

Movements During Colony Founding by Queens of the Honey Ant (*Myrmecocystus mimicus* Wheeler)

ABSTRACT.—Habitat selection by ant queens has been little studied even though it may be a critical component of colony founding. We describe the movement pathways of honey ant queens (*Myrmecocystus mimicus* Wheeler) searching for sites on the ground to initiate nests. Typical paths may include segments of directional movement that are interrupted by segments of area-restricted search. Mechanisms producing area-restricted search might include variable step lengths and looping behavior. Cues that prompt the switch to local search remain undetected.

INTRODUCTION

Most ant colonies are essentially sessile, so habitat selection by ants is mainly by queens during colony founding. Mortality of foundresses (Whitcomb *et al.*, 1973; Hölldobler and Wilson, 1990) and young colonies (Wiernasz and Cole, 1995) may be extremely high. Natural selection among queens for behavioral mechanisms to avoid predators and select suitable nest sites should be intense during this brief, but critical, period of colony founding (Hölldobler and Wilson, 1990). However, the assertion made by Wilson and Hunt (1966) over 30 y ago still holds: “In spite of its probable importance, habitat selection by queens has been one of the least studied aspects of ant biology.” This gap in knowledge is due to the difficulty of studying movements of queens. For many species of ants, colony founding events are triggered by environmental conditions that may occur only on a few days each year (Hölldobler and Wilson, 1990) and sometimes only on a single day (Mull and Crist, 1993). Insights into this crucial aspect of colony founding may depend, in part, on opportunistic observations of queen movements.

For ant species with nuptial flights, habitat selection by queens can be considered at two spatial scales (Wilson and Hunt, 1966). Selection of macrohabitat occurs during flight and selection of microhabitat (nest sites) occurs through movements on the ground after the flight. Although Wilson and Hunt (1966) described the movements of queens of two ant species (*Lasius neoniger* and *Solenopsis molesta*) as nondirectional, looping paths with random searching, we are unaware of any quantitative descriptions of movements by ant queens. Herein, we describe the movement paths of honey ant queens (*Myrmecocystus mimicus* Wheeler) searching for nest sites on the ground during colony founding. To our knowledge, these observations represent the first attempt to quantify movement patterns of ant queens in the wild.

METHODS

Myrmecocystus mimicus is a diurnal predator-scavenger that forages for insects, gathers floral nectar and tends aphids (Hölldobler, 1981). Winged male and female reproductives likely mate in the air during the nuptial flight, after which the mated queens land and shed their wings (Bartz and Hölldobler, 1982). Colonies are often founded by >1 queen (pleometrosis), but workers in the incipient colony eliminate all but one queen and mature colonies are monogynous (Bartz and Hölldobler, 1982). Incipient colonies of *M. mimicus* are aggregated in space (Bartz and Hölldobler, 1982), but intraspecific raiding and predation lead to overdispersed mature colonies (Hölldobler, 1981).

We recorded the movements of *Myrmecocystus mimicus* queens between 1130 and 1330 h on 27 June 1996 in creosote-tarbrush (*Larrea tridentata*-*Flourensia cernua*) shrub habitat in Chihuahuan desert at the Jornada Experimental Range, which is located 37 km north of Las Cruces, New Mexico. Nuptial flights were ongoing earlier that morning (0830 h) following heavy rains of 26 and 27 June. We mapped pathways of six foundress queens and then collected five of them to verify identification. Using standard protocol for measuring insect movements (Turchin *et al.*, 1991; Wiens *et al.*, 1993), we marked the location of each ant with numbered flags at 20-s time steps for ≤ 30 steps. To avoid disturbing the ant we waited ≥ 1 time step before placing the flags. We mapped the locations of the flags on each pathway with a compass and a measuring tape. Although we observed ≥ 2 queens digging nests together in the area, the paths that we measured were for queens moving individually. Air temperatures were ca. 22

TABLE 1.—Parameters of movement pathways of *Myrmecocystus mimicus* queens during colony founding. Values are based on six replicate paths. The parameters are defined in the text

