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Foraging strategies may mediate the coexistence of ant species attending *Kerria yunnanensis* on their host plant

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Abstract

The role of different foraging strategies in the coexistence of ant species is poorly understood. In this study, we examined the effects of accessibility of food resource (more / less accessible environment) and food type (carbohydrates and protein) on discovery dominance trade off, and which foraging traits are related this trade off in a guild of ants attending lac insect (*Kerria yunnanensis* Ou et Hong) on their host plant (*Dalbergia obtusifolia* Prain) in the Yunnan province, China. We found that: 1) the ant assemblage on *D. obtusifolia* comprised 11 ant species; ant species differed significantly in relative abundance; 2) there was a discovery dominance trade-off among ant assemblage. Ant species with fewer individuals discovered more food relative to abundant ant species; *Crematogaster macaoensis* Wheeler dominated most of the baits. Once the food resources were discovered by *C. macaoensis*, they monopolized them; any other closing ant species were attacked. Though some ant species were quick in finding new food resources, they were unable to monopolize them; 3) the type of accessibility to food resources affected the success of discovering food resource. Some ants discovered more food in more accessible environments, relative to less accessible environments, some ants discovered more food in less accessible environments relative to more accessible environments. *C. macaoensis* dominated more in less accessible environments than that in more accessible environments; 4) protein attracted more than twice as many species compared to carbohydrates in two environments of different accessibilities; 5) the ant community on lac insect host plant exhibits foraging strategies such as foraging at low-medium rates for short distances and foraging at high rates for long distances. Foraging at low-medium rates for short distances was advantageous in a less accessible environment but disadvantageous in a more accessible environment, and vice versa; 6) We recommend that an approach which combines foraging features of ants under different accessibility to food resource with their relative foraging success may provide a good understanding of ant community structure.

Key words: Ant community, discovery-dominance trade off, foraging behaviour, lac insect, *Dalbergia obtusifolia*.

Introduction

Competitive interactions are assumed to play a key role in structuring ant communities (Blüthgen and Fiedler, 2004; Blüthgen *et al.*, 2004; Davidson, 1998; Lach, 2005; Raine *et al*, 2004; Sarty *et al*, 2006; Savolainen and Vepsäläinen, 1988; Tilman, 1982; 1999). The success of most opportunistically foraging ants critically depends on arriving early in a new habitat, recruiting many individuals and quickly leaving from the habitat once the aggressive territorial species arrive there (Planqué *et al.*, 2010). Not surprisingly, ants vary substantially in running speed and running distance (Hölldobler and Wilson, 1990) and this variation may affect the ways they interact with competitors and the habitat (Morrison, 1996; Kay, 2002; 2004; Kay and Adler, 2003). Oster and Wilson (1978) coined the terms "high tempo" and "low tempo" foragers to describe the different activity levels of foraging ants, which has important implications for the type of diet consumed, dominance status, colony size and size of the foraging area covered.

Coexistence in ant communities can be explained by several hypotheses. The most influential model has been the competition-colonization trade-off, which predicts that better competitors are inferior colonizers, and vice versa (Levins and Culver, 1971; Tilman, 1994; Yu and Wilson, 2001; Yu *et al.*, 2001; Crowley and McLetchie, 2002). Fellers (1987) suggested the discovery-dominance trade-off mechanism operating in ant communities, which is the ability to discover food versus the ability to dominate and consistently recruit to a food resource. And the size-grain hypothesis (SGH) (Kaspari and Weiser, 1999) proposed that coexistence between ant species is facilitated by differential habitat use according to body size. Size dependent differences in habitat use and its potential role for species coexistence have also been suggested for communities of other terrestrial insects (Kaspari and Weiser, 1999; Farji-Brener *et al.*, 2004; Sarty, 2005; Sarty *et al.*, 2006). The similarity of these hypotheses or mechanism is their contribution to explain ant coexistence. However, each hypothesis (mechanism) has its own focus. Competition-colonization trade-off emphasized the ability of competition resources and colonization; discovery-dominance trade-off emphasized the ability of discovering and dominating resources; and size-grain hypothesis focused differential habitat use according to body size. To test these hypotheses, most manipulation experiments using ants have been conducted in simple environments with food baits placed on the ground or on tree trunks. Some studies have documented the effects of accessibility to resources (the difficulty for ants to locate, exploit and recruit to resources), which can lead to foraging partitioning, and is important for ant coexistence and community structure (Davidson, 1977; Kaspari, 1996; Schooley *et al.*, 2000; Tanner, 2009; Tanner and Adler, 2009).

