Sociobiology 61(3): 258-264 (September 2014) DOI: 10.13102/sociobiology.v61i3.258-264

Sociobiology
An international journal on social insects

RESEARCH ARTICLE - ANTS

Competitive Interactions in Ant Assemblage in a Rocky Field Environment: Is Being Fast and Attacking the Best Strategy?

TA Sales, IN Hastenreiter, LF Ribeiro, JFS Lopes

PPGCB: Comportamento e Biologia Animal, Universidade Federal de Juiz de Fora, Juiz de Fora, Minas Gerais, Brazil

Article History

Edited by
Gilberto M M Santos - UEFS, Brazil
Received 14 January 2014
Initial acceptance 29 April 2014
Final acceptance 06 June 2014

Keywords
behavior, competition, discovery ability, ecologically dominant

Corresponding author
Tatiane Archanjo de Sales
PPGCB, Comportamento e Biologia Animal
Universidade Federal de Juiz de Fora
Instituto de Ciências Biológicas
Campus Universitário s/n
Juiz de Fora, Minas Gerais, Brazil
36036-300
E-Mail: tatiane.archanjo@gmail.com

Abstract

The ant assemblage structure can be molded by mechanisms such as competition and discovery-dominance trade-off. In harsh circumstances it is likely that ant species that control the food resource are the first to arrive at the food source, the most aggressive (behavioral dominance), abundant (numerical dominance) and, thus, ecologically dominant. By these characteristics combination, the discovery-dominance should not be a trade-off, but a positive relationship. Here, we examined the interactions among nine ant species in a rocky field area, in the Ibitipoca State Park, Minas Gerais, Brazil. By offering attractive baits at field, we determined the discovery-dominance ability and the frequency of attack, avoidance and coexistence behaviors of each species. We showed that *Crematogaster sericea*, *Pheidole obscurithorax* and *Pheidole radoszkowskii* abundance has a positive and significant correlation with their discovery ability. They were the first to arrive at the baits (best discoverers) and were numerically dominant, being thus considered ecologically dominant. Despite *P. radoszkowskii* being part of this relationship, this interpretation should be taken cautiously. Its dominance was assured by their high discovery ability and abundance, but the behavioral strategy exhibited was avoidance, not attacking as *C. sericea* and *P. obscurithorax*. The discovery-dominance trade-off could be broken by the linked characteristics that define the ecological dominant status of the ant species studied. Also, *P. radoszkowskii* demonstrates that other strategies could surpass the combination of being fast and attacking, and thus this is not the best strategy for all. In harsh circumstances each species has its own best strategy.

Introduction

The structure of an ant assemblage can be influenced by various factors, the main ones being mutualism, competition, parasitism and predation. Competition plays an important role in the structure of the assemblage, since competitive interactions could control the access of different species to resources (food and nesting sites), thus determining the coexistence among species within an assemblage. Evidence which supports the role of competition as a structuring factor of ant assemblages comes from observation of physical and chemical aggression among species to protect resources and territorial limits (Parr & Gibb, 2010). The high competitive potential of each ant species arises from the fact that most of them are omnivorous. This increases the competition effect and its importance in structuring ant assemblages (Benson & Harada,1988), which leads ants to exhibit various strategies to obtain food resources (Carroll & Janzen, 1973; Detrain & Deneubourg, 1997).

The competitive strategy of some species to control the food source is through numerical dominance, with the predominance of particular species in numbers, biomass and/or frequency of occurrence (Davidson, 1998). Others exhibit aggressive behaviors which forces their competitors to avoid them (behavioural dominance) (Bestelmeyer, 2000; Davidson, 1998; Fellers, 1987). However, this dominant status is not immutable. A study conducted by Markó and Kiss (2002) indicates that *Myrmica ruginodis* changes its behavior from aggressive to submissive in the presence of a stronger competitor (*Manica rubida*). Espírito-Santo et

ISSN: 0361-6525

al. (2012) showed that the presence of a strong competitor (*Camponotus sericeiventris*) leads *C. rufipes* to show different degrees of aggressiveness. When conspecific from different origins meet, the behavior of *Camponotus sericeiventris* workers also changes from the simple inspection to foreigner-chasing (Yamamoto & Del-Claro, 2008).

