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 phenomena (Holden 2006) or focus on population-level dynamics (Bowler and Benton 2005; Holyoak et al. 2008; Schick et al. 2008; Wittmer 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 Pisanski 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; Oriel 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; Peke 1978; Zimmerman 1979; Hoffman 1983; Dusenberry 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 foragers 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 (Cellis 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 lobolly pine (Pinus taeda). The Arizona plots were located in mixed forests containing Chihuahuan pine (Pinus thurifera 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. emeryi, Myrmica strigosaster, 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 thermohygro meter (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 species-specific mean clip length ranged between 45 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 [MC, 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 m² 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$_i$ × HT$_i$)$^{-1}$, or the proportion of baits a species discovered when it was around to discover them.

Statistical analyses

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

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.
speed (millimeters/second), turning rate (degrees/second), and turning intensity (i.e., mean degrees turned in seconds needed to travel 3 × 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 non-significant ($F = 0.11$, 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 ($q^b = 0.05$) (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 (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 deviations 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: $F_{\text{species}} = 28.7$, df = 5.92, $P < 0.001$; AZ: $F_{\text{species}} = 27.3$, df = 3.64, $P < 0.001$) (Figure 2a,d) and, in the Texas community, also turned at different rates (degrees/second) (TX: $F_{\text{species}} = 8.5$, df = 5.95, $P < 0.001$) (Figure 2b). The ants in Arizona turned at the same rate (AZ: $F_{\text{species}} = 2.5$, df = 3.62, $P > 0.05$) (Figure 2e). Turning intensity (mean degrees turned in seconds needed to travel 3 × thorax length) was also significantly different among species (TX: $F_{\text{species}} = 34.3$, df = 5.95, $P < 0.001$; AZ: $F_{\text{species}} = 20.8$, df = 3.64, $P < 0.001$) (Table 1; Figure 2c,f). Some species, such

| Species | Speed (mm/sec) | Turning rate (degrees/second) | Turning intensity (deg/body length) |
|---------|---------------|-------------------------------|-----------------------------------|
|         | N  | Mean  | 95% CI | Mean | 95% CI | Mean | 95% CI |
| **Texas** |     |       |        |       |       |       |       |
| Brachymyrmex depilis | 13 | 14.6 | 12.9–16.6 | 87.0 | 3.2 | 13.5 | 0.5 |
| Monomorium minimum | 13 | 7.0 | 6.0–8.2 | 76.1 | 2.8 | 20.3 | 0.7 |
| Myrmecina americana | 20 | 23.5 | 19.6–28.1 | 66.2 | 5.0 | 9.7 | 0.8 |
| Peratrechus terricola | 14 | 15.7 | 13.8–18.0 | 84.1 | 3.3 | 17.9 | 0.7 |
| Pheidole dentata | 19 | 17.6 | 15.0–20.8 | 76.4 | 2.8 | 15.1 | 0.5 |
| Ph. metallescens | 20 | 16.3 | 14.3–18.6 | 82.6 | 2.0 | 15.9 | 0.3 |
| **Arizona** |     |       |        |       |       |       |       |
| Dorymyrmex insanus | 17 | 16.7 | 13.8–20.1 | 60.5 | 2.4 | 11.8 | 0.6 |
| Mo. emersoni | 15 | 6.8 | 5.8–7.9 | 59.7 | 3.4 | 15.7 | 0.6 |
| Myrmica striolagaster | 20 | 12.3 | 10.7–14.1 | 56.9 | 2.4 | 19.6 | 0.8 |
| Ph. diversifolia | 16 | 10.1 | 8.5–12.0 | 68.6 | 3.1 | 16.3 | 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 0.5 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.
as *Mo. minimum* and *Myrm. 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 *Myrm. 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 2](https://academic.oup.com/beheco/article-abstract/22/3/501/267968/505)

![Figure 3](https://academic.oup.com/beheco/article-abstract/22/3/501/267968/506)
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 legs...
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 predictions 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 constrains 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 Myrme. strigifrons and Myrme. 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 pronounced (Cody 1971; Jander 1975; Pyke 1978; Zimmerman 1979; Hoffman 1983; Dunseberry 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 generally 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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**REFERENCES**

Adler FR, Gordon DM. 1992. Information collection and spread by networks of patrolling ants. Am Nat. 140:373–400.

Adler FR, LeBrun EG, Feener DF. 2007. Maintaining diversity in an ant community: modeling, extending, and testing the dominance-discovery trade-off. Am Nat. 169:325–333.

Andersen AN. 1991. Sampling communities of ground-foraging ants: pitfall catches compared with quadrat counts in an Australian tropical savanna. Aust J Ecol. 16:273–279.

Andersen C, McShea DW. 2001. Individual versus social complexity, with particular reference to ant colonies. Biol Rev. 76:211–237.

Angilletta MJ Jr., Roth TC 2nd, Wilson RS, Niehaus AC, Ribeiro PL. 2001. Influence of hunger level and prey density on searching behaviour of the redwood predator *Rhyacornis marginatus* (Fabricius) (Heter., Reduviidae). J Appl Entomol. 127:42–45.

