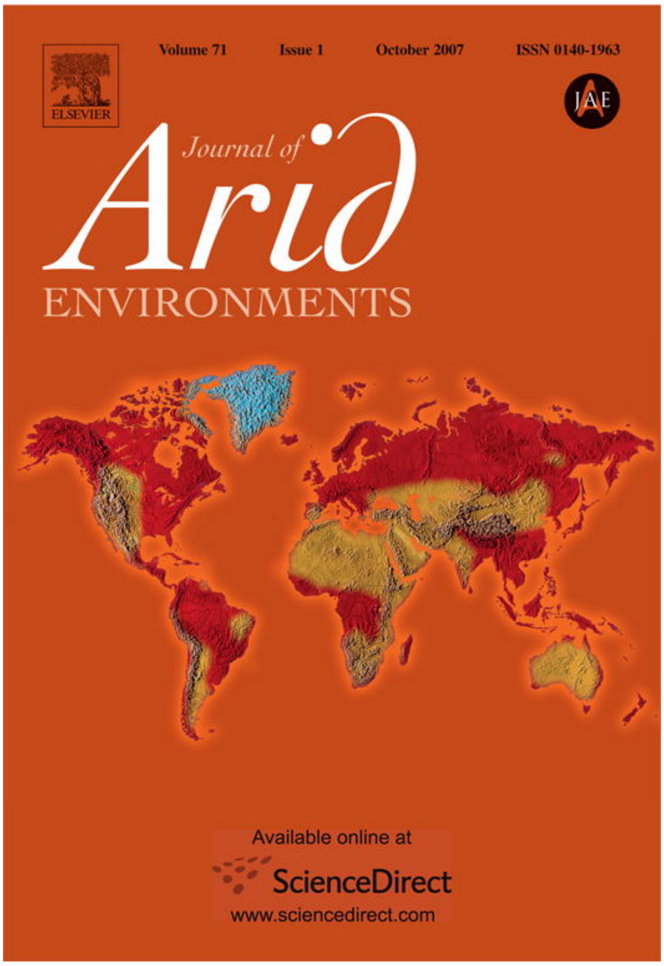
Volume 71
Issue 1
October 2007
ISSN 0140-1963
ELSEVIER
JAE
Journal of Arid ENVIRONMENTS
Available online at
ScienceDirect
www.sciencedirect.com

ELSEVIER
Journal of Arid Environments 71 (2007) 29–44
Journal of Arid Environments
www.elsevier.com/locate/jaridenv

Spatial and temporal foraging overlaps in a Chacoan ground-foraging ant assemblage

T. Delsinne[a,b,*], Y. Roisin[b], M. Leponce[a]

[a]*Conservation Biology Section, Royal Belgian Institute of Natural Sciences, 29 rue Vautier, 1000 Brussels, Belgium*
[b]*Université Libre de Bruxelles, 50 avenue Roosevelt, Behavioral & Evolutionary Ecology—CP 160/12, 1050 Brussels, Belgium*

Received 12 September 2005; received in revised form 22 January 2007; accepted 24 February 2007
Available online 24 April 2007

Abstract

In arid habitats ant temporal foraging results from a set of trade-offs between species food discovery and food domination ability and between species thermal tolerance and behavioral dominance. We investigated how this set of trade-offs structures the spatial co-occurrence of ants during foraging, hence focusing on interspecific competition. The consequences of food type on the spatio-temporal foraging structure were also studied because food preferences were expected to optimize the restricted foraging time and space of thermophilic species. The food partitioning between 24 species attracted to protein or carbohydrate baits was studied in a dry forest of the Paraguayan Chaco. Baits were spaced at one meter intervals and inspected every 15 min over 90-min sessions conducted during mornings and afternoons. Null model analyses revealed a temporal food partitioning during afternoon sessions and a spatial partitioning, influenced by both thermal conditions and interspecific competition. Bait type did not influence the spatio-temporal foraging. Unexpectedly, evidence of interspecific competition was scarce and avoidance rather than overt conflicts appeared to be the rule of thumb. Overall, the spatio-temporal food exploitation at a small scale was affected by temperature and stochastic processes. This demonstrates that chance structures ant foraging even in constraining arid environments.

Keywords: Food partitioning; Formicidae; Interspecific competition; Null model analysis; Species coexistence; Temperature

---

[*]Corresponding author. Conservation Biology Section, Royal Belgian Institute of Natural Sciences, 29 rue Vautier, 1000 Brussels, Belgium. Tel.: +32 2 627 43 64; fax: +32 2 649 48 25.

E-mail addresses: Thibaut.Delsinne@naturalsciences.be (T. Delsinne), yroisin@ulb.ac.be (Y. Roisin), Maurice.Leponce@naturalsciences.be (M. Leponce).

0140-1963/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jaridenv.2007.02.007

1. Introduction

Space, food type and time are the three most important niche axes which may be partitioned among species in order to facilitate their coexistence (Schoener, 1974). In ground-foraging ant assemblages species coexistence is eased by temporal segregations occurring at seasonal (Fellers, 1989; Greenslade, 1971; Herbers, 1989; Levings, 1983; Lynch, 1981; Rissing, 1988) and nycthemeral scales (Bernstein, 1974; de Biseau et al., 1997; Vepsäläinen and Savolainen, 1990). At even shorter temporal scales (60–90 min), food exploitation is also temporally segregated among species depending on their resource discovery and food dominance abilities (Fellers, 1987; Wilson, 1971). Competitive hierarchy theory predicts the existence of three categories of species classified according to their food exploitation behavior: "opportunists", "insinuators" and "extirpators". Opportunists are subordinate species, capable of finding food quickly but which are displaced when extirpators, aggressive ant species, arrive later. Insinuators are discreet ant species able to steal food pieces from opportunists and extirpators (Davidson, 1998; Wilson, 1971). This classical trade-off between resource discovery and resource dominance abilities has been demonstrated in various temperate and tropical ant assemblages (Andersen, 1992, 1995, 1997; Perfecto, 1994; Savolainen and Vepsäläinen, 1989).

Nevertheless at the same short time scale ant competitive hierarchy is modified in habitats where thermal conditions may be stressful, as in arid or semi-arid habitats (Bestelmeyer, 2000; Cerdá et al., 1998a; 1998b; Retana and Cerdá, 2000). In particular, Bestelmeyer (2000) attracting ants with tuna baits in the Argentinean dry Chaco has demonstrated that the trade-off between food resource discovery and food resource domination is associated with a second one opposing thermal tolerance to behavioral dominance. Extirpators were most active at moderately high temperatures whereas opportunists were active at extreme ones. This set of trade-offs structures the ant temporal foraging (Bestelmeyer, 2000) and allows arid environments to support a higher diversity of ant species than expected under these stressful conditions (Cerdá et al., 1998a). Our aim here was to refine the Bestelmeyer study on temporal foraging, bringing to the fore the simultaneous presence of species, by a spatio-temporal foraging analysis taking into account also the species co-occurrence at baits, hence focusing on interspecific competition. This spatio-temporal analysis was performed at a small scale and with a randomization algorithm (null model) allowing the distinction between deterministic and purely stochastic patterns (Gotelli and Graves, 1996; Ribas and Schoereder, 2002). In addition we considered the influence of the type of the food resource by using not only proteins but also carbohydrates as baits.

