

Demography and Reproduction in the Cavity-dwelling Ant *Stenamma diecki* (Emery) (Hymenoptera: Formicidae)

Vickie L. Backus^{1,*} and Joan M. Herbers²

Abstract - *Stenamma diecki* is a small ant with a widespread distribution. Systematic plot excavations in two locations have allowed us to collect data on a large number of *S. diecki* nests in order to examine seasonal and spatial differences in nest demography and allocation decisions within this species. Populations of this species from New York and Vermont nest in cavities far more commonly than has been reported, and thus we could compare our results with data on this species and with patterns of demography and reproduction for two other well-studied cavity-dwelling ants. We found nests were monogynous at all locations, but showed considerable variation in mean queen number and mean worker number. Most nests did not produce any males or reproductive females in a season, and this pattern was also site specific. Sexual and reproductive allocation was similar for all sites tested. Finally, demographic patterns within a site over 3 seasons are consistent with those predicted by seasonal polydomy.

Introduction

Stenamma diecki (Emery) (subfamily Myrmicinae, tribe Stenammini) is a small, cavity- and soil-dwelling ant with a widespread distribution in the US and southern Canada (Bolton et al. 2007). Its small size and cryptic habits have meant that few researchers have reported on its natural history. Cole (1940) reported that it is typically found in wet forests and *Picea rubens* Sarg. (Red Spruce) forests in the Great Smoky Mountains National Park. Subsequent reports have confirmed this habitat preference in populations as far north as near Montreal, PQ, Canada (Francoeur 1965, 1966; Letendre and Pilon 1972) and across the US, including Michigan (Talbot 1975) and California (Smith 1957, Snelling 1973). Where nests have been censused, worker numbers are typically low (mean worker number ranges from 31.8 per nest [Francoeur 1965] to 56.0 per nest [Talbot 1975]). Nests are generally headed by a single queen (Francoeur 1965, Letendre and Pilon 1972, Talbot 1975), although 0 queen nests are occasionally found (Letendre and Pilon 1972); polygyny seems to be absent from this species (Talbot 1975).

While these reports seem to provide a complete description of the natural history for this species, they have several limitations. In all cases, sample size is low: $n = 7$ in Francoeur (1965), $n = 10$ in Letendre and Pilon (1972), and $n = 15$ in Talbot (1975). In these studies, the collection of nests was made using a non-systematic sampling scheme, and in two cases (Letendre and Pilon 1972, Talbot 1975), over a time span of several years.

¹Department of Biology, Middlebury College, Middlebury VT 05753. ²Department of Evolution, Ecology, and Organismal Biology, Aronoff Laboratory, OH State University, 318 West 12th Avenue, Columbus, OH 43210. *Corresponding author - backus@middlebury.edu.

Recent work in northeastern temperate forests have shown that important nest parameters such as number of queens, number of workers, and both sexual and reproductive allocation ratios can vary both in time and space for a guild known as the small, cavity-dwelling, northern temperate forest ants. Two species in particular have been well studied: *Temnothorax* (formerly *Leptothorax*) *longispinosus* (Roger) (Backus 1995, Herbers 1990), and *Myrmica punctiventris* Roger (Backus et al. 2006; Banschbach and Herbers 1996a, b; DeHeer et al. 2001). Detailed analysis of these two species has shown that reports focused on a single season, a single location, or with low sample sizes such as those listed above for *S. diecki* may miss important patterns in temporal and geographic variation in basic life-history traits for a species.

Systematic plot excavations in New York and Vermont starting in 1980 by our laboratory have allowed us to collect data on a large number of *S. diecki* nests, far exceeding the data available in the literature. Analysis of these data and comparison with the published data on other cavity-dwelling ants from the northern temperate forest will allow us to present a clearer picture of the natural history of this small ant. In this paper, we examine seasonal and spatial differences in nest demography and allocation decisions within this species in order to present a more complete representation of its natural history.

Methods

Table 1 shows the sources of the data we have included in this analysis; data are available in **Supplemental File 1 (available only online at <http://dx.doi.org/10.1656/N695.s1>)**. Collection methods for each of the sources varied. The data obtained from nests in Quebec (Francoeur 1965, Letendre and Pilon 1972) as well as the nests collected in Michigan (Talbot 1975) were collected at large.

