

Fast food in ant communities: how competing species find resources

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Abstract An understanding of foraging behavior is crucial to understanding higher level community dynamics; in particular, there is a lack of information about how different species discover food resources. We examined the effect of forager number and forager discovery capacity on food discovery in two disparate temperate ant communities, located in Texas and Arizona. We defined forager discovery capacity as the per capita rate of resource discovery, or how quickly individual ants arrived at resources. In general, resources were discovered more quickly when more foragers were present; this was true both within communities, where species identity was ignored, as well as within species. This pattern suggests that resource discovery is a matter of random processes, with ants essentially bumping into resources at a rate mediated by their abundance. In contrast, species that were better discoverers, as defined by the proportion of resources discovered first, did not have higher numbers of mean foragers. Instead, both mean forager number and mean forager discovery capacity determined discovery success. The Texas species used both forager number and capacity, whereas the Arizona species used only forager capacity. There was a negative correlation between a species' prevalence in the environment and the discovery capacity of its foragers, suggesting that a given

species cannot exploit both high numbers and high discovery capacity as a strategy. These results highlight that while forager number is crucial to determining time to discovery at the community level and within species, individual forager characteristics influence the outcome of exploitative competition in ant communities.

Keywords Community ecology · Forager density · Forager discovery capacity · Formicidae · Resource discovery

Introduction

Foraging for food is a necessity faced by almost all animals, and differences in how species accomplish this task influence niche segregation (Emlen 1966; MacArthur and Pianka 1966), contribute to species coexistence (e.g., Brown and Davidson 1977; Pulliam 1985; Kotler and Brown 1988), and stabilize food webs (Kondoh 2003; Beckerman et al. 2006). Consequently, understanding foraging behavior is crucial to understanding higher level processes (Werner 1992; Beckerman et al. 2010), especially when considering species coexistence in communities of generalists that use the same resource base (Tilman 1982; Kneitel and Chase 2004). In general, much more is known about how species differ in efficiency during resource harvest (Brown 1989; Ziv et al. 1993; Brown et al. 1994) as opposed to resource discovery (Westoby et al. 2002), even though resource discovery is the first step in the foraging process and, as such, may reveal more about the intensity of competition and its influence on species interactions (Vincent et al. 1996; Calcagno et al. 2006; Adler et al. 2007).

Ant communities represent an ideal study system for examining the dynamics of foraging behavior, as most

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species compete fiercely for the same pool of plant and insect matter (Pontin 1963; Brown et al. 1979; Davidson et al. 1984; Davidson 1985; Davidson et al. 1985; Hölldobler and Wilson 1990), and their behavior is directly observable. A trade-off between the ability to arrive at resources first and the ability to control them during harvest has been proposed as a mechanism for species coexistence (Vepsäläinen and Pisarski 1982; Fellers 1987; Morrison 1996; Davidson 1998; Holway 1999; LeBrun and Feener 2007; Feener et al. 2008). As is true in other systems, past work has focused almost exclusively on resource dominance (Fellers 1987; Savolainen and Vepsäläinen 1988; Savolainen et al. 1989; Andersen 1992; Morrison 1996; Andersen 1997; Cerdá et al. 1998b; LeBrun 2005), to the detriment of understanding how food is found.

In ants, as in other generalist foragers, the challenge is to locate diverse food resources that are both unpredictably located and renewed (Harkness and Maroudas 1985; Jones et al. 2001), and it appears discovery is not directed by resource signals (Pearce-Duvet and Feener 2010). As social insects, they can enhance the probability of encountering food indirectly via both the number of foragers employed as well as through those foragers' individual traits. It has long been assumed that resource discovery relies on species-specific forager number (Johnson et al. 1987; Jaffe and Deneubourg 1992; Kaspari 1993b; Dechaume-Moncharmont et al. 2005; Avgar et al. 2008). In particular, ant colonies are thought to contain a finite number of foragers that are divided into scouts which search independently for food and recruits which are summoned to collect or fight for food, and this mechanistic trade-off is thought to underlie species co-existence (Johnson et al. 1987; Feener 2000). Yet, the relationship between forager number and resource discovery has not been examined explicitly. It is also unknown if scout number is a species-specific trait that accounts for discovery ability or if individual foragers of certain species have a greater capacity for discovery.

How abiotic factors affect resource discovery is also largely uncharacterized, although their influence on resource dominance is well described (Cerdá et al. 1997, 1998a, b; Bestelmeyer 2000; Santini et al. 2007; Lessard et al. 2009). In North American and Mediterranean ant communities, many species have been found to trade off between behavioral dominance and thermal tolerance, with behavioral subordinates being more likely to forage during thermally extreme times (Cerdá et al. 1997, 1998a, b; Lessard et al. 2009; Wiescher et al. 2011) (although see Santini et al. 2007). These results generate a hypothesis for discovery dynamics: good discoverers, which are often behavioral subordinates, should show greater abiotic tolerance.

