Resource discovery in ant communities: do food type and quantity matter?

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Abstract. 1. Omnivorous woodland ant species trade off between the ability to find and behaviourally control food resources. Dominant species can limit the ability of subordinates to harvest certain food items. However, subordinate species, by being faster discoverers, could gain access to such food items by arriving at them first.

2. In this study, we tested the hypothesis that resource-directed discovery occurs in ant communities and that good discoverers preferentially discover high value resources. We did this by measuring time to discovery and the number of discoveries of high and low levels of two resource types, crickets and honey, for species occurring in Texas and Arizona woodland ant communities.

3. Ants discovered resources roughly 10 times faster in Texas than in Arizona. They discovered crickets more rapidly than honey in both communities, but there was no difference in the discovery of different resource levels. We also found that species were not biased in their discovery of different resource types or levels.

4. These results provide indirect evidence that discovery is directed by resource stimuli but that such directedness does not impact interspecific exploitative competition.

Key words. Ants, competition, foraging behaviour, Formicidae, resource discovery, search behaviour.

Introduction

All organisms face the challenge of acquiring sufficient food to fuel growth and reproduction. Foraging success relies on two main components: effectively encountering food items (Stephens & Krebs, 1986; Bell, 1991) and effectively harvesting them once found. The latter is of particular concern to central place foragers, organisms that return to a central point with acquired resources (Orians & Pearson, 1979; Schoener, 1979; Wetterer, 1989). One important and unavoidable limitation faced during both stages by foragers is competition by other species, whose presence depresses resource levels, leading to both diminished encounter rates (Mitchell et al., 1990) and/or costly physical battles to determine resource control (Ydenberg et al., 1986).

In temperate ant communities, the majority of species are omnivores, competing for the same resource pool of insect and plant matter (Vepsäläinen & Pisarski, 1982; Fellers, 1987; Hölldobler & Wilson, 1990; Retana & Cerdá, 1994; Morrison, 1996; Holway, 1999; Fiedler et al., 2007). They are also, with few exceptions, central-place foragers (Holldobler & Wilson, 1990) that specialise on different components of foraging success, trading off between discovery (resource encounter) and dominance (resource harvest and control) abilities (Vepsäläinen & Pisarski, 1982; Fellers, 1987; Morrison, 1996; Davidson, 1998; Holway, 1999; LeBrun & Feener, 2007). In the traditional interpretation of the trade-off, good discoverers are subordinate species that maximised their resource encounter rates so as to access resources before being displaced from them by behavioural dominants during harvest (Vepsäläinen & Pisarski, 1982; Fellers, 1987; Morrison, 1996). Individual foragers of subordinate species may pre-empt competitive interference at resources by arriving first at small resources that they can quickly exhaust or carry away (LeBrun, 2005; Adler et al., 2007). Being a good discoverer may also be a means by which subordinates access preferred resources. Omnivorous ant species often prefer different sizes and types of food both in the absence of competitors (Sanders & Gordon, 2000, 2003) and during recruitment (Savolainen, 1991; Yanoviak & Kaspari, 2000), yet dominant species often
monopolise these preferred items in nature (Sanders & Gordon, 2003).

Specific morphological and behavioural traits underlie the dominance–discovery trade-off. The mechanisms by which competitive dominants usurp and control resources are well characterised and diverse. Dominant species are often characterised by chemical weaponry (Fellers, 1987; Davidson, 1998), large colony size (Holway, 1999), the presence of a morphologically specialised soldier caste (Wilson, 1975, 1976; Wilson, 1978; Morrison, 2000), and large body size (Fellers, 1987). They can also maintain resource control via high tempo movement (Davidson, 1998) or by recruiting large numbers of small workers to resources using pheromone trails (Holway, 1999). Presumably, dominant species trade off investment in foragers that can usurp and/or control resources at the expense of having scouts available to find it first (Johnson et al., 1987), although empirical support for this mechanism is lacking.

In contrast, perhaps because of the historical focus on resource dominance, very little is known about how ants discover resources, despite its potential importance in understanding how communities are organised (Adler et al., 2007). Finding food resources relies on enhancing the probability of encountering randomly located and unpredictably renewed food items (Harkness & Maroudas, 1985). The way in which this is achieved, however, is largely undescribed and the traits that characterise good discoverers are a topic of current investigation. It has been hypothesised that colonies may maximise discovery by deploying a larger number of scouts because more scouts mean greater environmental coverage (Johnson et al., 1987; Schmid-Hempel, 1987; Holway & Case, 2001; Roulston & Silverman, 2002). Indeed, having more scouts outside the nest leads to more rapid resource discovery (Pearce, 2008) and, in polydomous species, forager number can potentially interact with nest number to enhance coverage and discovery (Holldobler & Lumsden, 1980; Traniello & Levings, 1986; Pfeiffer & Linsenmair, 1998; Holway & Case, 2001). However, this hypothesis has been put into question by the fact that differences among species in discovery ability are more influenced by characteristics of individual foragers than by the number of foragers in the vicinity of the resource (Pearce, 2008), highlighting the need to examine forager discovery ability in greater detail.