The new data reported here used a systematic nest-excavation technique described elsewhere (Herbers 1990). Two locations were extensively sampled: the Edmund Niles Huyck Preserve in Albany County, NY and Mallet's Bay (now Niquette Bay) State Park in Chittenden County, VT. Briefly, at each location, 25-, 36- or 49-m² plots were set up, and every potential nesting place was examined for ants. While our sampling methods are not designed to explicitly detect soil-nesting species, all litter was

Table 1. Data sets used in this study. Nests are defined as those that contain at least 1 queen and ≥ 1 worker or 0 queens and ≥ 5 workers.

Site	Source	Number of defined nests
Michigan	Talbot 1975	12
Quebec	Francoeur 1965, Letendre and Pilon 1972	9
New York	Our data	101
Vermont	Our data	58

removed from the forest floor, and the bare soil was observed for the presence of ants. Typically, *S. diecki* nests located in soil are superficial and located underneath a covering rock or piece of wood (Smith 1957), and we are confident that we have been able to find the majority of the nests in each plot. The type of nest material being used was recorded at the time of collection. Nests were brought, intact, to the laboratory where the species identity was confirmed and the nests were censused. The census data we analyzed below includes: number of dealate queens, number of workers, number of male pupae and adult males, number of queen pupae and virgin queens, and number of worker pupae. We weighed individual dealate queens, males, and alate queens from several nests. Voucher specimens have been deposited in the collection maintained by the University of Vermont (Burlington, VT) and in J.M. Herbers' personal collection.

These counts and weights were used to determine several commonly reported socio-biological measures. The number of dealate queens in a nest is a measure of that nest's gyny level; monogynous nests are defined as those with 1 queen present, whereas nests with greater than 1 dealate female are defined as being polygynous. Worker number is a standard estimate of the size of the nest. There are two commonly calculated investment ratios that are reported for ant nests. The first, the sexual investment ratio is the biomass of males reared relative to total biomass of new sexuals corrected by the individual female:male energetic cost ratio (Boomsma 1989). For this analysis, we used the energetic cost ratio published by Trivers and Hare (1976). The second investment ratio is the reproductive allocation ratio, calculated as the biomass of both male and female sexuals reared relative to all new biomass, including workers; this calculation estimates the nest's investment in reproduction compared to growth (Herbers and Banschbach 1998).

Preliminary examination of the data showed that some of the nests brought to the laboratory were very small with no queens present, which may represent transient groups of foragers. Thus, in order to be conservative, we have chosen to limit the analysis to nests that had either: at least 1 queen and ≥ 1 worker or 0 queens and ≥ 5 workers. Incipient nests (those with just 1 queen) were excluded from the analysis. For this analysis, we use the word nest to refer to a group of individuals, as defined above, which occupies a place at the same time. Colonies represent a group of genetically related ants that may occupy multiple nests. Since we have not undertaken a detailed genetic analysis of this species, we are able to present data for nests only. For many of the sites and years data had been collected for fewer than 10 nests, requiring us to combine sets for years in order to ask questions about site effects on nest demographics. Preliminary analysis showed that there was no effect of year on nest demography (V.L. Backus and J.M. Herbers, unpubl. data), and thus we are confident that we are not confounding questions of the effect of site with the effect of year in this analysis.

Results

Over the years, we excavated 73 plots in NY and 54 in VT. We found *S. diecki* nests in 37 and 26 of those plots, respectively. Most plots had no *S. diecki* nests, while a few had high density (Fig. 1). To determine if nests were distributed in space randomly, we compared the observed number of nests per plot with those expected if nests were distributed randomly under a Poisson distribution. The difference between the observed number of nests and expected was significantly different for both sites (NY: $\chi^2 = 127.10$, $df = 3$, $P < 0.001$; VT: $\chi^2 = 89.74$, $df = 3$, $P < 0.001$ for nests collected in the summer only). This species therefore has a patchy spatial distribution, and we were unable over the years to tie its occurrence to any obvious ecological variable such as litter depth, canopy cover, or soil moisture. Rather, nests occur in some parts of the forest and not in others; such a patchy distribution is the rule rather than the exception for this guild of forest ants.

