

Resource partitioning among epigaeic and hypogaeic ants (Hymenoptera: Formicidae) of a Brazilian cocoa plantation

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Resumen. Usando cebos de azúcar, carne y harina de mandioca sobre la superficie del suelo y enterrados, estudiamos los patrones de uso de substrato y de procura de alimento en una comunidad de hormigas en una plantación de cacao en el Brasil. Fueron registradas 49 especies de hormigas, incluyendo 10 especies de Pheidole. *Solenopsis geminata* fue dominante tanto en los distintos tipos de cebo como en los distintos estratos. El mayor número de especies fue encontrado en cebos de azúcar y carne en la superficie, con cada tipo de cebo caracterizado por una Fauna particular. La Fauna epigaeica fue mas variada que la Fauna hipogaeica. Por lo menos cuatro grupos Funcionales fueron identificados: las hormigas cultivadoras de hongo, las nectívoras epigaeicas, las carnívoras epigaeicas, y las hormigas hipogaeicas. La reducción en la amplitud del nicho, con la Formación de grupos Funcionales, permite la coexistencia de un gran número de especies en esta comunidad de hormigas del suelo de una plantación tropical.

Abstract. Patterns of dietary and Foraging strata utilization by the ground ant community of a Brazilian cocoa plantation were examined using sugar, meat and Flour baits on the surface as well as buried. A total of 49 ant species was recorded, including 10 species of Pheidole. Strong dominance was exercised by *Solenopsis geminata* at both surface and subterranean strata, and at all Food resources. More ant species attended sugar and meat baits on the surface, although each type of bait was characteristically frequented by particular ant species. The dissimilarity matrix of the epigaeic ant Fauna was much greater than that for the hypogaeic species. At least four guilds were identified: the fungus-growing ants, epigaeic nectivores, epigaeic carnivores, and hypogaeic Foragers. Niche breadth reduction, leading to the formation of guilds, permits the coexistence of many species in this ground ant community from a tropical cocoa plantation.

Introduction

In species-rich ant communities, resources are principally exploited through interference competition (Andersen 1991, Davidson 1980). Competition is minimized by various mechanisms, principally the use of different activity times (Fowler et al. 1991), specialized sizes or types of food (Fowler et al. 1991), or through divergence in the foraging strata explored (Fowler et al. 1991). Based upon the results of bait studies, it has been claimed that most ant species exploit similar food resources (Andersen 1991). However, little evidence substantiates this hypothesis. In fact, niche theory predicts species-rich communities should have more specialized resource exploiters, and food and foraging strata niche breadth should be smaller than in species-poor communities (Holldobler and Wilson 1990, Fowler et al. 1991).

Assemblages based upon exploitation of particular food resources can be considered as feeding guilds (Root 1967). In spite of our accumulated knowledge of the natural history of ants (Holldobler and Wilson 1991), critical experiments which look at quantitative aspects of the food, using different bait types, and foraging strata dimension are few (Chew 1977, Davidson 1980, Torres 1984, Marsh 1985, Fowler 1988).

In this paper we examine the feeding characteristics of a species-rich tropical ground ant community in Brazil (Delabie and Fowler 1995). We ask whether assemblage structure is due to the presence of a dominant species (Risch and Carroll 1982), or to a multiplicity of potential non-dominant species. To answer this, we examine the types of food resources exploited at vertical strata. Specifically, we ask whether guilds of ants exist, whether patterns of dominance are related to foraging strata or to types of food resources exploited, and what are the relative frequencies of foraging strata and food resource specialists.

Materials and Methods

The experimental site was located in the Cocoa Research Center (CEPLAC) in Ilheus, Bahia, Brazil (14° 45' S, 39° 13' W), situated in relict fragments of the South American Coastal Atlantic Forest. The climate is characteristic of the humid tropics, with two seasons, marked principally by temperature variations rather than by precipitation, which is irregular. We used an old cocoa (*Theobroma cacao* L.) plantation which had not received any chemical treatment over the last 20 years. Shade was heterogenous, made up of secondary-growth trees, 10 to 20 meters tall. Cocoa tree density of the plantation was approximately 600 trees per ha. Further details on the climatic conditions, vegetation and arboreal ant fauna can be found in Leston (1978) and Delabie (1990). The soil of the plantation was podzol (Leite 1987), uniformly covered by 1 to 7 cm of dry litter. Litter mass was estimated to be 6.9 t/ha, which was low in relation to commercial plantations of the same region (Leite 1987). As litter depth is an important variable correlated with ant species diversity (Fowler et al. 1991), thicker litter layers in productive cocoa plantations may vary in the number of ant species present.