Cody M. 1971. Finch flocks in the Mohave desert. Theor Popul Biol. 2:142–158.

Corbara B, Dejean A. 2000. Adaptive behavioral flexibility of the ant *Pachycondyla analis* (= *Megaponera fonts*) (Formicidae: Ponerinae) during prey capture. Sociobiology. 36:465–483.

Davidson DW. 1998. Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. Ecol Entomol. 23:484–490.

Dongou S, Lauga J, Dejean A. 2001. Intensive food searching in humid patches: adaptation of a myrmicine ant to environmental constraints. Behaviour. 138:251–259.

Dusenberry DB. 1989. Ranging strategies. J Theor Biol. 136:309–316.

Feener DH Jr., Lighton JRB, Bartholomew GA. 1988. Curvilinear allometry, energetics and foraging ecology: a comparison of leaf-cutting ants and army ants. Funct Ecol. 2:590–592.

Fellers JH. 1987. Interference and exploitation in a guild of woodland ants. Ecology. 68:1466–1478.

Fiedler K, Kuhlmann F, Schlick-Steiner B, Steiner F, Gehaver G. 2007. Stable N-isotope signatures of central European ants—assessing positions in a trophic gradient. Insects Soc. 54:393–402.

Gordon DM. 1995. The expandable network of ant exploration. Anim Behav. 50:995–1007.

Harkness RD, Maroudas NG. 1985. Central place foraging by an ant (*Cataglyphis bicolor* Fab.): a model for searching. Anim Behav. 33:916–928.

Heinzel H, Waldhöhr T, Mittlöbck M. 2005. Careful use of pseudo R-squared measures in epidemiological studies. Stat Med. 24:2867–2872.

Hoffman G. 1983. The random elements in the systematic search behavior of the desert isopod *Hemipterus raunowi*. Behav Ecol Sociobiol. 13:81–92.

Holldobler C. 2006. Inching toward movement ecology. Science. 313:779–782.

Hölldobler B, Wilson EO. 1990. The ants. Cambridge (MA): Harvard University Press.

Holway DA. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. Ecology. 80:238–251.

Holyoak M, Casagrandi R, Nathan R, Revilla E, Spiegel O. 2008. Trends and missing parts in the study of movement ecology. Proc Natl Acad Sci U S A. 105:19060–19065.

Hurlbert AH, Ballantyne F, Powell S. 2008. Shaking a leg and hot to trot: the effects of body size and temperature on running speed in ants. Ecol Entomol. 33:144–154.

Jander R. 1975. Ecological aspects of spatial orientation. Annu Rev Ecol Syst. 6:171–188.

Jindrich DL, Full RJ. 1999. Many-legged maneuverability: dynamics of turning in hexapods. J Exp Biol. 292:1603–1623.

Johnson LK, Hubbell SP, Feener DH Jr. 1987. Defense of food supply by eusocial colonies. Am Zool. 27:347–358.

Jones SR, Phillips SA Jr. 1990. Resource collecting abilities of *Solenopsis invicta* (Hymenoptera: Formicidae) compared with those of three sympatric Texas ants. Southwest Nat. 35:416–422.

Kareiva PM, Shigesada N. 1983. Analyzing insect movement as a correlated random walk. Oecologia. 56:234–238.

Kaspari M, Weiser MD. 1999. The size-grain hypothesis and interspecific scaling in ants. Funct Ecol. 13:530–538.
LeBrun EG. 2005. Who is the top dog in ant communities? Resources, parasites, and multiple competitive hierarchies. Oecologia. 142:643–652.

LeBrun EG, Feener DH Jr. 2007. When trade-offs interact: the balance of terror enforces the dominanceinance-trade-off in a local ant assemblage. J Anim Ecol. 76:58–64.

Lynch JF, Balinsky EC, Vail SG. 1980. Foraging patterns in three sympatric forest ant species. *Prenolepis imparis, Paratrechina melanderi, and Alphaenogaster rudis*. Ecol Entomol. 5:353–371.

Mitchell WA, Abramsky Z, Kotler BP, Pinshow B, Brown JS. 1990. The effect of competition on foraging activity in desert rodents: theory and experiments. Ecology. 71:844–854.

Morrison LW. 1996. Community organization in a recently assembled fauna: the case of Polynesian ants. Oecologia. 107:243–256.

Mueller T, Fagan WF. 2008. Search and navigation in dynamic environments—from individual behaviors to population distributions. Oikos. 117:654–664.

Nathan R. 2008. An emerging movement ecology paradigm. Proc Natl Acad Sci U S A. 105:19050–19051.

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE. 2008. A movement ecology paradigm for unifying organismal movement research. Proc Natl Acad Sci U S A. 105:19052–19059.

Orivel J, Souchal A, Cerdan P, Dejean A. 2000. Prey capture behavior of the arboreal ant *Pachycondyla goeldii* (*Hymenoptera: Formicidae*). Sociobiology. 35:131–140.

Oster GF, Wilson EO. 1978. *Social insects in the tropics*. Paris: Universite´ Paris-Nord. p. 59–73.