Previous studies have reported that the preferred nest material for *S. diecki* is in shallow soil nests or in the soil under rocks and logs (Cole 1940, Smith 1957), and the data from MI and PQ sites confirm these reports. In contrast, we found 67.7% of the NY nests and 87.5% of the VT nests were in cavities (empty nuts, empty acorns, and intact sticks) compared to non-cavity sites (litter, soil, or rotten sticks). There was a significant difference between the NY and VT populations ($G = 7.76$, $df = 1$, $P < 0.05$) with VT nests being in cavities more often than their NY counterparts.

There was a wide difference in the mean number of queens found in the nests for the sites (Fig. 2A). At each site, except PQ, a few nests had more than 1 queen present. Nests in NY and VT tended to have more nests with 0

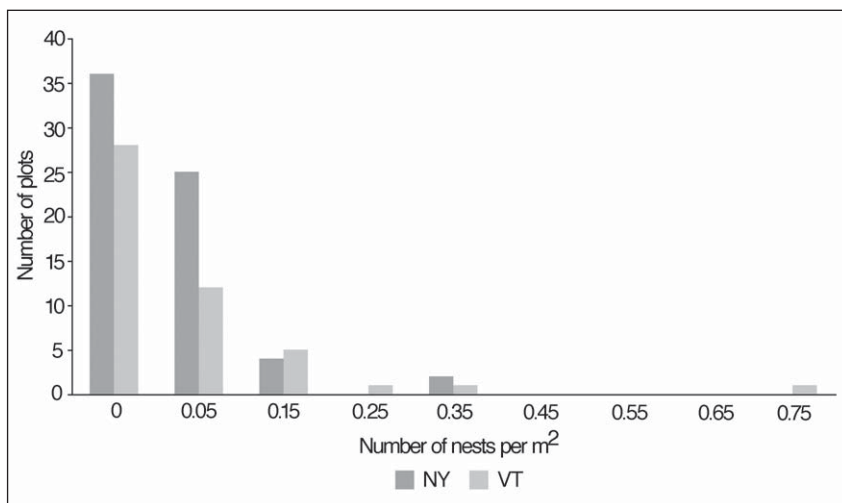


Figure 1. Density of nests per m² for the NY and VT sites. The number of plots sampled was 73 in NY and 54 in VT.

queens than those in MI or PQ. A G test of Independence showed that queen presence was site specific ($G = 24.36$, $df = 6$, $P < 0.001$) with the NY and VT sites having more 0 queen nests than reported for other sites.

Worker number was also variable between the sites. Nests from PQ and MI were larger than nests from VT and NY (Fig. 2B) ($F = 17.16$, $P < 0.0001$). The mean number of workers was similar for nests from MI and PQ and nests from VT and NY were similar in size and significantly smaller than those from MI and PQ.

As with the demographic measures, patterns of production were quite variable for new females, males, and workers (Table 2). While most nests produced some offspring each year, a small proportion of the nests in NY and

