected ants were kept in a lidded plastic containers (12 cm × 9 cm) with a cotton ball soaked in water-diluted honey and remained isolated (at 25°C and 70% humidity) for 24 hours before performing the experiment. During this period, the samples were exposed to similar stress of collecting and travelling, and subsequent resting in the laboratory. The resting period and the experiments took place at the Myrmecology Laboratory of UFJF during the months of December 2007 and January 2008.

At each dyadic encounter, two ants of the same caste were placed in an arena (6 cm diameter) with Fluon at the edges to prevent their escape. To relieve the stress of transferring, the ants were separated by a partition in the arena for 10 minutes. Afterwards, the partition was removed, and their behaviour was registered during 5 minutes (*ad libitum* [23]). The observed behavioural acts were divided into three categories: action, reaction, and nonaggressive.

We manipulated six types of encounters (Table 1) and each one was repeated 10 times. After each repetition, the experimental arena was cleaned with alcohol 50% to eliminate any ant odour, so as to not interfere with the results of the next repetition. For the repetitions involving ants of the same species, the individuals were marked on the pronotum with nontoxic ink using an Edding 750 pen [25].

Aggression was calculated according to a modified index of aggressiveness from Errard and Hefetz [26]. The assigned values represent degrees of aggressiveness: 0 = “touched antennae and retreated”, 1 = “on alert and charged”, 2 = “bite”, 3 = “torsioned gaster” and 4 = “fight”. The resulting index for each treatment was subjected to the Kruskal-Wallis test, followed by the post-hoc Student-Newman-Keuls test, at 5% significance level (Table 2), using Biostat 4.0 software. This study was performed under licence permission from

TABLE 1: Dyadic encounters occurring at the laboratory of the Federal University of Juiz de Fora (UFJF) for all treatments and species involved.

	Treatment	Species
1	Control <i>C. rufipes</i> Itacolomi	<i>C. rufipes</i> Itacolomi × <i>C. rufipes</i> Itacolomi
2	Control <i>C. rufipes</i> UFJF	<i>C. rufipes</i> UFJF × <i>C. rufipes</i> UFJF
3	Control <i>C. sericeiventris</i> UFJF	<i>C. sericeiventris</i> UFJF × <i>C. sericeiventris</i> UFJF
4	Neighbours	<i>C. rufipes</i> UFJF × <i>C. sericeiventris</i> UFJF
5	Same species	<i>C. rufipes</i> UFJF × <i>C. rufipes</i> Itacolomi
6	Different species	<i>C. rufipes</i> Itacolomi × <i>C. sericeiventris</i> UFJF

Itacolomi = Itacolomi State Park; UFJF = Campus of the Federal University of Juiz de Fora.

TABLE 2: Student-Newman-Keuls ( $H = 77.1648$ ) comparisons for each treatment of dyadic encounters listed in Table 1 (significant  $P$ -values in evidence).

		1	2	3	4	5	6
		Control <i>C. rufipes</i> Itacolomi	Control <i>C. rufipes</i> UFJF	Control <i>C. sericeiventris</i> UFJF	Neighbours	Same species	Different species
1	Control <i>C. rufipes</i> Itacolomi	—	<b>0.0031*</b>	0.7043	< <b>0.0001*</b>	< <b>0.0001*</b>	0.4172
2	Control <i>C. rufipes</i> UFJF		—	<b>0.0008*</b>	0.0344	0.0355	<b>0.0002*</b>
3	Control <i>C. sericeiventris</i> UFJF			—	< <b>0.0001*</b>	< <b>0.0001*</b>	0.6659
4	Neighbours				—	0.9891	< <b>0.0001*</b>
5	Same species					—	< <b>0.0001*</b>
6	Different species						—

Itacolomi: Itacolomi State Park; UFJF: Campus of the Federal University of Juiz de Fora.

the State Forestry Institute, and it followed university's ethic requirements for experiments with alive animals.

### 3. Results

**3.1. Field Experiments.** Nine morphospecies of ants were registered in experiments conducted in the Itacolomi State Park and 12 in the UFJF Campus. Fourteen types of behaviours were registered with the bait. The behaviour exhibited by the ants is categorized and described in Table 3.