Ant preferences for a certain food are suspected to occur when the nutrients contained in the food are usually less available or more limited in the environment (Kay, 2004). We hypothesized that in arid or semi-arid habitats species with narrow thermal requirements exhibit a food preference in order to optimize their restricted foraging time. Ant competitiveness is affected by food type, quantity and/or patchiness (Chew and de Vita, 1980; de Biseau et al., 1997; Detrain et al., 2000; Gibb, 2005; McGlynn and Kirksey, 2000; Vepsäläinen and Savolainen, 1990). However, it is still unclear how this may affect spatially and temporally the ant foraging at the assemblage level.

To attain our objectives we: (1) first verified the influence of the set of trade-offs on the temporal foraging activity of the assemblage considered before (2) to study the dynamic of the ant spatial foraging overlap and (3) the consequences of food type on spatio-temporal foraging patterns.

2. Materials and methods

2.1. Study site

The study site was located inside Teniente Enciso National Park in northeastern Paraguay (Lat: S 21°12′; Long: W 61°39′). The habitat is a xeromorphic forest called "Quebrachal" (Ramella and Spichiger, 1989). The upper vegetation stratum is composed of emerging trees (*Aspidosperma quebracho-blanco* Schlechtendal 1861 and *Chorisia insignis* Kunth 1822) and treelike cacti (*Stetsonia coryne* (Salm-Dyck) Britton and Rose 1920, *Cereus stenogonus* Schumann 1899). The lower vegetation stratum is composed of shrubs (*Ruprechtia triflora* Grisebach 1879, *Capparis* spp. and *Ziziphus mistol* Grisebach 1874). The ground vegetation includes bromeliads (*Bromelia* spp., *Dyckia* spp.) and cacti (*Opuntia* spp., *Cereus* spp., *Cleistocactus baumannii* (Lemaire) Lemaire 1861) (Ramella and Spichiger, 1989). Precipitations range between 500 and 800 mm per year (Ramella and Spichiger, 1989), mean temperature is 26 °C.

2.2. Experimental protocol

Experiments were conducted in September 2002 in nine contiguous 4 × 4 m plots, covering a total area of 144 m^2. The studied area was elected in order to maximize the homogeneity in terms of exposure to the sun, soil texture and leaf-litter cover. Each plot consisted of a grid with 25 points at 1 m intervals (Fig. 1). The plot constituted the experimental unit. Bait sessions were carried out with protein (3 g of natural canned tuna fish) or carbohydrate baits

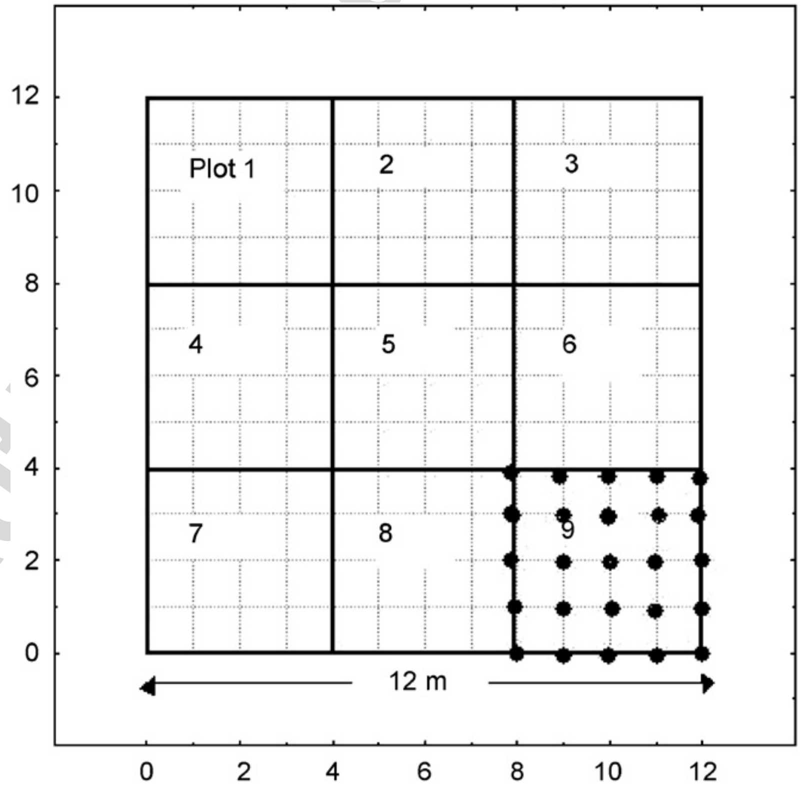

Fig. 1. Experimental protocol. Nine contiguous 4 × 4 m plots covering a total area of 144 m^2 were studied. Each plot was constituted of a grid of 25 baiting points at 1 m interval (illustrated in Plot 9).

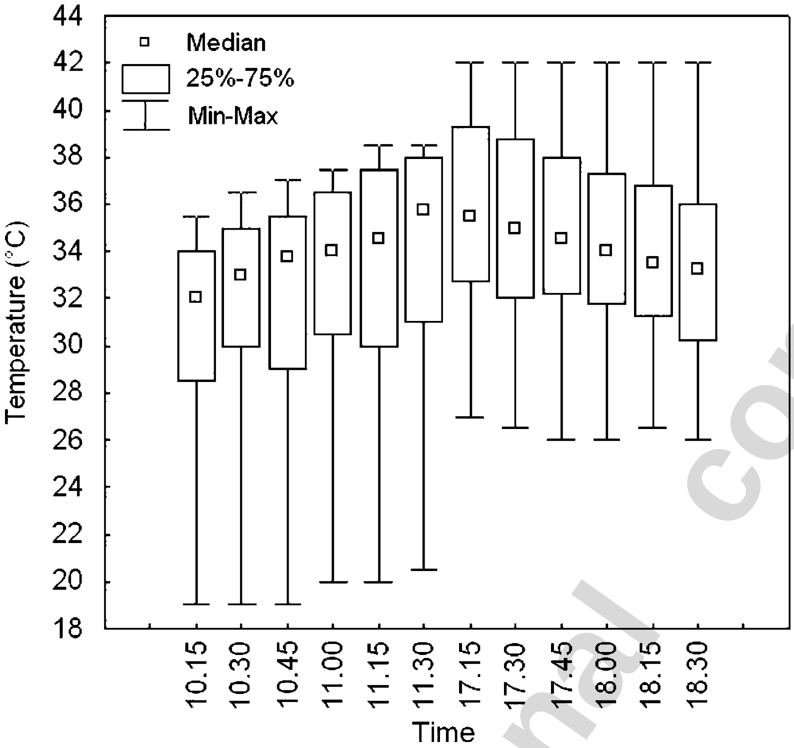

Fig. 2. Atmospheric temperature (°C) over time during the experiment.

(two drops of liquid honey). Baits were installed on a 2 cm-side square of aluminum foil that prevented ants from foraging below the bait. Ant species attracted to each bait were identified and their abundances noted every 15 min over a 90 min period (= 6 successive records). Voucher specimens were collected for later identification in the laboratory. All collected ants were identified to species or morphospecies.