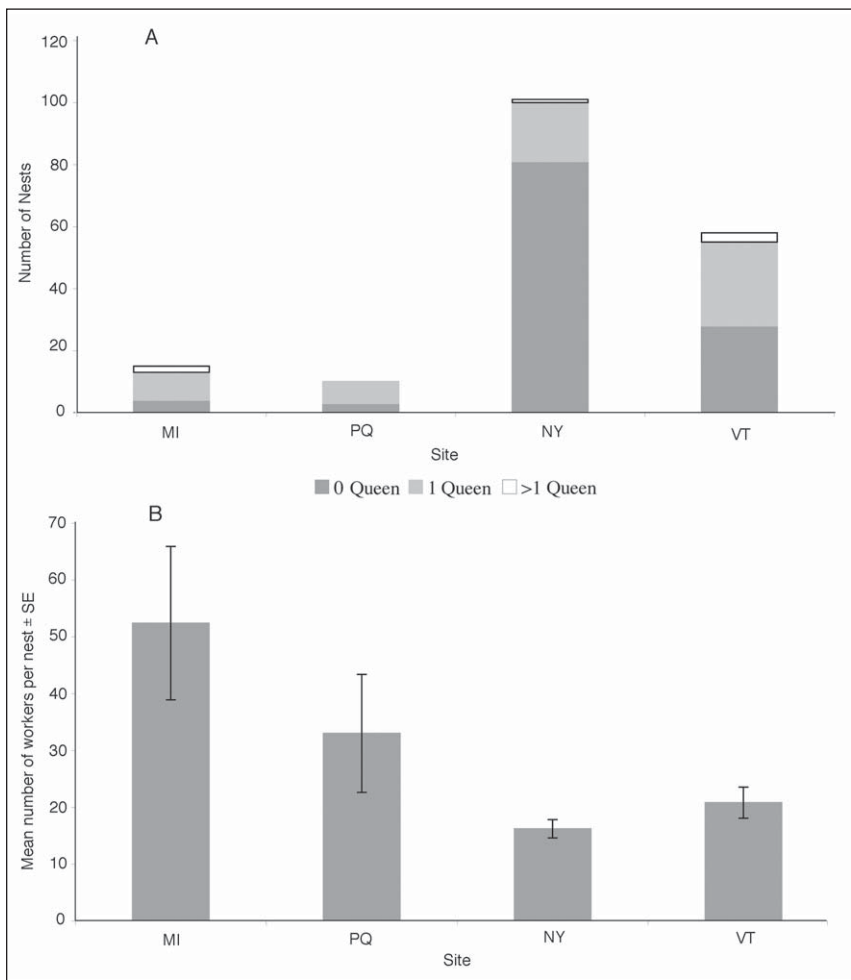


Figure 2. Nest demographic patterns for the 4 sites. A. Number of nests at each location that contained 0 queen, 1 queen, or >1 queen. B. Mean \pm SE number of workers per nest.

VT failed to rear any brood to eclosion in a season. Following the classification used by Herbers (1990), we assigned each nest to a producer class: none (produced 0 sexuals), minor (produced 1–4 sexuals) or major (5 or more sexuals produced). Due to sample size problems (Fig. 3), only nests from VT and NY were statistically compared to determine if there was an effect of site on sexual production. Nests from Vermont were assigned to the major producer class more often than nests in NY, which tended to show very little reproduction ($G = 15.25$, $df = 2$, $P < 0.05$).

Two additional measures were calculated: sex allocation and reproductive allocation. In order to reduce the skewing of the data by nests that produced very few sexuals we used the convention of Herbers (1990) to determine allocation patterns for nests only in the major producer class. Low sample size meant that nests from PQ were excluded from the analysis. While it appears as if the nests from NY produced slightly more males than females (Fig. 4A), there was no significant difference in sexual allocation between the 3 sites tested (ANOVA on arcsine transformed proportions $F = 2.94$, $P > 0.05$). In addition, there was no effect of site on the allocation of resources between

Table 2. Production data for the MI, NY, and VT sites. Values are the percent of nests producing at least 1 offspring of each type. The PQ site has not been included due to low sample size.

Type of offspring	MI	NY	VT
Males	69.2	42.7	60.7
Females	61.5	25.6	57.1
Workers	100.0	85.4	89.3
No brood	0.0	11.0	5.3

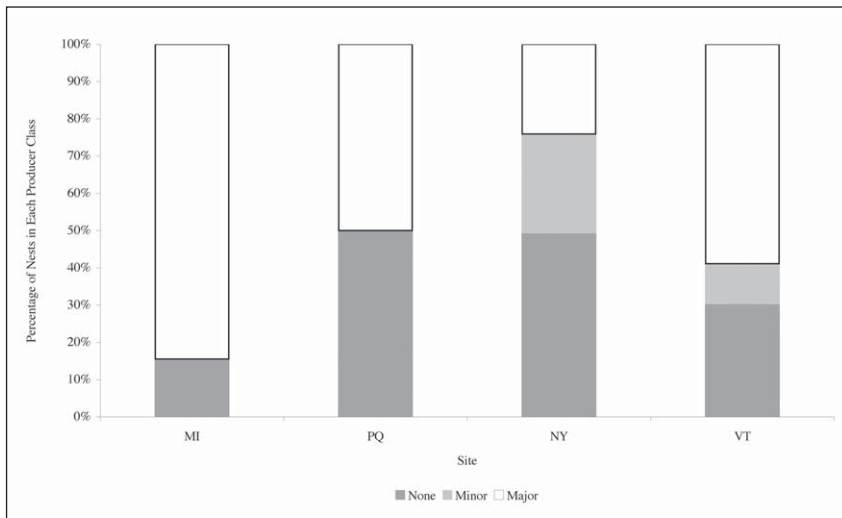


Figure 3. Percentage of nests in each producer class at each site. Classes are defined as follows: none = no reproductives produced that season, minor = 1 to 4 reproductives produced that season, and major = 5 or more reproductives produced that season.

sexual production and growth (new workers) (Fig. 4B) (ANOVA on arcsine transformed proportions $F = 0.83$, $P > 0.05$).