The most frequent behaviours for the ants in the two experimental sites were “quietly feeding” and “exploring the surroundings” (Table 4). When observing interactive behaviour in Itacolomi, *C. rufipes* was the species that most engaged in the aggressive actions of “charge” and “bite” ( $\chi^2 = 88.3, P < 0.001$ ). *Myrmelachista* sp.1 was the one that most engaged the reactions of “flee” and “gaster torsion” ( $\chi^2 = 15.65, P < 0.05$ ) (Figure 1). For all the other species together, only two registers were recorded for the “charge” behaviour, while the “avoid”, “flee”, and “retreat” were the most frequent ones ( $\chi^2 = 15.65, P < 0.05$ ), suggesting that they were submissive to the aggressiveness of *C. rufipes*.

In UFJF campus, *C. rufipes* and *C. sericeiventris* frequently showed aggressive behaviour through the actions of “charge” and “bite” ( $\chi^2 = 45.78, P < 0.05$ ) with no statistical

difference between these species in terms of the amount of these acts performed ( $\chi^2 = 3.43, P > 0.05$ ). All other morphospecies showed significantly more defensive behaviour, especially “retreat” and “flee” reactions ( $\chi^2 = 18.9, P < 0.05$ ) (Figure 2).

When comparing behaviour of *C. rufipes* workers from the two sites, the UFJF individuals bit more than the Itacolomi individuals, which showed more of “avoid” aggressors act ( $\chi^2 = 19.34, P < 0.05$ ) (Figure 3). Concerning reaction behaviours, the *C. rufipes* from the UFJF colony tended to “retreat”, especially in the presence of *C. sericeiventris* ( $\chi^2 = 23.9, P < 0.05$ ) (Figure 2).

**3.2. Laboratory Experiments.** Fifteen types of behaviours were registered in the laboratory, which are categorized and described in Table 3. According to the calculated aggressiveness index, the more aggressive encounters were between *C. rufipes* workers from the two areas and between *C. rufipes* from Itacolomi and *C. sericeiventris*, thus, between workers whose colonies are far apart from each other (Figure 4). Colony workers had an average agonistic response significantly larger than that observed between themselves in the control experiment (Table 2).

Considering the mortality at the encounters, we verified that 70% of *C. rufipes* workers were dead in less than 2

TABLE 3: Description of behavioral acts displayed by the ants on Itacolomi State Park (Itacolomi) and the Campus of Federal University of Juiz de Fora (UFJF) during field experiments (\*\*) and laboratory experiments (dyadic encounters) occurring at the lab of the Federal University of Juiz de Fora (\*).

Action	Reaction	Nonaggressive
Charge—an ant approaches the other with its mandible open	(**) Remain on the bait—after any types of the listed actions, the ant remains in the area, eating the bait	(**) Quietly eating—when an ant is standing still, only eating the bait
Bite—grips part of the body of another individual with its mandibles	(**) Flee—after any types of these actions it flees not only from the area, but also from the bait	(**) Food transport—the individual carries part of the bait to the colony
Esponaneous gaster torsion—the ant curls its abdomen to emits formic acid	(**) Retreat—after the mentioned actions, it retreats from the other individual, but does not leave the bait and eats it	Autogrooming—cleaning itself
Avoid—when perceiving the proximity of another individual, the first moves away, avoiding the encounter	Defensive gaster torsion—after these actions, it exhibits aggressive behaviour by curling its abdomen to emit formic acid	Trophallaxis—exchange of regurgitated liquid from one individual directly into the crop of the other
(*) Antennal touching—an ant exchanges antennal touches with the other for identification	Fight—after mentioned actions, it grabs the other individual with its jaws and emits formic acid	Exploring the surroundings—walking around, touching its antennae on the whole extension of the paper where the bait was placed
(*) On alert—an ant stands still with its head and antenna raised, and with its gaster torsed in the posterior-anterior position ready to emit formic acid, if necessary	(*) Bite—grips part of the body of another individual with its mandibles in response to any action act  (*) Charge—the ant advances in the direction of the other with its mandible open ready to bite back	(*) Trying to escape—the ant stays on the border of the arena, trying to climb its wall

(\*) Only in lab experiments; (\*\*) Only in field experiments.

minutes (mostly in seconds) in the encounters between *C. rufipes* from Itacolomi and *C. sericeiventris*. (Kruskal-Wallis, Student-Newman-Keuls = 23.12,  $P < 0.035$ ). For the remaining 30%, *C. rufipes* killed *C. sericeiventris* in one case, and two other times there were fights without deaths.

