

Research article

Change in movement and subdivision of *Myrmica punctiventris* (Hymenoptera, Formicidae) colonies in north temperate forests is related to a long-term shift in social organization

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Abstract. We assessed temporal and spatial patterns of nest site use in the cavity dwelling ant, *Myrmica punctiventris* in a well-studied temperate forest site in central New York State. We evaluated changes in nest site use by repeatedly censusing the ants inhabiting artificial nests (hollow dowels) for three consecutive growing seasons. We confirm a shift towards more polydomy in this population of *M. punctiventris*, first reported by DeHeer et al. (2001), but extend these findings by demonstrating that this shift has occurred gradually over several years. We are unable to determine if this polydomy is seasonal or year round. We explore various explanations for the occurrence of polydomy and suggest that long-term changes in sex allocation are indirectly driving the shift in nesting strategies.

Keywords: Polydomy, *Myrmica punctiventris*, nest relocation, ants.

Introduction

Location in time and space is an important component of ecological success. For social organisms, nest site location constrains an individual's use of time and space and thus may have profound effects on both the individual and the group (Hölldobler and Wilson, 1990; Yamauchi et al., 1981). These constraints are particularly evident in complex insect societies that use central place foraging, such as honeybee

hives and ant colonies. The sessile nature of these nests is thought to be imposed either by intense competition for food (Ryti and Case, 1984), space (Wiernasz and Cole, 1995), or are dictated by the energetic costs of moving (Seeley, 1985). Yet some ant species move frequently. For example, 56% of the *Aphaenogaster rudis* nests and 78% of the *Tapinoma sessile* nests in a temperate forest changed location within 21 days (Smallwood and Culver, 1979); these rates are typical for temperate forest ants. Even ants with nest structures that represent substantial investments in time and energy are more prone to move than one might expect. In Brazil, approximately 50% of the colonies of the tropical disturbance specialist *Solenopsis richteri* moved within 30 days (Briano et al., 1995) and its relative *S. invicta* changed its nest site on average once per year in introduced U.S. populations (Hays et al., 1982). Species that are normally thought of as completely sessile can also be mobile; Gordon (1992) reports that 10% of the desert harvester ant nests (*Pogonomyrmex barbatus*) changed nest sites over the course of a season. In spite of these data, however, our understanding of the forces prompting nest movement, as well as its implications, is rudimentary.

Wholesale nest movements may be caused by a number of factors. Foitzik and Heinze (1998) proposed physical deterioration of the nest structure as the driving force behind nest movement in the cavity dwelling ant *Leptothorax nylanderi*. Gibb and Hochuli (2003) showed that shading and nest temperature were important proximate cues for nest relocation in *Polyrhachis ammon*. Exhaustion of food supplies has been invoked to explain movement of large colonies, especially those that use a central-place foraging strategy (Herbers and Tucker, 1986; Traniello and Levings, 1986).

Additional complexity occurs when colonies occupy multiple locations at one time (polydomy). Ant colonies may be polydomous year round or seasonally; in the latter case, colonies divide into subunits during the spring and fuse into a single nest site before over-wintering. Seasonal polydomy has been demonstrated to be a function of queen-worker conflict over sexual allocation decisions in some populations of the ant *Myrmica punctiventris* (Snyder and Herbers, 1991). Alternatively, seasonal polydomy may simply be a strategy to increase food supplies or provide more space for brood maturation during the reproductive season (Traniello and Levings, 1986; Banschbach and Herbers, 1999).

