



RESEARCH ARTICLE - ANTS

Evaluation of Insects that Exploit Temporary Protein Resources Emphasizing the Action of Ants (Hymenoptera, Formicidae) in a Neotropical Semi-deciduous Forest

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Abstract

The majority of the ants is opportunistic and generalist foragers, commonly feeding on vegetable secretions, seeds, and living or dead animal material. They may be present on any type of substrate even, occasionally on carcasses. This work, then, aimed to evaluate the action of insects, especially ants, in the exploitation of protein resources in forest environment. Monthly collections were made over a year and, in each collection, were made observations during 12 consecutive hours. To simulate exposure of protein resources we used three types of baits, sardines, beef liver and chicken. To evaluate the importance of ants on protein resources for each type of bait there was a control replica with physical barrier to prevent their access. The ants were observed on all baits throughout the collection period. In total, the baits were visited by 34 species of ants. The main genus of ants to visit the baits were: *Pheidole*, *Crematogaster* and *Solenopsis*. These results demonstrate that the presence of ants is important to ecological succession on temporary protein sources in forest environments interfering in the occurrence of other frequent groups in this type of resource, such as flies, for instance. The species that dominated the baits, when presents, were those that regardless of size and aggressiveness, presented mass recruitment and exploited the baits with large flow of individuals. Although some species that exhibit certain characteristics can locate the baits faster and eventually dominate them at some point, depending on the ants species that co-occur, the results for the sequence of colonization can be modified.

Introduction

The insects of the order Hymenoptera have a wide diversity of habits and complex behaviors, culminating in the social organization of wasps, bees and ants (Wilson, 1971; Triplehorn & Jonnson, 2011; Rafael et al., 2012). In the tropics, ants have a strong presence in most terrestrial ecosystems (Fittkau & Klinge, 1973, Erwin, 1989, Stork, 1991, Longino et al., 2002; Ellwood & Foster, 2004). These insects have broad geographic distributions and high species richness, forming one of the most ecologically successful groups (Hölldobler & Wilson, 1990; Longino et al., 2002), and more than 2000 species are estimated to inhabit the Neotropical Region (Fernández, 2000). The evolutionary success of ants is due to several aspects of social life, but especially the strategies for obtaining resources, particularly food, for their colonies.

Some groups have a more specialized feeding mode, such as fungi cultivators (Weber, 1972); others particularly prefer liquid food (Delabie & Fernández, 2003); and, mostly, ants are opportunistic and generalist foragers, commonly feeding on vegetable secretions, seeds, and living or dead animal material (Fowler et al., 1991; Kaspari, 2000). Ants may be present on any type of substrate if conditions are favorable for foraging. According to Clark and Blom (1991), vertebrate or invertebrate carcasses, even if only occasionally, can be a source of additional food for ants that normally feed on seeds, for example.

The decision made by an ant when locating a resource is to maximize the energy balance, in order to obtain a higher gain at low energetic cost for obtaining food, as predicted by the optimal foraging theory (Sih, 1982 a, b, Stephens & Krebs 1986). Due to restrictions on dominating and carrying



resources, small ants should recruit other ants to ensure their domination after encountering a resource, avoiding the loss of that resource to a larger ant, or other animals (Pearce-Duvet & Feener Junior, 2010). Additionally, the recruitment speed is directly related to the amount of resources that an ant can carry. Therefore small ants should recruit faster than larger ants, since the smaller body size is satisfied quickly. The speed of food sources recruitment can be an important determinant of ant's communities, since the evolutionary trade-off between exploitative and interference competition may be a key influence to the dominance of resources (Davidson, 1998; Parr & Gibb, 2012).

The intra or interspecific competition during the foraging activity occurs when individuals exploit similar resources (Begon et al., 2006). The competition also occurs when there is an overlap of activity periods and areas for several species of ants that visit the same food source employing similar foraging strategies (Petal, 1978; Brandão et al., 2000; Hölldobler & Wilson, 1990). A species is competitively superior and considered dominant when it presents features that allow the monopoly of the resource, such as aggressive behavior or mass recruitment. The other species that co-occur with the dominant and do not have these characteristics are considered subordinate and usually have alternative strategies for obtaining resources (Andersen, 1992; Brandão et al., 2000). An example of these strategies is the infiltration behavior, in which some individuals of a subordinate species infiltrate among the dominants using a small fraction of the available resources (Brandão et al., 2000; Parr & Gibb, 2010). These aggressive behaviors between individuals can lead in some resource domination cases by workers of one of the species preventing the access of others (Brandão et al., 2000).