Baits were used to characterize the ant species feeding habits. Within a 1000 m² area of the plantation, we marked out 70, 5 x 5 m plots. Small piles of dry sugar, meat and manioc flour were placed on separate 6 cm diameter ceramic dishes (one of each type per plot), and were either buried in the soil at the depth of 5-15 cm or placed on the soil surface (one of each per plot). Baits were exposed for 8 hr periods, from dusk to dawn, during the summer (January). Bait stations were collected into plastic bags, and ant species were sorted in the laboratory. A total of 140 baits of each type were used during these studies. These data provide indications on the feeding habits of ant species as well as their ability to explore new food resources through recruitment (Holldobler and Wilson 1990).

Rarefaction (Simberloff 1979) was used to examine patterns of species richness at bait types for both surface and subterranean conditions. This method is independent of sample size and reduces the observed samples to a common size. Species are ranked according to their relative representation in the sample, and cumulative percentages are calculated. Using this method, species richness is estimated for that expected in a sample of individuals of some designated (rarefied) size. Rarefaction curves, based on the number of baits per species for each combination of bait type and location, were calculated. Dietary and vertical niche dimensions were estimated using a dissimilarity matrix (Cody 1974). The Bray-Curtis (1957) distance for each combination of bait type and location, considered as one resource state, was used as the dissimilarity index. The Bray-Curtis distance was then subjected to ordination by Kruskal's (1964) nonmetric multidimensional scaling (Austin 1976). Species loadings were used for guild assignments (Pielou 1984). Guilds were established based upon the type of bait foraged as well as the substrate used (Digby and Kempton 1987). Co-dominants were defined as those species which foraged in all bait types in all foraging strata. Generalists were those which used at least three bait types, while opportunists used at least two bait types.

Results

The species rank-abundance curve (Figure 1), indicated a strong dominance of bait-exploiting ant species. The dominant species, *Solenopsis geminata*, was twice as abundant (192 occupied baits) as

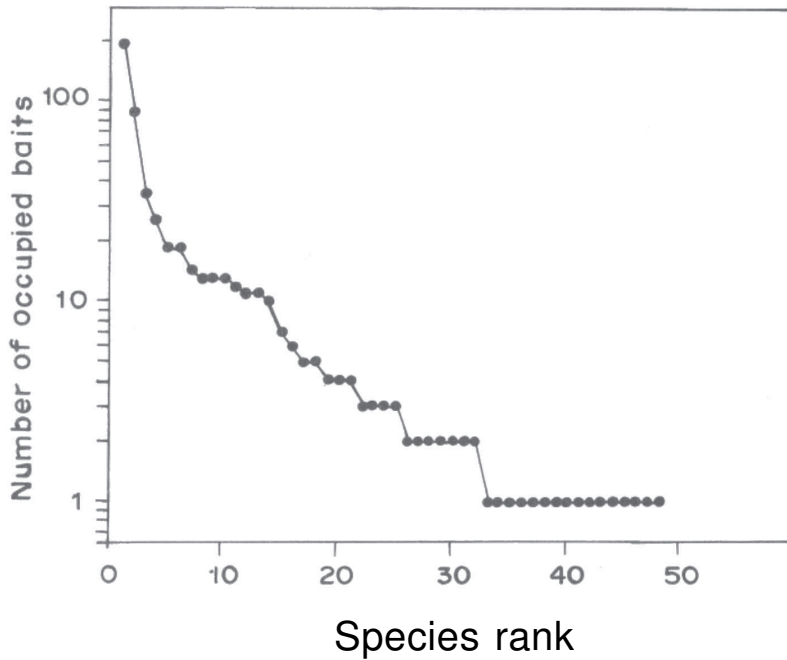


Figure 1. Overall rank-abundance relation based upon total bait occupancy of all species summed over all baits. The dominant species is *Solenopsis geminata*.

