Original Article

Walking the line: search behavior and foraging success in ant species

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Finding food is one of the most important tasks an animal faces. Although the impact of behavior and morphology on individual foraging success is well characterized, an understanding of the extent of interspecific differences in these traits as well as their influence on resource competition is lacking. Temperate ant communities represent an ideal opportunity for examining how search behavior and morphology affect a species' ability to find food first because ant species demonstrate both a wide range of foraging patterns and intense interspecific competition for food resources. For 10 species across 2 communities, species-specific speed and turning rate were quantified by filming their foraging behavior in nature; we also measured the ratio of leg length to body length of their foragers. Food discovery ability was determined by observing which species found baits first when they were present in the immediate environment. Our results show that foraging patterns are species specific, suggesting that search behavior is an important component of niche separation in ant communities. We also suggest that ant species maximize discovery success at the community level using both behavioral and morphological mechanisms. Good discoverers moved in straighter lines, thereby possibly increasing their chances of finding food, and had longer legs relative to their body size, increasing their efficiency of movement. *Key words:* ant morphology, ant movement, discovery ability, foraging behavior, Formicidae. *[Behav Ecol 22:501–509 (2011)]*

INTRODUCTION

The question of why and how organisms move is one of the most basic concerns in the study of behavior (e.g., Nathan et al. 2008). One of the most important reasons why animals move is to search for food (Stephens and Krebs 1986; Bell 1991); the specifics of how they do so is the subject of a rich theoretical and an empirical literature (Mueller and Fagan 2008). However, the fields addressing Tinbergen's ultimate ("why") and proximate ("how") questions have remained isolated (Nathan 2008; Nathan et al. 2008; Schick et al. 2008). Although the gap is narrowing, movement research often overlooks ecological context (Börger et al. 2008; Holyoak et al. 2008) and ecological studies similarly tend to ignore the relevance of movement patterns in ecological phenomenon (Holden 2006) or focus on population-level dynamics (Bowler and Benton 2005; Holyoak et al. 2008; Schick et al. 2008; Wittemyer et al. 2008). Because competition from other species is an important aspect of the search for food (Ydenberg et al. 1986; Mitchell et al. 1990), it is particularly essential to understand how movement patterns and mechanisms may impact species competitive ability.

Temperate ant communities represent an ideal opportunity for examining individual search patterns within the framework of community ecology because ant species demonstrate both a wide range of foraging patterns that rely on the coordinated behavior of individual foragers and intense interspecific competition for food resources (Hölldobler and Wilson 1990). Most ant species are central-place omnivorous scavengers (Hölldobler and Wilson 1990; Fiedler et al. 2007) and niche variability between species stems particularly from differences in the ability to discover versus dominate resources (Vepsäläinen and Pisarski 1982; Fellers 1987; Morrison 1996; Davidson 1998; Holway 1999; LeBrun and Feener 2007). Because resource discovery is the first rate-limiting step in the subsequent cascade of competitive interactions ending in dominance, it is central to understanding competition overall (Calcagno et al. 2006; Adler et al. 2007). Furthermore, although the behaviors underlying dominance are well elucidated (e.g., chemical interference, deployment of polymorphic castes, and morphological specialization) (Hölldobler and Wilson, 1990), the mechanisms underlying discovery ability in natural communities have not been quantified.

For omnivorous scavengers (and many other organisms as well), resource discovery is about maximizing the chance of running into randomly located and unpredictably renewed food items (Harkness and Maroudas 1985). This major challenge for ant colonies is largely resolved by maximizing individual forager discovery capacity, that is, how quickly an individual forager arrives at resources as opposed to mean forager number (Pearce-Duvet et al. 2011). Individual discovery capacity could be enhanced through 1) the sensory ability to detect food resources (Weseloh 2000; Wolf and Wehner 2000; Schatz et al. 2003), 2) optimized search behavior (Jander 1975; Bell 1991; Gordon 1995), and 3) adapted morphology, such as long legs to run faster (Kaspari and Weiser, 1999). Past research suggests that the sensory perception of food items appears to contribute minimally to resource discovery by ants (Pearce-Duvet and Feener 2010; Pearce-Duvet et al. 2011), likely operating only when an individual is within close range of the resource (Corbara and Dejean 2000; Orivel et al. 2000; Pearce-Duvet and Feener 2010) or in highly specialized species (Weseloh 2000; Wolf and Wehner 2000; Schatz et al. 2003). As a result, optimized search behavior and morphology should be the major determinants of discovery ability.