The relationship between dominant and subordinate species can also be influenced by environmental factors. This influence can occur by direct physiological effects resulting from the tolerance of each species to microclimatic variations (De Bie & Hewitt, 1990). In particular, when competing species are subjected to a limiting condition, the dominant species may no longer use the resource as a way to reduce the physiological stress. Consequently, subordinate species may take a risk under such adverse conditions and use the resource (Bestelmeyer, 2000). In this sense, especially for ants, temperature is one of the most important factors, since the myrmecofauna is sensitive to desiccation. Thus, high temperatures can influence the foraging strategy of ants and therefore their interactions on resource places (Cerdá et al., 1997, 1998).

Therefore, this study aimed to evaluate the action of ants, especially the interspecific relationships, while visiting temporary protein sources in a forest environment.

Material and Methods

Samples were collected monthly between June 2010 and July 2011 in a forest fragment of around 800,000 sqm

(square meters). This area is semi-deciduous forest, according to the classification system of IBGE, the Brazilian Institute of Geography and Statistics (Veloso et al., 1991), and is located in Dourados, Mato Grosso do Sul (S 22°12'56.63" – W 54° 54'57.05"). The area was divided into 20 quadrats of 40,000 sqm. The quadrats were numbered from 1 to 20, and in each collection month, each quadrat was randomly assigned a number which then was removed to avoid repetition. Samples were collected for 12 consecutive hours from 06:00 to 18:00.

To evaluate the effect of ants under temporary protein sources in forest environments, 50g of each of three different baits were used at each collection point. The baits consisted of sardines, which are commonly used as bait for ant collections (Benson & Brandão, 1986; Moutinho, 1991; Brandão et al., 2000), as well as beef liver and chicken.

At each collection point, the three types of baits were placed on disposable plates directly on the ground, 10m apart, in a straight line. The use of plates prevented access by some species of ants that can exploit baits beneath the plant litter. In this way, it was possible to monitor the interaction of all the species that occur only on the substrate. In order not to overestimate the occurrence and probable dominance of any species of ant, before the baits were installed at each site, a systematic search was made to avoid installing the bait on or near ant nests.

To evaluate more specifically the action of ants at the baits, isolated control baits were installed, under the same conditions, with a physical barrier (colorless and odorless gel) around the plate, thus preventing access by any insect that was foraging on the soil.

The consumption of baits was determined at the end of each collection, with the aid of an analytical scale, determined by the difference in weight between the beginning and the end of the period of exposure. Occasional weight loss from drying was not taken into account.

To evaluate whether the difference in consumption between the baits with and without barriers was significant, we applied a T test (using a 0.05% confidence level) to compare them. To evaluate whether the change in climatic conditions during the two seasons in the state of Mato Grosso do Sul (Zavattini, 1992) affected the richness and number of interactions between ant species that occurred on the baits, in the first 15 minutes of each hour of observation, temperature and relative humidity were measured with a hygrometer, and these data were evaluated by a Pearson correlation test.

Throughout the observation period, the individual acts of behavioral interactions between different species of ants that co-occurred on the baits were quantified and qualified, according to the following parameters adapted by Brandão et al. (2000): Action: **Going forward** = Going toward an individual of another species with jaws open in an abrupt movement; **Biting** = Claspings body parts of the other individual with the jaws; **Exhibiting the stinger region or sting** = turning the gaster downward from the abdomen; **Lifting the gaster** =

Shaking the gaster to expel pheromones; **Killing** = Attacks that resulted in the death of the individual attacked. Reaction: **Staying on bait** = The individual does not leave the bait even after attacked; **Escaping** = The attacked individual leaves the bait quickly; **Exhibiting the stinger region or stinging the aggressor** = The attacked individual displays the sting, and/or stings the attacker; **Lifting the gaster expelling pheromones** = The attacked individual displays the gaster region, expelling toxic substances; **Fighting** = The attacked individual defends itself, struggling with the attacker by using the jaw or other body parts; **Killing** = The attacked individual, when defending itself, kills the attacker.

The time that the species spent to locate and exploit the bait was quantified, as well as the number of individuals of each species present on the bait, in 1-minute intervals (flow of individuals). The mean flow was categorized as: **Weak flow**: 3 to 10 individuals per minute; **average flow**: 11 to 30 individuals per minute; **intense flow**: more than 30 individuals per minute.