Parameter	\bar{x}	SD	Range
No. of steps	25	5.1	18–29
Path length (m)	17.15	6.7	12.80–26.15
Net displacement (m)	4.90	3.50	2.37–11.78
Mean step length (m)	0.67	0.18	0.44–0.90
Locomotor rate (m/s)	0.034	0.009	0.022–0.045
Proportion of steps moving	0.86	0.14	0.64–1.00
Mean turning angle	–58.8	57.3 ¹	211 ²
Mean vector length	0.25	0.18	0.06–0.48

¹ Mean angular deviation, which is equivalent to SD for linear statistics

² Smallest arc that contains all of the mean turning angles (Batschelet, 1981)

C, soil surface temperatures were ca. 21.5 C and relative humidity at the soil surface was 82% during the observations.

For each movement pathway we calculated several descriptive parameters (Bell, 1991; Crist *et al.*, 1992). The net displacement is the straight-line distance between the initial and final locations. The mean step length is the mean distance moved during each 20-s time step. A turning angle is the angle formed by the change in direction between consecutive time steps. The mean turning angle is the trigonometric mean of the turning angles within a path (Batschelet, 1981). As a measure of directionality we used the mean vector length (r), which is a unit vector measure of the dispersion of turning angles (Batschelet, 1981). The mean vector length varies from 0.0 (uniform) to 1.0 (perfectly directional).

For testing hypotheses, individuals should be used as replicates (Turchin *et al.*, 1991; Wiens *et al.*, 1993) by first reducing the data from each path to summary parameters, such as calculating a mean turning angle from the individual steps within a path and then performing a test using the summary parameters. We performed such a second-order analysis to test whether the movements by the ant queens were directional with Moore's test, which is a nonparametric test based on mean turning angles and mean vector lengths of the replicate paths (Batschelet, 1981).

For additional descriptive purposes several within-path analyses are appropriate. In particular, tests for serial correlations in turning angles, step lengths and cross-correlations between these two parameters can provide insights into movement behavior. For instance, several mechanisms for producing area-restricted searching (Bell, 1991) may be detected with such tests. Serial correlations in turning angles can create looping patterns, which are one way of restricting search to an area. Variable move lengths, such as short moves within resource patches and long moves between patches, can result in serial correlations in step length. Finally, these within-path tests are useful in evaluating some of the assumptions of the correlated random walk (CRW) model, which may be a useful general model of animal movement (Turchin, 1998). The CRW model assumes that there are no serial correlations in turning angles and step lengths. We tested for serial correlations in turning angles with runs tests (Cain, 1989; Crist and MacMahon, 1991). For step lengths we calculated Pearson's correlation coefficients for time lags 1 through 4. The correlation for lag 1 was between a step length (time n) and the preceding step length (time $n - 1$). The correlation for lag 2 was for step length at time n with time $n - 2$, and so forth. We then treated each path as a replicate and calculated the mean and CI (± 2 SE) for each lag to determine if it differed from zero (Turchin, 1998). Finally, we conducted Spearman's rank correlation tests between turning angles and step lengths. We used the absolute values of the turning angles and, thus, ignored the direction of the turn (right or left).

RESULTS AND DISCUSSION

In general, *Myrmecocystus mimicus* queens moved in the patches between shrubs and they sometimes stopped briefly to examine areas under twigs and other ground litter. One of the queens that we