Although the optimization of individual search behavior has received much attention, its role in resource competition is far from clear. In general, when searching for randomly located and unpredictably renewed food items, the most efficient search path is one that is straighter because it is costly to search the same area twice (Cody 1971; Pyke 1978; Zimmerman 1979; Hoffman 1983; Dusenbery 1989; Bovet and Benhamou 1991). Although this prediction may not apply to all central-place foragers because of the energy costs associated with returning discovered food to a central point, it should hold for social insects, like ants, because they are highly efficient load-bearers (Weier and Feener 1995; Weier et al. 1995), and those discovering food often do not harvest it (Johnson et al. 1987). Encounters with sparse and immediately depleted resources, such as those likely experienced by omnivorous ants (Cerdá et al. 1998; LeBrun 2005), are increased when foragers cover greater distances (i.e., greater mean displacement) (Viswanathan et al. 1996, 1999) (seabirds and plankton) and overlap themselves less (Ramos-Fernández et al. 2004) (spider monkeys). However, turning more could also increase the probability of finding food depending on resource conditions (Bell 1991; Bovet and Benhamou 1991; Viswanathan et al. 1999; Bartumeus et al. 2002; Claver and Ambrose 2003; Biesinger and Haefner 2005) and the cost of overlapping one's own search path (Cody 1971; Stillman and Sutherland 1990). For instance, Argentine ants turn less when fewer foragers are around, presumably because they must search the environment more efficiently (Adler and Gordon 1992; Gordon 1995). The specific pattern of movement, straighter or curvier, varies between species and is hypothesized to affect a forager's relative ability to find food (Oster and Wilson 1978; Lynch et al. 1980; Jones and Phillips 1990). The extent of the variability that exists in the movement patterns of ant species has not been broadly characterized nor is it clear which movement pattern would give species a competitive advantage in finding food first.

Morphology could also affect discovery ability, particularly through its effect on speed, because faster moving foragers have been hypothesized to be better discoverers (Oster and Wilson 1978). Mechanistically, longer legs mean larger strides (Zollikofer 1994) and thus allow faster movement. Indeed, speed positively correlates to leg length within ant species (Hurlbert et al. 2008); in army ants, long-legged individuals tend to travel faster and further (Franks 1985, 1986; Feener et al. 1988; Schöning et al. 2005). Furthermore, data obtained in leaf-cutter ants suggests there may be a biomechanical trade-off between traveling fast and turning (Angilletta et al. 2008), which could affect discovery by compelling species to follow either straighter or more curvy paths but not both. Leg length may also independently contribute to discovery by affecting an ant's ability to navigate complex habitats: Ants with relatively longer legs are better at foraging in planar environments and over the top of litter (Kaspari and Weiser 1999; Sarty et al. 2006). However, because previous work has almost always taken place in artificial and often extreme conditions and has focused on single species or species drawn from disparate communities (Angilletta et al. 2008; Hurlbert et al. 2008), it is unclear how such morphological relationships and constraints correspond to foraging behavior in nature. In order to understand the ecological implications of the relationship between morphology, movement, and discovery ability, natural behavior of freely moving animals in the comparative context of intact communities must be observed.

This study characterizes the mechanisms underlying species-specific discovery ability in natural communities of interacting species. In nature, we digitally recorded and quantified the foraging behavior of 10 common species found in 2 communities. We also quantified the morphometric parameters of their for-agers and determined species-specific discovery ability using bait trials. These data were used to answer 3 questions. First, are there differences in the foraging behavior of different species of omnivorous ants? Second, how is morphology related to differences in search patterns? Third, how do search patterns and morphology interact to frame species-specific discovery ability?

MATERIALS AND METHODS

Study sites and species

The data were collected during the summers of 2005 and 2006, on 6 plots in Texas and 5 plots in Arizona. Our sampling took place during the peaks of ant 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 (lat ~30°17′N, long ~97°46′W, elevation ~145 m) and 3 were located at the Stengl "Lost Pines" Biological Station (lat ~30°04′N, long ~97°10′W, elevation ~140 m). The Brackenridge plots were characterized by sugarberry (*Celtis laevigata*), Ashe's juniper (*Juniperus ashei*), and cedar elm (*Ulmus crassifolia*), and 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 (*Pi. leiophylla var. chihuahuana*), gray oak (*Q. grisea*), and alligator juniper (*J. deppeana*); 3 plots were located on the eastern side of the Chiricahua Mountains, near Portal (lat ~31°54′N, long ~109°14′W, elevation ~1700 m), and 2 plots were established on the western side of the range, on the El Coronado Ranch near Pearce (lat ~31°51′N, long ~109°22′W, elevation ~1700 m).

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. Using results obtained from pitfall traps and visual surveys (Andersen 1991; Bestelmeyer et al. 2000) performed at all of the stations on all of the plots, we identified stations with high ant activity and made them the focus of video sampling (see below).

We focused our study on a total of 10 species: 6 species in Texas (*Brachymyrmex depilis, Monomorium minimum, Myrmecina americana, Paratrechina terricola, Pheidole dentata*, and *Ph. metallescens*) and 4 species in Arizona (*Dorymyrmex insanus, Mo. emersoni, Myrmica striolagaster*, and *Ph.e diversipilosa*). Based on field observations (visual and/or pitfall sampling), we identified these species as being the most commonly observed generalized scavengers in their communities. They exploit the same types of food resources, are common at both insect and sugar baits, and exhibit overlapping patterns of daily activity (LeBrun 2005; Pearce-Duvet et al. 2011). Consequently, they were also the species for which we were able to collect the most instances of video.

Movement pattern quantification

Filming took place in the summer of 2006. We obtained video footage from multiple stations across all of the plots in order to sample individuals from a diversity of colonies. Video was taken during the day, when temperatures ranged between 26–36 °C. The filming arena was a circular blank index card of 15 cm in diameter onto which a circle cut from engineering paper (5 sq cm), 9.5 cm in diameter, was glued; the entire arena was laminated. We dusted the card with nearby soil and placed it on a level ground surface, even with the surrounding litter. A digital camcorder (Sony Handycam MiniDV DCR-HC32) was attached to a tripod and fixed pointing down to the card. A small box level was secured to the back of the camcorder to ensure that the lens was always on the same plane when filming; zoom was kept consistent.