Individual discovery ability could be enhanced using either undirected or directed search strategies. In an undirected search, the likelihood of resource encounter is optimised by the features of the search pattern. For instance, an individual forager could have a greater chance of bumping into a resource if it more thoroughly searched an area by turning more (Lynch et al., 1980) or covered greater distances by moving in straighter lines (Jander, 1975; Jones & Phillips, 1990; Bell, 1991; Zollner & Lima, 1999), although a colony’s search pattern may be mediated by the number of foragers present (Adler & Gordon, 1992; Gordon, 1995). Furthermore, a forager might be able to cover more ground and increase encounter probabilities by enhancing biomechanics, such as the ratio of leg to body size (Kaspari & Weiser, 1999; Sarty et al., 2006).

Ants could also employ directed searches that rely on external environmental cues. For instance, some species rotate or constrain the routes that foragers follow, resulting in greater search thoroughness and minimised search overlap (Bernstein, 1975; Franks & Fletcher, 1983; Fresneau, 1985; Buchkremer & Reinhold, 2008). Such searches are guided by polarised light (Wehner, 1997), the sun (Müller & Wehner, 2007), magnetic fields (Banks & Srygley, 2004), and habitat landmarks (Judd & Collett, 1998; Fukushi & Wehner, 2004). It is less clear how frequently directed searches rely on cues directly associated with the resource itself. There is ample evidence that foragers can and do assess resource desirability and quantity upon encounter with food items and that they communicate resource characteristics to the nest (de Biseau & Pasteels, 1994; Dethier & Deneubourg, 1997; Robson & Traniello, 1998; Mailleux et al., 2000; Lenoir, 2002; Cassill, 2003). However, the degree to which sensory assessment operates to direct the search is not well-characterised. The use of vision and olfaction has been documented in a few specialised predaceous species (Schatz et al., 1997; Dejean et al., 2001; Durou et al., 2001) and in even fewer omnivorous species (Wolf & Wehner, 2000; Schatz et al., 2003). The role of resource-directed discovery in the community context is entirely unknown.

Our study assesses the contribution of resource-based cues to discovery in two different ant communities by examining evidence for two emergent predictions. First, if ants are using resource cues to discover resources, we would predict that resources that differ qualitatively in composition and/or in size or concentration will be discovered at different rates. Second, if subordinate species use resource cues to arrive at preferred resources first, thereby enhancing access, good discoverers should show a greater bias in the discovery of certain resource types and larger/more concentrated resources. Poor discoverers should either show a weaker bias or none at all since, as behavioural dominants, arriving later matters less; their access to preferred resources is almost guaranteed at the recruitment stage.

Materials and methods

Study plots and systems

We collected data on the foraging patterns of woodland ant communities on five plots in Arizona in August–September of 2004 and six plots in Texas in May–June 2005. We sampled during the seasonal peaks of ant activity in each location. Texas plots were located at the Brackenridge Field Lab (three plots: ~ 30° 17′N, ~ 97° 46′W, elevation ~ 145 m) and at the Stengl ‘Lost Pines’ Biological Station (three plots: ~ 30° 04′N, ~ 97° 10′W, elevation ~ 140 m). Plots at Brackenridge were characterised by sugarberry (Celtis laevigata), Ashe’s juniper (Juniperus ashei), and cedar elm (Ulmus crassifolia). The Stengl plots were dominated by varying mixtures of blackjack oak (Quercus marilandica) and loblolly pine (Pinus taeda). The Arizona plots were located in the Chiricahua Mountains of Arizona, in mixed forests containing Chihuahuan pine (Pinus leiophylla var. chihuahuana), gray oak (Quercus grisea), and alligator juniper (Juniperus deppeana). Three plots were located on the eastern side of the range, near Portal (~ 31° 54′N, ~ 109° 14′W, elevation ~ 1700 m), and
two plots were established on the western side, on the El Coronado Ranch near Pearce (~31°51’N, ~109°22’W, elevation ~1700 m).