Another mechanism widely investigated related to competition and coexistence in ant assemblages is the discovery-dominance trade-off. Various authors have cited that there is a balance between discovery ability and resource dominance (Vepsäläinen & Pisarski, 1982; Fellers, 1987; LeBrun & Feener, 2007; Pearce-Duvet et al., 2011), wherein dominat species which are slower to find food have greater capacity to defend it. On the other hand, species that are good at finding food can be classified as subordinate and their strategy for success is to find food quickly so as to exploit it partially before being dislodged by a dominant species (Vepsäläinen & Pisarski, 1982; Fellers, 1987; LeBrun & Feener, 2007). However, this trade-off can be broken by ecological dominant ant species (Davidson, 1998), invasive ant species (Holway, 1999) and the presence of parasitoids (Lebrun & Feener, 2007), in structurally complex habitats (Gibb & Parr, 2010) or at high temperatures (Bestelmeyer, 2000).

In highly diverse ant assemblages high variation of the competitive interactions is likely to exist (Andersen, 2008). The rocky field area, located at State Park of Ibitipoca, Minas Gerais, Brazil, besides having an impressive richness of ant species (Lopes et al., 2012), is an environment considered extreme and hostile, where food resources become scarce in certain periods (Fowler et al., 1991). Matching up all these characteristics is likely to find at rocky field-type habitats a more enhanced competition among ant species, wherein species that will control the food resource will be very aggressive (behavioral dominance), abundant (numerical dominance) and, wherefore, ecologically dominants (Davidson, 1998). If this is true, the discovery-dominance will be a positive relationship and not a trade-off.

Here, we examine the interactions among nine ant species in a rock field, considered a harsh environment due to extreme daily variation of temperature and humidity; patches with different levels of sun incidence daily; and swallow soils (Rodela & Tarifa, 2002). By offering baits, we aimed to verify which kind of relationship between dominance and food discovery is found for ants in such environment. Also we evaluated if the aggressiveness level is related to the dominance status of ant species.

Material and Methods

Study site

The study was conducted in a rocky field area, at State Park of Ibitipoca (Parque Estadual do Ibitipoca-PEIb), Minas Gerais, Brazil (S 21º42.493', W 043º53.738'). The region has a humid mesothermal climate, with a mild summer and dry winter seasons and at 1500m average elevation (Rodela, 1998). Mean annual precipitation is 1532 mm (being high between months December and January). The average summer-maximum and winter-minimum temperatures are 36ºC and -4ºC, respectively, with extremes daily fluctuations of temperatures (Rodela & Tarifa, 2002). The studied rocky field is characterized by grassland vegetation consisting of grass, herbs and shrubs on outcrops of quartzitic rocks associated with shallow soils and high solar incidence (Rodela, 1998). Vegetations composition includes Velloziaceae, Compositae, Melastomataceae, Orchidaceae, Gramineae, Asclepiadaceae, Eriocaulaceae, Bromeliaceae and Cyperaceae (Rodela, 1998).

Experimental design

We carried out the observations between June 2010 and February 2011. The experimental system consisted of six contiguous plots measuring 8 x 8 m, each one included 25 points set out 2m from each other in a grid pattern. Of these 25 points, the 16 edge points were not utilized, and the 9 internal points constituted the bait stations (Delsinne et al., 2007 adapted) (Fig. 1).

The plots order for baits offer was randomly chosen, so that each one of the six plots was sampled 10 times. At each of the nine bait stations, we placed 3g of sardine with honey (1:1; g:g) over a square PVC plate (10x10 cm). The nine baits were monitored until the appearance of the first forager ant at one of the baits, which lasted at maximum 15 minutes. Then we removed the other eight baits not visited, in order to reduce the excess of resources available, thus avoiding the distribution of potential competitors over the baits spread through the experimental system. In the first discovered bait, we started recording by filming for 40 minutes. The temperature and relative humidity were measured at the beginning of each recording session. This procedure was repeated until we obtained 60 recording sessions, totalizing 40 hours of records. The experiment was always carried out between 8:00 AM and 3:00 PM. Voucher specimens were collected for later identification in the laboratory. At the end of the observations we removed the bait with a plastic bag.

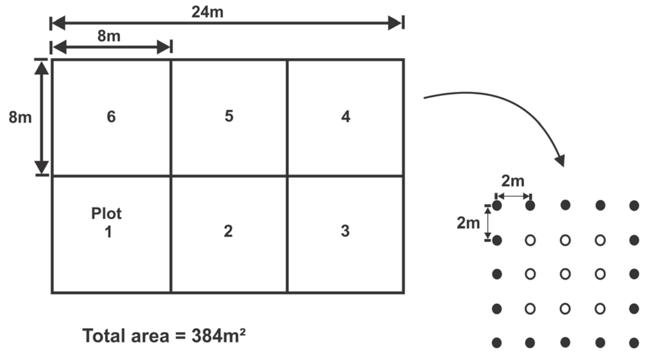

Fig 1. Diagram of the plots with the bait stations. Empty circles represent sites where the baits were offered.