We initiated recording when an ant moved onto the card, and we stopped it shortly after the ant left the card. Date, location, and time were noted for each observation. The temperature at the time of the observation was measured using a digital thermohygrometer (Forestry Suppliers Inc., Jackson, MI) placed nearby. Although there is the potential for ants to behave abnormally on the card, many studies of ant movement have been performed successfully utilizing entirely artificial foraging arenas (e.g., Bovet et al. 1989; Jones and Phillips 1990; Durou et al. 2001; Challet et al. 2005). Ours took place in nature, and additionally, the cards are approximately the size of leaf litter that ants may encounter.

Overall, we recorded a total of 5 and 2.5 h of digital footage in Texas and Arizona, respectively. This difference stemmed from differences in overall ant abundance in the 2 communities. Approximately 45 min of video of highly variable quality was obtained for each species. Footage was transferred to a computer and processed into individual clips. We analyzed between 13 and 20 of the best quality video clips for each species; species-specific mean clip length ranged between 5 and 22 s. The ant's position in the arena was automatically extracted from the individual clips frame-by-frame using a custom-built program developed in MATLAB (The MathWorks, Natick, MA). From these position data, the total path could be reconstructed (Figure 1).

The native time interval of the digital camcorder was a standard 33 ms (30.33 frames/s). We transformed this original time interval to a more biological relevant timescale of 0.3 s (Kareiva and Shigesada 1983; Gordon 1995), which corresponded to the time it took the largest ant species sampled

to move one body length (Tourtellot et al. 1991). We estimated body length as $3 \times TL$, where TL is thorax length (see below). From the ant's movement, we determined the mean of instantaneous speeds (millimeters/second) (hereafter called mean speed) and the mean turning rate (degrees turned/second) for each clip. Mean speed was found by calculating the speed for each time step (distance traveled divided by 0.3 s) and taking the overall mean of all of the steps in the clip. The mean degrees turned per second was obtained by calculating the absolute difference in angular orientation between adjacent time steps, dividing it by 0.3 s, and taking the overall mean. In order to characterize each species' movement relative to its own body size, the data were discretized a second time. In this case, the time interval was calibrated to the amount of time it took a particular species to travel 3 times its thorax length. We then calculated turning intensity as the mean degrees turned per this time interval.

Ant morphology measurements

We estimated ant body size allometry by measuring the thorax length and leg length of 6–10 individuals of each species filmed. The individuals measured came from pitfall trap sampling performed following site establishment. Measurements were made using a Zeiss Stemi SV 6 stereo microscope (Carl Zeiss, Inc., Oberkochen, Germany). In dimorphic genera (e.g., *Pheidole*), only minor workers were measured because they are the ones that discover resources (see Wilson 1984; Pearce-Duvet JMC, personal observation). Thorax length was defined as the distance between the anterior edge of the pronotum and the posterior edge of the propodeum. The length of the hind femur and hind tibia were each measured and summed to yield hind leg length. The hind femur length was defined as the distance from the femur's connection to the trochanter and its attachment to the tibia. The hind tibia was defined as the linear distance from the articulation with the femur to the articulation with the tarsus.

Quantification of discovery ability

We estimated species' discovery ability in the field using baiting trials (LeBrun and Feener 2007) in the summer of 2005 (Pearce-Duvet et al. 2011). Resource discovery trials were performed twice at each of the 25 study stations located on each plot: once during the day (between 9:00–17:00 h in Texas and 13:00–17:00 h in Arizona) and once at night (21:00–1:00 h in Texas and 20:00–1:00 h in Arizona). Overall, this resulted in a total of 550 observations (TX = 6 sites × 25 stations × 2 time periods = 300; AZ = 5 sites × 25 stations × 2 time periods = 250).

We placed a hoop encompassing an area of 0.25 m^2 at the station. The area inside the hoop was observed for a period of 5 min, during which time the number and identity of the ants present was noted. We then placed a piece of hot dog on a blank bait card in the center of the hoop and observed it until it was discovered, that is, an ant made physical contact with the bait, or an hour had passed without discovery; the species identity of the discoverer was noted. The bait cards used in the baiting trials were different from the cards used to film movement. We quantified the discovery ability of species i (DA_i) as the number of discoveries by species i (DI_i) divided by the total number of times species i was observed in the hoop (HT_i): ($DA_i = DI_i \times HT_i^{-1}$), or the proportion of baits a species discovered when it was around to discover them.
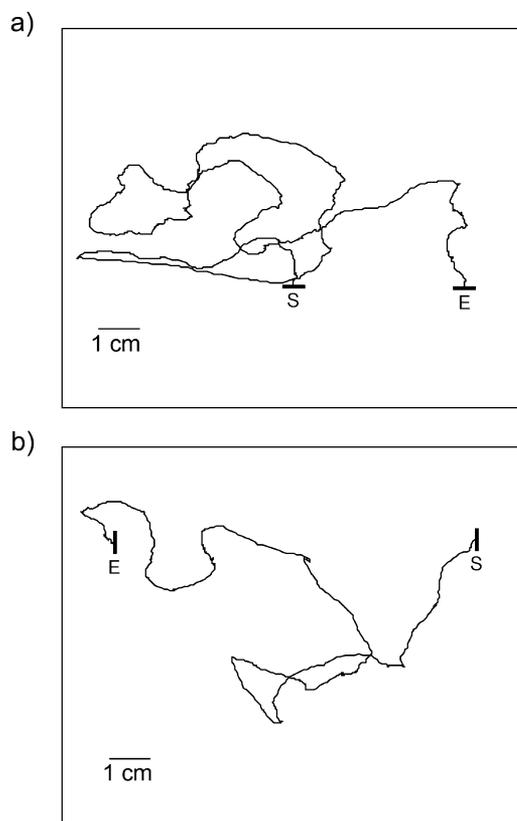
a)

b)