Table 1. Frequency Bray-Curtis dissimilarity matrix of foraging strata and food resource based upon ant species visitations.

| Bait | Surface | | | Subterranean | | |
|--------------|---------|------|-------|--------------|------|-------|
| | Sugar | Meat | Flour | Sugar | Meat | Flour |
| Surface | | | | | | |
| Sugar | | 0.60 | 0.65 | 0.77 | 0.77 | 0.88 |
| Meat | | | 0.80 | 0.64 | 0.68 | 0.65 |
| Flour | | | | 0.77 | 0.71 | 0.89 |
| Subterranean | | | | | | |
| Sugar | | | | | 0.30 | 0.45 |
| Meat | | | | | | 0.44 |
| Flour | | | | | | |

the second most abundant bait monopolizer *Pheidole* sp. 4 (86 occupied baits).

Subterranean bait collections were used to determine hypogaeic foraging species, which can be compared with those where the baits were placed on the litter surface to collect epigaeic foragers (Appendix). Mean numbers of ant species at the surface baits were 1.02 for sugar, 1.09 for meat, and 0.82 for flour. These values were significantly lower than corresponding values for subterranean baits (3.42, 3.10, and 1.65, respectively). However, for the combined baits, significantly more species were taken at surface baits (38) than at subterranean baits (19) ($X^2 = 5.25$; $P < 0.05$) (Appendix). Moreover, 30 species were only found on the surface baits, as compared with only 11 species confined to buried baits ($X^2 = 10.00$; $P < 0.05$). However, almost half of the former (13) were

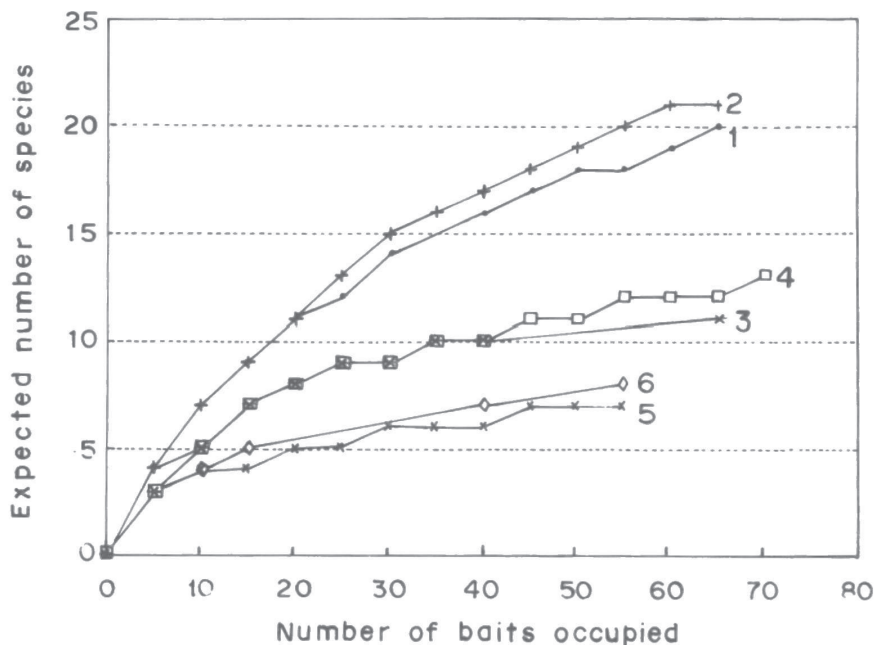


Figure 2. Comparison of associated guilds of ant species using different food resources in different foraging strata. Rarefaction curves indicate expected species abundance for varying numbers of occupied baits. Bait types: Surface 1-3; 1= sugar, 2= meat, 3= flour; Subterranean 4-6: 4= sugar, 5= meat, 6= flour.

characterized as predominant or frequent arboreal foragers, and of these only 4 of these found at subterranean baits (Appendix).