Cavity-dwelling species, because of their willingness to utilize engineered nesting sites, provide a unique opportunity to experimentally test how movement or polydomy might vary with ecological context. The cavity dwelling ant *Myrmica punctiventris* has been the focus of a series of studies primarily performed within two study sites in the northeastern United States. These studies revealed considerable diversity in the social organization and nest-site utilization within and between populations of both species (e.g., Herbers, 1986; Snyder and Herbers, 1991; Banschbach and Herbers, 1996a; Herbers and Banschbach 1998). In particular one population of this species shows a consistent pattern of seasonal polydomy (Snyder and Herbers, 1991; Banschbach and Herbers, 1999), whereas another population of the same species has changed its behavior from being primarily monodomous, polygynous and having a strongly male-biased sex ratio (Banschbach and Herbers, 1996a) to being polydomous, with lower queen numbers and a less male-biased allocation ratio (DeHeer et al., 2001). The conclusion that this population has changed its behavior results were based on data collected at the end of a three-year experiment; here we augment those observations with data collected throughout the experiment's duration in order to determine if apparent the apparently new behavior of polydomy occurs in a seasonal cycle.

Materials and methods

This study was conducted in mixed species, deciduous forests on the E.N. Huyck Preserve, Albany County, New York. The ant community there was described by (Herbers, 1989) and comprises 17 species. Most of these species utilize plant cavities for their nesting space (acorns, twigs, fallen logs), with soil-nesters being in the minority (Herbers, 1989).

Twelve plots were set up in the woods, each 7 m by 7 m, organized into three blocks of four plots each. In each block, we randomly chose two plots to receive additional nesting sites and two to remain as intact control plots. Nest sites were engineered by drilling a 4mm diameter hole lengthwise through a 10-cm birch carpentry dowel. These methods replicated an experiment conducted in a Vermont site by Banschbach and Herbers (1999).

The experiment commenced on May 17, 1996 and was terminated the first week of August 1998. Every three weeks from mid-May to the end of August (five time points each in 1996 and 1997, three in 1998) we inspected the dowels for occupancy. Any dowel containing ants was collected and returned to the lab. There we extracted ants, identified them to species, censused them, and allowed them to re-settle into the dowel. Dowels and their ant occupants were returned to the same locations in the field on the following day. Repeated censusing of dowels does not

provoke either colony movement or polydomy (Banschbach and Herbers, 1999) and the ants quickly re-settle into the dowels following censusing, often within an hour (pers. obs.).

For each census period we characterized the condition of each dowel as inhabited or empty, with notes on the inhabitants' species identity and composition. We considered a dowel to be inhabited if it either contained a queen, brood with at least one worker, or at least four workers. This decision rule eliminated observations of just a few workers that may have been foraging or scouting for empty nest sites; we did not record such transient visits as true occupations. The occupancy data were then compared between time intervals and events recorded as: immigration (empty at time i and occupied at time $i + 1$); emigration (occupied at time i and empty at time $i + 1$); turnover (occupied by one species at time i and another species at time $i + 1$); or stasis (the same species occupying a dowel at time i and at time $i + 1$). Immigrations and turnover events imply colonies moving from one nest site to another, emigrations result from colonies moving or dying, and stasis assumes that the nest at time i is the same nest at time $i + 1$. These rules differ from those employed by Banschbach and Herbers (1999) and lead to a more conservative estimate of nest movement because any dowel inhabited by the same species in consecutive censuses was assumed to not have undergone a change. For example, a dowel might contain one queen, 14 workers, and 24 larvae at one census and 0 queens, 10 workers, and 5 larvae of the same species at the next census. Such changes in numbers of queens, workers, and brood are consistent with both intraspecific colony turnover and fission/fusion events (Herbers and Tucker, 1986). We had no good way to distinguish among these possibilities, and thus adopted the conservative strategy of recording all consecutive occurrences of the same species as stasis events.

Results

Ants in this community readily used our engineered nest sites; within 3 weeks of setting the dowels in the woods we found that 10% of the dowels contained ant nests (Fig. 1). Occupancy rates for the dowels continued to be high over the course of the experiment with over 40% of the dowels being occupied during the summer for the last two seasons of the study.