Figure 1
Example traces of ant foraging patterns for (a) *Brachymyrmex depilis* (25 s of video) and (b) *Dorymyrmex insanus* (21 s of video). "S" indicates the start of the path and "E" indicates its end. *B. depilis* is one of the species that turns the most while foraging, whereas *D. insanus* is among those turning the least.

Statistical analyses

We used R 2.9.1 (R Development Core Team 2009) for all analyses unless otherwise indicated. Species differences in

speed (millimeters/second), turning rate (degrees/second), and turning intensity (i.e., mean degrees turned in seconds needed to travel $3 \times$ thorax length) were determined using analyses of covariance (ANCOVAs) in which species identity was a main effect. Our initial models included temperature and the temperature–species interaction to control for its potential effect on movement; model selection then identified the most parsimonious model. We found no significant interactions between temperature and species but temperature was retained a significant covariate in the model of Texas speed ($F = 8.4$, degrees of freedom [df] = 1,92, $P < 0.001$) and Arizona turning rate ($F = 6.5$, df = 1,62, $P = 0.01$). Speed in both locations was log transformed to meet assumptions of normality (Shapiro–Wilk) and homogeneity of variance (Fligner–Killeen). Turning rate in Texas could not be made to meet assumptions by transformation. As a result, we first performed an ANCOVA to determine if temperature contributed significantly to the model. When it was found to be nonsignificant ($F = 0.11$, df = 1,92, $P = 0.7$), species differences (main effect and post hoc) were confirmed using a more conservative nonparametric analysis (Kruskal–Wallis). No transformation was necessary for turning rate in Arizona or turning intensity in either location. The significance of all post hoc analyses was corrected using false discovery rate ($q* = 0.05$) (Benjamini and Hochberg 1995). We also examined the correlation (Pearson) between the species-specific means for speed and turning rate.

We analyzed ant allometry using the R smatr package (Warton et al. 2006). First, we determined the scaling relationship between thorax length (an estimate of ant body size) and leg length in all measured individuals using major axis line fitting (Warton et al. 2006). The slope and the elevation of the relationship between log_{10}-transformed thorax length and log_{10}-transformed leg length in Texas versus Arizona were then compared using a likelihood ratio test and Wald test, respectively. When the datasets were determined to be equivalent (see RESULTS below), we tested if the combined dataset differed significantly from the predicted isometric slope of 1.0 using a one-sample t-test (R package smatr; see Warton et al. 2006). We used the species-specific residuals of the relationship in subsequent analyses as an estimate of relative leg length. The

relationship between running speed, turning rate, and both absolute and relative leg length was examined using linear regression; absolute leg length was log_{10} transformed.

The relationship between speed, leg length, turning rate, and discovery success was examined using a generalized linear model with a binomial distribution. The number of successes and failures for each species was used as the dependent variable; the independent variables were species-specific mean speed, mean relative turning rate, and mean relative leg length. Relative leg lengths were the residuals taken from the species-specific regression of leg length against thorax length. Relative turning rate was the residuals of the species-specific regression of relative leg length to degrees turned per second. Relative turning rate was used rather than absolute turning because of the nonlinear correlation between the two (see RESULTS below); turning intensity was not used because it is calculated from data that is discretized in a species-specific manner and is thus not necessarily as comparable or biologically relevant. A quasibinomial distribution was utilized to correct for overdispersion in the data. The model that best fit the data was selected using a stepwise backward comparison of the variance explained by the model's terms starting from a saturated model including all interactions. A pseudo-R^2 was calculated using the deviances of the final model as compared with the null model (Heinzl et al. 2005) to estimate model fit.

RESULTS

Movement

Both ant communities studied here showed clear interspecific differences in how ants moved (Table 1). Species foraged at different speeds (TX: $F_{species} = 28.7$, df = 5,92, $P < 0.001$; AZ: $F_{species} = 27.3$, df = 3,64, $P < 0.001$) (Figure 2a,d) and, in the Texas community, also turned at different rates (degrees/second) (TX: $F_{species} = 8.5$, df = 5,95, $P < 0.001$) (Figure 2b). The ants in Arizona turned at the same rate (AZ: $F_{species} = 2.5$, df = 3,62, $P > 0.05$) (Figure 2e). Turning intensity (mean degrees turned in seconds needed to travel $3 \times$ thorax length) was also significantly different among species (TX: $F_{species} = 34.3$, df = 5,95, $P < 0.001$; AZ: $F_{species} = 20.8$, df = 3,64, $P < 0.001$) (Table 1; Figure 2c,f). Some species, such