Of the 49 recorded species taken at baits, 8 were found at both subterranean and surface baits. In particular, the codominants, *Solenopsis geminata* (Fr. Smith) and *Pheidole* sp. 4, were the only species found at all types of baits whether surface or subterranean, while the generalists, *Camponotus cingulatus* Mayr and *Wasmannia auropunctata* (Roger), were found at 5 of the 6 bait types (Appendix).

Based upon our bait studies, the exclusively hypogaeic foraging community consists of *Tranopelta* sp. 1, *Solenopsis* sp. 1 and sp. 2, *Rogeria* sp. 1, *Carabarella* sp. 1, *Pheidole* sp. 7, sp. 8, sp. 9, sp. 10, *Monomorium* sp. 1, and *Octostruma jheringhi* (Appendix). Species loadings on the first two non-metric dimension ordination (Appendix) permitted assignments of species into 13 distinct guilds, with the extremes being epigaeic nectar foragers and hypogaeic fungus-growers. Of the three codominant species identified, *S. geminata* and *Pheidole* sp. 4 were closely grouped in dimensional space at the separation of hypogaeic and epigaeic species, while *Wasmannia auropunctata* was contained within the guild of epigaeic carnivores.

By examining the resources explored independent of the foraging strata used, the number of species visiting flour baits (11) was significantly lower than for meat (29) or sugar baits (32). However, almost half of this number (5) was comprised of attine species. The number of bait types used independent of foraging substrate was strongly dominated by specialists, with significantly more species foraging on only one type (26), than those foraging on two (13) or three (10) types. Overall, more species differed between strata than between food types, implying that species are more strata than food specific. Non-metric dimensional ordination separated these groups into a finer array of species guilds (Appendix).

Faunal dissimilarity was found to be much less between subterranean baits, irrespective of the type (Appendix). Mean dissimilarity values of bait types were 0.40 for subterranean baits, 0.68 for

surface baits, and 0.75 between surface and subterranean baits. This indicates that there were more differences between strata than between food types. This was probably because the number of species visiting baits was smaller and the proportional usage of sugar and meat baits was higher (Appendix). The surface-active fauna had higher frequencies of specialists, foraging on only one bait type (Appendix), and this was reflected in the dissimilarity values (Table 1). Faunal dissimilarity with respect to substrate and strata foraged when examined through rarefaction curves (Figure 2) revealed that sugar and meat surface baits had significantly more species associated, followed by surface flour and subterranean meat baits. Significantly lower numbers of associated ant species were found with subterranean flour and meat baits (Figure 2).

Discussion

In litter and soil samples taken in the same area (Delabie and Fowler 1994), a total of 113 species were recorded in the soil stratum, and 69 species were collected in the litter stratum, with a combined species richness of 124 species. The subterranean baits we used to study the soil ant fauna revealed only 19 species, while surface baits registered 39 species, respectively 16.8% and 56.5% of the recorded ant fauna of each stratum. However, our baiting studies revealed 4 species not recorded in our (Delabie and Fowler 1994) soil and litter surveys (*Tapinoma* sp. 1, *Hypoclinea bidens* (L.), *Pachycondyla unidentata* (Mayr), and *Crematogaster* sp. 3). With the exception of *Pachycondyla unidentata*, all of the new registers are arboreal, and these were only captured at surface baits. Of the 49 species we collected during these baiting experiments, 35 species were known to occur in both litter and soil layers (Delabie and Fowler 1994), but only 9 were found at both surface and subterranean baits, 10 only at subterranean baits, and 30 only at surface baits. For the 9 species which were only collected in the litter layer, 8 were found at surface baits and only 1 at subterranean baits. Only 1 species previously recorded for the litter layer was present, and it was only found at surface baits.

With only two exceptions, the Myrmicinae dominated buried baits, with most species being characteristic of the litter layer. Even out of their normal substrate, species of this group are generally behaviorally dominants at food items (Fowler et al. 1991). The Myrmicinae are generally opportunistic foragers, whose activities are probably facilitated by chemical mass communication systems (Fowler et al. 1991).