This study examines the simple but unexplored question of how ants find food, using observations in two temperate woodland communities. First, we examine the ability of

scout number to explain discovery dynamics within local ant communities. Second, we ascertain whether differences in discovery ability among species could be explained by scout number, thus making community discovery dynamics an emergent property of the species' traits, or whether individual foragers have different discovery capacities. Third, we consider the effect of abiotic factors, such as time of day and desiccation risk, on discovery at the community and species level.

Materials and methods

Study sites and systems

In the summer of 2005, we collected data on resource discovery at six plots in Texas and five plots in Arizona. Sampling took place during the peaks of ant community activity in each location: May–June in Texas and July–August in Arizona. Three of the Texas plots were located at the Brackenridge Field Lab (latitude $\sim 30^{\circ}17'N$, longitude $\sim 97^{\circ}46'W$, elevation ~ 145 m), and three were located at the Stengl “Lost Pines” Biological Station (latitude $\sim 30^{\circ}04'N$, longitude $\sim 97^{\circ}10'W$, elevation ~ 140 m). The Brackenridge plots were characterized by sugarberry (*Celtis laevigata*), Ashe's juniper (*Juniperus ashei*), and cedar elm (*Ulmus crassifolia*), while the Stengl plots were dominated by varying mixtures of blackjack oak (*Quercus marilandica*) and loblolly pine (*Pinus taeda*). The Arizona plots were located in mixed forests containing Chihuahuan pine (*Pinus leiophylla* var. *chihuahuana*), grey oak (*Quercus grisea*), and alligator juniper (*Juniperus deppeana*); three plots were located on the eastern side of the Chiricahua Mountains, near Portal (latitude $\sim 31^{\circ}54'N$, longitude $\sim 109^{\circ}14'W$, elevation $\sim 1,700$ m), and two plots were established on the western side of the range, on the El Coronado Ranch near Pearce (latitude $\sim 31^{\circ}51'N$, longitude $\sim 109^{\circ}22'W$, elevation $\sim 1,700$ m). Based on species observations at baits and from pitfall traps, Texas and Arizona communities were equivalently rich, with a mean of 21 species in Arizona (range = 20–22) and 22 species in Texas (range = 17–27) ($t = 0.5$, $df = 5.3$, $P = 0.6$; corrected for unequal variance). There was extensive genus but limited species overlap.

Experimental design

Each plot measured 50 m by 50 m and was divided into 25 evenly spaced stations. Stations were located 10 m apart and individually marked by a survey flag. In order to measure forager density, we placed a circular hoop encompassing 0.25 m^2 at each station on all plots and visually scanned the area inside the hoop for 5 min. The identity and the

number of ants present in the hoop were recorded; ants on recruitment trails or which were clearly returning with food were not counted. We felt confident about accurately estimating ant presence, as visual surveys provide reliable estimates of ant presence when leaf litter is limited (Andersen 1991). Also, we performed a validation trial in which we visually surveyed ants using the hoop and then collected and filtered the underlying litter using a Berlese funnel (4 samples per site). Both the presence and number of ants were positively correlated between the visual survey and litter sample (presence: GLM binomial, $z = 5.4$, $df = 130$, $P < 0.001$; number: Pearson correlation; $r = 0.54$, $df = 42$, $P < 0.001$).

At the end of the 5 min, we placed a clean bait card of laminated plastic measuring 9 cm in diameter on the ground in the center of the hoop. A large piece of a hot dog frank (Bar-S Foods; approx. 3 g) was placed in the center of the card. We used hot dog franks, as they contain a mixture of nutrients that are attractive to ants (11:3:4 mass ratio of lipids:carbohydrates:protein; 33 mg sodium/3 g), and thus tried to limit bias due to bait type. However, it is important to point out that bait type and quality do not appear to bias species-specific resource discovery (Pearce-Duvet and Feener 2010). We observed the bait until it was discovered or until 1 h had passed, measuring the time between bait placement and bait discovery in addition to the identity of the discoverer. Discovery was defined as the time at which the ant made physical contact with the food item. We performed hoop trials twice at each station, once during the day and once at night, during periods when ant species were most active, which differed for each community. Trials took place between 900 and 1,700 h (day) and 2,100–100 h (night) local time in Texas, and between 1,300 and 1,700 h (day) and 2,000–100 h (night) local time in Arizona.

We measured temperature and relative humidity every five minutes at the center of each plot by a HOBO H8 Pro Series logger (Onset Computer Corp., Bourne, MA, USA). Water vapor pressure deficit values (VPD) were calculated from the recorded temperature (T) and relative humidity (RH) measurements (Weast 1973; Lighton and Feener 1989), where $VP = 512 + 73.662T - 0.72645T^2 + 0.079616T^3$ and VPD (kPa) = $(VP - (VP \times RH)/100)$. Vapor pressure deficit is a proxy for ant desiccation risk (Lighton and Feener 1989; Kaspari 1993a).

Statistical analyses

All statistical analyses were performed in R 2.5 (R Development Core Team 2007). We controlled for multiple comparisons using the false discovery rate correction employing $q^* = 0.05$ (Benjamini and Hochberg 1995). This approach controls the proportion of erroneously rejected hypotheses as opposed to the possibility of a single false

rejection, thus resulting in more power than in traditional multiple comparison methods (Garcia 2003).