Unlike the encounters with the neighbouring *C. rufipes* and *C. sericeiventris* from UFJF, the fight lasted longer and all the repetitions severally resulted in death; 60% of the *C. sericeiventris* and 40% of the *C. rufipes* died. It is worth noting that when *C. rufipes* were killed, the trial was faster than when it was not killed. Finally, in the treatment between *C. rufipes* from the two studied sites, the ants from the Itacolomi colony died in half of the repetitions without causing a single death among the ants from UFJF (Table 1).

## 4. Discussion

**4.1. Field Experiments.** Regardless of the advantage of aggressiveness, high costs of competing may mean that its selective advantage is only sustainable if associated with the minimization of conflicts. An evidence is that the behaviours most frequently exhibited by all ants species from both sites were “quietly feeding” and “exploring the surroundings”. According to ethograms found in the literature, the most common behavioural acts are into the categories of grooming, feeding, and exploring surroundings [19, 27–29].

Likewise, the “dear enemy” hypothesis [30] predicts that ant species are capable of recognizing and discriminating their neighbours (species/individuals), and then they are

normally more aggressive with the “foreigners”, saving energy by avoiding unnecessary conflicts with species or colonies with which they have already defined their boundaries [31, 32]. The species that live together adjust to the habitat and share resources, while foreigners may threaten this balance [30]. In addition, the constant contact among all coexisting ants followed by autogrooming results in a common Gestalt odour, that decreases the aggressiveness among all the species that share the same space [4]. Finally, for canopy ants, it has been reported that various species have the habit of foraging over great distances, presenting familiarity with the place, and tolerating the presence of neighbour species [33].

Both experiments suggest that these species tend to have a territory which is aggressively protected, and thus are able to dominate numerically in the canopies. Both species seem to have defensive behavior across the complete territory, instead of only at the nest or some particular feeding resource, as aggressive actions have been observed everywhere in the studied forest (pers.obs.) and have been corroborated experimentally. The dominant position could be taken by *C. rufipes* where *C. sericeiventris* does not occur, while in the presence of the latter, *C. rufipes* may still keep high abundance (mainly by combining foraging in different habitats, such as the canopy and in the litter) and codominate the assemblage.

Concerning other observed species, distinct behaviours at the bait reflected their recruiting and foraging strategies and, in many cases, their attack and defence tactics. Many species proved to be opportunists, eating rapidly until being

TABLE 4: Occurrence of behaviours for the morphospecies of ants in the Itacolomi State Park (Itacolomi) and the Campus of Federal University of Juiz de Fora (UFJF) during field experiments.