There was a clear seasonal pattern to nest movements; *M. punctiventris* nests showed more frequent movement early in the season than late in the season (1996 $G = 20.56$, $df = 3$, $p < 0.05$; 1997 $G = 41.1$, $df = 4$, $p < 0.05$; 1998 $G = 42.74$, $df = 3$, $p < 0.05$) a pattern which is consistent with seasonal polydomy. In addition, the tendency for a nest to move was related to the presence of brood; nests with sexual brood were less likely to remain in place (show stasis) than nests without sexual brood (mean \pm se, proportion stasiswith = 0.55 ± 0.04 ; proportion stasiswithout = 0.65 ± 0.04 ; $t = 2.41$, $df = 14$, $p = 0.04$).

We counted inhabitants of dowels throughout the experiment, thereby tracking demographic shifts. Comparison of ant nest demography between natural nests and nests in dowels at the end of the experiment gave similar numbers of queens and workers (DeHeer et al., 2001). Thus we assume that demographic data for our engineered nests reflect demography in undisturbed nests nearby; that assumption allows us to infer ant behavior throughout our experiment.

Seasonal polydomy is expected to result in temporal oscillations in the numbers of queens and workers per nest (Snyder and Herbers, 1991; Banschbach and Herbers, 1999).

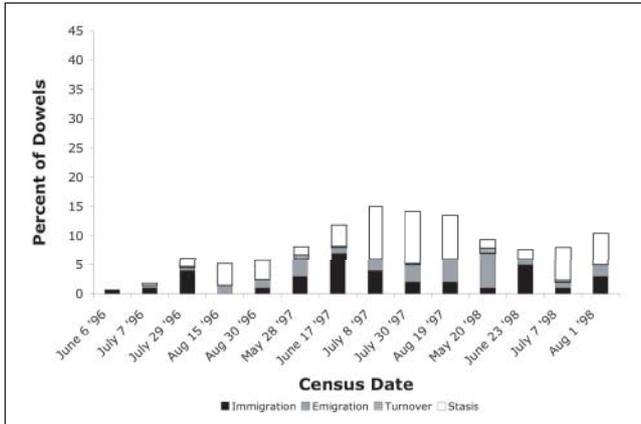


Figure 1. The inhabitants of dowels were compared between consecutive time periods to classify each dowel's state as unoccupied (data not shown); immigration; emigration; stasis; or species turnover. Census date is the calendar date that the dowels were collected; each bar represents activity since the last time census period.

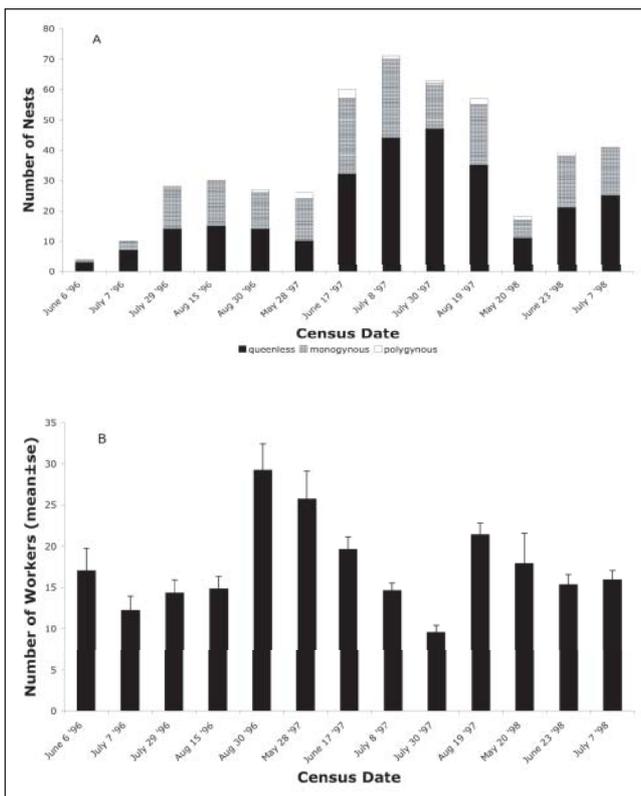


Figure 2. Demography of *M. punctiventris* nests inhabiting dowels at each census period. A) Queen class B) Mean \pm se worker number.