We examined overall discovery dynamics in each community using survival analysis, specifically the Cox proportional hazards approach (Cox and Oakes 1984; Therneau 2007) (R: survival package). Although these CPH 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; Pearce-Duvet and Feener 2010) (e.g., discovered bait = “dead” bait). In the output of such 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 relative to the baseline hazard rate. In this context, positive coefficients signify faster discovery times and negative coefficients signify slower discovery times. Survivorship models also account for the potential problem created by censorship of data—the discovery time for a bait that remains undiscovered at the end of the hour or for a species present in the hoop but that was not the first discoverer—by including a dependent variable for discovery status, 0 (no discovery) or 1 (discovery).

We ran separate survivorship models for Texas and for Arizona and included forager number, time (day vs. night), VPD, and site as covariates. Time to discovery was the dependent variable. Although forager number was the main term of interest, the others were included to control for their effects on the results. The number of ants in the hoops was transformed by $\log(\text{number of ants} + 1)$ in order to linearize the values with respect to discovery time. In order to account for repeated sampling (day–night) at the individual stations, “frailty” was incorporated into all models (Therneau et al. 2003). The most parsimonious model describing the data was selected using backwards elimination of terms.

We then performed a series of analyses to further clarify species-specific aspects of resource discovery. First, survival models were run for each species. The terms included were forager number, time, and VPD; the best-fit model was selected by backwards elimination of terms. We transformed forager number by $\log(\text{number of ants} + 1)$ as before. Species present in the hoop that did not discover the bait first were assigned a discovery status of 0 and the discovery time x of the discovering species in that hoop; this indicated to the analysis that that species had not discovered the bait as of discovery time x , at which point the observation ended. The magnitude of the coefficient relating forager number to discovery time provided an estimate of the discovery capacity of individual foragers, or the per capita rate of discovery, for that species. Only species for which more than ten discoveries were obtained were used; below this set point, confidence intervals for model coefficients could not be reliably calculated. These species-specific survival models clarified three aspects of resource

discovery. They indicated whether forager number significantly affected discovery time at the species level. They also revealed the individual forager capacity for that species, as reflected in the per capita coefficient, which is an indication of how efficient an individual ant is at discovering a resource. Finally, they indicated how desiccation risk (as reflected by vapor pressure deficit) and time of day acted on resource discovery in a species-specific way.

Second, we related species-specific differences in mean forager number and discovery capacity (the per capita coefficient) to overall discovery ability and to each other. Mean forager number was the mean number of ants present in the hoop belonging to a particular species. Discovery capacity was, as stated above, how good an individual forager of a given species was at finding food. We defined discovery ability by counting the number of successful discoveries relative to the number of “failed” discoveries; i.e., when a species was present in the survey hoop but did not discover the bait first. A high number of successful discoveries relative to failures signified a consistent ability to locate resources before other species. This method is similar to that used in a past work assessing discovery ability, in which species presence in the bait area prior to discovery trials was assessed using 48-h pitfall trap sampling (LeBrun and Feener 2007). However, by assessing species presence immediately prior to bait placement using our 5-min surveys, we were able to more precisely capture discovery dynamics.

The relationship between mean forager number, forager discovery capacity, and overall discovery ability was then examined in each community. First, we tested if mean forager number and forager discovery capacity were significant predictors of discovery ability using a generalized linear model with a binomial distribution. We found the best-fit model via backwards elimination of terms. Second, in order to determine if a trade-off existed between mean forager number and forager discovery capacity, we performed a Pearson correlational analysis. Third, because mean forager number only reflects forager number when the species is present in a survey hoop, another metric of forager

abundance—the number of hoops in which a species occurred—was also examined. This estimate of species prevalence reflects the number of foragers present at the broader community level instead of the mean number counted only when the forager was locally present in the hoop.

Results

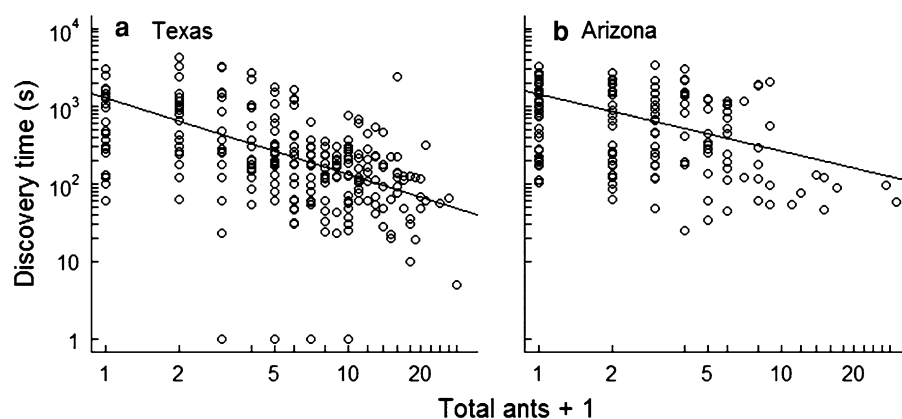
Community-wide patterns of resource discovery