We conducted 18 baiting sessions including four "food resource–time of day" combinations consisting of 3 "honey/morning" (75 baits), 5 "honey/afternoon" (125 baits), 7 "tuna/morning" (175 baits) and 3 "tuna/afternoon" sessions (75 baits). Morning sessions were from 10.00–11.30 h and afternoon sessions from 17.00–18.30 h. In total, our study was based on 450 baits and 2700 (450 baits × 6 records) data collection points.

Each plot was studied two or three times but with a different combination separated by more than 48 h. At the end of each experiment, baits were cleared to avoid a food saturation of the habitat.

To evaluate temperature influence upon observed foraging patterns, ambient air temperature was measured every 15 min during the experiments, from which mean temperature was calculated for each baiting session (Fig. 2). It is likely that ants are more sensitive to ground temperature rather than to that of the ambient air. However, we assumed that these variables were correlated.

2.3. Analyses of ant foraging

- *Food preferences*. For the nine most frequent ant species, we tested food preferences by Chi-square analyses of contingency tables of species occurrences accompanied by Yates corrections for continuity.

- *Influence of temperature*. The Pearson product moment correlation was calculated (1) between temperature and the occurrence of each frequent ant species and (2) between temperature and the abundance of every frequent ant species. If occurrences or abundances increased with temperature, this indicates that thermal conditions may influence the ability of ants to discover or to dominate baits, respectively.
- *Behavioral dominance*. We noted any aggressive behavioral interactions (biting or stinging) that occurred between ant species at baits. The number of times that a given species initiated an attack indicated its aggressiveness, which is a critical trait of behaviorally dominant ant species (i.e. extirpator ants) (Fellers, 1987; Wilson, 1971).
- *Food exploitation and recruitment strategy*. To classify the frequent ant species and to investigate their recruitment strategy we represented the cumulative abundance of ants at baits as a function of time from the beginning to the end of the baiting session. By definition, opportunistic ant species are abundant at baits at the beginning of the baiting session and then, decrease in abundance at the benefit of extirpator species. The abundance of insinuator species is independent of time.

2.4. Null model analysis

To determine the stochastic and deterministic parts of observed patterns of species occurrences and abundances at baits, we compared the observed matrices (see below) to those expected under the null hypothesis of random occurrence/abundance of species and generated by null model randomizations (Gotelli and Graves, 1996).

2.4.1. Matrices of data

Temporal analysis. Rows of the data matrix represented species foraging at least once at baits. Columns corresponded to the time from the start of the experiment. Entries in the matrix consisted of the number of bait occurrences for each species. The data obtained for the four "food resource–time of day" combinations were analyzed separately.

Spatial analysis. Rows of the data matrix represented species while columns represented baits. Entries in the matrix consisted of the species abundance at each bait. The data obtained for the four "food resource–time of day" combinations and for the six sampling points in time following the start of the experiment were analyzed separately. Only species that occurred at least at one bait during the given observation time were included in this analysis. Points common to two contiguous plots were excluded from the analysis.

2.4.2. Quantification of spatial and temporal foraging overlaps between species

To quantify spatial and temporal foraging overlaps, we calculated the Pianka index of niche overlap between each pair of species (Pianka, 1973):

$$O_{12} = O_{21} = \frac{\sum_{i=1}^{n} p_{2i}p_{1i}}{\sqrt{\sum_{i=1}^{n}(p_{2i}^2)(p_{1i}^2)}}.$$

In this formula, O_{12} is the overlap between species 1 and 2, p_{1i} and p_{2i} represent the utilization of time i (for temporal analyses) or bait i (for spatial analyses) by species 1 and 2, respectively. Pianka index is symmetric, so $O_{12} = O_{21}$, and ranges from 0, for pairs of species that share no spatial or temporal resource state, to 1, for pairs that present an identical resource utilization. To describe the observed spatial and temporal foraging overlaps of the entire ant assemblage, we calculated the observed mean and variance of foraging overlap indices for each data matrix.

We compared the values with those derived from 1000 iterations. All null model simulations were performed with Ecosim software (Gotelli and Entsminger, 1999). We used the randomization algorithm 3 (RA3) of Winemiller and Pianka (1990) which corresponds to a simple reshuffling of each row of the matrix and which is often recommended to create null matrices (Gotelli and Graves, 1996). All resources (time or bait) were considered equiprobable. We did not use any adjustments for multiple tests because we were interested in the overall pattern of which data sets showed significance and which did not.

2.4.3. Interpretation of results

If ant species forage at the same time or at the same location more often than expected by chance it can be interpreted as an effect of abiotic factor (Albrecht and Gotelli, 2001; Gotelli and Graves, 1996). Here, temperature was the more plausible abiotic factor constraining ant foraging (Bestelmeyer, 2000). By contrast, interspecific competition tends to segregate ant species more often than expected (Albrecht and Gotelli, 2001; Gotelli and Graves, 1996; Sale, 1974).

The study of foraging overlap variances informs about the ant assemblage structure. An internal guild structure in the assemblage, in which some species pairs are very similar in resource use while others are very dissimilar, leads to an observed variance index superior to those generated by null models (Albrecht and Gotelli, 2001; Winemiller and Pianka, 1990). No guild structure can be demonstrated when the indice is inferior.

3. Results

3.1. Ecology of ants attracted to baits

Overall baits attracted 24 species (Table 1). Most baits were exploited by a single ant species during the time of the experiment. Only 28% of baits attracted more than one species (up to 4) (Fig. 3). The "food resource–time of day" combination did not influence the mean number of species per bait (one-way ANOVA, $df = 3$, $P = 0.55$).

Only nine direct interspecific aggressions were observed at baits. *Pseudomyrmex denticollis* attacked *Wasmannia auropunctata* ($n = 2$) and *Pheidole radoszkowskii* ($n = 1$). *Camponotus crispulus* attacked *Ps. denticollis* ($n = 4$), *Solenopsis* sp. A attacked *W. auropunctata* ($n = 1$) and this latter species attacked *Solenopsis* sp. B ($n = 1$). A conflict generally resulted in the retreat of the species attacked. A single aggressive intraspecific interaction was observed between *Ps. denticollis* workers.

The numerical dominance of six ant species was influenced by temperature. Their abundances were either negatively ($n = 4$ species) or positively ($n = 2$) correlated with temperature (Pearson product moment correlation analysis, $P \leqslant 0.05$, Table 1). Identical results were obtained by considering their occurrences (number of baits visited by contrast to number of individuals observed in the area) according to the temperature indicating that temperature also influenced bait discovery for these six ant species.