The levels of ant aggression were categorized during interactions in values from 0-2 (0 = not aggressive; 1 = aggressive, 2 = very aggressive), taking into account the following parameters: **Not aggressive**: they always fled and displayed no agonistic behavior; **aggressive**: they moved most of the time, but did not maintain any physical contact; **very aggressive**: they bit and/or killed, or even performed another aggressive act that caused injury to another individual.

The types of interactions that mainly indicate the dominance or exclusion of other ants from the food source, according to Brandão et al. (2000), were categorized as follows: Dominated by being the only individual on the bait; dominated by being abundant; dominated by being aggressive; dominated by being abundant and aggressive; excluded other ants from the bait.

To evaluate whether there was any relationship between the size of the species and the strategy adopted during the interactions between the species, the alitrunk of each individual collected on the bait was measured. According to Brandão et al. (2000), this measurement is not affected by the individual's physiological state, and is traditionally termed in taxonomic articles on ants as the measure of Weber (WL). The sizes of the ants were categorized as: **Small**: from 0.01 to 1.0 mm; **average**: from 1.01 to 2.0 mm; **large**: above 1.2 mm.

All these parameters described above were correlated by a Jaccard cluster analysis, to attempt to identify groups of ant species that adopt the same behavioral strategies during interactions on baits.

After the interactions and/or consuming the baits, some foragers (one or two depending on the species) were collected while they were leaving the bait, and were placed in 70% ethanol for later identification at the genus level, using the keys of Bolton (1994, 1995 and 2003); and at the species level, when possible, by comparing with standard specimens in the Formicidae Reference Collection of the Museum of Myrmecology

CEPEC/CEPLAC - Ilhéus, Bahia. Vouchers from this study were deposited in this collection under number # 5675.

Specimens of other insects were collected with forceps and/or brushes and stored in jars containing 70% ethanol for later identification to family level, with the aid of the dichotomous key of Rafael et al. (2012) and by comparison with standard specimens in the Entomological Collection of the Museum of Biodiversity, UFGD/MS.

Results and Discussion

Occurrence of insects in general

The average consumption on baits without a barrier was $17.87\text{g} \pm 5.45$, and on baits with a barrier was $15.95\text{g} \pm 5.86$. The T test indicated no significant difference between these values ($F = 1.41$; $p = 0.261$). The presence or absence of ants, on these food sources, does not influence their consumption. Baits where ants do not occur must be consumed by other groups of insects.

During the months of collection, the mean temperature and relative humidity were $25.4^\circ\text{C} \pm 2.86\%$ and $56.58\% \pm 14.16$, respectively. There was no significant correlation between the consumption of baits and the temperature ($F = 2.83$; $p = 0.163$), or relative humidity ($F = 2.68$; $p = 0.163$), in both seasons.

In general, the assembly of insects varied little on both types of baits (Figs. 1 and 2).

Dipterans occurred most frequently on both baits (Figs. 1 and 2). According to Souza and Linhares (1997), the insects most frequently evaluated in this type of substrate are the dipterans, especially the families Calliphoridae, Sarcophagidae and Muscidae (Oliveira-Costa, 2003, 2008; Gullan & Cranston, 2008; Pujol-Luz et al., 2008). Fly larvae compete intensely for resources on the carcasses in an attempt to consume the largest possible volume of food before the resource is exhausted (Goodbrod & Goff, 1990).

Although coleopterans are also an important group

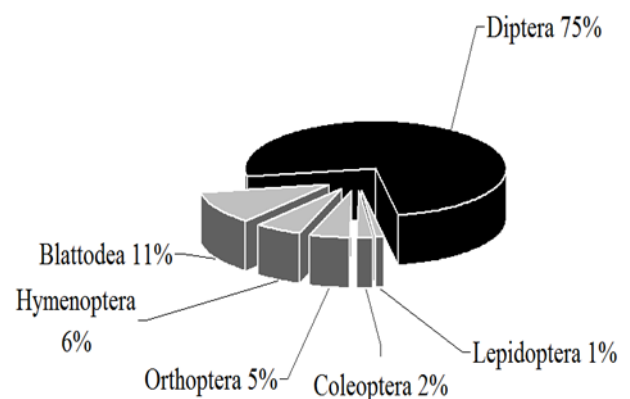


Figure 1: Relative frequency of the different insect orders that visited the 3 types of baits with physical barrier, exposed in forest areas between June/2010 to July/2011.

