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Research article

Settlement and distribution of colony-founding queens of the arboreal ant, *Crematogaster ashmeadi*, in a longleaf pine forest

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Abstract

Crematogaster ashmeadi is the dominant arboreal ant occurring on longleaf pines in the Apalachicola National Forest of northern Florida. Newly-mated *C. ashmeadi* queens preferentially founded colonies in abandoned beetle galleries in the dead branches of longleaf pine saplings. There was a positive association between the frequency of queens in trees, several size-related tree characteristics and the amount of insect boring activity in dead branches. The dispersion of newly-mated queens among trees was clumped, suggesting that these queens selected founding sites according to their suitability for colony founding, and that these favorable characteristics were clumped among saplings. The occurrence of founding nests was not related to the prior presence of other ants on the tree. Survival of incipient colonies during the first year was low (7.6%), and their dispersion was not different from random. One possible explanation for this change in dispersion over the year is aggressive interference competition between incipient colonies, although random mortality cannot be discounted. Overall, the distribution of young *C. ashmeadi* colonies in longleaf pine saplings was probably determined by several factors including: the distribution of saplings, the distribution of suitable founding sites within these saplings, and aggressive interactions among incipient colonies, conspecifics and heterospecifics. *C. ashmeadi* probably gains dominance through a combination of early colonization and aggressive interference competition.

Introduction

Crematogaster ashmeadi (Mayr) is an arboreal ant that nests in longleaf pine trees throughout the southeastern United States (Johnson, 1988). *C. ashmeadi* is the dominant arboreal ant in the Apalachicola National Forrest occupying roughly 50% of all pine trees (Tschinkel and Hess, in prep.) Like other dominant species (Greenslade, 1971; Room, 1971; Leston, 1973; Majer, 1976; Taylor, 1977; Cole, 1983; Savolainen and Vepsalainen, 1988; Hölldobler and Wilson, 1990; Tschinkel and

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Hess, in prep.), *C. ashmeadi* may play a large role in structuring the ant community in the longleaf pine forest. In areas where the distribution of the ant overlaps with that of the endangered red-cockaded woodpecker (*Picioides borealis*) its workers are a primary food item, making up 80% of the ingested arthropod biomass (Hess, 1997). The Apalachicola National Forest, the site of our study, contains the largest population of these woodpeckers. Because of its role in the diet of the woodpecker, study of *C. ashmeadi* may lead to a better understanding of the requirements of the bird and therefore to improved management.

Colonies of *C. ashmeadi* are relatively large and monogyne, and when mature, occupy a single tree each (W. R. Tschinkel, unpubl.). During the summer months mature colonies release sexuals (Deyrup and Trager, 1986). After mating, the females disperse to found new colonies. Singly, they seek out the abandoned galleries created by wood-boring beetles in the dead branches of young longleaf pines, seal themselves inside and raise the first brood of workers from their own storage tissues. This type of colony founding is termed haplometrotic and claustral (Hölldobler and Wilson, 1990). The period of site selection and colony founding is a particularly dangerous time during which newly mated queens of many species suffer high mortality (Whitcomb et al., 1973; Hughes, 1974; Rissing et al., 1986; Tschinkel, 1992).

Many authors have focused on the role competition plays in the structuring of arboreal ant communities, especially those associated with tree corps (Room, 1971; Majer, 1976 a, c; Leston, 1978; Taylor, 1977). However, few studies have focused on the role of habitat requirements and nest-site availability in structuring ant communities (Greenslade, 1979; Herbers, 1986, 1989; Majer, 1976 c). Habitat requirements may determine whether a site is suitable for colony founding and thus will be settled. For example, Rissing et al. (1986) determined that aggregation of newly inseminated *Acromyrmex versicolor* (Pergande) queens to sites under desert shrubs was caused by the relative ease of chamber excavation in the damp earth found there. This aggregation of newly mated queens affected the eventual distribution of mature colonies. Similarly, Cole (1983 a) showed that minimum size of mangrove islands guide colonization by the dominant species of arboreal ants (*C. ashmeadi* and *Xenomyrmex floridanus* Emery), thereby asserting a profound effect on the distribution of these species.

The distribution of *C. ashmeadi* foundresses is probably determined by both the distribution of young pines and the occurrence of suitable sites for founding on these young pines. Because newly mated queens require cavities, only certain trees and certain branches on trees are suitable for founding. The aim of this study was to determine what characteristics were associated with settlement and survival of newly mated queens of *C. ashmeadi* during colony founding, and to provide a foundation for the study of colony distribution and the interactions of *C. ashmeadi* with the other members of the ant community of the longleaf pine forest.

Methods

Numbered trees

Four sites of mature longleaf pine (*Pinus palustris*) forest were selected in the Apalachicola National Forest between 20 and 45 km southwest of Tallahassee, Florida.