Texas baits had a mean discovery time of 3.5 min (95% CI = 3.0–4.2), with 97.6% of the baits discovered (293 out of 300). In Arizona, the mean discovery time was 19.3 min (95% CI = 16.9–23.6), with 83.6% of the baits discovered (209 out of 250). There was a significant effect of forager number on discovery time in both communities (Fig. 1). In Texas, baits were discovered more quickly when more foragers were present across all sites (coefficient = 1.1, $\chi^2 = 88.2$, $n = 300$, $P < 0.001$), with forager number explaining 53% of the variation in discovery time. The best-fit model included forager number, VPD, site, and an interaction between VPD and site. The relationship between forager number and discovery held true in Arizona for three of the five sites (coefficient = 0.79, $\chi^2 = 6.8$, $n = 50$, $P = 0.009$; coefficient = 0.58, $\chi^2 = 7.0$, $n = 50$, $P = 0.008$; coefficient = 1.45, $\chi^2 = 25.1$, $n = 50$, $P < 0.001$); two sites showed no relationship between forager number and discovery ($\chi^2 = 1.7$, $n = 50$, $P = 0.2$; $\chi^2 = 0.1$, $n = 50$, $P = 0.7$). As such, the best-fit model included an interaction between forager number and site; there was also a significant interaction between site and time. Forager number explained 43% of the variation in discovery time in the Arizona community.

Species differences in resource discovery

Sufficient data for the species-specific survival models were obtained for seven species in Texas and seven species in

Fig. 1 Relationship between the total number of ants in a survey and the time to discovery of a bait placed immediately subsequent to the survey in ant communities in **a** Texas and **b** Arizona. Note the log scales used on both axes in the panels. Higher numbers of ants significantly decrease time to discovery in both communities, but more of the variation in discovery time was explained by forager number in Texas (53%) than in Arizona (43%)



Arizona. Although there were many more species observed at our baits (25 species in Texas and 23 species in Arizona), the seven species examined in each community were responsible for the majority of discoveries in each location: 88% (270/306) in Texas and 66% (148/224) in Arizona.

Forager number was a significant predictor of discovery time in all of the species-specific models, with the exception of *Camponotus vicinus* in Arizona (Table 1). In all of the significant cases, forager number significantly increased how quickly a species discovered the resource. The lack of a relationship in *C. vicinus* may relate to its larger body size and thus its potential ability to traverse longer foraging distances; the scale of the visual surveys (0.25 m²) may have been too small to detect a relationship with forager density (although this was not an issue for the other *Camponotus* species observed). Alternatively, discovery in this species may rely on other mechanisms, such as detection of resource-based cues.

When forager number and forager discovery capacity were related to species differences in overall discovery ability (proportion of baits discovered first), forager discovery capacity appeared to be the more important determinant of discovery success, whereas mean forager number played a more minor role (Table 2). In Texas, there was a significant interaction between mean forager number and the per capita coefficient in predicting species discovery success

($z = -3.1, df = 6, P = 0.002$). This pattern was driven by the fact that two discovery mechanisms are operating in Texas but are differentially utilized by species (Fig. 2a): *Aphaenogaster texana* and *Camponotus americanus* appear to rely on a few, highly capable foragers while *Pheidole dentata* has many less capable foragers. In Arizona, in contrast, species differences in discovery success were related entirely to individual forager discovery capacity ($z = 3.5, df = 5, P = 0.0004$) (Fig. 2b). There was no correlation between forager number and forager discovery capacity in either community (TX: $t = -0.2, df = 5, P = 0.8$; AZ: $t = 1.7, df = 4, P = 0.2$) (Fig. 2).

Species prevalence did not correlate with mean forager number in either Texas or Arizona (TX: $t = 0.9, df = 5, P = 0.41$; AZ: $t = -0.7, df = 4, P = 0.49$) (Fig. 3a, c). However, there was a significant negative correlation between a species' occurrence and its per capita coefficient in both Texas and Arizona (TX: $t = -2.5, df = 5, P = 0.05$; AZ: $t = -2.9, df = 4, P = 0.04$) (Fig. 3b, d). The relationship in Texas remained even when the statistical outlier *P. dentata* (Grubbs' outlier test $z = 2.14, n = 7, P = 0.01$) was removed ($t = -5.6, df = 4, P = 0.005$). Although this species was an extreme outlier in terms of its inordinately high number of occurrences, it still followed the trend set by the other species and therefore did not have high leverage (Fig. 3b).