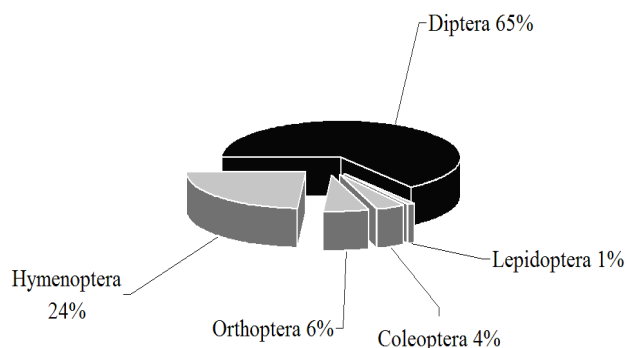


Figure 2: Relative frequency of the different insect orders that visited the 3 types of baits without physical barrier exposed in forest areas between June/2010 to July/2011.

that occurred in this type of resource according to the literature (Oliveira-Costa, 2003; Rafael et al., 2012), they occurred in relatively low frequency compared to the other groups; as Lepidoptera and Orthoptera (Figs. 1 and 2). Souza et al. (2008) reported that insects such as coleopterans, even if frequent, most frequently visit protein sources only at the initial stage of putrefaction.

Cruz and Vasconcelos (2006) discussed that the low occurrence of Blattodea and Orthoptera is associated with their feeding habits. Most representatives of the latter group are phytophagous, occurring almost as accidental visitors (Oliveira-Costa, 2003). Blattodea are opportunistic insects that exploit the most easily available resource. In general they are omnivorous, feeding on organic matter of any kind; however, they are sometimes also predators and attack other insects (Triplehorn & Jonnson, 2011). In this study, Blattodea were present only on baits that were surrounded by a barrier (Fig. 1) and hence without ants, indicating that the presence of ants seems to inhibit the action of this group.

The baits with barriers were visited by insects of the orders Diptera (75%), Blattodea (11%), Orthoptera (5%), Coleoptera (2%) and Lepidoptera (1%); the order Hymenoptera was represented only by wasps (6%) (Fig. 1). These results demonstrate that ants can inhibit the occurrence of wasps. Moretti et al. (2011) demonstrated that these types of substrates may be an additional food source for the wasps; they observed wasps feeding directly on the baits and preying on adult insects.

Also for baits with barriers, Coleoptera of the family Staphylinidae and Diptera of the family Calliphoridae were very common. Calliphorid flies occur in great abundance in this type of substrate, and are very common in manure and carrion (Oliveira-Costa, 2003; Gullan & Cranston, 2008; Triplehorn & Jonnson, 2011).

The baits without barriers were visited by Diptera (65%), Hymenoptera (24%), Orthoptera (6%), Coleoptera (4%) and Lepidoptera (1%) (Fig. 2). On two occasions, baits without barriers were visited by spiders of the family Lycosidae. According to Centeno et al. (2002), and Oliveira-Costa (2008), this group of spiders plays an ecological role as predators of

insects that belong to the cadaverous fauna.

The frequency of occurrence of flies was about 10% lower on bait without barriers, which allowed ants to visit (Table 1). Even so, flies were the most frequent group, as described in trials such as those of Souza and Linhares (1997), Oliveira-Costa (2008), and Rafael et al. (2012). Still, this clear effect on the occurrence of flies should be analyzed with caution because it is a very common group in this type of resources besides being highly important to Forensic Entomology (Oliveira-Costa, 2003; Pujol-Luz et al., 2008).

Table 1.: Frequencies relative (%) of occurrences of different orders and families of insects in the three types of baits exposed forested areas between the period June/2010 July/2011.

| Insects | | Baits (%) | | |
|-------------|---------------|-----------|---------|-------|
| Order | Family | Chicken | Sardine | Liver |
| Hymenoptera | Formicidae | 34.73 | 33.22 | 32.04 |
| | Vespidae | 69.56 | 21.73 | 8.69 |
| Diptera | Calliphoridae | 81.25 | 15.62 | 3.12 |
| | Sarcophagidae | 67.98 | 24.02 | 8.00 |
| | Muscidae | 80.01 | 15.96 | 4.03 |
| | Syrphidae | 66.66 | 20.00 | 13.33 |
| Coleoptera | Staphylinidae | 87.09 | 12.9 | 3.22 |
| | Scarabeidae | 75.00 | 20.83 | 4.11 |
| Orthoptera | Histeridae | 96.87 | 3.12 | 0.00 |
| | Gryllidae | 42.85 | 50.00 | 7.14 |
| Blattodea | Blattellidae | 35.71 | 35.71 | 28.57 |