The absence of arboreal species was expected in the buried baits. However, this was not expected for the Ponerinae, some of which are truly terrestrial. The ponerines constituted 16.3 % of the species found. Not one individual of the ponerinae was taken in the buried baits, while 8 species were taken with the surface baits. These results can be interpreted in several ways. First, due to the lack of a chemical mass recruitment system, the Ponerinae would not be able to compete with dominants for subterranean food items. Even if this is true, this does not justify the difference observed at the surface baits. Because they tend to forage individually, many ponerine species are not frequently captured at baits that are only checked once. Second, the Ponerinae should visual signs to locate prey or any food item, but this is probably not true for all the species (Fowler et al. 1991). Third, the true cryptic Ponerinae are specialist predators, specializing upon unique macroarthropod prey in the litter layer (Fowler et al. 1991) and cannot be taken by baits.

Seven species, representing genera of Attini, or 14.3 % of the species present, were collected at the surface baits, but only one species was found in the buried baits. This result, coupled with the fact that we have never seen any of these species on the vegetation, suggests that they forage in the litter layer. The high species richness of attines found foraging in the same 1000 m² is probably a record for local species richness of the fungus-growing ants (Holldobler and Wilson 1990).

Pheidole was the dominant genera, with 20.4 % of the ant species collected. However, the dominant species was *Solenopsis geminata*, which was by far the most wide ranging forager, both in terms of vertical distribution, as well as in food items explored. The co-dominant *Pheidole* sp. 4 was always less frequent at all niche dimensions than *Solenopsis geminata*. *Solenopsis geminata*, the most

common species of the litter, was the most able to dominate food resources underground, even in the presence of *Pheidole* sp. 4 and *Wasmannia auropunctata*, which soil samples had previously indicated to be more numerically abundant (Delabie and Fowler 1995). In epigeaic conditions in the same area, *Pheidole* sp. 4 was equally dominant with *Solenopsis geminata*, while, on an arboreal substrate, *Wasmannia auropunctata* was the dominant of the three species (Medeiros et al. 1994).

Guild sizes associated with foraging stratum and food resources varied greatly, as determined by rarefaction estimates. Surface-active species which exploited sugar or meat formed significantly larger guilds than others found exploiting flour or subterranean resources. This pattern is marked due to dietary specializations. The majority (33 %) of the strictly epigeaic ants foraged only on meat, while 23 % foraged only on sugar, leading to high dissimilarities. In contrast, low dissimilarity levels were found among the subterranean foragers, which tended to exploit more food resources. The only characteristic species of the soil which was frequently found was the Basicerotini *Octostruma jheringhi*, which was expected to be carnivorous, but is, in fact, a generalist. *Carebarella* sp. 1, for which we had no previous information, appears to be carnivorous, as was expected (Fowler et al. 1991), but can apparently take advantage of other available foods.

Based upon our results, we conclude that guilds do indeed exist in ground ant communities. Foraging strata has a stronger effect on guild structure than does bait type. The subterranean fauna, although richer in species (Delabie and Fowler 1995), is characterized by few species found at baits. These species, however, generally exploit more food types than do their epigeaic counterparts. However, the most common species in soil samples, *Acropyga* cf. *paramaribensis* and *Tranopelta* are extreme food specialists, depending principally upon root mealybugs (Delabie and Fowler 1994), and consequently do not appear at even sugar baits. The surface guilds are comprised of nectivores, carnivores, and the attine ants, which collect vegetable material or insect frass for culturing their substrate. A few species exist which transverse these guilds, but only a few are able to attain dominant status. In particular, *Solenopsis geminata*, the most common ant in litter samples (Delabie and Fowler 1995), maintains its spatial dominance at food resources, and also under hypogaeic conditions, where it is not numerically abundant. The subdominant *Pheidole* sp. 4, attains a higher ranking than expected based upon its lower rank abundance (17) in litter samples (Delabie and Fowler 1995). We suggest that this may be due to efficient scouting and recruitment behaviors.