Based on species observations at baits and from pitfall traps, the two communities were equally rich, with a mean of 21 species in Arizona (range = 20–22) and 22 species in Texas (range = 17–27) (t = 0.5, d.f. = 5.3, P = 0.6; corrected for unequal variance). There was extensive overlap at the genus level, but limited overlap at the species level. Even though predatory genera such as Ponera and Neivamyrmex were observed in pitfall traps and thus contributed to species richness, the majority of the ants observed at baits belonged to omnivorous, ground-nesting species. Finally, although we initially intended to study native species, we also frequently observed Solenopsis invicta, the red imported fire ant, in Texas plots.

**Experimental design**

Each plot measured 50 m x 50 m and was divided into 25 evenly spaced stations located 10 m apart. Baiting trials took place from 09.00 to 19.00 hours in Texas and from 07.30 to 17.30 hours in Arizona during peak activity.

We evaluated the discovery of two bait types representative of those exploited by ants in nature: pure clover honey diluted in water and freezer-killed crickets (Fluker’s Cricket Farm, Inc., Port Allen, Louisiana). Two levels were used: 20% and 80% honey (approx. 8% fructose and 6% glucose in the 20% solution and 31% fructose and 25% glucose in the 80% solution) and small (mean = 0.053 g) and large (mean = 0.36 g) crickets. The sugars found in clover honey, glucose, and fructose are the main components of the honeydew and nectars exploited in natural communities (Blüthgen & Fiedler, 2004; Woodring et al., 2004) and the concentrations we used fall towards the ends of the spectrum found in nature (Blüthgen & Fiedler, 2004). The crickets were representative of the proteinaceous resources frequently exploited by ants. In using these sizes and concentrations, we were attempting to generate a large gap in the quantity of a given resource type so as to maximise the likelihood of seeing a difference.

We applied bait conditions in pairs. On a given day, all stations on a plot received a single bait type; half received the low level treatment and half the high level treatment in an alternating pattern. The following day we used the same bait type but we switched treatment levels. Overall, each station experienced each bait (type + level) once for a total of four sampling periods on each plot. Sampling of a given plot was always conducted at the same time of day. We allowed at least 1 day to pass between sampling pairs in order to minimise any effects of ant entrainment. We randomised the order of bait types that plots experienced.

At the beginning of the sampling period, we placed a clean bait card of laminated plastic measuring 9 cm in diameter on the ground near the survey flag. The designated bait (type and level) was placed in the centre of the card using forceps to minimise human-related odour. For crickets, this consisted of either a single large cricket or a single small cricket. For the honey bait, a single 1 cm³ piece of unscented cellulose sponge soaked in the appropriate solution was used; it contained approximately 0.7 ml of liquid. We observed the bait until it was discovered or until 1 h had passed, noting both the time to discovery as well as the discoverer’s identity. A maximum of three neighbouring baits were observed at any given time.

Discovery was defined as the time at which an ant made physical contact with the food item. The ant was aspirated off the resource immediately, either into 70% ethanol for later identification at the University of Utah or into a holding vial until the end of the sampling session when it was released off-site. In a minor number of cases, the discoverer escaped collection. However, because we removed the discoverer and the bait immediately after its discovery, the effects of recruitment and resource supplementation on subsequent sampling periods should have been limited. Our estimates of discovery time should directly estimate pre-contact assessment of resource size and type by ant species, given that we closely observed baits for discovery and removed resources and discoverers immediately following discovery.

We measured temperature and relative humidity every 5 min at the centre of each plot using a HOBO H8 Pro Series logger (Onset Computer Corp., Bourne, Massachusetts) and used the values to calculate water vapour pressure deficit at the time of discovery (Lighton & Feener, 1989). Vapour pressure deficit is a proxy for ant desiccation risk (Lighton & Feener, 1989; Kaspari, 1993) and affects ant activity.

**Data analysis**

We performed all statistical analyses in R 2.9.1 (R Development Core Team, 2009). We examined discovery time data using Cox proportional hazards (CPH) survival models (Cox & Oakes, 1984). Although these models were originally developed to estimate risks of patient survival in medical studies, they are equally applicable in ecological analyses in which time-to-event data are collected (Muenchow, 1986) (e.g. discovered bait = ‘dead’ bait). In the output of CPH models, the value of the coefficient associated with each covariate conveys how much the covariate affects the hazard or risk of the time-to-event above the baseline hazard rate. In the context of resource discovery, positive coefficients are associated with faster discovery times (increased risk of bait ‘death’) and negative coefficients signify slower discovery times (decreased risk of bait ‘death’). In all models, the P-values for multiple comparisons were adjusted using the false discovery rate method (q* = 0.05) (Benjamini & Hochberg, 1995).