The most frequent insects on the sardine baits without barriers were members of the family Gryllidae (50%); on beef-liver baits, Formicidae (32.04%); and Histeridae (96.87%) were most frequent on chicken baits (Table 1). As seen in Table 1, the chicken bait was the most frequently visited overall. Although subjective, the reason may be the strong odor emitted by the chicken bait on decomposition, compared to the others.

Occurrence of ants

Ants occurred on all types of baits throughout the collection period (Table 2), although some species occurred more frequently on a certain type of bait than on another. However, one should take into account that the low occurrence of a species in different areas of collection may explain its low frequency on a specific type of bait.

Throughout the collection period, 34 ant species were observed (Table 2); however, only 27 (80%) interacted with other species of ants. The other species were alone when visiting the baits, with no other ant species at that time. We quantified 194 behavioral acts during interactions between species (Table 3). The most effective act involving action was biting (43.75%).

Table 2.: Relative frequency (%) of occurrence of different species of ants in each type of bait attractive exposed in the forest, between the period of the June/2010 July/2011.

| Species | Baits | | |
|--|---------|---------|-------|
| | Chicken | Sardine | Liver |
| SUBFAMILY: PONERINAE | | | |
| <i>Odontomachus meinerti</i> Forel, 1905 | 1.29 | 0.00 | 0.00 |
| <i>Odontomachus chelifer</i> (Latreille, 1802) | 1.29 | 0.00 | 0.00 |
| <i>Pachycondyla striata</i> Smith, 1858 | 3.89 | 2.12 | 0.00 |
| <i>Pachycondyla verena</i> (Forel, 1922) | 5.19 | 4.25 | 1.92 |
| <i>Pachycondyla villosa</i> (Fabricius, 1804) | 11.68 | 8.51 | 3.84 |
| SUBFAMILY: ECTATOMMINAE | | | |
| <i>Ectatomma brunneum</i> F. Smith, 1858 | 1.29 | 4.25 | 1.92 |
| <i>Ectatomma tuberculatum</i> F. Smith, 1858 | 1.29 | 2.12 | 1.92 |
| <i>Ectatomma permagnum</i> Forel, 1908 | 0.00 | 2.12 | 0.00 |
| <i>Gnamptogenys</i> sp. | 0.00 | 2.12 | 5.76 |
| SUBFAMILY: DOLICHODERINAE | | | |
| <i>Azteca</i> sp. | 1.29 | 2.12 | 0.00 |
| <i>Linepithema iniquum</i> (Mayr, 1870) | 0.00 | 4.25 | 1.92 |
| <i>Linepithema pulex</i> Wild, 2007 | 3.89 | 0.00 | 0.00 |
| SUBFAMILY: FORMICINAE | | | |
| <i>Camponotus crassus</i> Mayr, 1862 | 5.19 | 2.12 | 3.84 |
| <i>Camponotus fastigatus</i> Roger, 1863 | 0.00 | 2.12 | 3.84 |
| <i>Camponotus melanoticus</i> Emery, 1894 | 3.89 | 2.12 | 5.76 |
| <i>Camponotus (myrmaphaenus)</i> sp | 0.00 | 2.12 | 3.84 |
| <i>Camponotus sericeiventris</i> Guérin, 1838 | 2.59 | 0.00 | 0.00 |
| <i>Nylanderia</i> sp. | 3.89 | 0.00 | 0.00 |
| <i>Nylanderia guatemalensis</i> (Forel, 1885) | 0.00 | 0.00 | 5.76 |
| SUBFAMILY: ECITONINAE | | | |
| <i>Labidus coecus</i> (Latreille, 1802) | 0.00 | 2.12 | 1.92 |
| SUBFAMILY: PSEUDOMYRMECINAE | | | |
| <i>Pseudomyrmex tenuis</i> (Fabricius, 1804) | 2.59 | 6.38 | 1.92 |
| SUBFAMILY: MYRMICINAE | | | |
| <i>Acromyrmex coronatus</i> (Fabricius, 1804) | 2.59 | 0.00 | 0.00 |
| <i>Atta sexdens rubropilosa</i> Forel, 1908 | 2.59 | 2.12 | 7.69 |
| <i>Crematogaster nigropilosa</i> Mayr, 1870 | 3.89 | 8.51 | 0.00 |
| <i>Crematogaster limata</i> Smith, 1858 | 6.49 | 10.63 | 5.76 |
| <i>Pheidole oxyops</i> Forel, 1908 | 6.49 | 10.63 | 7.69 |
| <i>Pheidole pubiventris</i> Mayr, 1887 | 7.79 | 10.63 | 5.76 |
| <i>Pheidole radoszkowskii</i> Mayr, 1884 | 6.49 | 0.00 | 5.76 |
| <i>Sericomyrmex</i> sp. | 2.59 | 0.00 | 1.92 |
| <i>Solenopsis invicta</i> Buren, 1972 | 6.49 | 0.00 | 10.00 |
| <i>Solenopsis</i> sp. | 0.00 | 0.00 | 7.69 |
| <i>Trachymyrmex iheringi</i> (Emery, 1888) | 2.59 | 2.12 | 0.00 |
| <i>Trachymyrmex</i> sp. | 1.29 | 2.12 | 1.92 |
| <i>Wasmannia scrobifera</i> Kempf, 1961 | 1.29 | 4.25 | 0.00 |