These were not random sites, but were purposely chosen in order to represent "natural" longleaf pine habitat with sufficient regeneration. In addition to mature trees each site contained 130–140 marked longleaf saplings between 2 and 10 cm diameter at breast height (DBH) and 2 and 12 m tall. The patchy nature of longleaf pine regeneration allowed marked trees to be grouped into several patches within each site. Site and patch size varied according to the natural distribution of the pine regeneration. Each sapling was labeled with an individual number and the following measurements were taken: tree height (m), DBH (cm), number of live branches and number of dead branches. These numbered trees were assumed to be representative of the population of young trees available for colony founding.

Baiting

To determine the presence of ants, all numbered trees were baited at the beginning of June 1995. A 1 cm disk of filter paper was dipped in a slurry of Alpo's Ocean Whitefish Treat cat food (2 parts) blended with water (1 part) and vegetable oil (0.5 parts) and was placed at breast height on both the north and south sides of all young trees. Baits were checked after 40–60 minutes and the species and number of foragers on the bait were recorded. All trees were baited again immediately prior to branch collection to determine the ant fauna on each tree at that time.

Sampling and analysis of dead branches

During the summer of 1995 sampling was carried out during three periods chosen to include the majority of the summer mating flights (June 27th – July 4th, July 25th – 31st, and August 29th – September 4th). During the summer of 1996 sampling for surviving colonies from 1995 was carried out during two periods that preceded the majority of the summer mating flights (May 6th – 16th, and May 23rd – June 4th). The presence and location of newly mated queens and incipient colonies was determined by removing all dead branches from a randomly chosen subset of twenty trees in each site during each of the three sampling periods in 1995 (239 trees) and the two sampling periods in 1996 (160 trees). The dead branches were brought back to the lab and stored in a cold room until they could be dissected. Each branch was dissected by stripping off all the bark to expose subcortical galleries and by splitting the wood and pith to expose deeper cavities. The following data were taken for each branch: tree of origin, height of the branch on the tree (m), length of the branch (cm), diameter of the branch at base (cm), approximate percent of subcortical gallerying, number of subcortical entrance holes into cavities in the pith or wood, the approximate percent of the pith removed, and the number and condition of all ants found. In addition, all other insects were also collected and preserved for later identification.

Patch mapping

Each patch of numbered trees was mapped using polar coordinates from a central stake. These polar coordinates were then transformed into Cartesian graphs to display the spatial distribution of trees and ants within a patch.

Statistical analysis

Exploratory data analysis was used to determine relationships between foundresses and characteristics measured at three different spatial levels; patches, trees, and branches. The dispersion of queens was tested against the Poisson distribution, and a coefficient of dispersion was used to determine the direction of the effect. Data were transformed to stabilize the variance where necessary. Since the relationships between founding nests and measured tree characteristics were not significantly different between sites, data were pooled for all four sites to provide a larger sample size for analysis. Analysis of variance, chi-square tests, and multiple regression analysis were used, as appropriate, to determine relationships between measured characteristics and the distribution of incipient colonies.

Results

Wood-boring insects

All insects found during dissection of branches were collected. Ants were identified to species, and beetles to genus. The following woodboring beetles were found: *Glyptoscelimorpha* sp. (Buprestidae), *Monochamus* sp. (Cerambycidae), and *Ips* sp. (Scolytidae). The galleries or pith-cavities of all but the smallest scolytids were used as founding chambers by newly-mated queens of *C. ashmeadi* (Fig. 1). Several non-wood-boring beetles were found: *Temnochila* sp. (Ostomidae), and *Thanasimus* sp. and *Pelonium* sp. (Cleridae). These were assumed to be predators of wood borers.

Patch mapping

All twenty-four patches of longleaf saplings were mapped (Fig. 2). In those patches with sufficient numbers of queens for statistical testing, queens were not randomly distributed among patches, but were clumped, so that some patches had more queens and some fewer than would be predicted by the Poisson distribution (Goodness of Fit test: $X^2 = 2540$, df = 10, $p < 0.001$; Coeff. of dispersion (CD) = 8.7, df = 10, $X^2 = 87$, $p < 0.001$).

Queen distribution, summer 1995

Of the 239 trees sampled, 78 (33%) contained queens, and 37 (16%) contained more than one queen, with a maximum of 16 queens on a single tree. Of the 1129 branches collected, 138 (12%) branches contained queens, and 31 (3%) of them contained more than one queen for a total of 197 queens.