The video allowed us to identify the species that was the first to find the food source, the number of species that visited each bait and its respective abundance. Interactions at baits were also observed and registered by frequency of occurrence into three categories, following Fellers (1987): attack, avoidance and coexistence. An attack constituted of when one ant bit, turned its gaster toward another ant or there was an outright fight. We considered it to be avoidance when ants fleed or avoided direct confrontation with an individual of another species. Lastly, coexistence was considered when two or more workers of different species fed at the same bait without any interaction. Using this classification, we registered the frequency of each behavioral category for ant species.

Data analysis

We restricted our analyses to species which occurred in at least 10% of the baits in order to obtain sufficient numbers of behavioral interactions to reliably assess their dominance. Using this method, we sorted the nine most common species, coincidentally the same number of species used in other studies (Fellers, 1987; Lebrun, 2005; Delsinne et al., 2007).

For data analysis, we divided the 40 minutes of observation into 5-minute intervals, in which we registered the abundance of each species, which enables the calculation of specific average abundance.

The discovery ability of each species (DA) was the number of baits at which the species was the first to arrive (NF) divided by the total number of baits in which that species was observed (NO): (DA = NF / NO). Values near 1 indicate higher discovery ability (Pearce-Duvet et al., 2011). We analyzed the relationship between the specific average abundance (log10x+1 transformed) and their respective discovery ability by fitting a linear regression model.

To verify whether there was a dependence between the frequency of occurrence of each behavior category (attack, avoidance and coexistence) and the species, we subjected the data to the independence Pearson's chi-squared (χ^2) test for contingency tables, in order to access if a species exhibits more often one of the behavioral categories. When attacks occurred more than expected, the species was considered aggressive. We used the R program for all the analyses, at 5% significance in all cases (R Development Core Team, 2013).

Results

We sampled a total of 20 ant species, which belong to 11 genera, distributed into 6 subfamilies: Ectatomminae, Ponerinae, Formicinae, Dolichoderinae, Pseudomyrmicinae and Myrmicinae. Nine of these twenty species were observed at more than 10% of the baits (Table 1). The majority of the baits were visited by more than one species, while only 7% attracted only one species (Fig. 2). *C. crassus* and *C. renggeri* visited more baits than the other species, while *Pheidole* sp.1 exploited the smallest number (Fig. 2).

The specific average abundance calculated for each species showed a positive and significant correlation with their discovery ability (df=7, $P<0.001$, $R^2=0.91$), showing that the best discoverer species were also numerically dominant. Conversely, for the species that were not the first ones to arrive at the baits, we registered lower values of abundance (Fig. 3).

During the experimental period, the average temperature was 29.2 ± 4.0 ºC (39.9 – 19.5 ºC) and the relative humidity was 50.5 ± 10.5% (75.4 – 28.6%). Through the results of the regression analyses it was not possible to show a significant effect of these abiotic variables on the abundance for any of the nine species.

Table 1. Frequency of occurrence of the ant species sampled at 60 baits in Ibitipoca State Park, Minas Gerais, Brazil. * Indicate the species used in the analyses (observed at more than 10% of the baits).

Subfamily	Species	Baits (%)
Formicinae	*Camponotus crassus* Mayr, 1862*	65.0
Formicinae	*Camponotus renggeri* Emery, 1894*	48.0
Ectatominae	*Ectatomma edentatum* Roger, 1863*	38.3
Formicinae	*Camponotus genatus* Santschi, 1922*	35.0
Myrmicinae	*Pheidole obscurithorax* Naves, 1985*	35.0
Ponerinae	*Pachycondyla striata* Smith, 1858*	23.3
Myrmicinae	*Pheidole radoszkowskii* Mayr, 1884*	21.7
Myrmicinae	*Pheidole* sp1*	18.3
Myrmicinae	*Crematogaster sericea* Forel, 1912*	16.7
Dolichoderinae	*Linepithema cerradense* Wild, 2007	8.3
Myrmicinae	*Pheidole* sp3	8.3
Myrmicinae	*Pheidole* sp2	6.7
Myrmicinae	*Cephalotes pavonii* (Latreille, 1809)	5.0
Myrmicinae	*Cephalotes pusillus* (Klug, 1824)	5.0
Ectatomminae	*Ectatomma* sp1	5.0
Ponerinae	*Odontomachus* sp1	3.3
Myrmicinae	*Solenopsis* sp1	3.3
Formicinae	*Myrmelachista* sp1	1.7
Myrmicinae	*Pheidole* sp4	1.7
Pseudomyrmicinae	*Pseudomyrmex* sp1	1.7