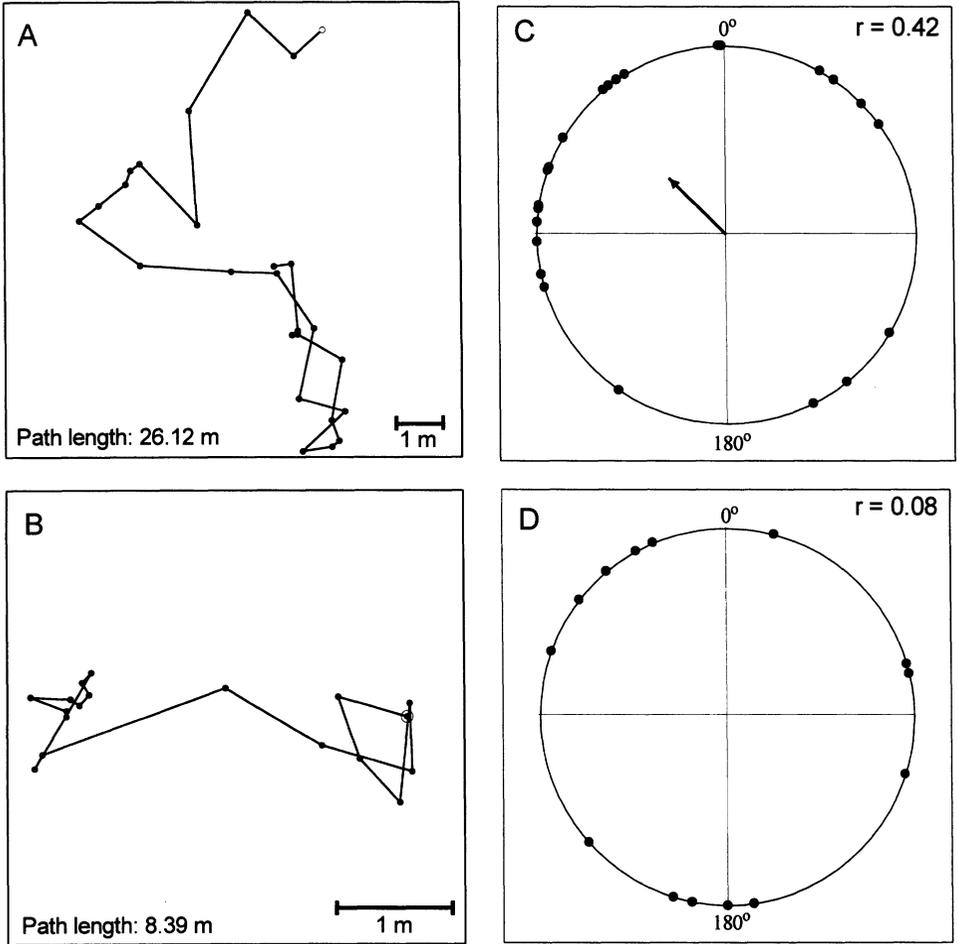


FIG. 1.—Representative pathways of two types of movement observed for *Myrmecocystus mimicus* queens searching for a nest site during colony founding. (A) A longer path with moderate directionality and (B) a shorter path without directionality. The open circles are the starting locations and the closed circles are sequential locations at 20-s intervals. Note the difference in scale: the top frame is 10×10 m and the bottom frame is 4×4 m. (C) Circular scatter plot of turning angles for the trail depicted in A and (D) similar plot for the trail depicted in B. Zero degrees indicates a straight movement. The mean vector length (r) in (C) is represented by the arrow, which points to the mean turning angle.

followed stopped for ca. 2 min to investigate a nest that was being excavated by another queen, but then continued moving. We stopped observations on another of the queens when she started to excavate her own nest.

For the observed queens, the total path length averaged 17.2 m and net displacement averaged 4.9 m, but these parameters were variable among paths (Table 1). The mean step length ($\bar{x} = 0.67$ m/step) was much greater than that reported by Crist and Wiens (1994) for workers of western harvester ants (*Pogonomyrmex occidentalis*) foraging in shortgrass steppe habitat (means ranged from 0.18–0.28 m/step after adjusting for different time-step intervals). Direct comparisons are difficult, however,