Of the 239 trees baited, 103 trees (43%) showed no ants at baits. Of the remaining 136 trees that had foragers on baits, 49 (20% of all trees) had *Crematogaster ashmeadi* (Mayr); 36 contained other arboreal ants, primarily *Camponotus*

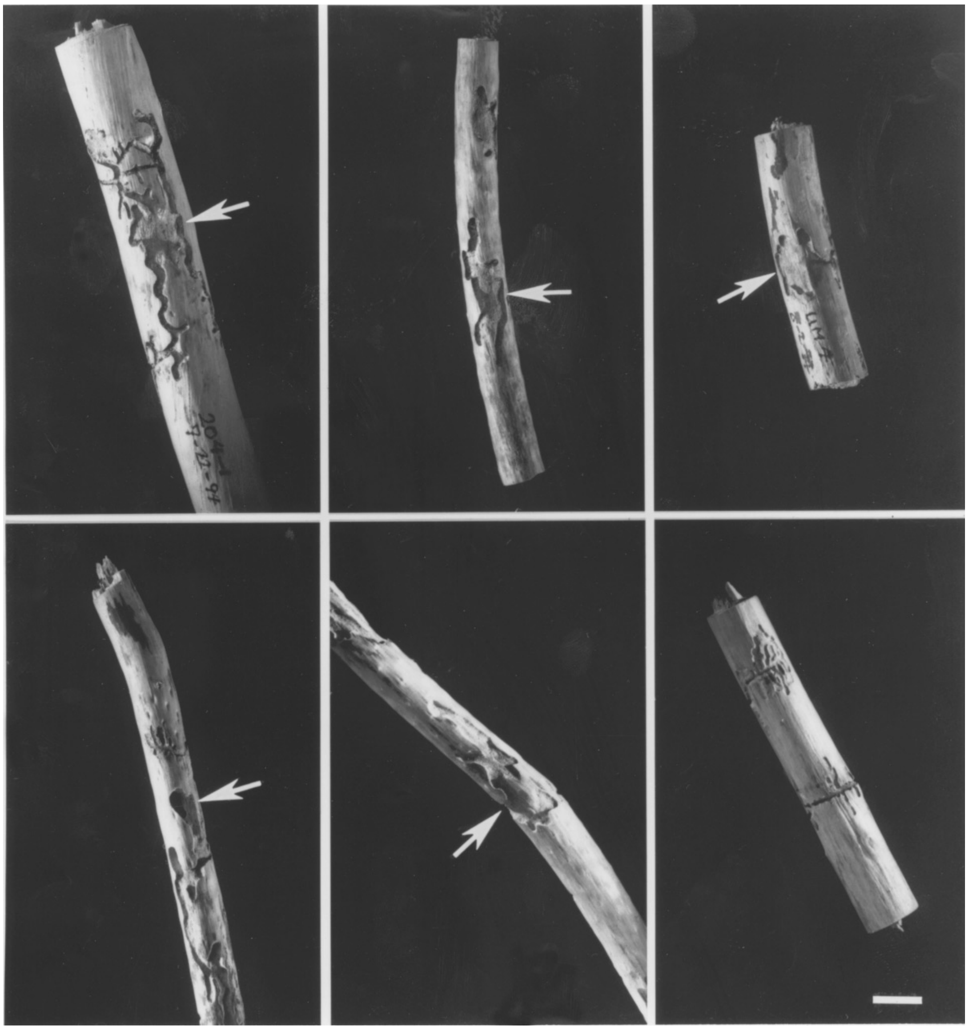

Figure 1. Sections taken from the dead branches of longleaf pine saplings and stripped of bark to show the types of galleries made by woodboring beetle larvae. The arrows indicate the locations of colony-founding queens of *Crematogaster ashmeadi.* Galleries in the lower right panel are too small to shelter queens. Scale bar at lower right indicates 1 cm

nearcticus (Emory) and *Solenopsis picta* (Emory), and 73 trees showed foraging activity by various ground nesting ants, most commonly *Pheidole anastasii* (Emory) (36 trees) but also occasionally *P. dentata* (Mayr), *Solenopsis geminata* (F.), *S. invicta* (Buren), *Monomorium viridum* (Brown), *Forelius humilis* (Roger) and *Camponotus floridanus* (Buckley). On a few occasions, two or more species of ant occurred on baits simultaneously. The distribution of newly mated queens was not significantly influenced by the presence of foragers of any species on the same trees, as