These results imply that bait dominance is more pronounced in the epigeaic ant fauna, and also more species are limited to a specific bait type than is found in the hypogaeic fauna. Because baiting studies do not easily detect species which are specialists on certain food items, especially root mealybugs, or certain arthropod prey, we know that more dietary specialists exist in the hypogaeic fauna than the surface fauna (Delabie and Fowler 1995). Baiting studies, however, do reveal potential interactions between species which recruit workers to food items, and which probably dominate the major part of energy flow and nutrient cycling (Fowler et al. 1991).

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Appendix. Frequency occurrences of species (baits occupied by one species/ all species occurrences at baits of that type occupied) at surface and subterranean stations in Brazilian cocoa plantations. Bait types: S= sugar; M= meat; F= flour. Also shown are the first 2 dimensions of nonmetric scaling based upon the Bray-Curtis dissimilarity matrix.

| Baits: > Species | Surface | | | Subterranean | | | Dimension Loadings | | |
|---------------------------------------|---------|-----|-----|--------------|-----|-----|--------------------|------|-------|
| | S | M | F | S | M | F | I | II | Guild |
| <i>Trachymyrmex</i> sp. 2 (l) | | | .09 | | | | 1.27 | -.47 | e/a |
| <i>Mycocrepus goeldi</i> (l) | | | .06 | | | | 1.24 | -.49 | e/a |
| <i>Sericomyrmex</i> sp. 1 (l) | | | .03 | | | | 1.23 | -.50 | e/a |
| <i>Sericomyrmex</i> sp. 1 (l) | | | .24 | | .00 | | 1.06 | .08 | h-e/a |
| <i>Pheidole</i> sp. 8 (l,s) | | | | .00 | | | .92 | .99 | h/n |
| <i>Pheidole</i> sp. 9 (l,s) | | | | .00 | | | .94 | 1.00 | h/n |
| <i>Rogeria</i> sp. 1 (s) | | | | .00 | | | .92 | .99 | h/n |
| <i>Carebarella</i> sp. 1 (s) | | | .03 | | .19 | .06 | .88 | .70 | h/p |
| <i>Tranopelta</i> sp. 1 (s) | | | .00 | | | .01 | .85 | 1.17 | h/n |
| <i>Pheidole</i> sp. 10 (l,s) | | | .01 | | | .01 | .78 | 1.07 | h/n |
| <i>Monomorium</i> sp. 1 (l,s) | | | .02 | | | | .77 | .97 | h/n |
| <i>Solenopsis (Diplorhoptrum)</i> sp. | | | .03 | | | | .67 | .96 | h/n |
| <i>Solenopsis (Diplorhoptrum)</i> sp. | | | .05 | | .00 | .01 | .59 | .91 | h/g |
| <i>Octostruma jheringhi</i> (5) | | | .10 | .04 | | .09 | .45 | .97 | h/g |
| <i>Pheidole</i> sp. 6 (l,s) | | .04 | | .05 | .01 | | .45 | .12 | g |