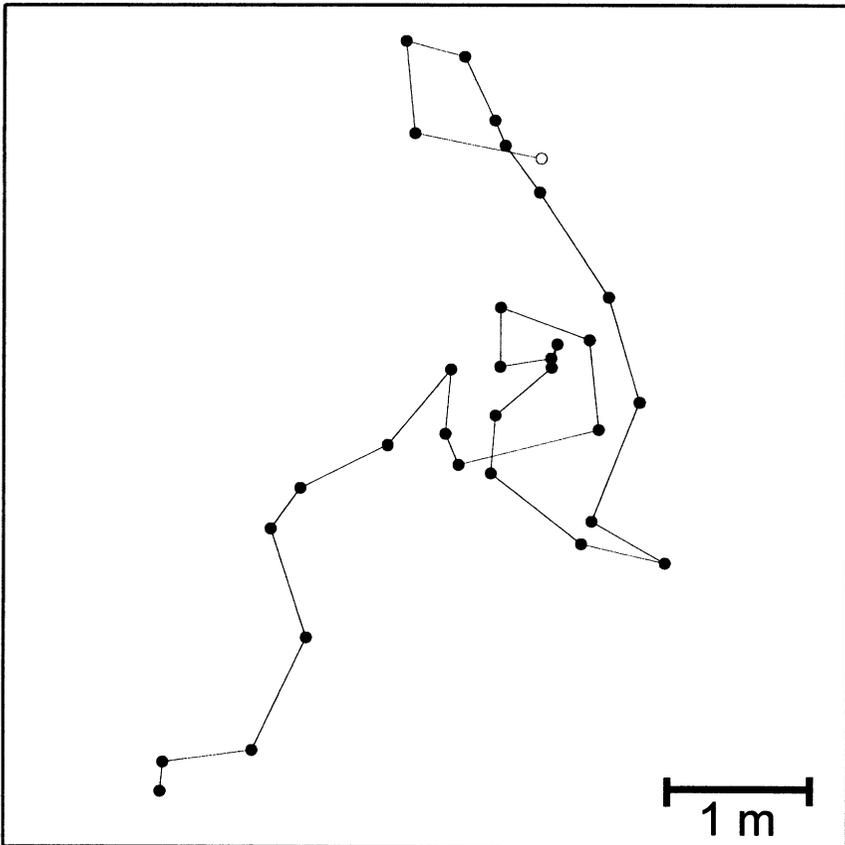


FIG. 2.—Movement pathway of a *Myrmecocystus mimicus* queen that includes some looping behavior within a longer path with moderate directionality (mean vector length = 0.48). The open circle is the starting location and the closed circles are sequential locations at 20-s intervals

because vegetation structure can influence movement patterns of insects (Crist and Wiens, 1994; Wiens *et al.*, 1997), and our study site contained more bare ground cover than does shortgrass steppe habitat.

As a whole, the paths of the searching ant queens were nondirectional with the mean turning angles no different from an independent and uniform distribution (Moore's Test, $P > 0.10$, $D' = 0.89$). However, there may be two groups of distinct path types (Fig. 1). Three longer paths ($\bar{x} = 28.3$ steps) with greater net displacement (4.6–11.8 m) had moderate directionality ($r = 0.35$ – 0.42), whereas three shorter paths ($\bar{x} = 21.7$ steps) with lower net displacement (2.6–3.4 m) had little directionality ($r = 0.06$ – 0.16). Mean vector lengths can depend on sample sizes, but a decrease in sample size results in an increase in mean vector length (Batschelet, 1981). Thus, the difference in directionality between the two groups is not due to a sampling artifact. Instead, we believe that the typical path probably is represented by the longer paths, in which periods of directional movement are interspersed with periods of local search with low directionality. The shorter paths may thus have captured only these less directed sections of overall movements. Changing patterns in directionality were reported by Crist and MacMahon (1991) for foraging *Pogonomyrmex occidentalis* workers in shrub-steppe habitat. Workers running on trunk trails had high directionality ($r = 0.87$), but those searching for seeds between shrubs had reduced directionality ($r = 0.34$) and those searching under shrubs had little directionality

($r = 0.15$). *Myrmecocystus mimicus* queens also may have changed movement behavior when they encountered a favorable "patch" for searching, but in contrast to the *P. occidentalis* foragers, it is not clear what environmental conditions constitute such a patch for the queens. We observed no obvious patches that might have prompted the queens to alter their movements. The search behavior of workers of other ant species also may include relatively straight moves interrupted by phases of area-restricted search (Harkness and Maroudas, 1985; Traniello *et al.*, 1991; Fourcassie *et al.*, 1992).