Lac insects (*Kerria* spp., Rhynchota Kerriidae) are scale insects which occur naturally on various host plant species. They produce lac, a layer of red resin on the branches of their host trees on which they feed. Lac resin is biodegradable and non-toxic. It is widely used as food supplement, for textiles and in the pharmaceutical industry. Lac insects occur in tropical and subtropical regions of South Asia and Southeast Asia, and most of the lac-producing insects are economically important and often reared in agroecosystems (Chen *et al*., 2010). Ants feed on the honeydew excreted by lac insect, attend the lac insect colonies, and quickly reach high densities. Many ant species visit the host plants of the lac insects. The composition and abundance of ant assemblages vary substantially within plant parts of the host plant (unpublished data). However, the reasons for the variation are not clear. Understanding the mechanisms which likely affect the abundance and coexistence of ants is of fundamental importance to community ecology.

In this study, we examined the effects of different accessibility to food resource and resource type on foraging behaviour and competitive ability in a guild of ants attending *Kerria yunnanensis* Ou et Hong (Rhynchota Coccoidea Kerriidae) on their host plant *Dalbergia obtusifolia* Prain in the Yunnan province, China. We used field manipulation experiments to address how greater or lesser accessibility to food resources and resource type (carbohydrate and protein) affect the success of discovery and dominance food resources; which foraging characteristics (including the running distance before stopping / turning direction, the running speed, and the frequency of stopping / turning direction in searching for prey) of different ant species correlate their success in discovering food resources. In particular, we ask: First, was there a discovery dominance trade-off? And how does environmental accessibility and resource type affect this? Second, which foraging traits are related to the trade-off?

Materials and methods

Study system

This research was conducted in a lac insect agroecosystem in Mojiang county, Yunnan Province, south west of China (101°43'E 23°14'N 999.8-1056 m a.s.l.). The study site is characterized by an average annual rainfall of 1500-2100 mm (mostly in May to October) and a mean annual temperature of 18.2 °C (observations in recent 3 years). The total area of the research plot was 10 hectares. The lac insect agroecosystem is the main form of cultivation in mountainous regions between 900-1500 m a.s.l., with several plant species (plants are not used for anything other than lac production) as host for the lac insect, distributed along or among the semiarid agricultural plots. *K. yunnanensis* is reared by farmers on different plant parts throughout the year. On completing its first generation (from May to October), *K. yunnanensis* is collected by cutting the branches on which they feed, and transferring to alternative trees (other trees of the conspecific or different species can be selected) for the second generation (from October to May of the following year). As a consequence, resource availability can quickly change for established ant communities.

The experiments were performed in a lac plantation which was dominated by the lac plant *D. obtusifolia* with a density of 1500 trees per hectare. On *D. obtusifolia*, *K. yunnanensis* settles on the main branch, shoots and even leaf stalks. On reaching the adult stage, lac insects excrete larger quantities of honeydew, some of which may stick to the body of lac insects and accumulate in small droplets. Honeydew is also flicked away from the body and accumulates on the surface of leaves and branches. Many ant species, such as *Crematogaster macaoensis* Wheeler, *Dolichoderus thoracicus* Smith, and *Camponotus parius* Emery visit *D. obtusifolia* and often co-forage on the same tree. However, some ant species, like *C. parius* Emery and *Polyrhachis tibialis* Smith, prefer to forage for food on the trunk, main branches and the surface of leaves, but less so on branches with a small diameter. Others, like *C. macaoensis* and *D. thoracicus* forage throughout a tree, including the trunk, branches, leaves, cavities and outgrowths of a branch. In this experiment, 5-year-old *D. obtusifolia* were selected, ranging between 2.5 m to 2.8 m in height and between 5 cm to 7 cm of diameter at breast height. All selected trees were used to rear *K. yunnanensis* and the experiments were conducted in 2009 and in 2010.