When two or more species were recorded foraging at the same bait, approximately 53% of the behaviors exhibited were avoidance. The chi-square test indicates dependence between the behavior category and species (Pearson's chi-squared test: df = 16, $\chi^2 = 356.84$, $P < 0.001$), supplying further evidence that the behavioral strategy shown by a

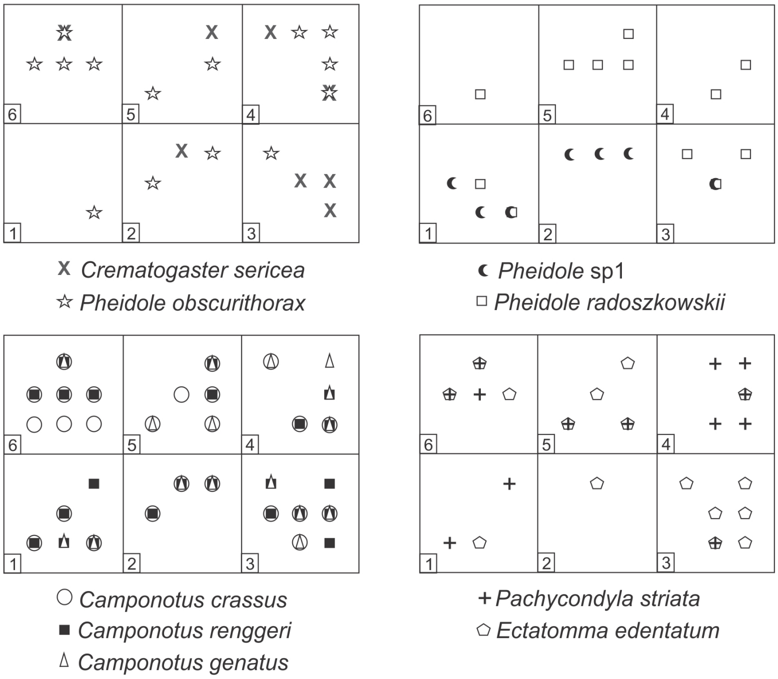

Fig 2. Bait occupancy by the nine species. The species are separated only for illustrative purposes.

species varies according to the species with which it interacts.

C. sericea, *P. obscurithorax* and *C. renggeri* attacked more than expected. However, such aggressiveness only assured dominance of the bait for the first two species, not for *C. renggeri*. In the present study, the aggression exhibited by *C. renggeri* did not assure dominance at the baits, probably due to its low abundance per bait ($N_{max} = 2$). In turn, *C. sericea* stood out for the absence of avoidance behaviors (Table 2), which along with its abundance and discovery ability characterizes it as an aggressive species that can potentially exert a limiting effect of resource use by subordinate species.

P. radoszkowskii also presented a high abundance, but the workers exhibited avoidance behaviors more often than expected, suggesting is the avoidance strategy that assures its ability to remain at the resource (Table 2).

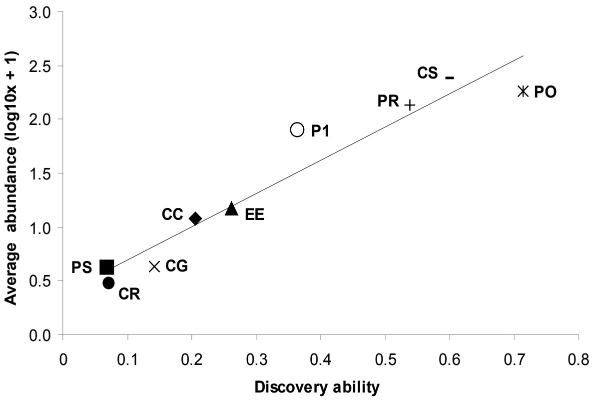

Fig 3. Relationship between the average abundance of the species at the baits and respective discovery ability. CC: *Camponotus crassus*, CG: *Camponotus genatus,* CR: *Camponotus renggeri*, CS: *Crematogaster sericea*, EE: *Ectatomma edentatum*, PS: *Pachycondyla striata*, PO: *Pheidole obscurithorax*, PR: *Pheidole radoszkowskii*, P1: *Pheidole* sp1.