Local	Espécie	Quietly eating	Exploring the surroundings	Autogrooming	Food transport	Charge	Bite	Spontaneous torsion gaster	Avoid	Remain on the bait	Flee	Retreat	Fight	Trofalaxis
UFJF	<i>Acromyrmex</i> sp.1	100%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
UFJF	<i>C. rufipes</i>	42%	21%	14%	0%	9%	10%	0%	0%	1%	0%	2%	0%	0%
UFJF	<i>C. sericeiventris</i>	69%	8%	12%	0%	4%	4%	0%	0%	0%	1%	1%	0%	1%
UFJF	<i>Camponotus</i> sp.5	82%	8%	2%	0%	0%	0%	0%	1%	0%	3%	3%	0%	0%
UFJF	<i>Camponotus</i> sp.6	41%	19%	5%	0%	0%	0%	0%	0%	0%	27%	3%	5%	0%
UFJF	<i>Camponotus</i> sp.7	50%	8%	7%	0%	2%	1%	0%	7%	0%	9%	15%	2%	0%
UFJF	<i>Camponotus</i> sp.8	100%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
UFJF	<i>Cephalotes</i> sp.2	100%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
UFJF	<i>Crematogaster</i> sp.1	98%	2%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
UFJF	<i>Pheidole</i> sp.2	75%	23%	0%	1%	0%	1%	0%	0%	0%	0%	0%	0%	0%
UFJF	<i>Pseudomyrmex</i> sp.2	69%	15%	3%	0%	3%	1%	0%	4%	0%	1%	5%	0%	0%
UFJF	<i>Solenopsis</i> sp.1	100%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
Itacolomi	<i>C. rufipes</i>	29%	40%	14%	4%	6%	3%	0%	4%	0%	0%	0%	—	—
Itacolomi	<i>Camponotus</i> sp.4	86%	7%	0%	0%	0%	0%	0%	0%	0%	0%	7%	—	—
Itacolomi	<i>Camponotus</i> sp.2	76%	6%	12%	0%	0%	0%	0%	0%	0%	6%	0%	—	—
Itacolomi	<i>Camponotus</i> sp.3	50%	17%	33%	0%	0%	0%	0%	0%	0%	0%	0%	—	—
Itacolomi	<i>Camponotus</i> sp.1	65%	22%	8%	0%	1%	0%	0%	3%	0%	0%	0%	—	—
Itacolomi	<i>Cephalotes</i> sp.1	80%	20%	0%	0%	0%	0%	0%	0%	0%	0%	0%	—	—
Itacolomi	<i>Myrmelachista</i> sp.1	95%	4%	0%	0%	0%	0%	0%	0%	0%	1%	0%	—	—
Itacolomi	<i>Pheidole</i> sp.1	100%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	—	—
Itacolomi	<i>Pseudomyrmex</i> sp.1	37%	46%	10%	4%	0%	0%	0%	2%	0%	0%	2%	—	—

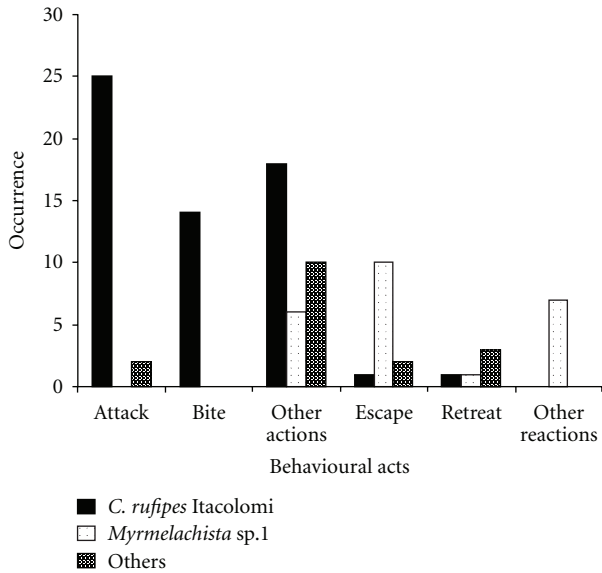


FIGURE 1: Action and reaction behavioural occurrences for *C. rufipes*, *Myrmelachista* sp.1 ants, and other morphospecies assemblages during field experiments in the Itacolomi State Park (Itacolomi). The “other actions” and “other reactions” behaviours are grouped together because of their low frequency.