Two of the paths suggested that looping behavior (Bell, 1991) may be a component of local search (Fig. 2). However, the runs tests indicated no significant serial correlation among turning angles for any of the paths (all $P \geq 0.20$). It may be difficult to demonstrate an overall nonrandom distribution of turning angles if loops are located within longer paths. There were also no correlations between turning angles and step lengths (all $P \geq 0.05$). Schmid-Hempel (1984) also found no relation between these two movement parameters for scavenging workers of the desert ant *Cataglyphis bicolor*. For the *Myrmecocystus mimicus* queens there was positive serial correlation in mean step length for lag 1 (Pearson's r , $\bar{x} = 0.44$, 95% CI = 0.22–0.66, $n = 6$), lag 2 ($\bar{x} = 0.33$, CI = 0.13–0.53) and lag 3 ($\bar{x} = 0.21$, CI = 0.01–0.41). The autocorrelation was strongest at lag 1 and decayed to zero by lag 4. Therefore, variable step lengths (shorter steps in favorable areas) may be one mechanism of area-restricted search used by *M. mimicus* foundresses.

As is typical for most initial studies, our quantitative assessment of movement behavior by *Myrmecocystus mimicus* queens raised many questions. If movement pathways are characterized by sections of moderate directionality interspersed with portions of area-restricted search, then the obvious question to ask is what cues cause the queens to change behavior. Are there physical environmental variables, such as soil-surface texture or soil moisture (Nagel and Rettenmeyer, 1973), which queens prefer for initiating nests? Are the queens responding to cues related to the distribution of possible predators? Foundress queens in our study area were preyed on by workers from mature colonies of *M. mimicus* and by other ant species, including *Aphaenogaster cockerelli* (André), *Myrmecocystus navajo* Wheeler and *Pogonomyrmex desertorum* Wheeler. Predation of *M. mimicus* foundresses is high within 3 m of mature *M. mimicus* colonies, and incipient colonies have low survival between 3 and 15 m of mature colonies (Hölldobler, 1981). Establishment of new colonies is also related to the distance to mature conspecific colonies in other species of ants (Ryti and Case, 1988; Wiernasz and Cole, 1995; Gordon and Kulig, 1996). Although the queens that we tracked were not obviously influenced by potential predators, they may have been responding to chemical cues for predation risk such as nest refuse (Kaspari and Vargo, 1994) or trail pheromones. Given that pleometrotic associations of foundresses are more successful at raising worker offspring than are solitary foundresses (Bartz and Hölldobler, 1982), could the movements of queens be influenced by trail pheromones of potential co-foundresses? Finally, are there similarities in the searching behavior of queens and of workers or do the constraints of central-place foraging and group-level behavior (Gordon, 1995) create fundamental differences in their movement patterns?

Acknowledgments.—We thank J. Rice for assisting in the field, D. Guertin for writing a computer program for calculating some of the movement parameters and T. Crist and R. Jander for providing helpful comments on the manuscript. Our observations were made while conducting research on ant communities funded by the National Science Foundation (DEB-95-27111 to J. A. Wiens).

LITERATURE CITED

- BARTZ, S. H. AND B. HÖLLDOBLER. 1982. Colony founding in *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae) and the evolution of foundress associations. *Behav. Ecol. Sociobiol.*, **10**: 137–147.
- BATSCHLET, E. 1981. Circular statistics in biology. Academic Press, London. 371 p.
- BELL, W. J. 1991. Searching behaviour: the behavioural ecology of finding resources. Chapman and Hall, London. 358 p.
- CAIN, M. L. 1989. The analysis of angular data in ecological field studies. *Ecology*, **70**:1540–1543.
- CRIST, T. O. AND J. A. MACMAHON. 1991. Individual foraging components of harvester ants: movement patterns and seed patch fidelity. *Ins. Soc.*, **38**:379–396.