One explanation for the nest size differences observed between the populations may be geographic variation in seasonal polydomy. Polydomy occurs when colonies fragment to occupy multiple nest sites at one time. Colonies can be polydomous year round or seasonally; in the latter case, colonies divide into subunits during the spring and fuse into a single nest before overwintering. Sample sizes across seasons were sufficient for the demographic analysis of NY nests only. The data show a pattern consistent

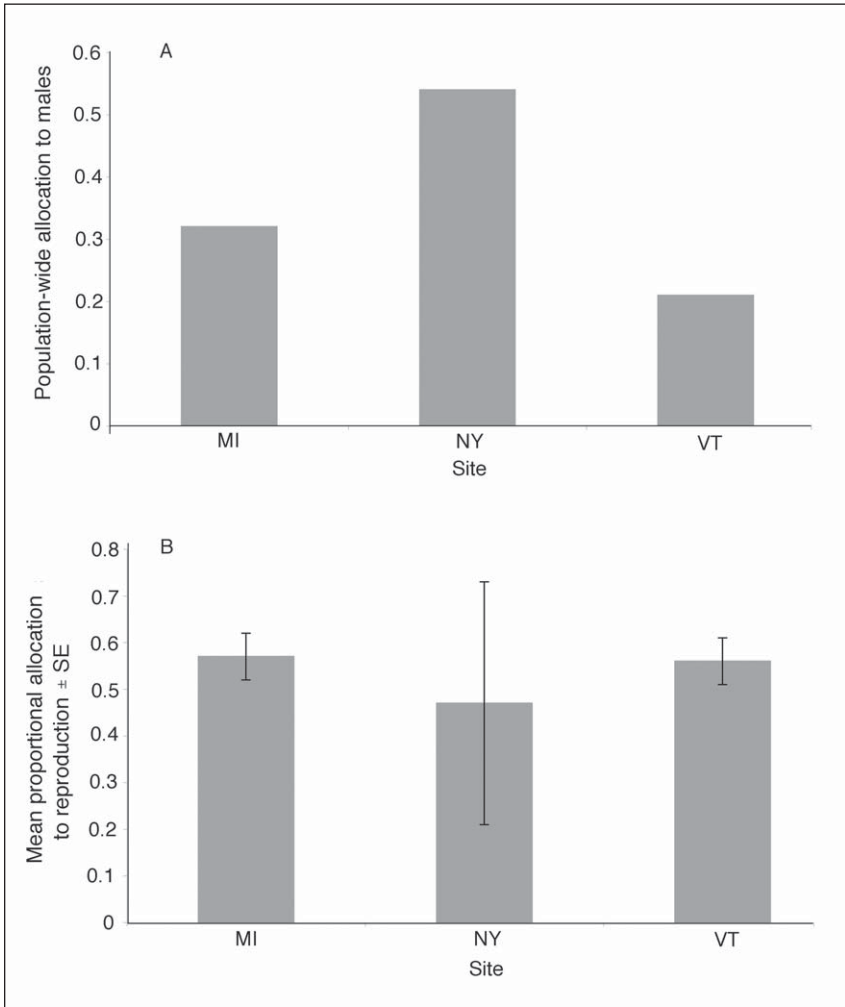


Figure 4. Allocation in nests during a season. A. Population-wide proportional investment in males based on dried weight. $P(m) = 1.0$ means that all sexual biomass was invested in males. B. Mean \pm SE. proportional investment in sexuals based on dried weight. $PR = 1.0$ means all new biomass produced was invested in sexuals with no growth (workers) produced.

with that predicted by a model of seasonal polydomy (Fig. 5 A, B), that is, nests have significantly more queens and more workers in the spring and in the autumn (during the coalescent phase of polydomy) and fewer queens and workers present in the nest during summer when the colony has undergone fission (ANOVA on square root transformed number: Queens— $F = 4.09$, $P = 0.02$; Workers— $F = 10.62$, $P < 0.0001$).

Discussion

The data presented here allow us to add to the existing body of knowledge concerning the natural history of *Stenemma diecki* and allow us to suggest some fruitful directions for future studies on this ant.