Composition and abundance of ant communities

Three patches (100 × 100 m) were selected in a lac plantation. In the first patch, more than 40 nests of *C. macaoensis* were found on *D. obtusifolia*, and we selected 30 plants without *C. macaoensis* nest. The distance between two plants was at least 5 m. In the second patch, no *C. macaoensis* nest was found on *D. obtusifolia*, and we randomly selected 30 plants also, the distance between each plant was at least 3 m. In the third patch, no *C. macaoensis* nest was found on *D. obtusifolia*, and the plants distribute along the edge of the paddy. 30 plants were selected, and the distances between each plant ranged from 5 - 20 m. The selected 90 trees were cultivated with *K. yunnanensis* in October, and ants were investigated in May next year.

The experiment was conducted between 09:00 AM and 12:00 AM. The ants were recorded and sampled on each tree by two investigators standing face to face, and searching for a period of 2 minutes (Del-Claro and Oliveira, 1996). Specimens were identified using the keys of Xu (2002) and also Wu and Wang (1995). Abundance of ant species was calculated in two ways using Andersen's (1991) methods: 1) relative abundance, which is the number of individuals of a particular ant species on all trees / the total number of individuals of all ant species on all trees per patch; and 2) relative frequency of occurrence, which is the number of emerging times of one species on trees / the total number of emerging times of all species on all trees per patch (irrespective of individual numbers). Together, these two types of information provide an idea of the relative performance of an ant species. MANOVAs were performed to analyze the effects of habitat type (as independent factor) and ant species on abundance of ants; analysis was also conducted to compare the abundance of all ant species based on data for 90 trees (as independent factor).

Discovery of food baits

As mentioned above, lac insect agroecosystem is a useful system for testing whether or not carbohydrate availability is important for structuring ant communities. However the viscous property of honeydew affects the behaviour of ants if not removed continuously. Therefore, it is difficult to use in controlled experiments. As an alternative resource, we offered bread crumbs (have lots of complex carbohydrates, varying from 0.1-2 mg in weight). While most ant species are thought to feed on carbohydrates (Blüthgen *et al.*, 2003), some feed preferentially on protein. Also, during reproduction, many ant species temporarily need protein to enhance the growth of their larvae. Thus, protein food was offered to lure ant species. In previous experiments, bread crumbs and small pieces of duck intestine proved suitable to attract ants.

The experiment was again conducted between 09:00 AM and 12:00 AM on *D. obtusifolia*, where food accessibility and food type as fixed factors were tested. In food accessibility experimental design, two levels (difficult access and easy access) were set to investigate the influence of accessibility to food resources on discovery of food by ants. In food type experimental design, two types (carbohydrates and protein) were set to investigate the influence of food types on discovery of food by ants. The approximate abundances of the lac insect and ants on the selected tree where the baits were experimentally set ranged from 20,000 - 30,000 and 10 - 30 (plant with ant nest was not selected), respectively. In the first stage, we used baits which were put in plastic cups (400 ml) as food bait and suspended from a tree with an iron wire 1.5 m above the ground, and the distance between cup and the tree was about 1.0 cm. Compared to food on small branches, this bait is more difficult to locate, exploit and recruit to, as cups did not touch the stem and the ants had to traverse the wire in order to get to the bait. This was defined as a less accessible environment. In total, 40 cups with bread crumbs were used with one cup per tree. The same procedure was used for cups containing small pieces of duck intestine. In total, 20 cups were put on different trees (one cup per tree). The second stage of the experiment was conducted with baits attached to the main trunk of *D. obtusifolia* using sticky resin 1.5m above the ground. This represents a more accessible environment for ants because the baits can be accessed from any direction. In total, 40 trees were selected for bread crumbs baits and 40 for duck intestine baits (one bait per tree). The trees were not previously used for other experiments. All trees used in the experiments were at least 3 m from each other. All baits were monitored every 15 min by four investigators, and the investigation lasted up to a maximum of 3 hours. Individual numbers of each species arriving at the baits were recorded.

MANOVAs were used to compare the ability of different ant species to discover different food resources, using ant species, food type and type of accessibility to food resources as influential factors, and data of ten trees were combined as one group; analyses were also conducted to compare the frequency of discovery food resource of all ant species based on data for 140 trees (the trees selected for discovery experiment, and tree as independent factor), but in fact not all baits on trees were discovered by ants, only tree with ant discovering bait came into the analysis. The frequencies that more than one species co-occurring on food resources were analyzed by means of one-way ANOVAs, using mean individual numbers of ants per cup and mean individual number of cups co- occurred by ants per 10 trees.