This behavior was also the most frequently described by Brandão et al. (2000) and it seems to be one of the most effective behavioral strategies to dominate a resource. The most frequent act involving reaction was lifting the gaster (66.32%). According to Longino (2003), species of the genus *Crematogaster* exhibit their gaster, raising it in order to demonstrate that it is apparently larger than it actually is; or it can be used to eject formic acid or other substances as chemical defenses, depending on the situation and also on the species.

Table 3: Relative frequency of action and reaction behaviors executed by different ant species during interactions in the 3 types of baits exposed in forest areas between June/2010 to July/2011.

| Action | % | Reaction | % |
|---------------|-------|--------------------|-------|
| Biting | 43.75 | Lifting the gaster | 66.32 |
| Going Forward | 26.04 | Staying on bait | 20.4 |
| Killing | 13.54 | Escaping | 13.26 |
| Expelling | 17.7 | | |

The results demonstrate that as the frequency of interactions between species on baits increased, the consumption decreased (Fig. 3 A, B and C). It seems that in most cases, the species opted to dominate the resource before exploiting it, which leads them to spend more time interacting with other species than consuming the resource.

The correlations between the number of species of ants that visited the baits ($F= 10.88$; $p= 0.030$) and the number of interactions ($F= 5.38$; $p= 0.01$) with temperature were significant and positive in the rainy season. That is, the more the temperature increased, the more the number of visitor species increased, and consequently the number of interactions on baits increased as well (Figura 4).

The temperature, especially at the soil surface, is one of the factors that regulate the activity of foraging ground insects. At higher temperatures and favorable relative humidity, ants tend to increase their foraging activities and consequently the number of interactions between species also increases (Hunt, 1974; Levings, 1983; Cerdá et al., 1997, 1998; Dajoz, 2000).

Several species of the Attini group visited and consumed the bait: *Atta sexdens rubropilosa*, *Acromyrmex coronatus*, *Sericomyrmex* sp. and *Trachymyrmex* sp. All of them carried pieces of bait to their colonies. However, these species are known to be restricted to feeding on fungi that grow on a composite substrate consisting mainly of plant material gathered by their workers (Weber 1972; Delabie & Fernández, 2003). On the other hand, Clark and Blom (1991) stated that vertebrate carcasses may be an additional food source for ants that feed on seeds, for example, considering the frequency of availability of carcasses. Conconi and Rodríguez (1977) suggested that species of *Atta* must feed on alternate materials such as meat. Marques and Del-Claro (2006), also observed that ants of the genus *Atta* was one of the most frequent visi-