Table 1
Ant species collected during the study with baits ($n = 450$)

Species attracted to baits ($n = 24$)	Percentage of occurrences at baits (%)	Food preferences	Correlation between ant abundance and temperature ($P \leqslant 0.05$)
Pseudomyrmex denticollis	46.9	Proteins**	Positive
Camponotus crispulus	10.0	Proteins**	No
Pheidole radoszkowskii	7.1	No	Negative
Wasmannia auropunctata	5.8	No	No
Pheidole sp. A	5.6	No	Negative
Brachymyrmex aphidicola	4.7	No	Negative
Brachymyrmex leuderwaldti	4.4	No	Negative
Crematogaster quadriformis	4.2	No	No
Forelius brasiliensis	4.2	Proteins***	Positive
Camponotus termitarius	3.6		
Pheidole jelskii	2.9		
Pheidole vafra	2.4		
Camponotus crassus	2.0		
Solenopsis sp. A	2.0		
Solenopsis sp. B	2.0		
Forelius nigriventris	1.6		
Ectatomma edentatum	0.7		
Pheidole sp. B	0.7		
Pheidole sp. C	0.7		
Solenopsis sp. C	0.7		
Pseudomyrmex acanthobius	0.4		
Ectatomma brunneum	0.2		
Ectatomma permagnum	0.2		
Odontomachus chelifer	0.2		

The percentage of the total number of bait used by each species is given. Food and temperature preferences of the nine most frequent ant species attracted to baits are indicated. Food preferences were tested by Chi-square analyses of contingency tables of species occurrences with Yates corrections for continuity. Correlation between the abundance of each species and temperature were calculated by Pearson product moment correlation analyses (**$P \leqslant 0.01$; ***$P \leqslant 0.001$).

Among the nine most frequent ant species attracted to baits, 3 exhibited a food preference, always for tuna baits (*Ps. denticollis*, $\chi^2 = 6.603$, $df = 1$, $P \leqslant 0.01$; *Ca. crispulus*, $\chi^2 = 9.133$, $df = 1$, $P \leqslant 0.01$; *Forelius brasiliensis*, $\chi^2 = 14.118$, $df = 1$, $P \leqslant 0.001$, Table 1). *Ca. crispulus* and *Ps. denticollis,* two relatively large ant species (over 1 cm) foraged mainly solitarily or in small groups and never recruited massively (maximal abundance at bait of 15 and 10 workers, respectively). *Ps. denticollis* was by far the most frequent species attracted to baits (Table 1). The other seven frequent ants whose workers are small (around 1 or 2 mm), often recruited massively (over 100 workers at some baits) over the 90 min period.

For each "food resource–time of day" combination, we plotted the cumulative abundance of ants at baits over time. With the exception of *Crematogaster quadriformis*, all species exhibited a similar curve for each combination. We thus represented the pooled data (Fig. 4). Among the nine most frequent species, abundance at baits of *Brachymyrmex aphidicola*, *B. leuderwaldti*, *Ph. radoszkowskii*, *Pheidole* sp. A and *W. auropunctata* globally

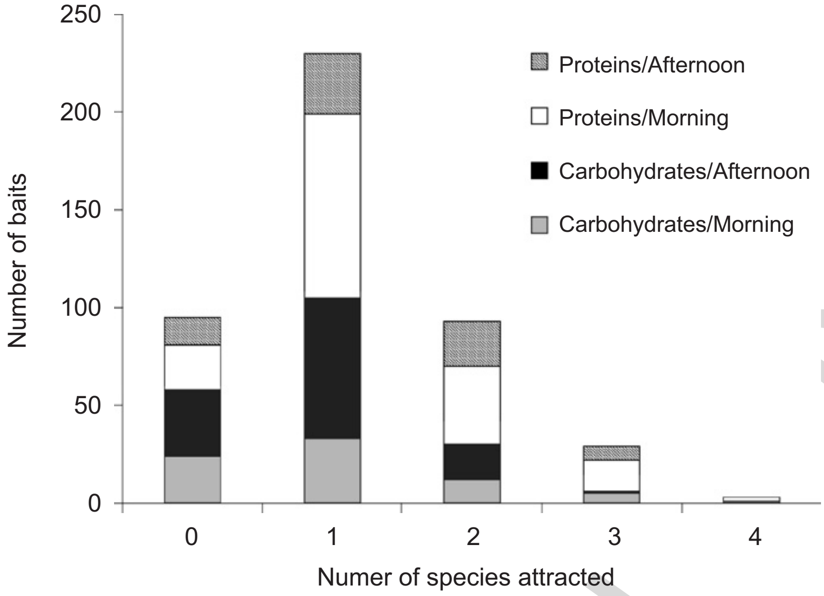

Fig. 3. Number of ant species attracted to baits ($n = 450$).