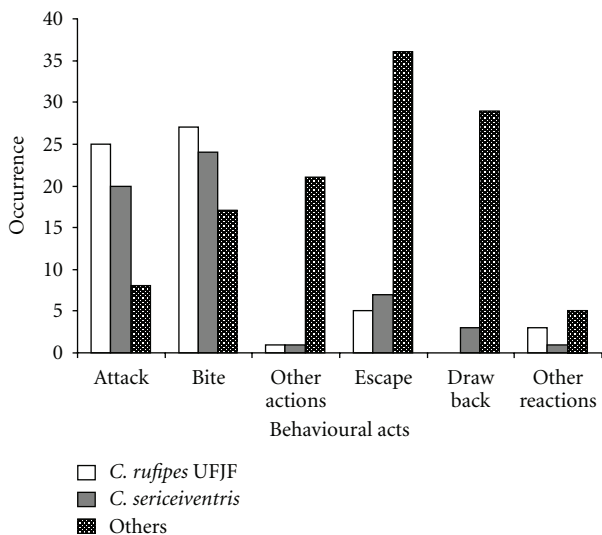


FIGURE 2: Action and reaction behavioural occurrences for *C. rufipes*, *C. sericeiventris*, and other morphospecies (grouped together) during field experiments at the Campus of Federal University of Juiz de Fora. The “other actions” and “other reactions” behaviours are grouped together because of their low frequency.

expelled by the dominant species, but avoiding interactive aggressive behaviour. In this study, the genera *Cephalotes* and *Pseudomyrmex*, along with some species of *Camponotus* (*C. crassus* and three nonidentified *Camponotus* species) exhibited this type of behaviour. The opportunistic or cowardly behaviour was previously recorded by *Cephalotes pusillus* in Byk and Del-Claro [34], as the species was never

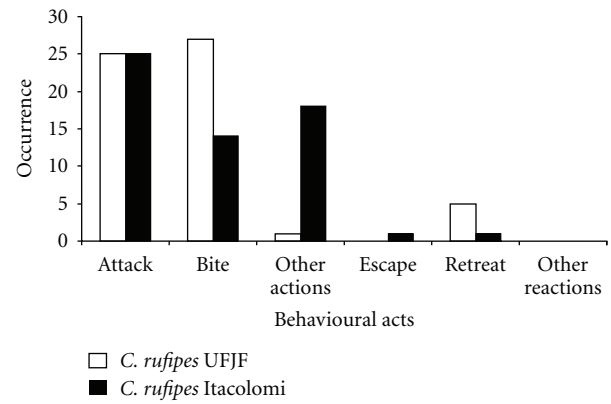


FIGURE 3: Action and reaction behavioural occurrences for the *C. rufipes* colonies at the Itacolomi State Park (Itacolomi) and campus of Federal University of Juiz de Fora (UFJF) during field experiments. The “other actions” and “other reactions” behaviours are grouped together because of their low frequency.

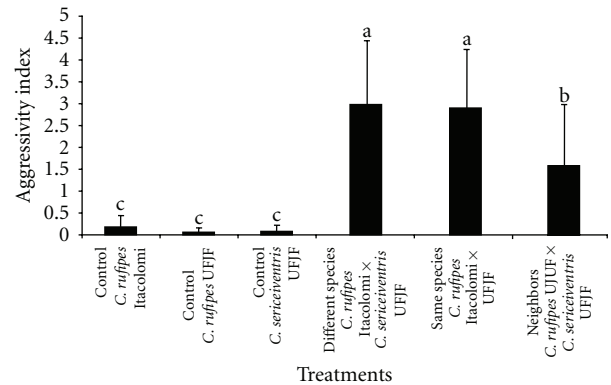


FIGURE 4: Aggressiveness index (mean and standard deviation) for each treatment of laboratory experiments (dyadic encounters) in which “control” is the manipulation with individuals from the same colony and species; “different species” between *C. rufipes* from Itacolomi State Park (Itacolomi) and *C. sericeiventris* from Campus of Federal University of Juiz de Fora (UFJF); “same species” between *C. rufipes* from both Itacolomi and UFJF; “neighbours” between *C. rufipes* and *C. sericeiventris* from UFJF.

observed attacking any insect, contrary to what is expected for a plan-ant-herbivore system.

To a certain extent, the coexistence of these species was possible due to behavioural diversity. For instance, we observed that different species place themselves almost opposite to the others when eating on the bait, thus avoiding conflicts while sharing the same resource at the same moment. In this study, at various times when the bait was exposed, there were around five ant species on it. An erroneous interpretation of this would be to say that there was no competition in place. However, upon behavioural observation *in locu*, it was evident that species placed themselves strategically on the bait, avoiding visual or chemical contact. Furthermore, when two species meet, there was aggressive behaviour, resulting in fleeing of one of them. It is worth noting, though, that

since baits were an energetic, unpredictable, and sufficiently abundant food source, it was possible for various species to eat at the same time without the need to expel or attack the others. Most of natural resources available ought to result in a tougher competitive environment than the one we manipulated.