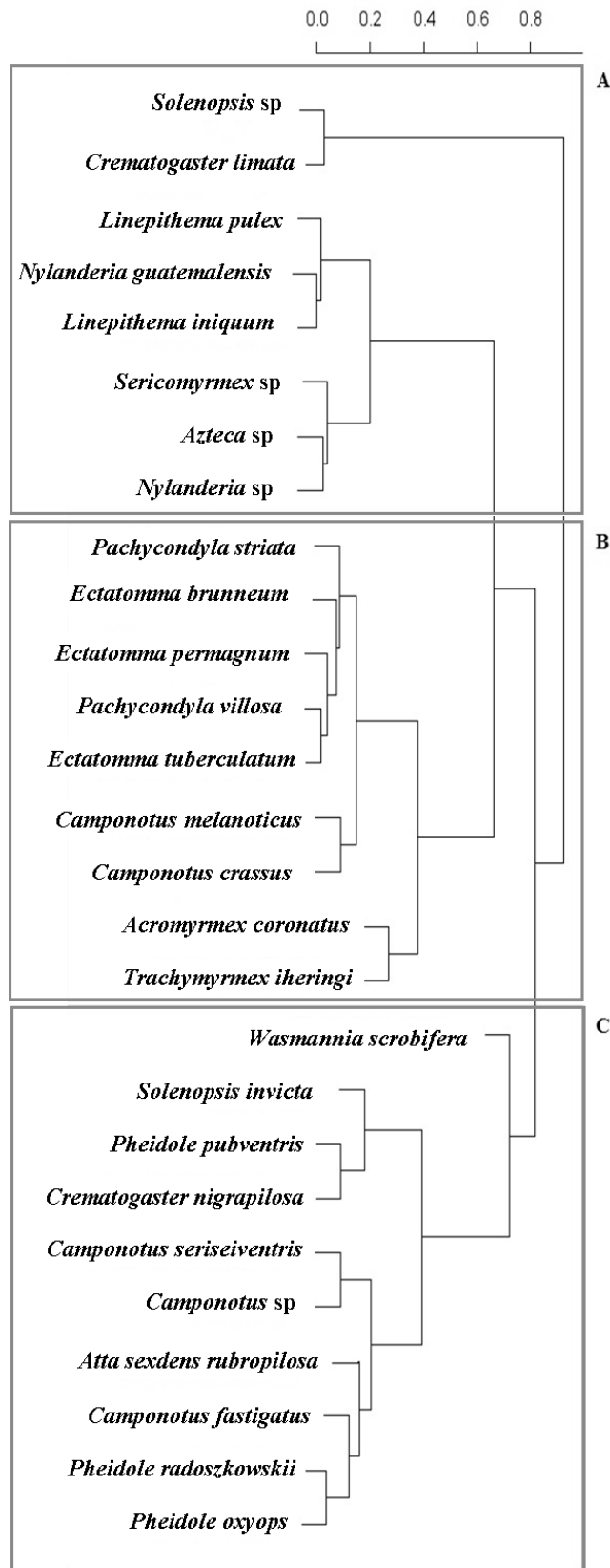


Figure 3: (Jaccard) Grouping evaluating size, aggressiveness and average flow of different ant species during interactions in baits. A: medium-sized species, medium foraging flow, little aggressive and not dominant, B: large species, low foraging flow, very aggressive and not dominant, C: small species, intense foraging flow, not aggressive and dominant.

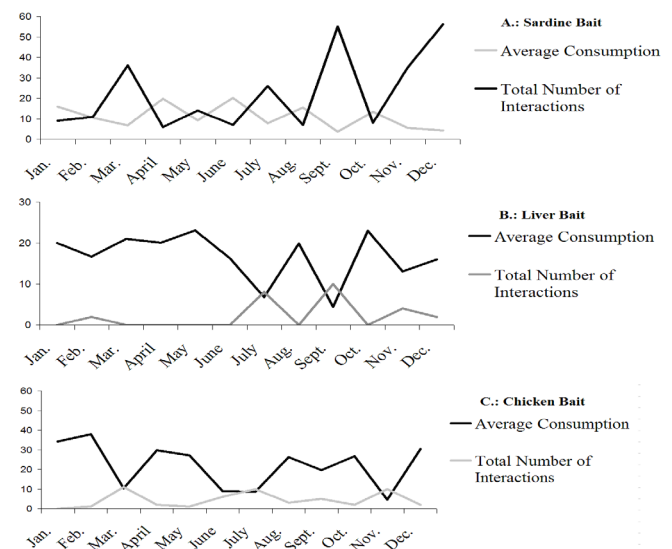


Figure 4: Average consumption and total number of interactions per collection of different ant species in the 3 types of baits without physical barrier, exposed in forest areas between June/2010 to July/2011.

tors in inventory held in a Cerrado area using sardine baits.