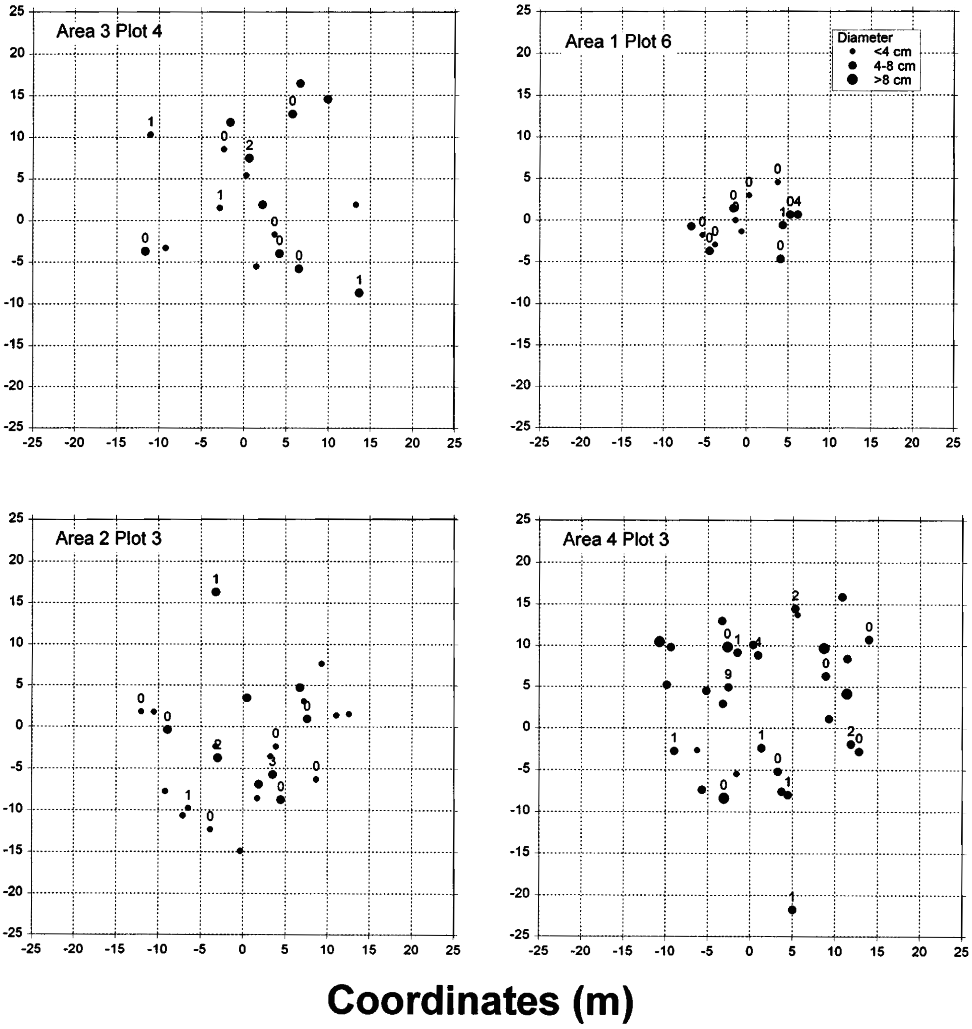

Figure 2. Maps of 4 representative patches of longleaf pine saplings, all to the same scale. The sapling size is indicated by the size of the symbol. The number above some of the symbols shows that the sapling was sampled and contained the indicated number of newly-mated queens. Saplings without numbers were not sampled

detected by baiting. Trees with ants foraging on baits did not have significantly fewer queens than trees without such foragers (Three way contingency table with absence or presence of newly inseminated queens, *C. ashmeadi* workers, and other ant workers: $X^2 = 0.7462$, df = 2, n.s.).

The freqency distribution of newly mated queens at the branch level was compared against the Poisson distribution and was determined to be significantly different (Goodness of Fit test: $X^2 = 202.5$, df = 3, $p < 0.001$). A coefficient of dispersion showed that the queens were clumped (CD = 4.5, df = 3, $X^2 = 13.5$, $p < 0.005$), with an

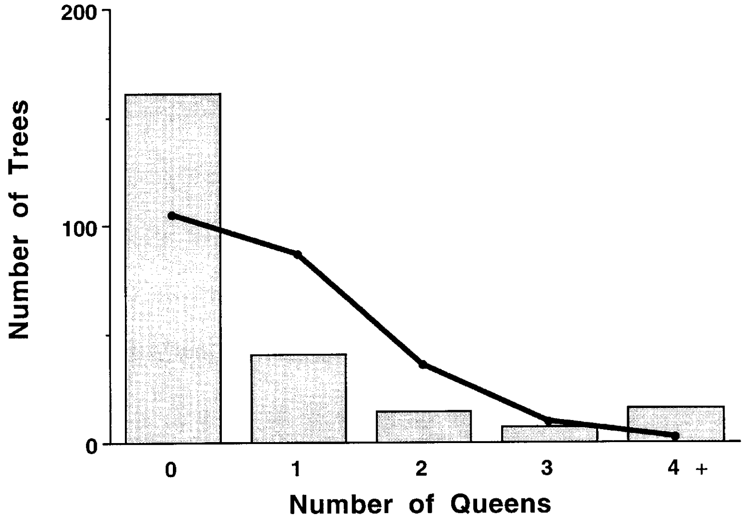

Figure 3. The frequency distribution of queens in saplings (columns) compared to the frequency expected from the Poisson distribution (curve). The queens were clumped on saplings, with a deficit of saplings having 1–3 queens and an excess having none or more than 3

excess of empty branches and branches with two or more queens, and a deficit of branches with only one queen. The distribution of queens among trees was also not random (Goodness of Fit test: $X^2 = 113.7$, $df = 4$, $p < 0.001$) (Fig. 3), but was clumped ($CD = 2.05$, $df = 4$, $X^2 = 8.2$, $p = 0.06$). This pattern of clumping at the branch, tree, and patch level suggested that newly mated queens were aggregating to a resource or resources that were favorable to colony founding.