Table 1

Movement patterns of ant species from Texas and Arizona communities

Species	N	Speed (mm/sec) Mean	95% CI	Turning rate (degrees/second) Mean	Turning tntensity (deg/body length) Mean
Texas					
Brachymyrmex depilis	13	14.6^c	12.9–16.6	87.0^a ± 3.2	13.5^c ± 0.5
Monomorium minimum	13	7.0^d	6.0–8.2	76.1^{bc} ± 2.8	20.3^a ± 0.7
Myrmecina americana	20	23.5^a	19.6–28.1	66.2^c ± 5.0	9.7^d ± 0.8
Paratrechina terricola	14	15.7^{bc}	13.8–18.0	84.1^{ab} ± 3.3	17.9^{ab} ± 0.7
Pheidole dentata	19	17.6^{ab}	15.0–20.8	76.4^{bc} ± 2.8	15.1^c ± 0.5
Ph. metallescens	20	16.3^{ab}	14.3–18.6	82.6^{ab} ± 2.0	15.9^{bc} ± 0.3
Arizona					
Dorymyrmex insanus	17	16.7^a	13.8–20.1	60.5 ± 2.4^a	11.8^c ± 0.6
Mo. emersoni	15	6.8^c	5.8–7.9	59.7 ± 3.4^a	15.7^b ± 0.6
Myrmica striolagaster	20	12.3^b	10.7–14.1	56.9 ± 2.4^a	19.6^a ± 0.8
Ph. diversipilosa	16	10.1^b	8.5–12.0	68.6 ± 3.1^a	16.5^b ± 0.8

N is the number of high quality clips available for that species. Speed and turning rate were calculated at a discretization level of 0.3 s. Turning intensity signifies the mean degrees turned in a time step when the data were discretized according to body length. Because the means given for speed are back-transformed from the log-transformed values used in the analysis, back-transformed 95% confidence intervals are reported instead of standard errors. The means for turning rate and intensity include standard errors. Significant differences after false discovery rate post hoc correction are indicated by unshared letters. If species share a letter, their means are not significantly different.
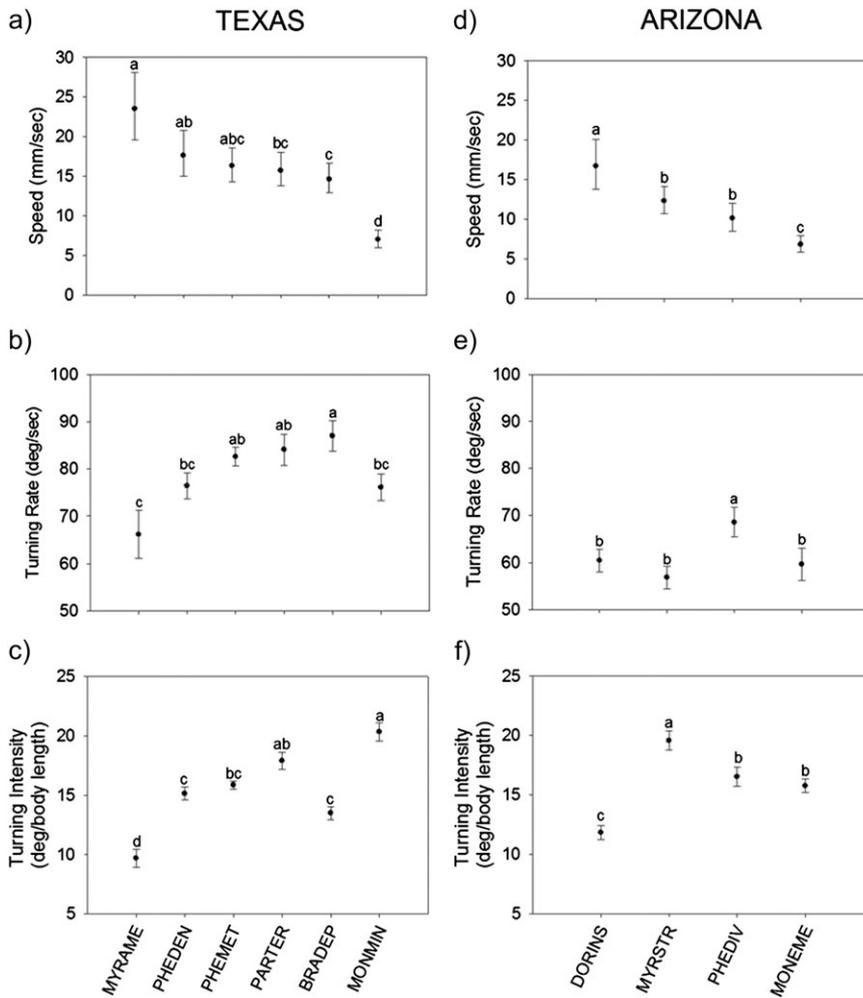
Figure 2
Speed, turning rate, and turning intensity (degrees turned/body length) for ant species in Texas and Arizona. Results for Texas species are depicted in (a-c), and results for Arizona species are depicted in (d-f). Species names are composed of the first three letters of the genus names followed by the first three letters of the species (Table 1). Unshared letters above the bars indicate significant differences in values after post hoc correction using false discovery rate. Because speed was log transformed to meet normality assumptions for the analysis, the back-transformed values have been plotted with 95% confidence intervals bars.

as *Mo. minimum* and *Myrmi. striolagaster*, turned even more than suggested by their simple turning rates when body length was taken into account. There was no relationship between mean speed and mean turning rate at the species level ($r = 0.2$, $t = 0.6$, df $= 8$, $P > 0.05$). The species investigated here display a range of movement patterns/strategies under natural foraging conditions, including both fast and curvy paths as well as straight and slow ones. Because these communities capture the wide variation of patterns present in nature, they are suitable for addressing how these patterns relate to foraging ecology.