| Baits: > | Surface | | | Subterranean | | | Dimension Loadings | | |
|--|---------|------|------|--------------|------|-----|--------------------|------|-------|
| Species | S | M | F | S | M | F | I | II | Guild |
| <i>Pheidole</i> sp. 4 (l,s) | .18 | .08 | .34 | .13 | .16 | .03 | .17 | .21 | c |
| <i>Solenopsis geminata</i> (l,s) | .08 | .24 | .06 | .43 | .52 | .54 | .13 | .33 | c |
| <i>Crematogaster</i> sp. 3 (a) | | .03 | | | | | .05 | -.88 | e/c |
| <i>Pheidole</i> sp. 7 (l,s1) | | | | | | .03 | .04 | 1.41 | h/s |
| <i>Pheidole</i> sp. 3 (l) | | .01 | | | | | .04 | -.95 | e/ca |
| <i>Acanthognathus</i> sp. 1 (l) | | .01 | | | | | .04 | -.95 | e/ca |
| <i>Hypoponera</i> sp. 1 (l) | | .01 | | | | | .04 | -.95 | e/ca |
| <i>Cyphomyrmex</i> sp 1 (1) | | .01 | | | | | .04 | -.95 | e/ca |
| <i>Acropyga</i> cf. <i>paramaribensis</i> | | .01 | | | | | .04 | -.95 | e/ca |
| <i>Wasmannia auropunctata</i> | .01 | .06 | | .06 | .00 | .01 | .04 | .13 | g |
| <i>Pachycondyla villosa</i> 1 | | .02 | | | | | .03 | -.92 | e/ca |
| <i>Crematogaster</i> sp. 1 (a,l) | | .02 | | | | | .03 | -.92 | e/ca |
| <i>Cephalotes atratus</i> (a,l) | | .02 | | | | | .03 | -.92 | e/ca |
| <i>Camponotus cingulatus</i> (a,l) | .07 | .02 | .03 | .00 | .01 | | -.03 | -.08 | h-e/g |
| <i>Monomorium floricola</i> (a,l,s) | .01 | .02 | | .00 | | .01 | -.08 | -.03 | h-e/g |
| <i>Pheidole</i> sp. 2 (l) | .11 | .01 | .04 | | | | -.28 | -.32 | e/g |
| <i>Crematogaster</i> sp. 2 (a,l) | .09 | .02 | .01 | | | | -.32 | -.36 | e/g |
| <i>Paratrechina</i> sp. 1 (a,l,s) | .02 | .04 | | | .00 | | -.36 | -.40 | e/o |
| <i>Pachycondyla venusta</i> (l) | .13 | .12 | | | | | -.46 | -.50 | e/o |
| <i>Camponotus</i> sp. 2 (a,l) | .02 | .02 | | | | | -.46 | -.56 | e/o |
| <i>Crematogaster</i> cf. <i>limata</i> (1,l) | .04 | .08 | | | | | -.49 | -.44 | e/o |
| <i>Pachycondyla apicalis</i> (l) | .01 | .12 | | | | | -.52 | -.53 | e/o |
| <i>Pheidole</i> sp. 5 (l) | .01 | .01 | | | | | -.54 | -.60 | e/o |
| <i>Trachymyrmex</i> sp. 1 (l) | | | .03 | | | | -.55 | 1.08 | e/a |
| <i>Odontomachus haematodus</i> (l) | .03 | .01 | | | | | -.56 | -.51 | e/o |
| <i>Pheidole</i> sp. 1 (l) | | | .01 | | | | -.68 | 1.10 | e/s |
| <i>Odontomachus minutus</i> (l) | .01 | | .01 | | | | -.88 | .15 | e/o |
| <i>Paratrechina</i> sp. 2 (a,l) | .02 | | | | | | -1.06 | -.05 | e/n |
| <i>Gnamptogenys striatula</i> (l) | .03 | | | | | | -1.07 | -.11 | e/n |
| <i>Tapinoma</i> sp. 1 (a) | .01 | | | | | | -1.08 | -.01 | e/n |
| <i>Myrmicocrypta</i> sp. 1 (l) | .01 | | | | | | -1.08 | -.01 | e/n |
| <i>Pachycondyla unidentata</i> (l) | .01 | | | | | | -1.08 | -.01 | e/n |
| <i>Camponotus</i> sp. 1 (a,l) | .01 | | | | | | -1.08 | -.01 | e/n |
| <i>Hypoclinea bidens</i> (a) | .01 | | | | | | -1.08 | -.01 | e/n |
| Total baits occupied | 82 | 87 | 66 | | 124 | 66 | | | |
| Species | 22 | 25 | 11 | 137 | 10 | 11 | | | |
| Mean number of spp. per bait | 1.0 | 1.09 | 0.82 | 16 | 3.10 | 1.6 | | | |

(l)= litter species;(s)= subterranean species; (a)= arboreal species
Guilds: e= epigaeic species; n= nectivorous, restricted to honey baits; h= hypogaeic species; a= fungus cultivador; o= opportunist, exploring two bait types; generalist= exploring all bait types; carnivore= carnivores, restricted to meat baits. a= attine; ca= carnivore; c= codominant; e= epi; g= generalist; h= hypo; n= nectar; o= opportunist; s= seed