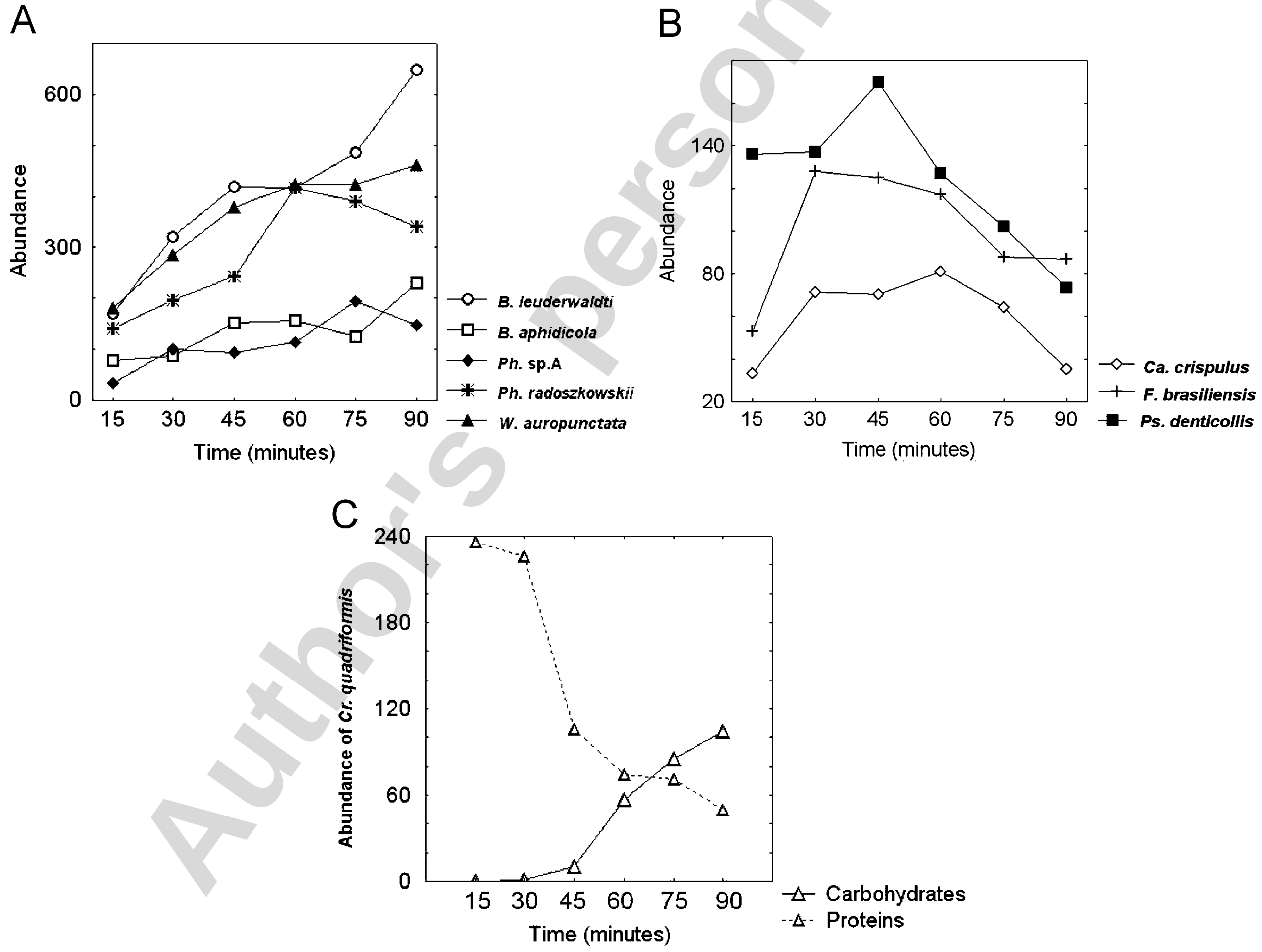

Fig. 4. Cumulative abundance at baits of the nine frequent ant species as a function of time. Five species are considered as extirpators because their cumulative abundance increased along with time (A). *Pseudomyrmex denticollis* is classified as opportunist because globally abundant at baits at the beginning of the baiting session and then scarcer (B). Two species exhibited an intermediate pattern (B). *Crematogaster quadriformis* behavior (C) is function of food type (see text).

increased over time, as expected for extirpators (Fig. 4A). The opposite was globally observed for *Ps. denticollis*, as expected for opportunists. *F. brasiliensis* and *Ca. crispulus* exhibited an intermediate pattern (Fig. 4B). *Cr. quadriformis* displayed an extirpator behavior for carbohydrates and an opportunist behavior for proteins (Fig. 4C).

3.2. Temporal foraging overlap

Temperature constrained the temporal foraging of ants (at both protein or carbohydrate baits) only during afternoons (observed mean indices greater than expected, Table 2).

An internal guild structure of the ant assemblage was revealed (observed variance greater than expected, Table 2) except during afternoons with proteins.

3.3. Spatial foraging overlap

In most cases ants were not constrained spatially to exploit particular baits (Table 3, 15 out of 24 observed mean indices not different from those generated by null models). However, at the end of morning sessions temperature influenced the spatial foraging structure (mean indices were greater than expected). By contrast, at the end of afternoon sessions, interspecific competition appeared as a structuring factor (mean indices were lower than expected).

Only at the end of morning experiments a guild structure was revealed (observed variance indices greater than expected, Table 3).

Food type did not influence the spatial foraging structure of the ant assemblage (similar results obtained with tuna or honey baits for mean or variance indices, Table 3).

All results of temporal and spatial null model analyses remained valid when the most frequent ant species was discarded from analyses. Therefore, they were valid for the whole assemblage and not distorted by the overdominance of *Pseudomyrmex denticollis*.

3.4. Spatial distribution of ants

Fig. 5 represents, for every frequent species and all unfrequent species cumulated, baits where the species were observed. Because bait type did not influence the spatio-temporal

Table 2

Determination of stochastic or deterministic influences on the observed pattern of temporal food resource exploitation and study of the ant assemblage structure

Food resource–time of day combination	Observed vs expected mean indices	Observed vs expected variance indices
Proteins–morning	$0.69 = 0.69$ n.s.	$0.09 > 0.07$***
Carbohydrates–morning	$0.76 = 0.76$ n.s.	$0.07 > 0.04$**
Proteins–afternoon	$0.8 > 0.76$***	$0.02 < 0.03$ n.s.
Carbohydrates–afternoon	$0.60 > 0.57$*	$0.1 > 0.07$***

Observed means or variances of temporal foraging overlap indices are compared with those expected under random for each "food resource–time of day" experiments. Expected values were calculated as the average temporal overlap in 1000 randomized assemblages generated by the randomization algorithm 3 of Ecosim (*$P \leqslant 0.05$; **$P \leqslant 0.01$; ***$P \leqslant 0.001$).

Table 3
Determination of stochastic or deterministic influences on the observed pattern of spatial food resource exploitation and study of the ant assemblage structure

	Morning		Afternoon	
Time (min)	Proteins	Carbohydrates	Proteins	Carbohydrates
Means of spatial overlap indices (observed vs expected values)				
15	$0<0.01$ n.s.	$0<0.03$**	$0.04>0.03$ n.s.	$0<0.02$ n.s.
30	$0.04>0.02$**	$0.01<0.03$ n.s.	$0.01<0.03$ n.s.	$0<0.02$ n.s.
45	$0.03>0.01$ n.s.	$0.01<0.02$ n.s.	$0.04>0.03$ n.s.	$0.02=0.02$ n.s.
60	$0.02>0.01$ n.s.	$0.01<0.03$ n.s.	$0.0<0.04$*	$0.01<0.02$ n.s.
75	$0.02>0.01$ n.s.	$0.02=0.02$ n.s.	$0.0<0.04$**	$0<0.02$***
90	$0.08>0.01$***	$0.08>0.02$**	$0<0.03$***	$0<0.02$***
Variances of spatial overlap indices (observed vs expected values)				
15	$0<0.01$ n.s.	$0<0.01$**	$0.02>0.01$ n.s.	$0<0.01$ n.s.
30	$0.02>0.01$ n.s.	$0<0.01$ n.s.	$0<0.01$ n.s.	$0<0.01$ n.s.
45	$0.01=0.01$ n.s.	$0<0.01$ n.s.	$0.02>0.01$ n.s.	$0.01=0.01$ n.s.
60	$0.02>0.01$ n.s.	$0<0.01$ n.s.	$0<0.01$ n.s.	$0<0.01$ n.s.
75	$0.01=0.01$ n.s.	$0.02>0.01$ n.s.	$0<0.01$*	$0<0.01$***
90	$0.05>0.01$**	$0.07>0.01$**	$0<0.01$***	$0<0.01$**

Observed means or variances of spatial foraging overlap indices are compared with those expected under random for each "food resource–time of day" experiments. Expected values were calculated as the average spatial overlap in 1000 randomized assemblages.

foraging overlap patterns, data for both resources were combined. Bait occurrences gave an indication over the extent of the foraging area for every species inside the studied 144 m^2. *Pseudomyrmex denticollis* exploited almost every available bait. Contrastingly, the other eight frequent species exploited a restricted number of baits, which were often clustered. This was particularly obvious for *Ph. radoszkowskii*, *Ph.* sp. A, *Ca. crispulus* and *W. auropunctata*. The foraging areas of these species virtually did not overlap. *Brachymyrmex leuderwaldti* and *B. aphidicola* were able to exploit baits present inside the foraging area of these species because, rather than foraging over a group of baits, they often exploited a single one which was exclusively dominated due to a high recruitment (Fig. 4). The largest species (*Ps. denticollis* and *Ca. crispulus*) were also those who exploited the largest number of baits (Table 1 and Fig. 5).