The above patterns suggested that trees are the primary unit of colonization for newly mated queens. Trees were assigned to four classes according to the number of queens they contained. Depending on whether the explanatory variable conformed to the assumptions of normality, mean or ranked tree characteristics were analyzed for these frequency classes by one way Anova or Kruskal-Wallis rank sums tests. Trees containing greater numbers of newly mated queens had higher values for all of the measured tree characteristics (Figs. 4 and 5). These results suggested that one or more of these correlated variables (Table 1) is important in the process of colony founding,

Multiple regression analysis was used to discern which tree characteristics were most closely associated with the distribution of foundresses. The model was built by the addition and removal of variables in order to distinguish those variables that contributed the greatest amount of explained variance in the distribution of newly mated queens. Mean dead branch length (BL) was found to be the best predictor of the presence and number of newly mated queens a tree would contain ($Q = -0.395 + 0.051$ (BL), $R^2 = 0.257$, $p_{intercept} = 0.031$, $p_{regr} < 0.001$). This indicates that dead branch length or some variable correlated with dead branch length is driving site selection and thus the distribution of newly mated queens, even though much of the variation remains unexplained by the model (74%).

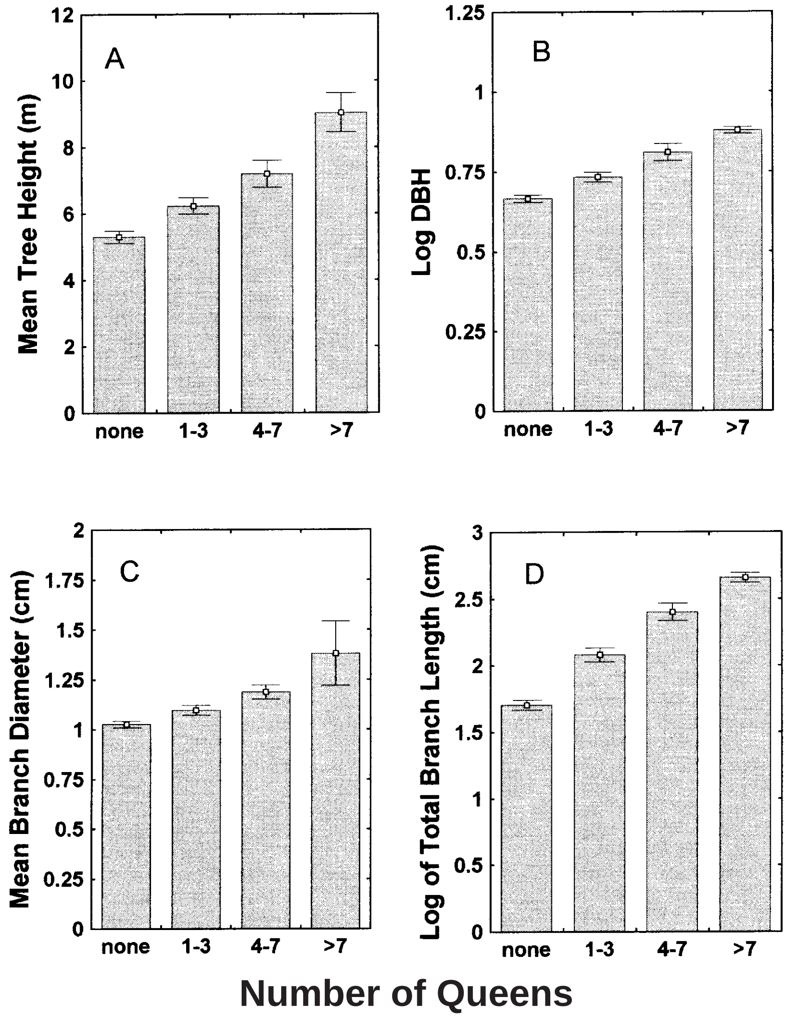

Figure 4. Attributes of trees classified by the numbers of newly-mated queens they contained. Trees with more queens had higher values of all of these size-related branch attributes. F-ratios (all with 3,265 d.f.) were as follows: tree height, 10.2; DBH, 11.65; branch diameter, 8.03; branch length, 25.11. Not shown as a graph was branch height (4.12). All p-values < 0.001

The validity of mean dead branch length as a predicting variable was confirmed in two ways. First, the model was compared to all possible other models. Second, the data set was randomly halved three times and the models produced on one half of the data were cross-validated against the other half (Table 2). The very low p-values eliminate selection effects of the addition and removal of variables in the model during the regression procedure, that magnify p-values, thus qualifying the predictor as valid. No other variable consistently explained a significant proportion of the variance in the data set and held up through the process of cross-validation.