Dominance at food baits

Five hours after the bait dominance experiment was terminated, the abundance of each ant species at the baits of each treatment was recorded. The selected trees and experimental designs and procedures were identical to those used in the discovery experiment, which is mentioned above in the last section. MANOVAs were used to compare the ability of different ant species to dominate different food resources, using ant species, food type and type of accessibility to food resources as influential factors, also data of 10 trees were combined as one group; analysis was also conducted to compare the dominance of food resource for all ant species based on data of 140 trees (the trees selected for dominance experiment, and tree as independent factor), but in fact not all baits on trees were discovered and dominated by ants, only tree with ant being dominating bait came into the analysis. The species turnover rate in time was calculated in the following way (after Magnuson *et al.*, 1994): $T = 100 (I + E) / (S1 + S2)$, where T is the turnover rate in time, I is the number of taxa newly emerging in baits in the dominance experiment and E is the number of taxa replaced between the two stage of the experiment (discovery and dominance experiment). S1 is the number of ant taxa found in the discovery experiment, S2 is the number of taxa observed in the dominance experiment. Differences of species turnover rates in time were analyzed by one-way ANOVAs.

Features of foraging

There are many examples in the literature of ants exhibiting characteristic foraging behaviours before reaching food resources. However, the foraging behaviours after ants reached the resources may be also important. Here, we investigated the foraging behaviour after ants reached *D. obtusifolia* for honeydew and other prey.

Five *D. obtusifolia* were selected in the patch where the discovery experiments were conducted. The height of the trees and the surface of the stem mirrored those of the bait experiments, including smooth and rough textured surfaces, number of branches, etc. Out of the 11 ant species found, seven ant species located both carbohydrate and protein food during the observation period, and we investigated their foraging features. After an ant reached the selected tree, we determined running speed, running distance, and the frequencies of stopping / turning directions while traversing the stem by each of five investigators. The number of replicates varied from 11 - 50 for different ant species, depending on their abundance. Individuals that were disturbed by other ants or arthropods while foraging were not included in the analyses. Two hundred and sixty seven measurements were performed in total for seven ant species. Each measurement was conducted in the lac plantation in the morning between 09:00 AM and 12:00 AM. Ant running speed and running distances (before stopping / turning directions) were analyzed by one-way ANOVAs. The frequencies of stopping / turning directions in foraging were recorded, based on running distance categories (20, 30, 100 cm). Correlation analyses (Pearson correlation index) were used to analyze the relationships between different foraging features of ant species and their relative frequency of discovering a food resource. Here, the data of relative frequency of discovering two food types were combined to compare the effect of two different accessibilities, and the mean running speed, mean running distance, and the relative frequency of discovering food resources entered the analysis. In analyses of ants foraging in more accessible environment, the seven ant species were divided into two groups, the ants with mean running distance (before stopping / turning directions) more than 100 cm as a group, and the ants with mean running distance (before stopping / turning directions) less than 100cm as a group; in analyses of ants foraging in less accessible environment, the seven ant species were divided into two groups based on running speed, the ants with mean running speed more than 5 cm/sec as a group, and the ants with mean running speed less than 5 cm/sec as a group.

Results

Was there a discovery dominance trade-off?

The ant assemblage on *D. obtusifolia* comprised 11 ant species, representing four subfamilies and eight genera. The number of ants on trees ranged from 1.5 - 1273 per patch; and the number of trees on which at least one ant was observed ranged from 1.5 - 20.3 per patch (table 1). Relative fewer ants were found on trees and fewer trees were found with ants in patch where trees distribute along paddy edge. For the investigated 90 trees, there was a significant difference in relative abundance among ant species (P = 0.02, $F_{0.05}$ (10, 12) = 3.566, n = 90). Abundance of ant species (based on % of all ants) ranked *Crematogaster macaoensis* > *Dolichoderus thoracicus* > *Crematogaster ferrarii* Emery > *Monomorium chinensis* Santschi > *Camponotus parius* > *Tetraponera allaborans* Walker > *Polyrhachis tibialis* > *Anoplolepis gracilipes* (Smith) > *Polyrhachis proxima* Roger > *Cataulacus granulatus* (Latreille) > *Camponotus lasiselene* Wang et Wu.