4. Discussion

4.1. Influence of the set of trade-offs on temporal ant foraging

The trade-off between food resource discovery and food resource domination (Fellers, 1987; Wilson, 1971) existed globally. We recognized five extirpators, one opportunist and two intermediate species. Furthermore, infrequent ant species possibly corresponded to insinuators since this behavior is often exhibited by cryptic ant species (Wilson, 1971). Temperature influenced both bait discovery and dominance abilities of frequent ant species as described by Bestelmeyer (2000) in the Argentinean Chaco (400 km away from our study site). *Forelius brasiliensis* was the most thermophilic species and exhibited a foraging

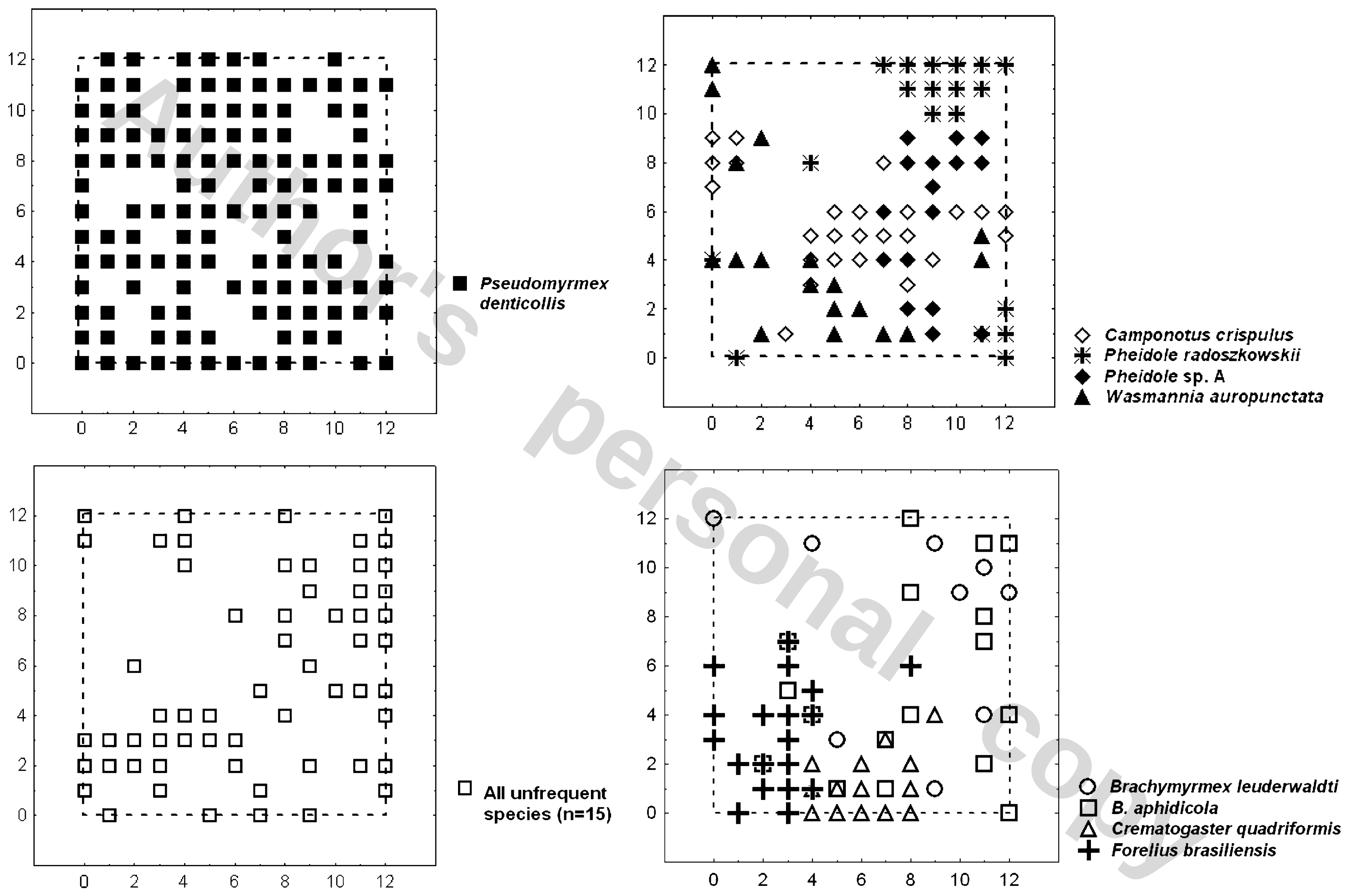

Fig. 5. Bait occupancy by species. For every frequent ants and all unfrequent species cumulated, baits where species was noted at least once during all baiting sessions are indicated.

behavior (fast worker displacement with raised abdomen) typical of thermophilic ants such as *Cataglyphis rosenhaueri* (Cerdá, 2001; Cerdá and Retana, 2000). Extirpators were competitive non-thermophilic ant species (*Brachymyrmex* spp., *Pheidole* spp., *Wasmannia auropunctata*), and opportunists were subordinate thermophilic ones (*Forelius* spp.). It appears that the coexistence of numerically dominant ant species was allowed by the coexistence of these two guilds. An internal guild structure in the assemblage was confirmed. It was sometimes difficult to establish the guild to which a particular species belongs, as for *Pseudomyrmex denticollis* (aggressive and thermophilic species whose cumulated abundance pattern was typical of opportunists), or for *Cr. quadriformis* (which appeared to change its food exploitation strategy according to food nature).

However, temperature and chance rather than interspecific competition structured the temporal foraging at the assemblage level. Indeed, during afternoons temperature strongly structured the temporal foraging but during mornings temporal foraging did not differ from random.

Interspecific conflicts observed at baits were rare and moreover, were rarely initiated by extirpators, which are supposed to be the most aggressive species (Wilson, 1971). Avoidance could be a typical interference behavior among ants. Fellers (1987) specified that interference between species in his study occurred on around 55% of the occasions when two or more species used the same bait and that avoidance behavior accounted for half of these observed interactions. Yanoviak and Kaspari (2000) also found a low frequency of aggresive bait defense at ground in a seasonally wet tropical forest of Panama. However, Bestelmeyer (2000) indicated that non-aggressive encounters between taxa were relatively infrequent at his baits and did not integrate them in his analyses.

Nevertheless, the apparent absence of interspecific competition in our temporal study may be an artifact. The high density of baits at small spatial-scale may allow subordinate species to move to a second bait when extirpators arrived at the first exploited. Hence, although a species turnover at one particular bait existed, at the scale of a whole baiting session, the coexistence time of the guild was increased. We never observed this directly but noted that 21% of the baits were never exploited by any ant species and that half of them (51%) attracted only a single species. This is rather unusual with bait experiments. Only invasive tramp-species are known to monopolize baits exclusively (Davidson, 1998). Here ants were confronted with unusually high quantities of food which could modify their foraging behaviors.

4.2. Influence of the set of trade-offs on spatial ant foraging

Our results show that ants in a semi-arid habitat adjust their foraging behavior to environmental conditions very finely in space. Variance indices of spatial foraging overlap indicated that several guilds foraged at the end of morning experiments (thermophilic and non-thermophilic ants probably) and only one guild foraged at the end of afternoon experiments, (non-thermophilic dominant and aggressive species which had excluded submissive thermophilic ants). In the morning, ants were able to forage randomly on the entire soil surface but when temperature became stressful (at the end of morning experiments), ants foraging was aggregated possibly around microsites where temperature was lower. Under high temperatures, only thermophilic ants were able to explore the environment randomly before being excluded by non-thermophilic ants as the temperature cooled down (at the end of the afternoon experiments). To sum up, the set of trade-offs structured the spatial ant foraging when thermal conditions were stressful. When temperature was not too high (during mornings), bait spatial exploitation appeared stochastic.