We would predict that queenless nests should increase in frequency, and worker number decrease, between our late spring census (early June in 1996, and late May in 1997 and 1998) and our mid-summer census (late July in 1996, early July in 1997 and 1998), and that queenless nests should decrease in frequency (and worker number increase) between

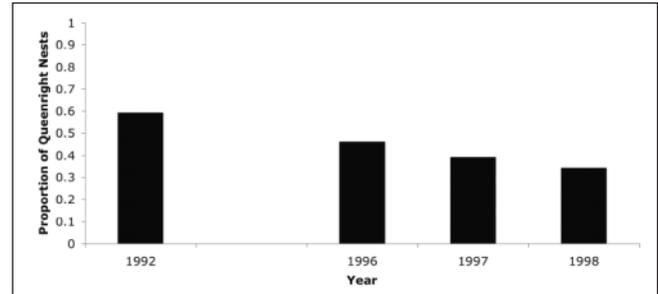


Figure 3. Proportion of queenright nests for *M. punctiventris*. We included in this analysis data from 1992 (Banschbach and Herbers, 1996a) and control plots from our final excavation from 1998 (DeHeer et al., 2001).

the mid-summer census and the late summer census (late August in 1996, middle August in 1997). However, we detected the expected change in the frequency of queenless nests for *M. punctiventris* (Fig. 2A) during only one of the five time periods (early 1997; Chisquare, $p = 0.039$; all other times $p > 0.50$). Support for these predictions based upon the expected changes in worker number were also mixed. Worker numbers (Fig. 2B) decreased significantly only in the spring of 1997 (Kruskal-Wallis; $p = 0.0025$; 1996 and 1998, both $p > 0.20$), but increased in the late summer during both years in which it was measured (Kruskal-Wallis; 1996, $p = 0.0002$, 1997, $p < 0.0001$).

We found significant variation between years in the frequency of queenright nests in *M. punctiventris*, suggesting that levels of polydomy or queen mortality were changing over time within this population. We included in this analysis data from 1992 (Banschbach and Herbers, 1996a) and control plots from our final excavation from 1998 (DeHeer et al., 2001). The proportion of queenright nests decreased in a nearly perfectly linear fashion from a high of nearly 60% in 1992 to 34% in 1998 (Fig. 3; linear regression, R-squared = 0.975, $p = 0.013$).

Discussion

Our results confirm that *M. punctiventris* change nest locations readily and suggest that the nest movement that we observe is due in part to an emerging pattern of polydomy in this population. The pattern of nest movement that we documented here is consistent with a long-term change of in the behavior of nests in this population that was first demonstrated by DeHeer et al. (2001), that is the ant nests were primarily monodomous and polygynous but are now polydomous with lower queen numbers. The near-line decline in proportion of queenright colonies from 1992 through 1998 confirms DeHeer et al.'s (2001) inference based on microsatellite data and clearly shows that major changes in this species, life history were occurring during our experiment.

What is unclear from these data is whether the pattern of nest movement that we saw was due to seasonal polydomy (colony fission followed by fusion within a season) or re-

flects year round polydomy. Nest movement occurs early in the summer when nests are being established, with a second burst of movement in late summer. This temporal pattern of movement is partially driven by this species's over-wintering strategy; ants over-winter underground (Snyder and Herbers, 1991) so the early burst of immigration reflects ants moving from underground to above ground cavities, while the late burst of emigration reflects ants moving back underground. Thus the over-wintering strategy of this species would obscure the expected temporal pattern of seasonal polydomy.