Movement and morphology

In both communities, larger ants had relatively longer legs (Figure 3). The lines describing the relationship between thorax length and leg length had same slope and elevation in both Texas and Arizona (slope: likelihood ratio statistic $= 0.39$, $P = 0.5$; elevation: t (Wald) $= 2.7$, $P = 0.1$), and thus the 2 data sets were combined. The slope of the combined data equaled 1.2 (95% confidence intervals $= 1.10$–1.29) and was significantly greater than the isometric value of 1 ($r = 0.49$, $P < 0.001$). We used the species-specific residuals of the relationship between thorax and leg length as an estimate of relative leg length below.

The speed at which a foraging ant moves was not determined by absolute or relative leg length (speed vs. absolute leg length: $t = 0.9$, $n = 10$, $P > 0.05$; speed vs. relative leg length: $t = 0.7$, $n = 10$, $P > 0.05$) (Figure 4a,b) when the entire dataset was

considered. As *Myrme. americana* appeared to be an outlier in this dataset, it was removed and the analysis was repeated. Absolute leg length still did not determine the speed at which the ants foraged ($t = 1.3$, $n = 9$, $P > 0.05$). In contrast, ant species with relative longer legs foraged at faster speeds ($t = 2.9$, $n = 9$, $P = 0.02$, $R^2 = 0.50$). The turning rate of foragers peaked at intermediate values of relative leg length (linear
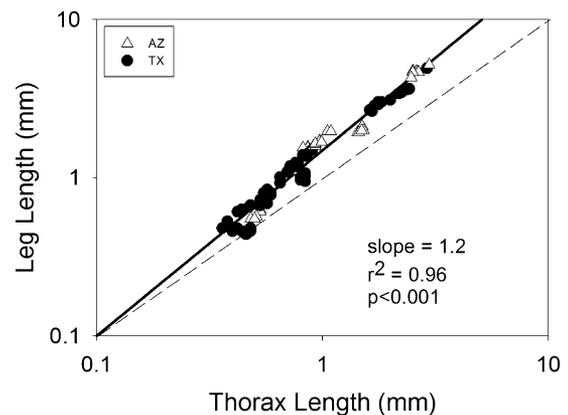

Figure 3
Relationship between thorax length and leg length. Both axes are $\log_{10}$ scaled. The slope is significantly different from the isometric expectation of 1.0 ($P < 0.001$) (hatched line), indicating that leg length gets disproportionately longer with increasing body length.
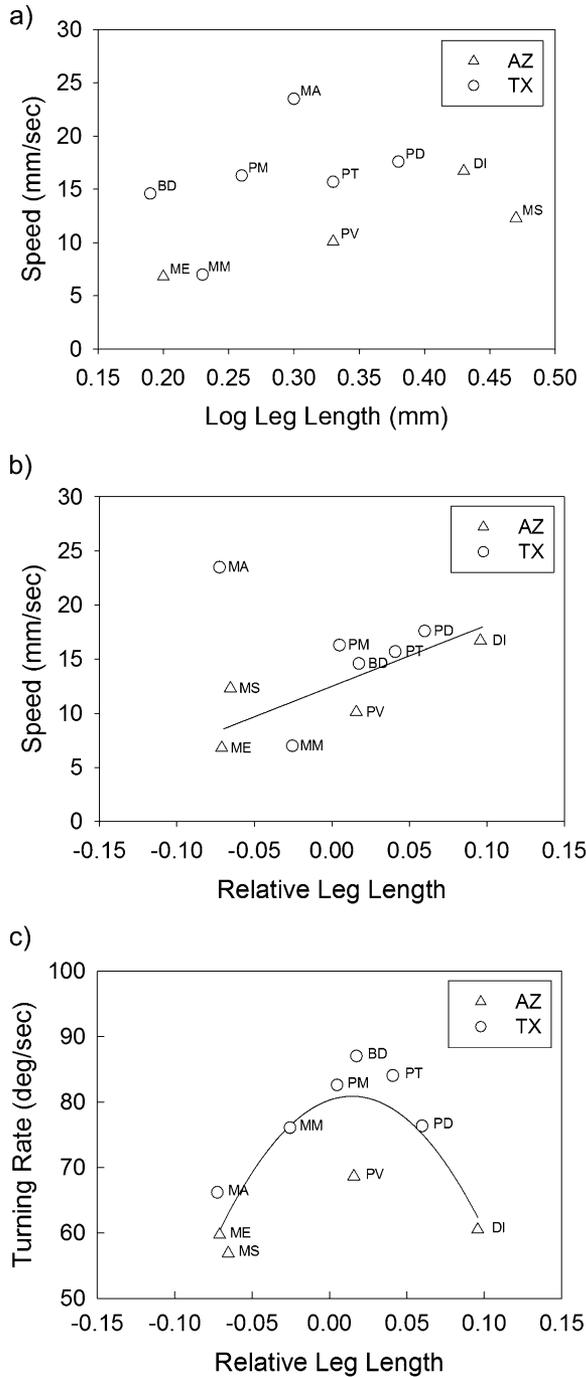
a)

b)

c)