Table 2. Relative frequency for the attack, avoidance and coexistence behaviors and standardized residuals in contingency tables (Pearson's χ^2 test for standardized residuals in contingency tables). In boldface behaviors that occurred above the expected (>+1.96) and behaviors that occurred below the expected (<-1.96).

Species	Relative Frequency of Behaviors (%)			*Standardized residuals in contingency tables (Z)		
	Attack	Avoidance	Coexistence	Attack	Avoidance	Coexistence
Camponotus crassus	27.43	51.43	21.14	*-2.09*	**3.21**	-1.79
Camponotus genatus	16.85	47.19	35.96	*-2.37*	0.95	1.60
Camponotus renggeri	73.63	2.75	23.63	**7.72**	*-6.52*	-0.61
Crematogaster sericea	69.64	0.00	30.36	**3.68**	*-3.72*	0.54
Ectatomma edentatum	29.00	31.00	40.00	-0.79	-1.07	**2.41**
Pachycondyla striata	3.85	46.15	50.00	*-2.17*	0.44	**2.06**
Pheidole obscurithorax	41.42	29.75	28.83	**2.33**	*-2.93*	1.11
Pheidole radoszkowskii	10.13	73.00	16.88	*-5.63*	**7.01**	*-2.61*
Pheidole sp1	22.06	50.00	27.94	-1.45	1.12	0.25

Species with low abundances (*C. renggeri*, *C. genatus* and *P. striata*) can be considered submissive. However, this does not necessarily imply absence of aggressiveness, only a lower competitive ability, as observed for *C. renggeri* (Table 2).

Attack behavior frequencies lower than expected were registered for *P. radoszkowskii*, *C. crassus*, *C. genatus* and *P. striata*. We believe that for these *Camponotus* this result can reflect their low abundance and discovery ability. In contrast, for *P. striata* the most probable explanation is its solitary foraging strategy, characteristic of the species. In the case of *E. edentatum*, the solitary foraging strategy also explains the lower than expected occurrence of avoidance behaviors (Table 2).

Discussion

The relationship between dominance and food discovery was a positive one and not a trade-off, at the rocky field studied. The discovery-dominance trade-off predicts that good discoverers are subordinate species, which maximize their rates of finding resources to access them before being dislodged by a behaviorally dominant species (Vepsäläinen & Pisarski, 1982; Fellers, 1987; LeBrun & Feener, 2007). Inversely, the ant assemblage here studied presents a set of ecologically dominant ant species that arrived first and controlled baits through the combination of numerical dominance and aggressive behavior, with the exception of one species that was not aggressive.

Species with the greatest discovery ability were those with the highest abundance at the baits. On the other hand, species with low discovery ability (bad discoverers) who are less abundant, visited a larger number of baits. One can therefore assume that the low discovery ability of these species could have been offset by exploitation of a broader area. Since these species have low capacity to defend resources, they probably search for food over a larger area. In contrast, for the species with high discovery ability and abundance, we can hypothesize that the baits exploited by them were within their territory and thus were more quickly located and successfully defended.

This positive relationship can also be a reflex of the typical environmental conditions of rocky fields. These areas are characterized by extreme daily fluctuations of temperature and relative humidity, plus the effects of winds and strong sunlight (Pirani et al., 1994). Besides, they are located at high altitudes (above 1,000 meters) and have soils with outcrops of quartzite rocks (Guedes & Orge, 1998). In extreme and hostile environments such as rocky fields, where food resources become scarce in certain periods (Fowler et al., 1991), it is reasonable to assume that after spending energy to find resources, an ant species must take maximum advantage of it. Also, we must consider that the relationships in rocky fields are more specialized, as shown for wasps, due to limitations in resource collection (Clemente et al, 2013). Therefore, after locating the resource, we noted that dominant species present a particular behavioral strategy to remain at the food source. This might also have been the reason why the average abundance of the species at the baits was not influenced by abiotic factors.