**4.2. Laboratory Experiments.** *Camponotus rufipes* and *C. sericeiventris* were able to recognize individuals of their colony and to differentiate them from other colonies and species. For *C. rufipes*, this capacity has already been registered [35]. Most importantly, the present experiment measured the aggressiveness between these species, which was high for *C. sericeiventris*, but also stronger for those individuals of *C. rufipes* that coexisted in the field with *C. sericeiventris*, compared with the Itacolomi's individuals. Since Itacolomi's ants have grown without any substantial competition in nature, they become pacifists.

Similar results were previously described for other systems. Lucas [36] observed three species of *Pachycondyla* (*P. villosa*, *P. inversa*, and *P. subversa*) during dyadic encounters and found out that they were able to recognize members of the same colony, of the same species and of different species, increasing aggressiveness in the same order. For *C. rufipes* at UFJF, there was no differentiation of aggressiveness between intra- and interspecific encounters, which means that their defensive behaviour against *C. sericeiventris* or a potential invader colony of their own species was similar and may reflect their establishment in a hostile environment.

Combative behaviours are widely described in the myrmecological literature. In the laboratory, *Oecophylla longinoda* (a dominant arboreal genera) was observed while fighting for its territory with two foreign individuals that entered simultaneously the arena [37]. This species was also observed in its natural habitat fighting and excluding other ant colonies in Africa. Similar results were encountered for *Oecophylla smaragdina* in Australia [38, 39]. De Vita [40] measured the aggressiveness of *Pogonomyrmex californicus* populations in their natural habitat and observed that 81% of the encounters resulted in some type of aggression and, in some cases, led to the death of the individuals. In addition, there was evidence that ants of the same species from different colonies showed aggression against each other. Aggression was also shown against potential competitors of another species, which resulted in fights or death in all repetitions.

The lack of aggressiveness from Itacolomi's *C. rufipes* corroborates the assumption that aggressive behaviour is more likely learned than inherited, especially since the same species (*C. rufipes* from UFJF) that coexists with competitors presents a greater level of aggressiveness and a greater capacity to fight with foreign species of the same size (*C. rufipes* from Itacolomi). Also, the data from the encounters among *C. rufipes* from Itacolomi and *C. sericeiventris* show that *C. rufipes* from Itacolomi was almost always attacked and killed. On the other hand, when the encounters were between *C. rufipes* and *C. sericeiventris* that coexisted in the same area (UFJF), the battles were more evensided, registering 40% of the deaths for workers of *C. rufipes* and 60% for

*C. sericeiventris*. In these cases, the aggressiveness index was higher; the ants fought for a longer time before one of them died. In the field experiments, there was no occurrence of a fight to death between *C. rufipes* and *C. sericeiventris*, as had occurred in the dyadic encounters. Nevertheless, a transposing experiment is needed to confirm whether such aggressiveness would be learnt or, otherwise, whether there could be a *C. rufipes* "pacifist genotype".

As generally observed in the field for all species, these two codominant species also avoid combative behaviour, in accordance with the prediction that a strategy of decreasing costs of combat is of great importance in behavioural evolution. This mutual avoidance during the field experiments could also be related to the abundance of food that the bait represents, which implies in no dispute. However, the dominant species was bothered by the presence of other species when they were encountered feeding at the same place in the bait. On the other hand, in the dyadic encounters in a small arena and with no escape route, the ants had no alternative other than to dispute that small space by attacking and killing the other individual.

In conclusion, direct contacts seem to be avoided between *C. rufipes* and *C. sericeiventris*, as is expected, since they are two species with similar feeding habits, nesting location, foraging strategy, and body dimensions. However, *C. rufipes* species from Itacolomi does not have a great fighting capacity, very likely because it does not coexist with any other similar competitor, showing that behavioural plasticity will always favour the cost-saving behaviour, namely avoiding conflict.

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