Here, the ants, regardless of species, required a mean of 4.1 ± 1.8 minutes to locate the bait, which was visited by a mean of 2.11 foragers per minute, regardless of the type of bait. Species of the genera *Pheidole* and *Crematogaster*, and *A. sexdens rubropilosa* were the first to find and exploit resources in 33%, 27.77% and 13.88% of cases respectively, always with a mean flow of over 22 foragers per minute. Species with mass recruitment and that forage in large flows are more likely to detect and numerically dominate food resources more rapidly, as noted by Holldöbler and Wilson (1990).

Brandão et al. (2000) argued that the order of arrival of species on the bait is not necessarily associated with their relative dominance, but rather with other factors such as proximity to the source of the nest, colony size, and foraging strategy.

The Jaccard cluster analysis ($J = 0.92$) indicated three distinct groups (Fig. 5). Group "A" included ants with a mean size of 1.24 ± 0.23 mm and a mean flow of 12 ± 7.0 foragers per minute. In this group 83% of the species were categorized as non-aggressive, unable to dominate the bait at any time. An exception in this group was *Azteca* sp. which was considered aggressive; however, its mean flow was 2.1 ± 2 foragers per minute, which was weak according to the criteria used here.

Group B (Fig. 5) included ants with a mean size of 3.28 ± 1.35 mm and a mean flow of 2 ± 0.5 foragers per minute. In this group, 95% of the ants were highly aggressive; however, they dominated the bait in only 5% of cases. In 60% of the cases in which species of this group dominated baits, it was because they were alone, as many species of poneromorphs that comprise this group forage individually (Fig. 5). According to Brandão et al. (2000), ants of this group, although they are large and generally aggressive predators, almost never dominate, and

when they do, it is because they are the only ones present on the baits. Their failure to dominate the bait when other species are present is due to their strategy of foraging individually. According to Brandão et al. (2000), ants of the genus *Pachycondyla*, for example, although they are relatively large, cannot monopolize baits and every time that they confront species that use group attack strategies, they are excluded from the baits. However, in 75% of the cases, although they may not dominate baits, they can remove relatively large pieces and carry them off, infiltrating between the dominant species.

Group "C" consisted of small ants (Fig. 5) with a mean size of 0.80 ± 9.5 mm and a mean flow of 35.45 ± 9.5 foragers per minute. In this group 81% of the species were not aggressive; however, they dominated baits in 85% of the cases. *Pheidole radoszkowskii*, was a typical species of this group, which, when it occurred, dominated baits in 95% of the cases, maintaining a continuous and intense flow, according to the criteria used here. In particular, in 80% of cases where they were present, *A. sexdens rubropilosa* dominated the bait by being abundant and also by maintaining an intense flow.

Throughout the exposure period of baits it was possible to observe that depending on the time there was one species predominating in number in the bait, demonstrating that there is a succession of dominant species in these food sources, competition occurs more intensively when there is an overlap of activity periods and collection sites by several species of ants visiting the same food source (Brandão et al. 2000). In this case, they can take very aggressive actions that may result in some cases of monopolization of the resource by workers of one species, preventing access by others. A species is considered dominant and competitively superior when it possesses features that allow it to monopolize a resource, such as aggressive behavior or mass recruitment. The other species that co-occur with the dominant species and do not possess these characteristics are considered subordinate and usually have alternative strategies for obtaining resources (Andersen, 1992). The relationship between dominant and subordinate species may also be influenced by environmental factors. This influence may occur through a direct physiological effect resulting from the tolerance of each species to microclimate variations (Bie & Hewitt, 1990), such as temperature, because the myrmecofauna is sensitive to desiccation. High temperatures may influence the foraging strategy of ants and therefore their interactions at sites where resources are present (Hunt, 1974; Levings, 1983; Cerdá et al., 1997 and 1998; Dajoz, 2000).

These results demonstrate that the presence of ants is important to ecological succession on temporary protein sources in forest environments interfering in the occurrence of other frequent groups in this type of resource. Their presence may simply inhibit the presence of other insects, especially those that also forage on the ground, or even flies that avoid landing on the resource when there is an intense flow of ants exploiting it. Another important action in this sense is when they prey on

immature, especially of flies and adults of other species that detect and exploit this type of resource. The results show that there are three distinct groups of ants that can interact in this type of resource according to size, flow and aggressiveness toward other species. However, the ones that dominate the source are always those that arrive with less flow of individuals regardless of whether or not detecting the resource first than other species. Therefore, depending on the ant species that co-occur, the results for the sequence of colonization can be modified.

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