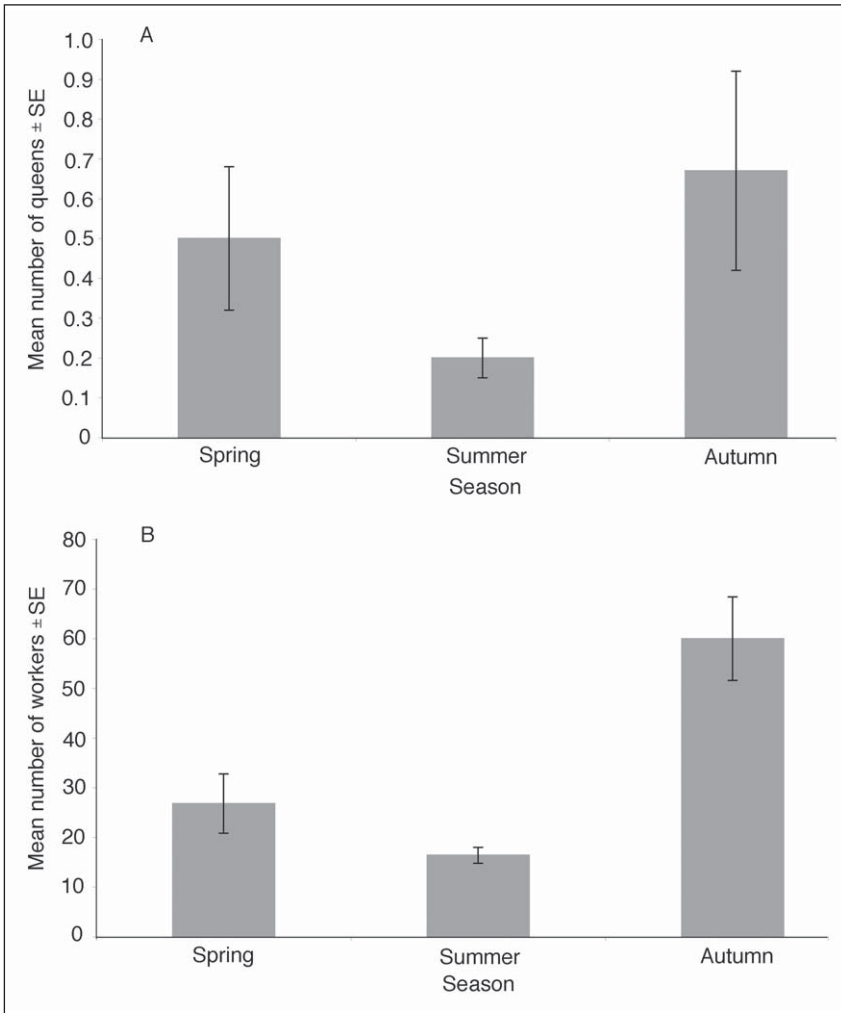


Figure 5. Nest demography for NY nests only over 3 seasons. A. Mean \pm SE number of queens per nest. B. Mean \pm SE number of workers per nest.

Our data represent an order of magnitude more nests than have previously been reported in the literature. Furthermore, by using a systematic collection scheme, we have a more complete idea of the range of nesting behavior and demography for this species than hitherto available. The results show that *S. diecki* uses cavities (empty nuts, empty acorns, and hollow, intact sticks) much more often than has been previously reported. Thus, this species clearly belongs to the guild of northeastern, temperate forest, cavity-dwelling ants that has been the focus of our research starting with Herbers (1986). Species in this guild have been well characterized on several important life-history traits, and we proceed to compare our results on *S. diecki* to species better known.

S. diecki nests tend to have 0 or 1 queen; multiple-queen nests occur only rarely. Indeed, Talbot (1975) concluded that this species was monogynous in spite of data showing that 2 of the 15 nests she collected had >1 queen. Our larger collections from VT and NY show that the proportion of multiple-queen nests in each population is very low but detectable. Talbot (1975) attributed the extra queens as new alates that were produced during that year; while reasonable, testing this hypothesis will require dissection and genetic analysis.