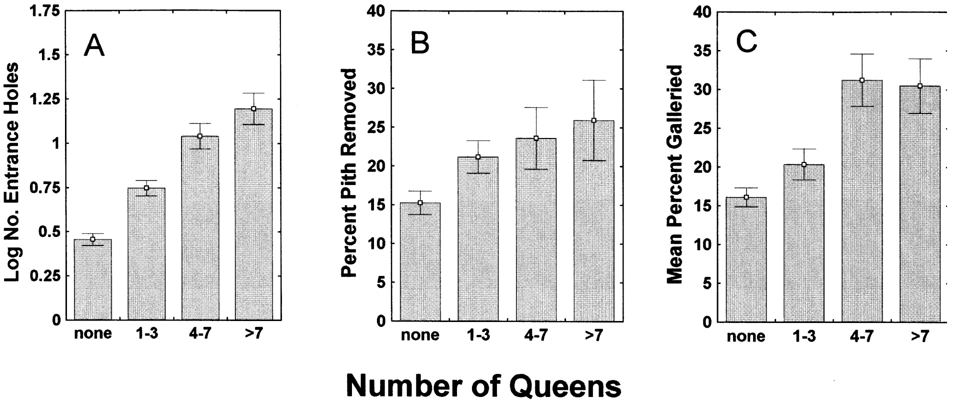

Figure 5. Branch attributes of trees classified by the number of newly-mated queens they contained. Trees with more queens had higher values of all of these size-related branch attributes. F-ratios (all with 3,265 d.f.) were as follows: entrance holes, 22.09; % pith removed, 20.89; % galleried, 20.21. All p-values < 0.001

Table 1. Pearson correlation coefficient among the tree characteristics. Branch length and diameter are both means by tree

	DBH	Tree height	# Dead branches	Branch height	Branch diameter	Subcort. galleries	Entrance holes	Pith removed	Branch length
Tree height	0.852								
# Dead branches	0.463	0.449							
Branch height	0.694	0.740	0.445						
Branch diameter	0.530	0.411	0.186	0.403					
Subcort. galleries	0.395	0.415	0.125	0.367	0.295				
Entrance holes	0.565	0.531	0.458	0.450	0.339	0.427			
Pith removed	0.341	0.353	0.041	0.314	0.061	0.497	0.520		
Branch length	0.605	0.570	0.735	0.531	0.433	0.217	0.677	0.129	
Queen number	0.337	0.319	0.308	0.286	0.284	0.238	0.472	0.159	0.538

Variables at the branch level were then analyzed by the same methods as above. A pair of characters consisting of dead branch length (BL), and the number of subcortical entrance holes (EH), was the best predictor of the presence and number of newly mated queens on a branch ($Q = -0.018 + 0.004\ (BL) + 0.066\ (EH)$, $R^2 = 0.106$, $p_{intercept} = 0.446$, $p_{BL} < 0.001$, and $p_{EH} < 0.001$). The stability of this pair of characters

Table 2. Regression parameters for the predicted number of queens on trees using branch length as the primary indicator. The original data were randomly separated into two halves three times, and the model generated on one half was validated with the other half

Run #	Initial samples				Validation sample			
	intercept	slope	R^2	p	intercept	slope	R^2	p
1	−4.63	0.058	0.263	<0.001	−2.84	0.042	0.186	<0.001
2	−0.019	0.031	0.117	<0.001	−0.357	0.044	0.250	<0.001
3	−0.257	0.048	0.203	<0.001	−0.259	0.050	0.259	<0.001

Table 3. Regression parameters for the predicted number of queens in branches, using branch length and sub-cortical entrance holes as the primary predictors. The original set was randomly divided into two halves, and the model generated on one half was validated with the other half

Run #	Initial samples						Validation sample					
	intercept	R^2	slope (1)	p (1)	slope (2)	p (2)	intercept	R^2	slope (1)	p (1)	slope (2)	p (2)
1	−0.32	0.121	0.004	<0.001	0.079	<0.001	−0.027	0.122	0.003	<0.001	0.075	<0.001
2	−0.03	0.124	0.004	<0.001	0.067	<0.001	0.009	0.057	0.003	<0.001	0.041	<0.002

was confirmed as above by splitting the data twice and cross-validating the model (Table 3). These results suggest that branch length is a primary factor driving site selection by newly mated queens with the number of sub-cortical entrance holes contributing to site selection at the branch level, even though much of the variation remains unexplained by the model (89%).

Mortality of newly mated queens was estimated by noting the condition of the queens at the time of their discovery. Of 197 newly mated queens 106 (54%) were found dead and 91 (46%) were found alive. There was no significant change in the observed mortality across the 1995 sampling periods ($X^2 = 1.338$, df = 2, n.s.).