- AND J. A. WIENS. 1994. Scale effects of vegetation on forager movement and seed harvesting by ants. *Oikos*, **69**:37–46.
- , D. S. GUERTIN, J. A. WIENS AND B. T. MILNE. 1992. Animal movement in heterogeneous landscapes: an experiment with *Eleodes* beetles in shortgrass prairie. *Func. Ecol.*, **6**:526–544.
- FOURCASSIÉ, V., D. COUGHLIN AND J. F. A. TRANIELLO. 1992. Fractal analysis of search behavior in ants. *Naturwiss.*, **79**:87–89.
- GORDON, D. M. 1995. The expandable network of ant exploration. *Anim. Behav.*, **50**:995–1007.
- AND A. W. KULIG. 1996. Founding, foraging, and fighting: colony size and the spatial distribution of harvester ant nests. *Ecology*, **77**:2393–2409.
- HARKNESS, R. D. AND N. G. MAROUDAS. 1985. Central place foraging by an ant (*Cataglyphis bicolor* Fab.): a model of searching. *Anim. Behav.*, **33**:916–928.
- HÖLLDOBLER, B. 1981. Foraging and spatiotemporal territories in the honey ant *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.*, **9**:301–314.
- AND E. O. WILSON. 1990. The ants. Belknap/Harvard Univ. Press, Cambridge, Massachusetts. 732 p.
- KASPARI, M. AND E. L. VARGO. 1994. Nest site selection by fire ant queens. *Ins. Soc.*, **41**:331–333.
- MULL, J. F. AND T. O. CRIST. 1993. Timing of mating flights in the western harvester ant, *Pogonomyrmex occidentalis* Cresson (Hymenoptera: Formicidae). *J. Kansas Entomol. Soc.*, **66**:372–375.
- NAGEL, H. G. AND C. W. RETTENMEYER. 1973. Nuptial flights, reproductive behavior and colony founding of the western harvester ant, *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae). *J. Kansas Entomol. Soc.*, **46**:82–101.
- RYTI, R. T. AND T. J. CASE. 1988. The regeneration niche of desert ants: effects of established colonies. *Oecologia*, **75**:303–306.
- SCHMID-HEMPEL, P. 1984. Individually different foraging methods in the desert ant *Cataglyphis bicolor* (Hymenoptera, Formicidae). *Behav. Ecol. Sociobiol.*, **14**:263–271.
- TRANIELLO, J. F. A., V. FOURCASSIÉ AND T. P. GRAHAM. 1991. Search behavior and foraging ecology of the ant *Formica schaufussi*: colony-level and individual patterns. *Ethol. Ecol. Evol.*, **3**:35–47.
- TURCHIN, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, Massachusetts. 396 p.
- , F. J. ODENDAAL AND M. D. RAUSHER. 1991. Quantifying insect movement in the field. *Environ. Entomol.*, **20**:955–963.
- WHITCOMB, W. H., A. BHATKAR AND J. C. NICKERSON. 1973. Predators of *Solenopsis invicta* queens prior to successful colony establishment. *Environ. Entomol.*, **2**:1101–1103.
- WIENS, J. A., T. O. CRIST AND B. T. MILNE. 1993. On quantifying insect movements. *Environ. Entomol.*, **22**:709–715.
- , R. L. SCHOOLEY AND R. D. WEEKS, JR. 1997. Patchy landscapes and animal movements: do beetles percolate? *Oikos*, **78**:257–264.
- WIERNASZ, D. C. AND B. J. COLE. 1995. Spatial distribution of *Pogonomyrmex occidentalis*: recruitment, mortality, and overdispersion. *J. Anim. Ecol.*, **64**:519–527.
- WILSON, E. O. AND G. L. HUNT, JR. 1966. Habitat selection by the queens of two field-dwelling species of ants. *Ecology*, **47**:485–487.

ROBERT L. SCHOOLEY¹ AND BRANDON T. BESTELMEYER, Department of Biology, Colorado State University, Fort Collins 80523. Submitted 23 December 1999; accepted 12 June 2000.

¹ Corresponding author: e-mail: schooley@lamar.colostate.edu