**Between community dynamics.** We compared overall discovery times between the two communities, Texas versus Arizona, in order to determine if overall discovery dynamics were similar between the two communities before beginning our more focused analyses. We used a CPH model in which state was a factor. As observations were repeated four times at each station, sampling station was treated as a random effect that we accounted for using ‘frailty’ (Therneau et al., 2003). The number of discovered and undiscovered baits across communities was compared using a χ² test.
Are different resources discovered at different rates? In order to examine the evidence for directed discovery within each community, we performed separate statistical analyses for Texas and Arizona. In these models, we included plot, sampling date, bait level nested in bait type, and vapour pressure deficit. Plot and vapour pressure deficit were included to account for temporal and spatial variation in ant activity. Sampling date accounted for the potential effect of prior experience encountering food at the stations, although we attempted to minimise such an effect with our methodological approach of staggered sampling and immediate removal of baits and discoverers. The cluster function was used to account for random effects associated with repeated sampling at the stations (Therneau, 2009). We selected the most parsimonious model describing the data using a stepwise backward comparison of the log likelihood of the models. The models were specifically structured to test the research questions specified above.

Are there species-specific differences in resource discovery? Species differences in resource discovery were examined for each community using a Poisson-distributed generalised linear model. The response variable was the number of discoveries and the model terms were species, bait type, and bait size. We only included species with more than 10 discoveries in the analysis. As we were particularly interested in the interaction between species and discovery of different resource types, we began with a model that included the three-way interaction between species and discovery of different resource types, and the model terms were species, bait type, and bait size. Additionally, the model terms were species, bait type, and bait size. We report deviance as it reflects the contribution of the selected using a stepwise backward comparison of the variance associated with repeated sampling at the stations (Therneau, 2009). We selected the most parsimonious model describing the data using a stepwise backward comparison of the log likelihood of the models. The models were specifically structured to test the research questions specified above.

Results

Between community dynamics

Resource discovery was 10 times faster in Texas than in Arizona (coefficient = 2.2, d.f. = 1, P < 0.001). The median discovery time for baits in Texas was 3.4 min (95% CI = 3–4 min) whereas it was 40 min in Arizona (95% CI = 32–46 min). Additionally, significantly more baits were discovered within 1 h in Texas than in Arizona: 95% (586/615) versus 63% (320/508) (χ² = 239, d.f. = 1, P < 0.001).

Are different resources discovered at different rates?

Ants discriminated between different types of resources during the discovery phase of foraging. Furthermore, despite large differences in discovery rate between the communities, the pattern of discrimination was nonetheless similar between the two. In Texas, ants discovered crickets more quickly than honey (coefficient = 0.29, z = 3.8, n = 615, P < 0.001) (Fig. 1a). Crickets were discovered in 3 min on average (95% CI = 2.3–3.1 min) whereas honey was discovered in 4 min (95% CI = 3.8–5 min). The trend was the same in Arizona (coefficient = 0.23, n = 508, z = 2.2, P = 0.02) (Fig. 1b); crickets were found in 33 min on average (95% CI = 27–44 min) whereas honey took 47 min (95% CI = 34–65 min) to be discovered. In contrast, resources of different sizes (crickets) or concentrations (honey) were discovered equally quickly in...
Are there species-specific differences in resource discovery?

Although foragers in general are capable of distinguishing between resource types, species did not bias discovery towards preferred resources. Six species in Texas and six species in Arizona had more than 10 observed discoveries and were included in the analysis. In both communities, species varied in discovery ability, as indicated by the numbers of baits discovered by each (Fig. 2). However, there was no interaction between species identity and resource type or size in either community, indicating that discovery ability did not have an impact on the type or size of resources likely to be discovered (Fig. 2). We also did not observe differences in the overall number of discoveries of either food types (TX: deviance = 0.38, d.f. = 1, P = 0.5; AZ: deviance = 0.004, d.f. = 1, P = 0.9) or sizes (TX: deviance = 0.01, d.f. = 1, P = 0.9; AZ: deviance = 3.5, d.f. = 1, P = 0.1). The invasive species, Solenopsis invicta, a clear behavioural dominant in the Texas ant community (J. M. C. Pearce-Duvet, pers. obs.), was not a particularly good discoverer in the plots where it occurred, ranking fourth in the total number of resources discovered first (Fig. 2).