Figure 4
Relationship of (a) absolute leg length (log transformed) with speed; (b) relative leg length with speed; and (c) relative leg length and turning rate. The values for relative leg length are the species-specific residuals of the linear relationship between thorax length and leg length. Species names are composed of the first three letters of the genus names followed by the first three letters of the species (Table 1); the only exception is PV = *Pheidole diversipilosa* (AZ) to avoid confusion with *Ph. dentata* (TX). Relative leg length predicts speed when *Myrmecina americana* is removed from the analysis (y = 12.55 + 54.42x).

regression: $F = 1.2$, $n = 10$, $P = 0.3$; quadratic regression: $F = 8.9$, $n = 10$, $P = 0.02$, $R^2 = 0.72$) (Figure 4c); this was not true for absolute leg length (linear regression: $F = 2.5$, $n = 10$, $P = 0.1$; quadratic regression: $F = 1.9$, $n = 10$, $P = 0.2$). As a result,

the residuals of turning rate regressed against relative leg length were used in the analysis below, that is, the relative turning rate. So, species with relatively longer legs moved faster, and ants of intermediate relative leg length turned more.

Movement, morphology, and discovery ability

The best fit model explaining discovery success included both relative leg length and relative turning rate, but not speed, as main effects (pseudo-$R^2 = 0.60$). Speed was dropped as a main factor in the model (model comparison $P = 0.6$). Relative leg length was retained (model comparison $P = 0.02$), as was relative turning rate (model comparison $P = 0.06$). Although relative turning rate was marginally significant, we retained it in the model for 2 reasons. First, power analysis suggested our ability to detect a relationship based on 10 species was low (actual power = 0.5 of a desired power of 0.8), and thus the negative result should be interpreted with caution; even with such low power, the term was nonetheless marginally significant. Second, a trend is clearly present in the data when viewed graphically. Ants with relatively longer
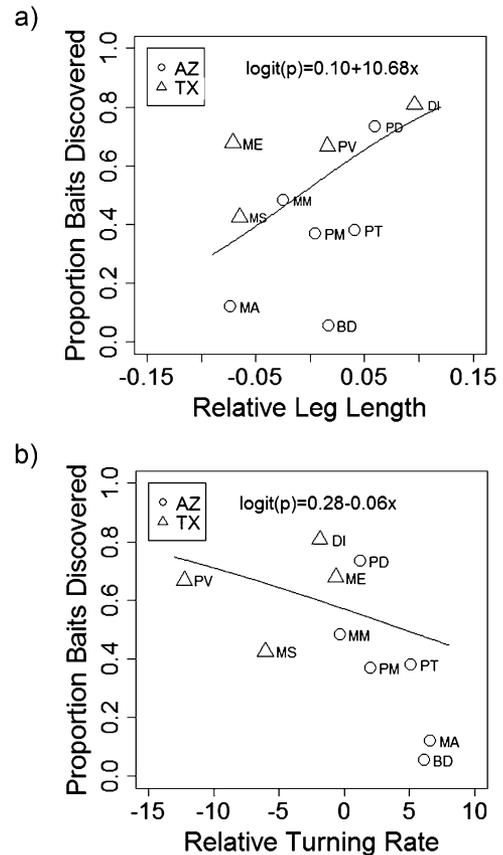
a)

b)

Figure 5
Relationship of (a) relative leg length and (b) relative turning rate to discovery success. The values for relative leg length are the species-specific residuals of the linear relationship between thorax length and leg length. The values for relative turning rate are the species-specific residuals of the nonlinear relationship between relative leg length and degrees turned per second. Discovery success is defined as the proportion of baits discovered when a species was present in a 5-min visual survey prior to bait placement. Species abbreviations are the same as for Figure 4. The fitted lines were calculated using the individual logistic regression model for each variable. The regression equations show the influence of each variable on the probability that a resource was discovered (logit(P)).

discovered a greater proportion of baits (coefficient value = 12.4) (Figure 5a). Ants that turned less also tended to be more successful (coefficient value = −0.1) (Figure 5b).

DISCUSSION

In this study, we investigated how different species approach the problem of finding food by focusing on the traits of their individual foragers. Using freely behaving ants in their natural habitat, our results show that species differ dramatically in their foraging patterns and that their movement is only partially driven by morphology. Furthermore, both morphology and movement contribute to successful discovery.

We showed that naturally behaving ant species have unique foraging patterns, demonstrating significant interspecific differences in both speed and turning (Figure 2). This pattern suggests that species employ many different combinations of speed and turning as part of their natural search behavior and a constant physical constraint between speed and turning during such movement is unlikely. Such variation may be important to niche partitioning within ant communities, especially as it contributes to differences in discovery ability among species. The absence of a significant correlation between speed and turning contrasts with a previously reported negative correlation between speed and tortuosity in leaf-cutter ants (Angilletta et al. 2008); turning rate and tortuosity are distinct but correlated measures. However, in that study, movement characteristics were not recorded during natural searching behavior but rather during the escape behavior provoked by the hand of the researcher tracing the path of the ant manually. During an escape response, many animals tend to move as fast and as far as possible, pushing their performance limits to survive. Under such extreme conditions, a negative correlation between speed and turning can be attributed in part to biomechanical incompatibilities between moving quickly and turning (Zollikofer 1994; Jindrich and Full 1999). If we want to understand the general patterns of ant movement, it is important to consider their most common behavior, which is foraging rather than escaping.