Pheidole radoszkowskii used the avoidance as behavioral strategy to remain at the baits. When faced with aggressive ants from other species, most of the time they responded with avoidance. Actually, *P. radoszkowskii* exhibits asymmetry in the competitive relationship with other dominant species (Perfecto, 1994). Our data does not exclude their potential for aggression or coexistence. Rather, they demonstrate its behavioral plasticity towards the species with which it co-occurs.

Further, *P. radoszkowskii* forms colonies with small populations (Perfecto, 1994), which can explain the avoidance strategy observed in the present study. In species with small colonies, direct confrontation represents a greater cost than it does for species with more numerous colonies (Carroll & Jansen, 1973). Therefore, avoidance - a typical interference behavior of ants (Fellers, 1987; Yanoviak & Kaspari, 2000; Delsinne et al., 2007) - seems to be more efficient to allow their use of the bait than attacking or giving up and seeking another resource.

Similarly, *P. obscurithorax* exhibited avoidance behaviors soon after locating the resource but became more aggressive after recruitment and the arrival of soldiers. Storz and Tschinkel (2004) reported a combination of foraging tactics of this species in function of the resource size. For small resources, the scouts carried the food back to the colony alone and only recruited when there was a larger resource. In the present study, the bait offered was hard to transport, thus requiring workers and soldiers recruitment to assure its use for a longer period.

Another strategy employed by *P. obscurithorax* to exploit the food resource was the use of tools. Workers took small pebbles and pieces of leaves onto the plate and placed them in contact with the bait, then removed these materials and transported them back to the nest altogether with the food. The use of tools to carry resources that are not represented by discrete units assures obtaining approximately 10 times more food than direct transport (Fellers & Fellers, 1976). In the case of a subordinate species, this behavior is also utilized to assure later use of the food, since the parts of the resource covered become unavailable to dominant species (Fellers & Fellers, 1976).

Mass recruitment was the strategy presented by *Pheidole* sp1 and *C. sericea* to dominate the bait. Such strategy assured *Pheidole* sp.1 the use of the resource towards *C. crassus* and *C. renggeri*, species with which it co-occurred most and which consequently presented low abundance. In general, the *Pheidole* soldiers are recruited to carry the resource (Mertl et al., 2010), but in the case of *Pheidole* sp.1, we observed soldiers acting only for defense.

The attacks exhibited by *C. sericea* combined with its lack of avoidance confirms this species' high aggressiveness (Longino, 2003). A considerable proportion of the attacks only consisted of turning the gaster up, in order to release small droplets of venom, which can be related to both offensive and defensive behavior (Buren, 1959). Therefore, its high abundance is due to a combination of aggressiveness and fast recruitment (Longino, 2003).

C. sericea, *P. obscurithorax* and *P. radoszkowskii* were considered ecologically dominants. This terminology is proposed by Davidson (1998) who named as ecologically dominant ant species those which are behavioral (due to superior fight and/or recruitment abilities) and numerically dominant. We can suppose that the discovery-dominance trade-off was broken by the linked characteristics that define the ecological dominant status of these species. Despite *P. radoszkowskii* being part of this relationship, this interpretation should be taken cautiously. Its dominance at the baits was assured by their high discovery ability and abundance, but the behavioral strategy exhibited was avoidance, not aggressiveness. *P. radoszkowskii* demonstrates that others strategies could surpass the set of being fast and attack, and thus this is not the best strategy for all. In harsh circumstances each species has its own best strategy, which is also illustrated by seed disperser ant species at Caatinga. In this case, high-quality disperser ant species showed a strong preference for diaspores with highest elaiosome mass, transporting the seeds for longest distances, until their nests, whereas to the low-quality disperser ants, the best strategy was fed on elaiosomes in situ, and never transporting the seeds to their nests (Leal et al., 2014).

The competitive interactions recorded show a range of foraging strategies employed by different ant species composing an assemblage that guarantees exploitation of food resources for all of them. The nature of the competition and the ant behavioral strategies have interesting implications in understanding the species' richness and composition of assemblages, especially in an environment where resources are scarce and ephemeral.

Acknowledgements

The authors are grateful to R. S. Camargo and K. Del-Claro for their constructive comments. Also we are grateful to the Fundação de Apoio e Amparo a Pesquisa do Estado de Minas Gerais (FAPEMIG grant No. 00411/08), the National Concil for Scientific and Technological Development (CNPq) for a fellowship granted to the last author (process No. 307335/2009-7) and Instituto Estadual de Florestas (IEF) from Minas Gerais in special to Clarice Nascimento Lantelme Silva for technical support at Ibitipoca Park..

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