Among species recognized as extirpators, two strategies of space occupation were observed (Fig. 5). Baits exploited by *Ph. radoszkowskii*, *Ph.* sp. A and *W. auropunctata* were clustered. It is plausible that these species defended a foraging area and only exploited baits located inside their territory (= "territorial species" following the three-leveled competition hierarchy of Savolainen and Vepsäläinen, 1988). Conversely, *B. aphidicola* and *B. leuderwaldti* seemed to defend a punctual food resource rather than a foraging area (= "encounterers species" of Savolainen and Vepsäläinen, 1988). They controlled the bait thanks to a massive recruitment, which allowed them to dominate it even inside the foraging area of other extirpators.

In numerous organisms as diverse as birds (Hyman, 2005), lizards (Trigosso-Venario et al., 2002) or termites (Kaib et al., 2002), it was observed that neighboring individuals avoid each other in order to reduce energetically expensive fighting. It was called the "dear-enemy phenomenon" (Fisher, 1954). In ants this effect also exists. Gordon (1989) has shown that *Pogonomyrmex barbatus* workers confronted with conspecifics from neighboring colonies detered foraging more frequently than with ants from geographically distant colonies. This behavior was also observed during interspecific encounters in two desert *Pheidole* species (Langen et al., 2000).

Here, a "dear-enemy" effect between interspecific neighboring colonies could explain: (1) a very low number of conflicts at baits; (2) no-overlap of foraging areas (Fig. 5) and small mean spatial foraging overlaps (Table 3); (3) a weak interspecific competition effect on the spatio-temporal foraging (Tables 2 and 3); (4) a very small number of baits exploited by more than a single species (Fig. 3).

Because abiotic conditions in arid and semi-arid habitats strongly constrain the ant foraging, the cost of fighting in these environments may be particularly strong and may allow the establishment of "a dear-enemy phenomenon" more easily than in temperate or tropical habitats. More studies are necessary to examine the importance of avoidance between neighboring interspecific colonies, its occurrence according to habitat type and season and its impact on space use and species coexistence.

Although a "dear-enemy phenomenon" may explain our observations, nonexclusive alternative hypotheses may also be proposed. *First*, our baiting protocol may have saturated the habitat with high quality food, decreasing the spatial foraging of ants. Indeed, optimal foraging theory (MacArthur and Pianka, 1966) predicts that the number of microhabitats visited by species during foraging decreases when the set of food resource increases. *Second,* it is possible that some areas were unfavorable due to high predation risks. High densities of antlion larvae, known to influence the spatial distribution of ants (Gotelli, 1993, 1996), were noted in some small patches of the studied area. *Third,* as we discussed above temperature appeared to influence strongly the foraging strategies exhibited by ants and it is not excluded that the majority of species in semi-arid habitat forage only near their nest entrance to decrease their exposure to stressful temperature.

4.3. Food type influence on spatio-temporal foraging

Food preferences were highlighted for three frequent ant species, always for proteins. As we predicted, two of them are thermophilic species: *Pseudomyrmex denticollis* and *Forelius* *brasiliensis*. Temperature restricted the foraging time and space of these species, which in turn exhibited a strong food selectivity to optimize their foraging. Kay (2004) found that species with relatively easy access to carbohydrates preferred proteins. In this direction, *Forelius* spp. are mainly plant nectar consumers. However, protein food preference of *Forelius brasiliensis* could be an artifact due to temperature constraints. Indeed, *F. brasiliensis* is a hot temperature specialist and only the experiment with the hottest temperature conditions (around 42 °C) was really attractive for this species and was carried out with protein baits. During this extremely hot episode, *F. brasiliensis* was the only ant species present at baits (sometimes along with *Ps. denticollis*). *Forelius* species forage usually in open areas under direct sunlight and rarely in forest where non-thermophilic and aggressive species are favored (Bestelmeyer, 1997, 2000). However, when ambient air temperature was high, and hence when competitors were less favored, the subordinate *Forelius* spp. were able to expand their foraging area into the leaf-litter. More replicates at very high temperature are necessary to confirm food preferences of *F. brasiliensis*.

Cr. quadriformis appeared to adapt its foraging behavior according to the bait nature, confirming that bait exploitation by ants could be different according to the food resource (de Biseau et al., 1997; Sanders and Gordon, 2000). However, even if we observed specific food preferences and foraging behavior changes according to food nature, it appears that this did not affect the global foraging at the assemblage scale.

Although it was possible that food preference may be confounded by texture preference (Kaspari and Yanoviak, 2001), we believe that bait exploitation was weakly biased by texture. Canned tuna contains water and salts, proteins and fats in solution, which were probably attractive to both liquid and solid feeders and we assumed honey to be thick enough to be exploited by both ant groups. In the future, it would be more precise to use nutrient solutions of sucrose or casein as Kay (2004) at the cost of realism (Kaspari and Yanoviak, 2001).

4.4. *General conclusions*

In hot and dry habitats the set of trade-offs between species food discovery and food domination ability and between species thermal tolerance and competitive dominance strongly influence the temporal foraging of ants (Bestelmeyer, 2000). The set of trade-offs has also consequences on the spatial co-occurrence of species during foraging. Nonetheless, temperature and chance rather than interspecific competition deeply structure the spatio-temporal foraging at the assemblage level. As for food preferences, no effect was detected at the assemblage scale. An interspecific "dear-enemy phenomenon" may explain the scarcity of evidences of interspecific competition. Albrecht and Gotelli (2001) already demonstrated the part of chance in the structure of the ant spatio-temporal foraging at both seasonal and nycthemeral scales in grassland ant assemblages from North America. Our results suggest that this finding can be extended to smaller spatio-temporal scales and to more constraining habitats as arid environments.

Acknowledgments

This study was made possible by financial support of the "Fonds pour la formation à la Recherche dans l'Industrie et l'Agriculture" and the King Leopold III Fund for Nature Exploration and Conservation. We thank the guards from Teniente Enciso National Park, John Kochalka, Bolivar Garcete-Barrett and Victor Filippi from the “Museo Nacional de Historia Natural del Paraguay” for their help during fieldwork or administrative procedures. Alex Wild from University of California at Davis and William MacKay from the Laboratory for Environmental Biology (University of Texas, El Paso) confirmed the ant identifications. The manuscript benefited from comments by two anonymous referees, Géraldine Kapfer, Laurence Theunis and René-Marie Lafontaine (RBINS). Lorraine Berry and Jennifer Boyle greatly improved the English version.

References

Albrecht, M., Gotelli, N.J., 2001. Spatial and temporal niche partitioning in grassland ants. Oecologia 126, 134–141.

Andersen, A.N., 1992. Regulation of “momentary” diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. American Naturalist 140, 401–420.

Andersen, A.N., 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. Journal of Biogeography 22, 15–29.

Andersen, A.N., 1997. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. Journal of Biogeography 24, 433–460.