Out of the 11 ant species, seven species found both carbohydrate and protein food in the experiment during the observation period (table 2). Sixty one baits were discovered by ants. The actual frequency (AF) of discovering food resources was significantly different

Table 1. The identity and relative abundance of dominant ant species on *D. obtusifolia* in lac plantations (mean ± 1 SE).

Subfamily	Genus	Species	Abundance and relative abundance (%)	Occurrence and relative frequency of occurrence (%)
Pseudomyrmecinae	*Tetraponera*	*allaborans*	13.0 ± 8.0 (3.0 ± 1.7)	8.7 ± 4.8 (15.6 ± 7.2)
Myrmicinae	*Cataulacus*	*granulatus*	1.5 ± 0.5 (0.6 ± 0.4)	1.5 ± 0.5 (2.9 ± 1.2)
Myrmicinae	*Crematogaster*	*macaoensis*	1273.0 ± 1056.0 (66.1 ± 26.5)	20.3 ± 6.9 (43.5 ± 18.2)
Myrmicinae	*Crematogaster*	*ferrarii*	11.0 ± 7.0 (4.8 ± 4.0)	4.0 ± 2.0 (7.8 ± 4.5)
Myrmicinae	*Monomorium*	*chinensis*	13.5 ± 4.5 (4.0 ± 0.4)	2.5 ± 1.5 (4.9 ± 3.3)
Dolichoderinae	*Dolichoderus*	*thoracicus*	120.0 (58.8)	7.0 (14.3)
Formicinae	*Anoplolepis*	*gracilipes*	2.0 (1.0)	2.0 (4.1)
Formicinae	*Polyrhachis*	*tibialis*	6.0 ± 4.0 (1.0 ± 0.1)	4.5 ± 2.5 (8.3 ± 3.2)
Formicinae	*Polyrhachis*	*proxima*	1.7 ± 0.7 (0.6 ± 0.5)	1.7 ± 0.7 (3.4 ± 1.4)
Formicinae	*Camponotus*	*lasiselene*	3.0 (0.1)	2.0 (5.1)
Formicinae	*Camponotus*	*parius*	9.7 ± 4.1 (3.4 ± 2.3)	7.0 ± 2.9 (13.7 ± 5.7)

Means were calculated for each patch and the overall mean values for the three experimental patches are provided here. *D. thoracicus*, *A. gracilipes*, and *C. lasiselene* were only found in one patch. 1) relative abundance is the number of individuals of a particular ant species on all trees / the total number of individuals of all ant species on all trees per patch, and 2) relative frequency of occurrence is the number of emerging times of one species on trees / the total number of emerging times of all species on all trees per patch (irrespective of individual numbers).

Table 2. Mean actual frequencies (AF) and relative frequencies (RF) of discovering different baits in different environments of accessibility during a three hour foraging period (mean ± 1 SE).

Ant species	More accessible environment		Less accessible environment	
	Bread crumbs	Duck intestine	Bread crumbs	Duck intestine
	AF (RF)	AF (RF)	AF (RF)	AF (RF)
T. allaborans	1.0 ± 0.0 (6.4 ± 0.0)	0 (0)	5.8 ± 1.1 (33.8 ± 7.9)	5.0 ± 2.0 (32.0 ± 12.8)
C. macaoensis	3.0 ± 0.6 (6.9 ± 1.3)	1.3 ± 0.3 (2.9 ± 0.6)	10.3 ± 2.3 (23.8 ± 5.4)	5.5 ± 4.5 (12.7 ± 10.4)
M. chinensis	1.0 (20.4)	0 (0)	0 (0)	1.0 (20.4)
D. thoracicus	1.0 (7.0)	1.5 ± 0.5 (10.5 ± 3.5)	2.0 ± 0.6 (14.0 ± 4.0)	3.0 (20.9)
P. tibialis	1.0 (12.0)	0 (0)	0 (0)	0 (0)
C. parius	1.0 ± 0.0 (7.3± 0.0)	1.0 ± 0.0 (7.3 ± 0.0)	2.3 ± 0.9 (17.0 ± 6.4)	2.0 (14.6)
A. gracilipes	0 (0)	2.0 (48.8)	0 (0)	0 (0)
C. lasiselene	0 (0)	0 (0)	1.0 (19.6)	0 (0)
C. granulatus	0 (0)	0 (0)	3.5 ± 2.5 (120.7 ± 86.3)	1.5 ± 0.5 (44.7 ± 24.3)
P. proxima	1.0 (29.4)	1.0 ± 0.0 (29.4±0.0)	0 (0)	1.0 (29.4)
C. ferrarii	2.8 ± 0.6 (35.3 ± 8.1)	2.7 ± 0.3 (34.2±4.3)	3.5 ± 2.5 (44.9 ± 32.1)	0 (0)