Incipient colony distribution, summer 1996

Of the 749 dead branches sampled from 160 trees, 10 incipient colonies were found complete with queen, 14 trees contained colonies in which the queen was not found. Twenty-two newly inseminated queens were found, all on trees taken during the later of the two sampling periods. Of the trees containing incipient colonies six contained only a single colony, and one tree contained three colonies, on the same branch. A comparison of the number of newly mated queens found in the summer of 1995 with the number of incipient colonies that were found in the summer of 1996 adjusted for the sample size yielded a survivorship of 7.6%, or mortality of 92.4% of the summer 1995 foundresses.

Of the 160 trees baited, 86 (54%) showed no foraging activity, somewhat higher than the previous year, but more trees (29%) had *Crematogaster ashmeadi*. Only 1 tree had another arboreal species *Camponotus nearcticus*, and 26 had other various ground nesting ants including *Solenopsis invicta, S. geminata, Pheidole anastasii,* *P. dentata, Camponotus floridanus, Monomorium viridum,* and *Forelius humilis*. The 8 trees that contained incipient colonies all had *C. ashmeadi* foragers on the baits. A chi-square contingency test, with the groups: no foragers, *C. ashmeadi* foragers, foragers of other arboreal ant species, and foragers of ground nesting ant species, showed a significant positive association between the presence of incipient colonies and foragers on a bait during the sampling periods in 1996 ($X^2 = 17.74$, $df = 3$, $p < 0.001$). There was no significant relationship between presence of an incipient colony in 1996 and the presence or type of ants foraging on it in 1995. This suggests that even small incipient colonies are able to dominate baits at the expense of other ants that may be in the area.

Incipient colonies were distributed randomly among trees ($X^2 = 2.26$, $df = 1$, n.s.) and among patches ($X^2 = 4.37$, $df = 2$, n.s.). At the branch level the distribution of incipient colonies was not testable because of the small sample size. Taken together the results of 1995 and 1996 suggest that the distribution of founding colonies is clumped among patches, branches, and trees in response to some resource or resources favorable to colony founding, and that incipient colonies eliminated each other through competition to produce a uniform dispersion by 1996. The number of trees that contained more than one queen in 1996 was significantly less than expected from the number of trees that contained more than one queen in 1995 ($X^2 = 2.21$, $df = 1$, $p < 0.001$).

Discussion

The period of time between insemination and sealing the founding chamber is a particularly perilous one for newly mated queens. The longer it takes a queen to find an appropriate founding site, the greater the chance of mortality due to environmental factors, such as desiccation (Hood and Tschinkel, 1990), or predation (Whitcomb et al., 1973; Rissing et al., 1986). In response to this, it would seem likely that newly mated *C. ashmeadi* queens should have evolved a system to maximize the likelihood of finding a suitable founding site and to minimize exposure time in order to reduce mortality. Previous studies have found that insects search for resources in a hierarchical manner (Bell, 1990). Thus, newly mated queens may also search for and choose founding sites hierarchically. Perhaps first, they choose a patch of young trees according to the likelihood of finding a suitable tree within it, i.e. patches with trees of appropriate size and dead branch length. Second, they may choose an individual tree with longer branches, or some character as yet unmeasured that is related to dead branch length. Finally, they may choose a suitable branch on a tree on the basis of the length of that branch and the number of subcortical entrance holes that branch contains or some other character related to one or both of these two variables.

Crematogaster ashmeadi is the dominant arboreal ant in the longleaf pines of the Apalachicola National Forest, occupying all but the yongest trees (Tschinkel and Hess, in prep.). As in the mangrove islands studied by Cole (1983a, b), *C. ashmeadi* gains dominance on longleaf pines through early colonization, and aggressive interactions with other ants (however, there is some doubt that the ants identified as *C. ashmeadi* in each of the studies are indeed the same species). In a study of the distribution of foraging ants on baits (Tschinkel and Hess, in prep.) it was found that

C. ashmeadi was by far the most common arboreal ant on all sizes of trees, yet the proportion of trees occupied by *C. ashmeadi* peaked in the 12 – 18 cm dbh range and then decreased as size class increased. In other words, densities of *C. ashmeadi* colonies decrease as trees grow larger, and larger trees are more likely to contain other arboreal species. In addition, preliminary data showed that *C. ashmeadi* queens rarely found colonies in the dead branches of mature trees (W. R. Tschinkel, unpubl.). This suggests that *C. ashmeadi* queens focus their founding efforts on small trees that are large enough to have dead branches and other necessary resources, such as abandoned beetle galleries, and small enough so that the likelihood of previous colonization is relatively low. The fact that other species of arboreal ant very seldom found colonies in small trees (D. A. Hahn, unpubl.) suggests that the early colonization is a primary factor leading to the dominance of *C. ashmeadi.* On the other hand, pines almost certainly live longer than *C. ashmeadi* colonies. Because over half of mature pines still contain *C. ashmeadi* colonies, there must be a mechanism for recolonizing trees or requeening orphaned colonies. No data on either exist.