Table 1 Summary of species-specific models of time to discovery in Texas and Arizona ant communities

Species	Best-fit model	Foragers <i>P</i>	VPD		Interaction	
			Coefficient	<i>P</i>	Coefficient	<i>P</i>
Texas						
<i>Pheidole dentata</i>	Foragers + VPD + time + VPD × time	<0.01			1.53	0.02
<i>Aphaenogaster texana</i>	Foragers + VPD	<0.01	1.89	0.01		
<i>Monomorium minimum</i>	Foragers + VPD + foragers × VPD				-1.17	0.04
<i>Camponotus americanus</i>	Foragers	<0.01				
<i>Paratrechina terriicola</i>	Foragers + VPD	<0.01	-2.51	0.07		
<i>Pheidole metallescens</i>	Foragers	<0.01				
<i>Solenopsis molesta</i>	Foragers	<0.01				
Arizona						
<i>Dorymyrmex insanus</i>	Foragers	<0.01				
<i>Monomorium emersoni</i>	Foragers + VPD	<0.01	1.31	<0.01		
<i>Pheidole diversipilosa</i>	Foragers	<0.01				
<i>Pheidole hyatti</i>	Foragers	<0.01				
<i>Camponotus vicinus</i>	VPD + time + VPD × time	0.66			5.10	<0.01
<i>Camponotus festinatus</i>	Foragers + VPD	<0.01	-1.55	0.07		
<i>Myrmica striolagaster</i>	Foragers + VPD + foragers × VPD				1.61	<0.01

The structure of the best-fit model for each species is provided. Statistical values for the models' factors are provided: forager number and/or VPD were often main effects, while time was only present in interactions. The *P* value is given for forager number, and both the coefficient and *P* value are given for VPD. The coefficient for forager number (otherwise known as the per capita coefficient of forager discovery or forager discovery capacity) is listed in Table 2. If the terms are involved in an interaction, the main effects are not reported; the coefficient and *P* value for the interaction are listed in the last set of columns

Table 2 Proportion discovered and traits related to discovery ability in ant species in Texas and Arizona communities

Species	No. discoveries	No. occurrences	Proportion discovered	Mean foragers	Per capita coefficient
Texas					
<i>Pheidole dentata</i>	186	254	0.73	4.68 ± 0.21	0.99 ± 0.11
<i>Aphaenogaster texana</i>	14	25	0.56	2.9 ± 0.29	4.07 ± 0.56
<i>Monomorium minimum</i>	15	31	0.48	5.64 ± 0.89	3.84 ± 0.85
<i>Camponotus americanus</i>	10	22	0.45	1.94 ± 0.35	3.98 ± 0.69
<i>Paratrechina terricola</i>	16	42	0.38	3.69 ± 0.46	2.38 ± 0.35
<i>Pheidole metallescens</i>	14	38	0.37	3.89 ± 0.48	2.71 ± 0.40
<i>Solenopsis molesta</i>	15	42	0.36	1.71 ± 0.21	1.85 ± 0.42
Arizona					
<i>Dorymyrmex insanus</i>	21	26	0.81	3.1 ± 0.71	2.70 ± 0.32
<i>Monomorium emersoni</i>	21	31	0.68	2.4 ± 0.41	1.81 ± 0.40
<i>Pheidole diversipilosa</i>	30	45	0.67	1.7 ± 0.17	1.99 ± 0.34
<i>Pheidole hyatti</i>	14	21	0.67	3.2 ± 1.38	2.79 ± 0.51
<i>Camponotus vicinus</i>	23	39	0.59	1.8 ± 0.34	NA
<i>Camponotus festinatus</i>	11	21	0.52	1.4 ± 0.23	1.84 ± 0.54
<i>Myrmica striolagaster</i>	28	66	0.42	2 ± 0.17	0.71 ± 0.50

The number of occurrences is the number of hoops in which an ant species was present. Mean foragers is the mean number of ants of that species in the hoop when it was present. The per capita coefficient is how quickly an individual ant of that species was able to arrive at baits, or the forager discovery capacity. Mean forager and per capita coefficient values include the associated standard error

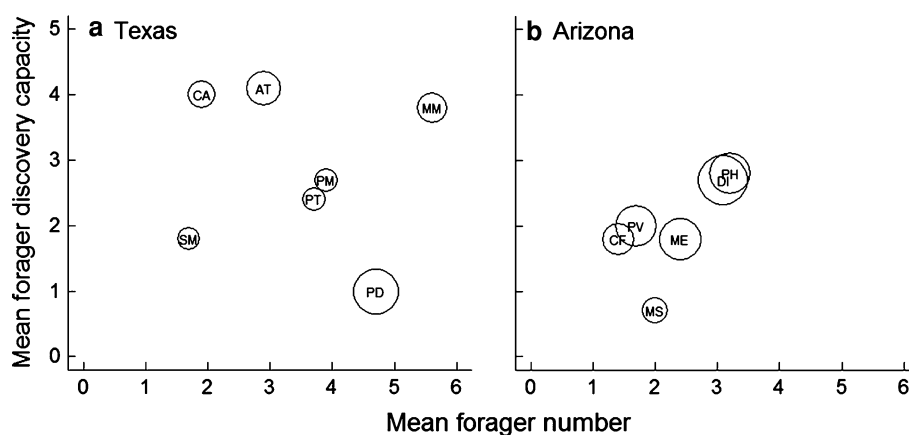


Fig. 2 Relationship between mean forager number, forager discovery capacity, and species discovery ability in **a** Texas and **b** Arizona. Bubble size represents the proportion of successful discoveries achieved by the species. The species abbreviations are as follows: in Texas: AT, *Aphaenogaster texana*; CA, *Camponotus americanus*; MM, *Monomorium minimum*; MA, *Myrmecina americana*; PT, *Paratrechina terricola*;