Mean actual frequencies (AF) were calculated per 10trees; relative frequencies (RF) mean relative frequency of occurrence of an ant species at baits per 10 trees. RF = AF/mean relative frequency of occurrence of a particular ant species per 10 trees (data shown in the last row of table 1).

among ant species (P = 0.019, $F_{0.05}$ (10, 33) = 2.593, n = 61), ant species with fewer individuals, such as *C. granulatus* and *P. proxima*, discovered more food relative to abundant ant species, such as *M. chinensis* and *P. tibialis*; What is also interesting is a comparison of the frequency of an ant species, irrespective of its initial abundance using occurrence data. Using these relative frequencies (RF = AF/ the relative frequency of occurrence of ants), ant species had a significant effect on the RF of discovering food resources (P = 0.013, $F_{0.05}$ (10, 33) = 2.798, n = 61) (MANOVAs), and many ant species had higher RF values than *C. macaoensis* (table 2).

Forty nine baits were found to being dominated by ants (table 3). Ant species had significant effects on the actual frequency (AF) of dominating food resources (P = 0.01, $F_{0.05}$ (8, 28) = 3.199, n = 49), with *C. macaoensis* dominating most of the baits. Once the food resources were discovered by *C. macaoensis*, they monopolized them by more than 10 individuals feeding on the baits; any other closing ant species were attacked. Though some ant species were quick in finding new food resources, they were unable to monopolize them. When compared with the relative frequencies (RF = AF / the relative frequency of occurrence of ants) of occurrence at the baits. Here also ant species had a significant effect on the RF of dominating food resources (P = 0.004, $F_{0.05}$ (8, 28) = 3.789, n = 49).

How does environmental accessibility and resource type affect this discovery dominance trade-off?

The actual frequency (AF) of discovering food resources was significantly different between the type of accessibility to food resources by the same ant species (P = 0.003, $F_{0.05}$ (1, 33) = 10.157, n = 61) (MANOVAs). *P. proxima* and *C. ferrarii* discovered more food in more accessible environments, relative to less accessible

Table 3. Mean actual frequencies (AF) and relative frequencies (RF) of dominating different baits in different environments of accessibility after five hours (mean ± 1 SE).

Ant species	More accessible environment		Less accessible environment	
	Bread crumbs	Duck intestine	Bread crumbs	Duck intestine
	AF (RF)	AF (RF)	AF (RF)	AF (RF)
T. allaborans	1.0 ± 0.0 (6.4 ± 0.0)	0 (0)	3.0 ± 0.4 (19.2 ± 2.6)	3.5 ± 2.5 (22.4 ± 16.0)
C. macaoensis	3.0 ± 0.6 (6.9 ± 1.3)	1.3 ± 0.3 (2.9 ± 0.6)	9.3 ± 1.3 (21.5 ± 3.1)	5.0 ± 4.0 (11.5 ± 9.2)
M. chinensis	0 (0)	0 (0)	0 (0)	1.0 (20.4)
D. thoracicus	0(0)	1.5 ± 0.5 (10.5 ± 3.5)	2.5 ± 0.5 (22.5 ± 8.6)	1.0 (7.0)
P. tibialis	0(0)	0(0)	0(0)	0(0)
C. parius	1.0 ± 0.0 (7.3 ± 0.0)	1.0 (7.3)	1.0 ± 0.0 (7.3 ± 0.0)	2.0 (14.6)
A. gracilipes	0 (0)	1.0 (24.4)	0 (0)	0 (0)
C. lasiselene	0 (0)	0 (0)	0 (0)	0 (0)
C. granulatus	0 (0)	0 (0)	0 (0)	1.5 ± 0.5 (44.7 ± 24.3)
P. proxima	1.0 (29.4)	0 (0)	0 (0)	0 (0)
C. ferrarii	2.5 ± 0.6 (32.0 ± 8.3)	2.7 ± 0.3 (34.2 ± 4.3)	3.5 ± 2.5 (44.9 ± 32.1)	0 (0)