The absence of clear evidence of polygyny in this species is somewhat surprising given both the widespread existence of polygyny in other cavity-dwelling ants from the same locations that we sampled, including: *Temnothorax longispinosus* (Herbers 1990), *T. ambiguus* (Emery) (Herbers and Grieco 1994), and *Myrmica punctiventris* (Banschbach and Herbers 1996a). Polygyny is a remarkably labile trait (c.f. Herbers 1993) and its causes and consequences are not well understood. Indeed populations of a single species (*M. punctiventris*) reported on here at the NY site have changed in their tendency to be polygynous over time (Backus et al. 2006, DeHeer et al. 2001); thus, it will be interesting to follow *S. diecki* to see if queen number is labile in this species as well.

We found strong geographic variation in the number of workers in a *S. diecki* nest. In large part, the differences in demography between MI and PQ populations and the VT and NY populations probably reflect collecting technique. Our systematic plot excavation methods in NY and VT insured that smaller nests were collected, whereas larger, more obvious nests were undoubtedly over-represented from MI and PQ.

On the other hand, geographic variation in nest demography is well documented for other cavity-dwelling temperate forest ants collected in these sites (Banschbach and Herbers 1996a, Herbers 1990) and it is possible that the differences between the MI and PQ populations and the NY and VT nests may be confirmed by systematic collection in the first two locations. Thus, more research is needed in order to understand how site affects demography in this guild.

One-third to one-half of *S. diecki* nests failed to rear any sexuals in a given year. Failure to reproduce may reflect the high cost of rearing

reproductives; it may be difficult for these small ants to accumulate enough resources to produce new males and females. Indeed, for a small proportion of nests, it seemed that producing any brood during a season was difficult. This interpretation is supported by our observation that VT nests had more major producers and fewer nests that failed to produce any brood than NY nests. The VT ant community is richer and denser than the NY community (Herbers 1989), and this robustness may be a function of increased resource availability at this location.

Given that life-history allocation decisions for social insects are often affected by location (Backus 1995, Herbers 1990), we were surprised to find no effect of site on either proportional allocation to males or allocation to reproduction. One reason for this result may be lack of statistical power. Studies of sex allocation and reproductive allocation in social insects require large sample sizes (Crozier and Pamilo 1996) and application of sophisticated multivariate techniques (Backus 1995). Our relatively small number of nests in any given season allowed us to ask only the simplest of questions from our data. Therefore a fuller understanding of what determines life-history allocation decisions in this species must await a much larger effort.

We provide strong evidence here, for the first time, that *S. diecki* colonies exhibit seasonal polydomy. This process is characterized by colonies that undergo fission in the summer to occupy multiple cavities and then coalesce in the autumn to overwinter. There are three lines of evidence to support an inference of seasonal polydomy for this species. Firstly, the non-random, patchy distribution of nests is characteristic for species that exhibit seasonal polydomy as satellite nests tend to be located close to the main nest. Secondly, the large number of queenless nests found in VT and NY are consistent with polydomy, with monogynous colonies including many satellite nests with workers and brood but no queen. Finally, the demographic patterns shown in Figure 4 clearly show that nests are bigger in the spring (after overwintering underground) and again in the autumn (prior to returning underground to overwinter) than in the summer. An alternative explanation for the demographic shifts from summer to autumn involves eclosion of new workers and adoption of newly mated queens by orphaned nests in the autumn. The only alternative explanation, however, for the change in demography from spring to summer is extremely high (and unlikely) worker mortality. In addition, preliminary microsatellite data (V.L. Backus and J.M. Herbers, unpubl. data) are consistent with those expected if nests undergo late spring fission followed by autumn fusion and lend support to a hypothesis that *S. diecki* undergoes seasonal polydomy. Thus, we are confident that *S. diecki*, like so many other species in its guild, has colonies that display an annual cycle of subdivision and recoalition.

Polydomy is a common phenomenon in cavity-dwelling ants and differences in levels of polydomy between populations in a species are accompanied by broad-scale differences in social organization (Bansbach

and Herbers 1996a, b). Changes in a population's pattern of polydomy can be accompanied by dramatic changes in social organization including sexual allocation strategies (Backus et al. 2006). Thus, long-term studies on polydomy in this species may be fruitful.

The cavity-dwelling ants of the north temperate forest are a remarkable group of ants. Long-term studies of multiple populations reveal interesting patterns for practically all life-history traits examined. Our data show that *S. diecki* fits firmly within this guild, and therefore it is likely that additional long-term studies of this species will prove useful for additional insights into forest ant ecology.