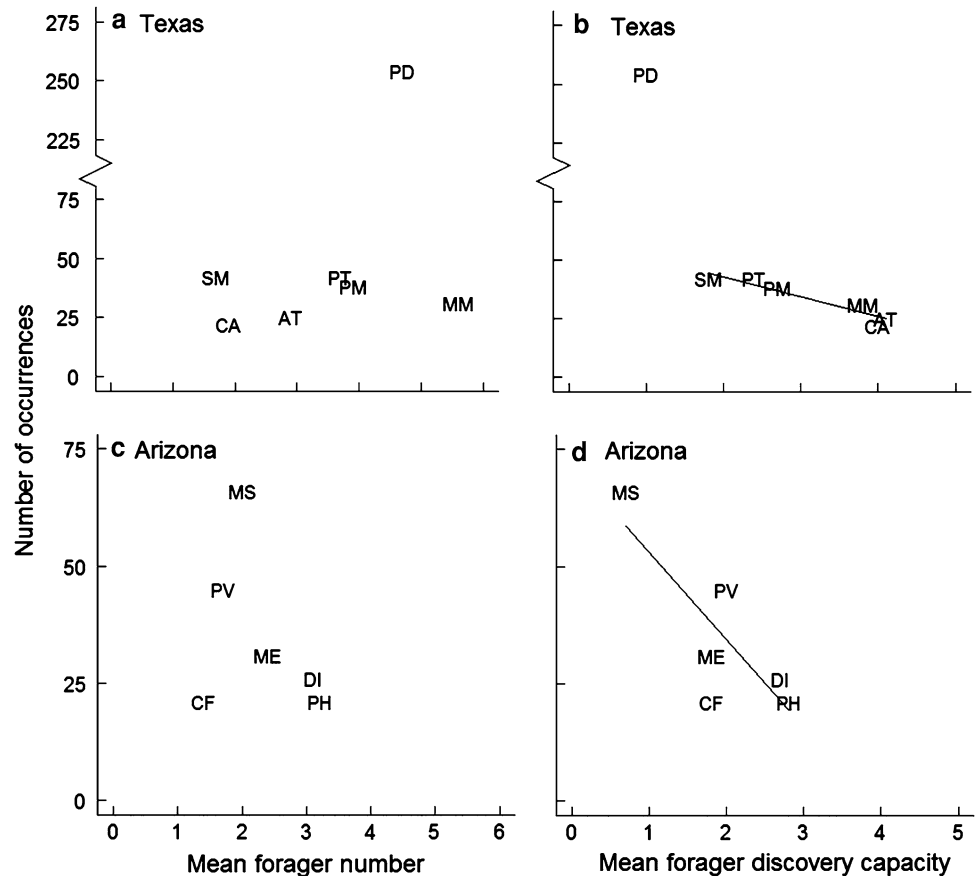
la; PD, *Pheidole dentata*; PF, *Pheidole floridana*; PM, *Pheidole metallescens*; and SM, *Solenopsis molesta*; in Arizona, CF, *Camponotus festinatus*; DI, *Dorymyrmex insanus*; ME, *Monomorium emersoni*; MS, *Myrmica striolagaster*; PV, *Pheidole diversipilosa*; and PH, *Pheidole hyatti*. We found no relationship between a species' mean forager number and its per capita coefficient (forager discovery capacity)

Abiotic effects on resource discovery

The survival analyses also quantified the role of abiotic factors, such as vapor pressure deficit, in partitioning resource discovery (Table 1). Some species appeared to be specialized for more challenging thermal conditions: *A. texana* and *Monomorium minimum* in Texas and *Monomorium emersoni* in Arizona discovered resources more rapidly as vapor pressure deficits increased. In the

case of *M. minimum*, its per capita discovery rate increased in response as well. Per capita discovery was also enhanced by increased vapor pressure deficit for *Myrmica striolagaster*, but, in contrast to *M. minimum*, this species was only observed foraging during the early morning, late afternoon and evening (Pearce-Duvet, personal observation). Thus, it was probably not a true thermophile, but rather responded positively to higher temperatures during overall cool periods.

Fig. 3 The relationship between mean foragers, mean forager discovery capacity, and the number of occurrences of species found in Texas (a–b) and Arizona (c–d). The number of occurrences is the number of times a species was present in a survey, and is a proxy for scout abundance at the community level. Species' names are coded as in Fig. 2. There was no relationship between mean forager number and the number of observations in either Texas (a) or Arizona (c). However, there was a significant negative relationship between a species' per capita coefficient (discovery capacity) and the number of observations of it in both communities (b and d)



Other species appear to be more susceptible to desiccation. Higher vapor pressure deficit slowed discovery time for *Paratrechina terricola* in Texas and *Camponotus festinus* in Arizona. *P. dentata* in Texas and *C. vicinus* in Arizona responded similarly to abiotic conditions: discovery times were lengthened by increasing VPD during the day, whereas increasing VPD speeded up discovery during the night. This is likely because higher vapor pressure deficit at night means ants are experiencing a higher temperature during a normally cooler thermal period, whereas higher VPD during the day signifies greater desiccation risk; vapor pressure deficit and temperature were significantly lower at night than during the day in both communities (repeated measures ANOVA: VPD: $t = 7.9$, $df = 9$, $P < 0.001$; temperature: $t = 12.5$, $df = 9$, $P < 0.001$).