In addition, we found mixed supporting evidence for seasonal polydomy based upon the expected cyclical changes in the proportion of queenright nests and worker numbers. There was an expected increase in number of workers per nest in late summer for 2 of the 3 seasons. This increase in number could be due to the eclosion of new workers from the current year's brood. It may be that polydomy is simply not seasonal in this population, but this would be somewhat surprising given that a well studied polydomous population (from Vermont) is seasonally polydomous (Snyder and Herbers, 1991). However, because polydomy was not as prominent here as it was in Vermont (DeHeer et al., 2001), our statistical power for detecting these seasonal changes in nest demography was necessarily more limited. Furthermore, previous studies have found that the most dramatic shifts in nest demography within seasonally polydomous populations occurred between April to May, and between August to September (Snyder and Herbers, 1991). Because we did not sample during April or September in the current study, we may have missed the largest shifts in demography, which would implicate seasonal polydomy.

Issues of seasonality of the observed polydomy aside, why would *M. punctiventris* change its behavior so dramatically such that a monodomy population has become suddenly polydomous? Snyder and Herbers (1991) reported predation on *M. punctiventris* workers and brood during nest movement, implying substantial costs to this behavior. If the movement patterns that we observed are indeed a result of a shift from being non-polydomous to polydomous it is possible that workers orchestrate colony fractionation in order to escape queen control over sex allocation (Snyder and Herbers, 1991; Banschbach and Herbers, 1996b). This hypothesis is supported by data from the VT population of *M. punctiventris* (Snyder and Herbers, 1991), but it has poor explanatory power for the NY population, for which no difference in sex allocation between queen-right and queenless nests occurs (DeHeer et al., 2001). Thus, if the movement that we have observed is due to an increase in the rate of polydomy shown over time by *M. punctiventris* in NY it cannot be explained by a change in the balance of power in queen-worker conflict over allocation ratios.

Other authors have proposed that both wholesale nest relocations and polydomy can occur when food resources become exhausted around the nest (Herbers and Tucker, 1986; Traniello and Levings, 1986). Yet we found that food supplementation had virtually no effect on nest movement (unpubl. data), which renders this explanation unlikely.

Decline in nest quality has also been proposed as a reason for ants to move nests (Foitzik and Heinze, 1998). We do not doubt that nest site quality degrades over time and can prompt colony migration, but it must contribute only weakly to the high rates of migration we observed: 16% of the dowels were occupied only once whereas others were occupied on-and-off the entire 3 years of our study. We could not tie that variation in occupancy to any indicators of nest site quality, since all dowels were prepared in the same way.

Banschbach and Herbers (1999) suggested that seasonal fission reflects the colony's need for more space as brood matures and workers eclose. Certainly for *M. punctiventris*, we found that nests rearing the very large sexual pupae moved more often than nests without sexual pupae. In addition, the shift from low to high polydomy over several years in this species coincided with this population shifting its sex allocation ratio from one that produced mostly males to one that produced mostly females, which are nearly three times heavier (DeHeer et al., 2001). Another possibility suggested by DeHeer et al. (2001) was that lower queen numbers and increased polydomy reflected an increased rate of new colony foundation by single queens (single-queen colonies are often polydomous in this species), which in turn has been driven by the greatly increased production of female sexuals. Patterns of sex allocation are more consistent with this latter hypothesis. First, 1996 was an extremely productive year, with nests producing on average more than four times as many new queens and twice as many new males as in 1998 (unpublished data). Nevertheless, based on the frequency of queenless nests, colonies were significantly more polydomous in 1998 than 1996. In contrast, if increased rates of new colony foundation are responsible for the changes in polydomy, we predict that the effect will be delayed several years while incipient colonies grow large enough to split into polydomous units, and this prediction is more consistent with the gradual increase in polydomy from 1996 through 1998 in the face of declining production of new queens. However, what drives changes in sex allocation is not yet understood.

It is clear that behaviors that are commonly thought to be separate, such as sexual allocation strategies and nest movement, are linked in social insects. Indeed, in depth study of a single species over multiple locations and times show that ants have remarkably labile life histories. Single time or location "snapshots" of many species may lead to erroneous conclusions about their behavior. Researchers need to be aware of the need for long-term studies of life history traits.

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