Mean actual frequencies (AF) were calculated per 10 trees; relative frequencies (RF) mean relative frequency of occurrence of an ant species at baits per 10 trees. RF=AF/mean relative frequency of occurrence of a particular ant species per 10 trees (data shown in the last row of table 1).

environments, while *D. thoracicus*, *T. allaborans* and *C. macaoensis* discovered more food in less accessible environments relative to more accessible environments. When RF data were used, *C. ferrarii* had the highest RF in more accessible environments; *C. granulatus* had the highest RF in less accessible environments. The type of accessibility to food resources had significant effects on the actual frequency (AF) of dominating food resources ($P = 0.019$, $F_{0.05}$ (1, 28) = 1.804, n = 49) (MANOVAs), with *C. macaoensis* dominating more in less accessible environments than that in more accessible environments. For example, in more accessible environments, baits discovered by *C. parius* were often replaced by *C. macaoensis*. In most cases, *C. macaoensis* attacked ant species which discovered the baits first, by more than three individuals, and until the ants gave up the food resources.

Protein attracted more than twice as many species compared to carbohydrates in two environments of different accessibilities. In 3 h bait trials, *C. macaoensis* recruited to 90% of located baits, while *T. allaborans* recruited to only 48% of located baits. Once baits were discovered, the two ant species differed significantly in the number of workers recruiting to baits over time ($P = 0.008$, $F_{0.05}$ (1, 26) = 8.208, n = 30).

More protein baits were dominated by ants than baits with carbohydrate. For the species turnover in time, protein baits had higher rates. In more accessible environments, the rates were 24.04% (at protein food) and 10% (at carbohydrate food); and in less accessible environments, the rates were 23.64% (at protein food) and 16.07% (at carbohydrate food).

Which foraging traits are related to the trade-off?

P. proxima showed the highest mean running speed and *C. ferrarii* the longest mean running distance of all studied species (table 4). In contrast, *M. chinensis* showed the slowest running speed and the shortest running distance. *D. thoracicus* and *C. macaoensis* showed a similar running speed, but *D. thoracius* tended to search longer distances (table 4). Ant species differed significantly in terms of mean running speed and mean running distance (before stopping / turning directions) ($P < 0.0001$, $F_{0.05}$ (6, 260) = 235.1, n = 267; $P < 0.0001$, F (6, 260) = 65.9, n = 267).

M. chinensis interrupted its searching activities and turned left / right or spun in circles usually after running distances of 0.1 m. *C. macaoensis*, *T. allaborans* and *D. thoracicus* started to show such a behaviour after running distances of about 0.2 m, while *C. parius* and *P. proxima* showed the least number of turns and only did so after running 1.0 m (table 4). Thus, the foraging behaviour of the ants visiting lac insects fell into three distinct classes: *C. ferrarii*, *C. parius* and *P. proxima* were high speed, long distance foragers, *M. chinensis* was a low speed short distance forager, and *C. macaoensis*, *T. allaborans* and *D. thoracicus* were intermediate foragers. That is, the ant community on lac insect host plant comprises all types of foraging strategies.

High tempo ants like *P. proxima* and *C. parius* preferred to forage in more accessible environments such as stem and main branch, and rarely in the less accessible environments, such as side shoots and leaf stalks. Low and medium tempo foragers, like *C. macaoensis* and *T. allaborans*, used both environments of differing accessibilities.

For ants foraging in more accessible environments, the mean running distance and mean running speed were positively correlated with the mean RF of discovering food items ($P < 0.0001$, $R^2 = 1.0$, n = 2). This suggests that ants with a higher running speed and longer running distances had a better chance to discover food resources. For ants foraging in less accessible environments, the mean running distance and mean running speed were negatively correlated with the mean RF of discovering food items. ($P < 0.0001$, $R^2 = -1.0$, n = 2). This suggests that ants with a lower running speed and shorter running distances had a better chance of discovering food resources.

Discussion

Was there a discovery dominance trade-off?