Discussion

Past studies of competition in ecological communities have largely focused on resource dominance, ignoring the first step in the competitive process: how organisms find food. Using ant communities, which have long served as model systems for understanding resource competition, we examine the process of resource discovery in greater detail. In

particular, this study examines the importance of forager number and forager discovery capacity for food discovery in two ant communities. We found that both factors function to frame discovery in different ways and at different scales.

Forager number and resource discovery

Forager number is crucial to discovery dynamics at both the community level and within species. When all ant species were pooled within their respective communities, more ants meant that baits were discovered more quickly. This pattern indicates that forager number is one of the core factors mediating discovery dynamics at the broad scale. Indeed, it explained over 53% of the variation in discovery time in Texas and 43% in Arizona. The number of ants locally present was also significantly correlated with discovery time within species, as revealed in the species-specific survival models. For a given species present in a local area, more individuals meant arriving at the bait faster. Taken together, these findings support the hypothesis that resource discovery is largely a matter of undirected processes, as previously found (Pearce-Duvet and Feener 2010). Omnivorous ants essentially bump into resources at a rate proportional to their abundance, as previously posited

(Schmid-Hempel 1987; Wehner 1987; Adler and Gordon 1992; Roulston and Silverman 2002) but never tested.

Future work aimed at sampling a broader suite of assemblages is clearly needed because our results suggest interesting differences in the discovery dynamics of different communities. The first was in mean discovery time in each community, which may be a proxy for the intensity of exploitative competition therein; discovery was much faster in Texas than in Arizona (AZ:TX survival coefficient = -1.1 , $\chi^2 = 6.8$, $df = 1$, $P = 0.009$). The second was in the relative importance of ant abundance in explaining discovery dynamics. Forager number explained a greater percentage of the variance in discovery time in Texas than in Arizona, and the best-fit model in Arizona demonstrated more ecological complexity, both spatially and temporally, than that in Texas. Since ant abundance is clearly related to discovery dynamics and the abundance of ants supported within a community is determined by primary productivity and mean temperature (Kaspari et al. 2000; Kaspari 2001), it could be useful to compare the relative importance of forager number and forager discovery capacity across productivity and temperature gradients. In fact, there may be communities in which forager discovery capacity entirely determines species differences in resource discovery and forager number is unimportant (Pearce-Duvet, unpublished data). Furthermore, the interaction between forager number and forager behavior may shift at different levels of ant abundance (Adler and Gordon 1992; Gordon 1995).

Ecological and evolutionary aspects of resource discovery

Although forager number determines how quickly a resource is discovered in the broader community and within species, its utility breaks down when examining interspecific competition. Good discoverers were not always the ones with the greatest numbers of foragers. Although some ants—like *Pheidole dentata* in Texas—use large numbers of foragers to arrive at resources first, drawing on the brute power of numbers, other good discoverers in both Texas and Arizona rely on fewer, more efficient scouts. As a result, interspecific competition for resources within communities is dictated mostly by forager discovery capacity, even though discovery time is tightly linked to forager number. This result is intriguing because it suggests the contrasting ecological and evolutionary contributions of forager number and forager discovery capacity to discovery dynamics.

Because forager number and discovery are correlated, it is not immediately apparent why species do not rely on large forager forces for interspecific competition. One possibility is that colony size is limited by evolutionary history; some ant species are found to attain large colony sizes, while other species always remain smaller in number.

The size of the scouting force will intrinsically be limited by the overall size of the colony. However, it is not clear that, even when colony size is variable within a species, it has any influence on discovery ability; in *Formica pratensis*, colony size did not influence the proportion of baits a colony discovered, suggestive of stereotyped species-specific foraging behavior (Jordan and Blüthgen 2007). Since, within species, the number of foragers in a colony is sensitive to ecological factors such as age, resource availability, and environmental conditions (Tschinkel 1988; Hölldobler and Wilson 1990; Gordon 1992) and can thus vary greatly, it may be a less viable target for selection.

Utilizing forager number solely may also make for inefficient foraging. Investment in scouts provides access to small, widely dispersed food items, and is predicted to be advantageous for small-sized colonies (Johnson et al. 1987). However, in larger colonies with more available foragers, allocation should shift towards recruits because they allow access to larger food items unavailable to solitary foragers, and these larger items can quickly amount to a majority of the colony's dietary biomass (Traniello 1983). Indeed, different foraging strategies are associated with different average colony sizes (Beckers et al. 1989). The addition of scouts, in contrast, does not add to the dietary breadth of the colony. Nor is there compensation through an increase in the physical foraging range of the colony. Instead, more scouts simply means more overlap in scout paths and thus greater local coverage of the pre-existing foraging territory (Gordon 1995). As a result, numerically speaking, investing in a recruit should provide a greater energetic return than investing in a scout when sufficient numbers of scouts are already available. If we accept prevalence as a proxy for colony size (Davidson 1998; Holway 1999; Adler et al. 2007), the negative correlation we observed between forager prevalence and forager discovery capacity supports the existence of differences in competitive strategy between large and small colonies. Less prevalent species, or those with smaller colony sizes, have more capable individual foragers, whereas more prevalent species, or those with larger colonies, have less capable foragers, perhaps because they have de-emphasized discovery capacity in favor of the more energetically profitable strategy of dominance.