Acknowledgments

Funding for this research has been provided to J.M. Herbers from the National Science Foundation and to V.L. Backus from the Edmund Niles Hyuck Preserve and Middlebury College.

Literature Cited

- Backus, V.L. 1995. Rules for allocation in a temperate forest ant: Demography, natural selection, and queen-worker conflict. *American Naturalist* 145:775–796.
- Backus, V.L., C. DeHeer, and J.M. Herbers. 2006. Change in movement and subdivision of *Myrmica punctiventris* (Hymenoptera, Formicidae) colonies in north temperature forests is related to a long-term shift in social organization. *Insectes Sociaux* 53:156–160.
- Banschbach, V.S., and J.M. Herbers. 1996a. Complex colony structure in social insects: I. Ecological determinants and genetic consequences. *Evolution* 50:285–297.
- Banschbach, V.S., and J.M. Herbers. 1996b. Complex colony structure in social insects: II. Reproduction, queen-worker conflict, and levels of selection. *Evolution* 50:298–307.
- Bolton, B., G. Alpert, P.S. Ward, and P. Maskrecki. 2007. Bolton's Catalogue of the Ants of the World. 1758–2005. CD-ROM. Harvard University Press. Cambridge, MA. Released February 28, 2007.
- Boomsma, J.J. 1989. Sex investment ratios in ants: Has female bias been systematically overestimated? *American Naturalist* 133:517–532.
- Cole, A.C. 1940. A guide to the ants of the Great Smoky Mountains National Park, Tennessee. *American Midland Naturalist* 24:1–88.
- Crozier, R.H., and P. Pamilo 1996. *Evolution of Social Insect Colonies: Sex Allocation and Kin Selection*. Oxford Series in Ecology and Evolution. Oxford University Press, New York, NY. 314 pp.
- DeHeer, C.J., V.L. Backus, and J.M. Herbers. 2001. Sociogenetic responses to ecological variation in the ant *Myrmica punctiventris* are context dependent. *Behavioral Ecology and Sociobiology* 49:375–386.
- Francoeur, A. 1965. Écologie des populations de fourmis dans un bois de chênes rouges et d'érables rouges. *Le Naturaliste Canadien* XCII:263–276.
- Francoeur, A. 1966. Le genre "*Stenammas*" Westwood au Québec (Hymenoptera, Formicidae). *Annals of the Entomological Society of Quebec* 11:115–119.

- Herbers, J.M. 1986. Nest site limitation and facultative polygyny in the ant *Leptothorax longispinosus*. Behavioral Ecology and Sociobiology 19:115–122.
- Herbers, J.M. 1989. Community structure in north temperate ants: Temporal and spatial variation. Oecologia 81:201–211.
- Herbers, J.M. 1990. Reproductive investment and allocation ratios for the ant *Leptothorax longispinosus*. American Naturalist 136:178–208.
- Herbers, J.M. 1993. Ecological determinants of queen number in ants. Pp. 263–293, In L. Keller (Ed.). Queen Number and Sociality in Insects. Oxford University Press, Oxford, UK. 546 pp.
- Herbers, J.M., and V.S. Banschbach. 1998. Food supply and reproductive allocation in forest ants: Repeated experiments give different results. Oikos 83:145–151.
- Herbers, J.M., and S. Grieco. 1994. Population structure of *Leptothorax ambiguus*, a facultatively polygynous and polydomous ant species. Journal of Evolutionary Biology. 7:581–598.
- Letendre, M., and J.-G. Pilon. 1972. Écologie des populations de *Leptothorax longispinosus* Roger et *Stenamamma diecki* Emery dans les peuplements forestiers des basses Laurentides, Québec (Hymenoptera: Formicidae). Le Naturaliste Canadien 99:73–82.
- Smith, M.R. 1957. Revision of the genus *Stenamamma* Westwood in American north of Mexico (Hymenoptera: Formicidae). American Midland Naturalist 57:133–174.
- Snelling, R.R. 1973. Studies on California ants 7. The genus *Stenamamma* (Hymenoptera: Formicidae). Contributions in Science, Natural History Museum of Los Angeles County 245:1–38.
- Talbot, M. 1975. Habitats and populations of the ant *Stenamamma diecki* Emery in Southern Michigan. Great Lakes Entomologist 8:241–244.
- Trivers, R.L., and H. Hare. 1976 Haplodiploidy and the evolution of the social insects. Science 191:249–263.