Eleven ant species were found to co-forage on honeydews excreted by *K. yunnanensis*. There was a significant difference in relative abundance among ant species. Ant species with fewer individuals, such as *C. granulatus* and *P. proxima*, discovered more food relative to abundant ant species, such as *M. chinensis* and *P. tibialis*. Dominant and aggressive species *C. macaoensis* is unable to exploit in environments of different accessibilities at all times, fugitive species such as *C. parius* and *T. allaborans* are able to invade habitats occupied by dominant ant species and exploit ephemeral resources. So there was a distinct discovery dominance

Table 4. Foraging speed and foraging distance of seven ant species on a stem of *D. obtusifolia*.

Ant species	Running speed Mean ± 1 SE (cm/sec)	Running distance Mean ± 1 SE (cm)	Frequency of stopping/turning directions after traversing certain distance (%)		
			20cm	30cm	100cm
T. allaborans	4.1 ± 0.2	14.7 ± 4.9	0	40.1	79.5
C. macaoensis	2.2 ± 0.2	30.4 ± 1.9	0	58	100
M. chinensis	1.3 ± 0.1	15.8 ± 1.6	0	91.7	100
D. thoracicus	2.1 ± 0.0	35.1 ± 3.0	0	51.9	100
C. ferrarii	3.1 ± 0.1	157.9 ± 12.3	0	0	0
C. parius	8.1 ± 0.4	136.4 ± 20.3	0	0	0
P. proxima	8.3 ± 0.3	153.9 ± 12.6	0	0	0

trade-off among ant species foraging on *D. obtusifolia* where *K. yunnanensis* hosting on, which was consistent with the result of Fellers (1987).

How does environmental accessibility and resource type affect this discovery dominance trade-off?

Besides the difference of discovery and dominance food resources among ant species, for the same ant species, they performed differently in terms of environmental accessibility and resource type. For example, *P. proxima* and *C. ferrarii* discovered more food in more accessible environments, relative to less accessible environments, while *D. thoracicus*, *T. allaborans* and *C. macaoensis* discovered more food in less accessible environments relative to more accessible environments. Though *C. macaoensis* dominated most of the baits, *C. macaoensis* dominated more baits in less accessible environments than that in more accessible environments. When come to food type, Protein attracted more than twice as many species compared to carbohydrates in two environments of different accessibilities. Protein attracted more ant species to dominate it also. So we predict that ants could adjust the balance of discovery dominance trade off plastically when confront different environment and food type. For high carbohydrate yields from scale exudates may afford these species high tempo activity (Oster and Wilson, 1978) and high dynamic density (workers/m^2, Hölldobler and Wilson, 1990) in preferred foraging areas, leading to more effective resource discovery, harvesting, and defence (Davidson, 1998). In a number of other ant communities, access to excess carbohydrates may enable species to "break" the trade-off in exploitation and interference competition, enhancing their ecological dominance (Davidson, 1998).

Which foraging traits are related to the trade-off?

A major challenge in community ecology is to understand the factors that confer co-occurrence or even coexistence (May, 1973; McCann *et al*., 1998). Our study shows that different accessibility to food resources and the presence/absence of different resource types modulate the foraging behaviour of ants and facilitate resource use by multiple species. On the main truck, main branch and leaves of lac insect host trees, high-tempo, long-distance ants gained a relative advantage because these species are able to access food resources earlier than *C. macaoensi*. Also, for food resources on small side shoots and leaf stalks of lac insect host trees, many were found by other ant species, of low to medium speed of foraging and frequent stopping/turning behaviour.

The differential effects of foraging strategies are important for ant community organization (Lach, 2005; Brown and Gordon, 2000; Nonacs and Dill, 1988; 1990; 1993). The results of our studies provide certain evidence that different parts of the lac insect host trees may represent different types of accessibility, and ant species could segregate into these within-tree parts of different accessibility to food resource on the basis of their foraging behaviour. Thus, the different foraging abilities might facilitate coexistence between large but rare ant species and small but abundant species on the same tree. Though the resources hanging off the stem and on the stem directly in the field manipulations were not equal to more and less accessible environments on lac host plants. Also, use of bread is somewhat problematic because of differences in the type and concentration of carbohydrates and because bread is solid. Most ants in experiments are not specialized to feed on liquid foods. In the dry season, many ants forage on honeydew droplets with less water, and bread in our baits was all eaten out within several hours; our results are thus reasonably robust.

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