If there is no advantage to be had in adding more scouts, selective pressure should work to refine the discovery capacity of those foragers available for scouting. Foraging capacity, as an intrinsic property of individual ants, also makes a more feasible target for selection than forager number. The particular pressure that may be acting could be the time costs incurred during foraging, a known foraging constraint in ants (Fewell 1988; Weier and Feener 1995). The foraging process can be divided into three components, outbound travel to the search site, the period of

active searching, and inbound travel to the nest, with the search phase representing the biggest time expense (Weier and Feener 1995). As a result, selection may have favored the evolution of a foraging strategy that minimizes the overall time spent searching, both per ant and summed over all scouts.

This idea contrasts with the assumption implicit in the hypothesis that forager number defines species discovery ability: namely, that scouts could theoretically be interchangeable with recruits. While it has long been recognized that certain traits are affiliated with behavioral dominance [chemical weaponry (Fellers 1987; Davidson 1998), soldier castes (Wilson 1975, 1976, 1978; Morrison 2000), and large body size (Fellers 1987)], the reverse—that similar, albeit more subtle, traits could be linked to superior discovery ability—has not been given much attention. Instead, an investment is being made in the traits that enhance the efficiency of individual ants in performing particular tasks, and it could be a trade-off in traits as opposed to numbers that forms the actual basis for the dominance–discovery trade-off in ant communities.

Although this study does not identify the particular features that may define individual forager capacity, the data both here and elsewhere (Pearce-Duvet and Feener 2010) suggest that resource discovery is undirected: ants run into resources somewhat like Brownian molecules. Furthermore, they suggest that biomechanics are important. First, the most efficient ants in Texas are the larger bodied and/or more gracile species *A. texana* and *C. americanus*. Second, *Monomorium minimum*—given its high forager density (statistically equivalent to *P. dentata*), a moderate per capita rate of discovery (significantly faster than *P. dentata*), and perhaps even a similar search pattern to *P. dentata* (Jones and Phillips 1990)—should have a comparable degree of discovery success, but it does not (Table 2). However, it is also a small ant, and thus may be limited from achieving such success because its size slows its progress through the local environment (Kaspari and Weiser 1999). These trends suggest that relative leg length and velocity will emerge as significant forces shaping scout discovery capacity. Significantly, leg length is one of the traits associated with the discovery success of the invader *Anoplolepis gracilipes* in Pacific island communities (Sarty et al. 2006), and the search patterns of Argentine ants have been linked to their first arrival at resources (Jones and Phillips 1990; Human and Gordon 1996).

Abiotic effects on resource discovery

Although forager density and discovery capacity are seminal to discovery dynamics, they do not exclusively shape competitive niches. Abiotic factors such as temperature and relative humidity also play an important role in resource

discovery. There was mixed evidence for the hypothesis that good discoverers demonstrate tolerance for challenging abiotic conditions. Certain good discoverers are less sensitive to desiccation risk; time to discovery by *A. texana* was enhanced by increasing vapor pressure deficit. However, others are actually detrimentally affected (*P. dentata*) or unaffected (*D. insanus*) by vapor pressure deficit, suggesting that more complex interaction between discovery, dominance, and thermal tolerance. It may be that forested communities of Texas and Arizona experience less overall abiotic pressure in comparison to the communities previously studied (Cerdá et al. 1997, 1998a, b; Santini et al. 2007; Lessard et al. 2009); certainly, trade-off expression within the same community appears to be dependent on environmental context (Wiescher et al. 2011). It may also be that more complex trade-off interactions are taking place. The relative importance of and interactions between multiple, co-occurring trade-offs remains to be studied (LeBrun and Feener 2007).

Conclusions

Although foraging behavior has long been considered key to understanding how communities are composed, the way in which species compete to discover food has largely been ignored. Our findings begin to correct this oversight by suggesting the importance of addressing discovery dynamics, not only in ants but in other systems as well. If discoverers determine the composition of their community, as recent theory indicates (Calcagno et al. 2006; Adler et al. 2007), then the nature of exploitative competition and the strategies being used to compete could have interesting implications for understanding the richness and specific composition of communities. Moreover, although forager number is important in determining how quickly food is discovered, confirming that ants encounter food in an undirected manner, it is not the basis for differences in discovery ability between species, as previously assumed. Instead, species differences in discovery ability are determined by how good the individual foragers of each species are at arriving at resources first, and the individual traits that enhance relative discovery ability in ants, and in other generalist species, should be given more attention. Indeed, they may form the basis for the trade-offs that mediate species coexistence. While many aspects of this research remain to be explored, this work has quantified the way in which some species perform the most basic and necessary of tasks: finding food fast.

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