Discussion

Ant species can distinguish between different resources (Abrams, 1975; Savolainen, 1991; Sanders & Gordon, 2000; 2003; Kay, 2002, 2004; Bihn et al., 2008; Kaspari et al., 2009), although resource assessment was only known to take place after contact with the food item (de Biseau & Pasteels, 1994; Detrain & Deneubourg, 1997; Robson & Traniello, 1998; Mailleux et al., 2000; Lenoir, 2002; Cassill, 2003). This study is the first to address whether ants can detect food characteristics prior to contact and whether such food detection influences exploitative competition between species. Our evidence is mixed, suggesting that ants do detect resources during the discovery process but that this ability does not bias species-specific patterns of discovery.

Individual foragers can distinguish between resources prior to physical contact with them, as indicated by the faster discovery of protein versus sugar baits. This result was consistent across both communities that we sampled, even though they had very different rates of overall discovery and thus presumably different intensities of resource exploitation. The fact that crickets were found more quickly than honey speaks to the general trend that nitrogen-rich resources are more valued than carbohydrate-rich resources (Kay, 2002, 2004; Bihn et al., 2008; Ness et al., 2009). Although we did not test the detection mechanism being used, previous evidence from predatory and omnivorous species suggests that olfaction, rather than vision, is the primary tool used to find food resources (Schatz et al., 1997, 2003; Schatz & Wcislo, 1999; Wolf & Wehner, 2000; Dejean et al., 2001; Durou et al., 2001).

Given that discovery was biased in both communities, each composed of a mean of 21 species, our results suggest that resource detection is more widespread than previously thought. Although, as mentioned above, it has been identified in predatory ants, its relevance for ants with a generalised diet was less clear. The two examples of sensory-directed discovery in omnivorous species come from ants living in specialised circumstances, such as inhabiting resource-depauperate deserts (Wolf & Wehner, 2000) or foraging on temporally and spatially predictable prey (Schatz et al., 2003; Schatz & Hossaert-McKee, 2003). In contrast, the species we studied are generalist omnivores found in woodland habitats, with a more abundant but varied and unpredictable resource base. Our work therefore suggests that resource detection is an important component of ant foraging ecology in general.
In contrast, ants did not find bigger or more concentrated resources faster. This can be interpreted two ways. First, it is possible that resource type matters more to a foraging ant than does resource level; for instance, a cricket may be a more valuable resource, whether big or small. Second, it may be that ants can distinguish gross differences in resource type but that their sensory abilities are not refined enough to distinguish different quantities of a given type without being in close range or direct contact.

It has been previously suggested that detection only operates when ants are within proximity of the resource (Drelle, 1998; Corbara & Dejean, 2000; Orivel et al., 2000; Wolf & Wehner, 2000; Schatz et al., 2003). In predaceous species, foragers show a detection radius between a few millimetres to a few centimetres (Schatz et al., 1997; Orivel et al., 2000). In this case, exploitative competition for resources would remain largely framed by undirected strategies that increase a scout’s possibility of ‘bumping’ into a resource. As a result, future work should focus on characterising the parameters of ant search paths, such as the interspecific variability in speed, turning angles, and locomotor biomechanics, in the context of discovery.

Although we hypothesised that, because behavioural dominants will monopolise preferred resources (Sanders & Gordon, 2003), it would be advantageous for fast subordinates to use resource detection to bias their discovery towards preferred resources, we found no support for this idea. Detection is clearly occurring, but it does not appear to bias discovery within species. In particular, ant species who are good discoverers do not arrive first more frequently at more valued baits, and thus detection is not a means by which they gain access to contested resources.

Instead, discovery may be a process by which colonies, using scouts, tailor their recruitment response to valued resources for maximal harvest. Scouts assess resource desirability and quantity upon encountering food items (Fourcassié & Traniello, 1993; de Biseau & Pasteels, 1994; Robson & Traniello, 1998; Mailleux et al., 2000; Lenoir, 2002; Cassill, 2003). If quality is low, scouts will continue searching (de Biseau & Pasteels, 1994). If the scout returns to the nest, the rapidity and intensity of the recruitment response depends on its communication of resource type and/or size given the current state of the foraging environment, known only at the colony level (de Biseau & Pasteels, 1994; Detrain & Deneubourg, 1997; Robson & Traniello, 1998; Lenoir, 2002; Cassill, 2003; Le Breton & Fourcassié, 2004). By having scouts that arrive at all resources more quickly, subordinate species are presumably able to more rapidly identify and initiate a recruitment response to valued resources. Consequently, future work should focus on disentangling the potential interaction between relative resource quality, discovery, and harvest.

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