It is well documented that interactions between ant species play a large part in the structuring of arboreal ant communities (Greenslade, 1971; Room, 1971; Leston, 1973; Majer, 1976; Taylor, 1977; Cole, 1983; Savolainen and Vepsalainen, 1988). *C. ashmeadi* acts aggressively towards both conspecifics and heterospecifics, and is capable of competing for baits with large, aggressive colonies of ground nesting ants such as *Solenopsis invicta* (W. R. Tschinkel, unpubl.). This aggressive nature coupled with large colony size suggests that *C. ashmeadi* should be considered as a primary dominant species (Cole, 1983; Savolainen and Vepsalainen, 1988). Such status suggests that *C. ashmeadi* probably plays a large role in the structuring of arboreal communities, and perhaps even affects the community composition of ground dwelling arthropods as well.

Studies of other arboreal ant communities have suggested that, in addition to aggressive interactions between species, habitat requirements are an underlying mechanism that determines the distribution of species (Greenslade, 1971; Herbers, 1986, 1989; Majer, 1976). The clumped dispersion of newly inseminated *C. ashmeadi* queens at the branch, tree, and patch levels suggests that these queens are aggregating at sites based on the distribution of resources favorable to colony founding. The use of branch length as a primary variable in the distribution of queens is a plausible one when one takes into account the correlation between it and percent subcortical gallerying and pith removed, i.e. branch length acts as a surrogate for galleries. Because newly mated queens require these subcortical and pith galleries for claustral founding chambers, it seems likely that they are choosing sites based on dead branch length because of the correlation between branch length and galleries. The longer the branch, the more likely it is to contain the sought-after chambers. We considered the idea that branch length might be the best predictor of the number of queens present because the likelihood that a queen will land on a particular branch increases with branch length, i.e. longer branches are able to "catch" more queens simply due to their length. However, there is a negative relationship between the number of queens per unit of branch area and branch length, i.e., longer branches have fewer queens per unit area than smaller branches. This suggests that other factors, besides just length, are playing a part in the selection of branches by queens. Additionally, in a corroborative study of colony founding in *C. ashmeadi*, it was found that the distribution of newly mated queens in an uncolonized longleaf pine plantation was reflective of the distribution of trees of the preferred size and dead branch characteristics, rather than proximity to the source population (W. R. Tschinkel, unpubl. data). These results strengthen the case that site selection is driven by the perception of resources by newly-mated queens.

Like other ants, mortality of *C. ashmeadi* colonies in the founding process is high (approximately 92% in 1 yr). Choice of an appropriate founding site, and interactions between young colonies and other ants, probably plays a large part in the resulting distribution of surviving incipient colonies. Whereas newly mated queens settled clumped together, the surviving incipient colonies were uniformly distributed. However, the sample size of incipient colonies may have been too small to detect an effect. This change in the dispersion may have resulted from competition between incipient colonies. It is likely that once foundresses raise several cohorts of workers, the foraging ranges of these workers overlap and they come into contact with each other, causing competition and fighting, until the mature condition of one colony per tree is attained. Unfortunately, because of the small number of incipient colonies, we cannot rule out that the observed pattern was produced by random mortality.

Although the prior presence of ants on trees might be expected to influence the settlement pattern of newly mated *C. ashmeadi* queens, there was no association between the occurrence or species of ants at baits and the probability of settlement on a tree (i.e., newly mated queens probably settle without regard to the ants already present). The prior presence of ants at baits in 1995 also did not affect the survival of colonies until 1996. Nevertheless, all baits on trees with incipient colonies in 1996 were dominated by *C. ashmeadi*. These results suggest that even small incipient colonies may be able to displace other ant species from baits, attesting to the competitive ability of *C. ashmeadi* relative to other ants in the longleaf pine forest.

While this work has allowed us to gain important knowledge about colony founding and distribution of young colonies of *C. ashmeadi*, the actual processes that drive site selection and the elimination of incipient colonies to produce the observed distribution remain unclear. The characters we chose to measure may not be causal in the process of site selection at all, and the remaining 70–80% of the unexplained variance could perhaps be accounted for if we knew more about the perceptual world and exact founding requirements of newly mated *C. ashmeadi* queens. Our study was not manipulative and was thus subject to many of the consequences of perceived and unperceived relationships that occur in nature.

The next step in this research would be the testing of tree characteristics in a manipulative experiment that reduced the correlations between variables. This would sort out causal relationships. Behavioral observations of newly mated queens during settlement would yield a clearer picture of the tree attributes and cues to which queens respond while seeking a founding chamber. Similarly the interference competition that occurs both between incipient *C. ashmeadi* colonies, and between *C. ashmeadi* and other ants, needs to be tested in a series of manipulative experiments, such as removals and additions, to determine the proximate mechanisms of this competition and to what extent it acts in the structuring of communities in the longleaf pine forest.

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