Bernstein, R.A., 1974. Seasonal food abundance and foraging activity in some desert ants. American Naturalist 108, 490–498.

Bestelmeyer, B.T., 1997. Stress tolerance in some Chacoan dolichoderine ants: implications for community organization and distribution. Journal of Arid Environments 35, 297–310.

Bestelmeyer, B.T., 2000. The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. Journal of Animal Ecology 69, 998–1009.

Cerdá, X., 2001. Behavioural and physiological traits to thermal stress tolerance in two Spanish desert ants. Etología 9, 15–27.

Cerdá, X., Retana, J., 2000. Alternative strategies by thermophilic ants to cope with extreme heat: individual versus colony level traits. Oikos 89, 155–163.

Cerdá, X., Retana, J., Cros, S., 1998a. Critical thermal limits in Mediterranean ant species: trade-off between mortality risk and foraging performance. Functional Ecology 12, 45–55.

Cerdá, X., Retana, J., Manzaneda, A., 1998b. The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. Oecologia 117, 404–412.

Chew, R.M., de Vita, J., 1980. Foraging characteristics of a desert ant assemblage: functional morphology and species separation. Journal of Arid Environments 3, 75–83.

Davidson, D.W., 1998. Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. Ecological Entomology 23, 484–490.

de Biseau, J.-C., Quinet, Y., Deffernez, L., Pasteels, J.-M., 1997. Explosive food recruitment as a competitive strategy in the ant *Myrmica sabuleti* (Hymenoptera, Formicidae). Insectes Sociaux 44, 59–73.

Detrain, C., Tasse, O., Versaen, M., Pasteels, J.M., 2000. A field assessment of optimal foraging in ants: trail patterns and seed retrieval by the European harvester ant *Messor barbatus*. Insectes Sociaux 47, 56–62.

Fellers, J.H., 1987. Interference and exploitation in a guild of woodland ants. Ecology 68, 1466–1478.

Fellers, J.H., 1989. Daily and seasonal activity in woodland ants. Oecologia 78, 69–76.

Fisher, J.B., 1954. Evolution and bird sociality. In: Huxley, J., Hardy, A.C., Ford, E.B. (Eds.), Evolution As A Process. Allen & Unwin, London, pp. 71–83.

Gibb, H., 2005. The effect of a dominant ant, *Iridomyrmex purpureus*, on resource use by ant assemblages depends on microhabitat and resource type. Australian Ecology 30, 856–867.

Gotelli, N.J., 1993. Ant lion zones: causes of high-density predator aggregations. Ecology 74, 226–237.

Gotelli, N.J., 1996. Ant community structure: effects of predatory ant lions. Ecology 77, 630–638.

Gotelli, N.J., Entsminger, G.L., 1999. Ecosim: null model software for ecology, version 3.0. Aquired Intelligence Inc. and Kesey-Bear 〈http://homepages.together.net/~gentsmin/ecosim.html〉.

Gotelli, N.J., Graves, G.R., 1996. Null models in ecology. Smithsonian Institution, Washington, pp. 368.

Gordon, D.M., 1989. Ants distinguish neighbors from strangers. Oecologia 81, 198–200.

Greenslade, P.J.M., 1971. Interspecific competition and frequency changes among ants in Solomon islands coconut plantations. Journal of Applied Ecology 8, 323–352.

Herbers, J.M., 1989. Community structure in north temperate ants: temporal and spatial variation. Oecologia 81, 201–211.

Hyman, J., 2005. Seasonal variation in response to neighbors and strangers by a territorial songbird. Ethology 111, 951–961.

Kaspari, M., Yanoviak, S.P., 2001. Bait use in tropical litter and canopy ants—evidence of differences in nutrient limitation. Biotropica 33, 207–211.

Kaib, M., Franke, S., Francke, W., Brandl, R., 2002. Cuticular hydrocarbons in a termite: phenotypes and a neighbour-stranger effect. Physiological Entomology 27, 189–198.

Kay, A., 2004. The relative availabilities of complementary resources affect the feeding preferences of ant colonies. Behavioral Ecology 15, 63–70.

Langen, T.A., Tripet, F., Nonacs, P., 2000. The red and the black: habituation and the dear-enemy phenomenon in two desert *Pheidole* ants. Behavioral Ecology and Sociobiology 48, 285–292.

Levings, S.C., 1983. Seasonal, annual, and among-site variation in the ground ant community of a deciduous tropical forest: some causes of patchy species distributions. Ecological Monographs 53, 435–455.

Lynch, J.F., 1981. Seasonal, successional, and vertical segregation in a Maryland ant community. Oikos 37, 183–198.

MacArthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. American Naturalist 100, 603–609.

McGlynn, T.P., Kirksey, S.E., 2000. The effects of food presentation and microhabitat upon resource monopoly in a ground-foraging ant (Hymenoptera: Formicidae) community. Revista de Biologia Tropical 48, 629–642.

Perfecto, I., 1994. Foraging behavior as a determinant of asymmetric competitive interaction between two ant species in a tropical agroecosystem. Oecologia 98, 184–192.

Pianka, E.R., 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4, 53–74.

Ramella, L., Spichiger, R., 1989. Interpretación preliminar del medio físico y de la vegetación del Chaco Boreal. Contribución al estudio de la flora y de la vegetación del Chaco. I. Candollea 44, 639–680.

Retana, J., Cerdá, X., 2000. Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment. Oecologia 123, 436–444.

Ribas, C., Schoereder, J.H., 2002. Are all ant mosaics caused by competition? Oecologia 131, 606–611.

Rissing, S.W., 1988. Dietary similarity and foraging range of two seed-harvester ants during resource fluctuations. Oecologia 75, 362–366.

Sale, P.F., 1974. Overlap in resource use, and interspecific competition. Oecologia 17, 245–256.

Sanders, N.J., Gordon, D.M., 2000. The effects of interspecific interactions on resource use and behavior in a desert ant. Oecologia 125, 436–443.

Savolainen, R., Vepsäläinen, K., 1988. A competitive hierarchy among boreal ants: impact on resource partitioning and community structure. Oikos 51, 135–155.

Savolainen, R., Vepsäläinen, K., 1989. Niche differentiation of ant species within territories of the wood ant *Formica polyctena*. Oikos 56, 3–16.

Schoener, T.W., 1974. Resource partitioning in ecological communities. Science 185, 27–39.

Trigosso-Venario, R., Labra, A., Niemeyer, H.M., 2002. Interactions between males of the lizard *Liolaemus tenuis*: roles of familiarity and memory. Ethology 108, 1057–1064.

Vepsäläinen, K., Savolainen, R., 1990. The effect of interference by Formicine ants on the foraging of Myrmica. Journal of Animal Ecology 59, 643–654.

Wilson, E.O., 1971. The Insect Societies. The Belknap Press of Harvard University Press, pp. 548.

Winemiller, K.O., Pianka, E.R., 1990. Organization in natural assemblages of desert lizards and tropical fishes. Ecological Monographs 60, 27–55.

Yanoviak, S.P., Kaspari, M., 2000. Community structure and the habitat templet: ants in the tropical forest canopy and litter. Oikos 89, 259–266.