Pearce-Duvet JMC, Moyano M, Adler FR, Feener DH Jr. Forthcoming. Fast food in ant communities: how competing species find resources. Oecologia.

Pearce-Duvet JMC, Feener DF Jr. 2010. Resource discovery in ant communities: do food type and quantity matter? Ecol Entomol. 35:549–556.

Pearce-Duvet JMC, Moyano M, Adler FR, Feener DH Jr. Forthcoming. 2011. Fast food in ant communities: how competing species find resources. Oecologia.

Pyke GH. 1978. Are animals efficient harvesters? Anim Behav. 26:241–250.

R Development Core Team. 2009. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.

Ramos-Fernández G, Mateos JL, Miramontes O, Cocho G, Larralde H, Ayala-Orozco B. 2004. Lévy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). Behav Ecol Sociobiol. 55:229–230.

Rettemeyer GW, Chadab-Crepet R, Naumann MG, Morales L. 1983. Comparative foraging by neotropical army ants. In: Jaisson P, editor. Social insects in the tropics. Paris: Université Paris-Nord. p. 59–73.

Sany M, Abbott K, Lester P. 2006. Habitat complexity facilitates coexistence in a tropical ant community. Oecologia. 149:465–473.

Schatz B, Anstett M-C, Out W, Hossaert-McKey M. 2003. Offactive detection of fig wasps as prey by the ant *Crematogaster scutellaris* (*Formicidae; Myrmicinae*). Naturwissenschaften. 90:436–459.

Schick RS, Loarie SR, Colchero F, Best BD, Boustan Y, Conde DA, Halpin PN, Joppa LN, McClellan CM, Clark JS. 2008. Understanding movement data and movement processes: current and emerging directions. Ecol Lett. 11:1338–1350.

Schöniger C, Kinuthia W, Franks NR. 2005. Evolution of allometries in the worker caste of *Dorylus* army ants. Oikos. 110:231–240.

Stephens DW, Krebs JR. 1986. *Foraging theory*. Princeton (NJ): Princeton University Press.

Stillman RA, Sutherland WJ. 1990. The optimal search path in a patchy environment. J Theor Biol. 145:177–182.

Taylor CR, Heglund NC, McMahon TA, Looney TR. 1980. Energetic cost of generating muscular force during running: a comparison of large and small animals. J Exp Biol. 86:9–18.

Tourtellot MK, Collins RD, Bell WJ. 1991. The problem of movement and turn definition in analysis of orientation data. J Theor Biol. 150:287–297.

Traniello JFA. 1989. Foraging strategies of ants. Annu Rev Entomol. 34:191–210.

Vepsäläinen K, Pisarski B. 1982. Assembly of island ant communities. Ann Zool Fenn. 19:327–335.

Viswanathan GM, Buldyrev SV, Murphy EJ, Prince PA, Stanley HE. 1996. Lévy flight search patterns of wandering albatrosses. Nature. 381:413–415.

Viswanathan GM, Buldyrev SV, Havlin S, da Luz MGE, Raposo EP, Stanley HE. 1999. Optimizing the success of random searches. Nature. 401:911–914.

Warton DI, Wright JJ, Falster DS, Westoby M. 2006. Bivariate line-fitting methods for allometry. Biol Rev. 81:259–291.

Weier JA, Feener DH. 1995. Foraging in the seed-harvester ant genus *Pogonomyrmex*: are energy costs important? Behav Ecol Sociobiol. 36:291–300.

Weier JA, Feener DH, Lighton JR. 1995. Inter-individual variation in energy cost of running and loading in the seed-harvester ant, *Pogonomyrmex maricopa*. J Insect Physiol. 41:321–327.

Weseloh RM. 2000. *Paths of Formica neoguayaca* (*Hymenoptera: Formicidae*) on tree and shrub leaves: implications for foraging. Environ Entomol. 29:525–534.

Wilson EO. 1984. The relation between caste ratios and division of labor in the ant genus *Pheidole* (*Hymenoptera: Formicidae*). Behav Ecol Sociobiol. 16:89–98.

Wittevanger G, Polansky L, Douglas-Hamilton I, Getz WM. 2008. Disentangling the effects of forage, social rank, and risk on movement autocorrelation of elephants using Fourier and wavelet analyses. Proc Natl Acad Sci U S A. 105:19108–19113.

Wolf H, Wehner R. 2000. Pinpointing food sources: olfactory and anemotactic orientation in desert ants, *Cataglyphis fortis*. J Exp Biol. 203:857–868.

Ydenberg RC, Giraldeau LA, Kramer DL. 1986. Interference competition, payoff asymmetries, and the social relationships of central place foragers. Theor Popul Biol. 30:26–44.

Zimmerman M. 1979. Optimal foraging: a case for random movement. Oecologia. 43:261–267.

Zollner PA, Lima SL. 1999. Stepping patterns in ants—fluence of body morphology. J Exp Biol. 192:107–118.

Zollner PA, Lima SL. 1999. Search strategies for landscape-level interpatch movements. Ecology. 80:1019–1030.