We found that morphology partially frames the speed at which ant species forage under natural conditions. Although absolute leg length is a strong predictor of how fast individuals within a species are able to move during maximal performance (Hurlbert et al. 2008), it does not account for the differences in foraging speed among species (Figure 4). Our data concur with findings by Hurlbert et al. (2008), who also found this pattern in a meta-analysis of widely distributed ant species (geographically and phylogenetically). Although they attributed their results to the inclusion of the specialized genera Cataglyphis and Eciton in their analysis, 2 genera uniquely adapted for fast running as a response to thermal pressure or a predatory lifestyle (Rettenmeyer et al. 1983; Anderson and McShea 2001), it is possible that absolute leg length is not the best predictor of species-specific speed. We found, in contrast, that relative leg length is more important in determining foraging behavior. Ants with relatively longer legs foraged more quickly (with the exception of Myrme. americana), and those of intermediate relative leg length turned more. Like Cataglyphis and Eciton species, Myrme. americana is also an outlier, moving at faster speeds than predicted by its relative leg length. Although its ecology is largely unknown, it too may be uniquely adapted for fast running.

Our finding that relative, but not absolute, leg length is correlated with speed suggests that the speed at which a species forages is tied to its efficiency of movement. Leg length increased allometrically with body size in both Texas and Arizona ant communities (Figure 3), which fits with the predic-

tions of the size-grain hypothesis (Kaspari and Weiser 1999). This hypothesis states that ants with relatively longer legs are better adapted to traverse planar environments and move more rapidly over the top of the litter. Here, we show that longer legged ants do forage at higher speeds, as predicted.

Stride frequency, rather than stride length, may contribute more to species locomotor differences. Although stride length is obviously constrained by leg dimensions, mean stride frequency may be differentially modulated, resulting in significantly different mean speeds even for species with very similar leg lengths (Zollikofer 1994). Although absolute leg length ultimately constraints the maximum speed at which a species travels, it does not appear to drive the tempo at which a species regularly searches. Species may make use of the range in stride frequency available to them to optimize their search patterns. This behavioral flexibility may be reflected in the remarkable suite of tempo combinations demonstrated by species of varying sizes; when turning intensity, a body size relative metric of turning, was examined, ants on opposite ends of the leg and body length continuum, such as Myrmi. striolagaster and Mo. minimum, showed markedly similar turning intensity (Figure 2).

Ants appear to maximize discovery success via at least 2 distinct mechanisms, the first morphological and the second behavioral (Fig. 5). First, good discoverers have relatively longer legs (Figure 5a), a trait that could enhance environmental coverage and thus the likelihood of running into food. Given the relationship between relative leg length and speed discussed above, we might predict that faster ants are better discoverers. However, speed did not predict a species' ability to find food, suggesting that the importance of leg length lies elsewhere. Rather, we suggest that long legs may allow ants to cover greater distances more efficiently. Relatively longer legs minimize locomotor costs because muscular metabolic costs are linked to the frequency of stepping cycles; the longer the legs, the longer the stride length, and the less frequent the stride cycle needs to be (Taylor et al. 1980). This pattern may reflect the adaptation of ant workers for locomotor performance (Weier and Feener 1995). Colonies can exploit such specialization to drive the energetic cost of foraging to a minimum (Weier and Feener 1995) because the wingless, sterile worker caste is not constrained by flight and reproduction costs (Traniello 1989).

Second, ants also enhance discovery success through behavior, by restricting the amount of turning during searches. Species moving in straighter lines tended to discover more baits (Figure 5b), even after controlling for leg length, suggesting it is a distinct and independent means of enhancing discovery. These results support the importance of more linear movement for resource discovery, which has long been propounded (Cody 1971; Jander 1975; Pyke 1978; Zimmerman 1979; Hoffman 1983; Dusenberry 1989; Bell 1991; Bovet and Benhamou 1991; Zollner and Lima 1999) but has only little empirical support in ants (Jones and Phillips 1990). Our findings directly contradict the prediction that more turning leads to greater discovery (Lynch et al. 1980) and may result because larger turning angles can lead to excessive overlap of one's own path (Ramos-Fernández et al. 2004) and/or that of fellow foragers (Adler and Gordon 1992). However, this result should be interpreted cautiously as the benefits of turning are greatly dependent on resource conditions (Bell 1991; Bovet and Benhamou 1991; Viswanathan et al. 1999; Bartumeus et al. 2002; Claver and Ambrose 2003; Biesinger and Haefner 2005) and the cost of search path overlap (Cody 1971; Stillman and Sutherland 1990). In other words, an ant could but may not always be better off searching a larger area less exhaustively than searching a smaller area more meticulously.

Many species, such as ants, face the challenge of discovering food that is unpredictably located in space and time. We show that, under natural conditions in intact communities, species-specific movement is as unique as it is diverse and, furthermore, that morphology may shape differences in ant foraging dynamics. We also found that discovery success is enhanced by mechanisms that increase the probability of running into food in an undirected manner. By having relatively longer legs and/or moving in straighter lines, foragers experience a greater and perhaps more efficient net displacement across the environment. Because our results come from groups of interacting species, we have caught a glimpse of how the mechanisms underlying movement translate into competitive ability within communities.

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