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The Natural History of the Arboreal Ant, *Crematogaster ashmeadi*

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Abstract

The arboreal ant, *Crematogaster ashmeadi* Emery (Hymenoptera: Formicidae), is the most dominant arboreal ant in the pine forests of the coastal plain of northern Florida. The majority of pine trees harbor a colony of these ants. The colonies inhabit multiple chambers abandoned by bark-mining caterpillars, especially those of the family Cossidae, in the outer bark of living pines. They also inhabit ground level termite galleries in the bark, often locating the queen in galleries. The density of chambers and ants is highest in the base of the tree and drops sharply with height on the trunk. Because chambers are formed in the inner layer of bark, they gradually move outward as more bark layers are laid down, eventually sloughing off the tree's outer surface. Chambers have a mean lifetime of about 25 yr. The abundant chambers in pine bark are excavated by a small population of caterpillars and accumulate over decades. Ant colonies also inhabit abandoned galleries of woodboring beetles in dead branches in the crowns of pines. Because newly mated queens found colonies in abandoned woodboring beetle galleries in the first dead branches that form on pine saplings, *C. ashmeadi* is dependent on cavities made by other insects throughout its life cycle, and does little if any excavation of its own. Mature colonies nest preferentially in chambers greater than 10 cm^2 in area, a relatively rare chamber size. In natural pine forests, this does not seem to limit the ant's populations.

Founding queens containabout 50% fat and lose about half of their dry weight during the claustral period, converting approximately half of this lost weight into progeny. The claustral period is about 40 to 50 days at 27 ^{o} C. Mature colonies contain several tens of thousands of workers (est. up to 80,000), and have a life expectancy of 10 to 15 years. Each colony occupies an entire tree, and sometimes two trees if they are close together. Within a colony, there is a single queen capable of laying up to 450 eggs/day during the warm season. Such queens weigh 12 to 18 mg, have 50 to 60 active ovarioles and 120 to 600 vitellogenic oocytes in their ovaries.

Mature colonies begin producing sexual brood in late April or early May. Sexual adults are present from late May through June. Mating flights commence in June and most sexuals have left their natal nests by late July. Female sexuals are an especially large investment;the energetic content of a single, flight-ready female sexual is almost 20 times that of a worker. The newly mated queen sequesters a mean of 2.64 x 10^6 sperm in her spermatheca, a supply that should last her for 16 years at the observed reproductive rates.

Keywords: Formicidae, nest chambers, arboreal ants, colony founding, seasonality, colony longevity, Cossidae, *Givira francesca* (Dyar), Buprestidae, Cerambicidae, woodboring beetles, longleaf pine, slash pine, *Pinus palustris*, *Pinus elliotti* , red-cockaded woodpecker.

Introduction

Crematogaster ashmeadi is a widespread arboreal ant of the southeastern United States, one of eleven species of this genus native to eastern North America. Deyrup and Cover (personal communcation) recently proposed that ants in pine trees are a distinct, previously unrecognized species. In the coastal plain forests of northern Florida, *C. ashmeadi* can be found in abundance on both longleaf (*Pinus palustris*) and slash (*P. elliotti*) pines. Their importance in this forest ecosystem is probably high, for they are by far the most abundant ant in the pine trees, making up 80 to 90% of the ant individuals there (Tschinkel and Hess, 1999).

C. ashmeadi is part of a relatively simple ant community with only four regularlypresent species. Among these, *C. ashmeadi* is strongly dominant. It reaches its maximum dominance in middle-sized trees and then declines somewhat in larger trees as the diversity of the arboreal ant community increases (Tschinkel and Hess, 1999). Because pine forests do not form a closed canopy, each tree acts as an island with its own ant community (Prather, 1997). There are no multi-tree ant mosaics such as occur in many tropical broadleaf forests and tree crops (Majer, 1976; Taylor, 1977; Leston, 1978; Cole, 1983; Adams, 1994; Majer et al., 1994; Demedeiros et al., 1995; Dejean et al., 1997).

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C. ashmeadi founding queens seek out sapling longleaf pines where they use abandoned woodboring beetle galleries in dead branches as founding chambers (Hahn and Tschinkel, 1997). Saplings are chosen according to their size and the number of dead branches (Baldacci and Tschinkel, 1999). Founding is claustral and haplometrotic, with low survival during the first year of life.

C. ashmeadi is of great interest to conservation efforts on behalf of the endangered red cockaded woodpecker, *Picoides borealis*, of the coastal plain forests of the southeastern United States. The largest remaining population of this endangered woodpecker occurs in the Apalachicola National Forest southwest of Tallahassee, Florida. *C. ashmeadi* workers make up the majority of this woodpecker's adult diet, especially in the winter (Hess and James, 1998). Adult woodpeckers forage for ants by flaking bark on living pines, and drill into the ant's brood chambers to collect food for their nestlings.

Until recently, little was known about the natural history of *C. ashmeadi*. However, its great abundance, link to conservation issues and obvious ecological importance has stimulated research into its biology. In this paper, some basic aspects of its natural history and its linkage to the activity of wood and bark-mining insects are described.

Materials and methods

The study was carried out from 1994 to 2000 in the Apalachicola National Forest in northern Florida, in second-growth longleaf pine forest regenerated naturally after having been cut 50 to 80 years ago.

Bark galleries

In order to study the dynamics of bark chambers and their contents, the bark of sample trees was shaved in elongate 0.33 m^2 areas down to the inner bark. On each tree, one sample area was located 1 m above ground level and the other at 5 m. Shaving was accomplished with a Pine-o-matic bark shaver constructed much like a large carrot-peeler (Ronco). With this device, I removed layers of about 1 mm per stroke, exposing chambers to view. Chamber outlines were traced on transparent acetate sheets, and their locations, living contents, approximate depth in the bark, and dimensions were recorded. At each of six sites, a minimum of 2 large, 2 medium and 2 small trees were shaved during the winter of 1995 (January-March), and again during the summer of 1995 (August-October). A total of 87 trees were shaved. From these datathe density of chambers (chambers/ m^2 of bark surface), and their total and mean areas in relation to tree diameter and height on the trunk, were derived.

Brood sampling and fat determination

On five dates between early May and late July 1999, shaving or chiseling the bark exposed two to four nest chambers on each of 9 to 14 trees. All chamber contents were collected, returned to the laboratory, sorted, dried, counted and weighed. All worker adult and brood samples with counts greater than 10 (85-90% of samples) were placed into perforated gelatin capsules in a Soxhlet extractor and were extracted with diethyl ether for 24 hr. All sexual forms were extracted. This was followed by drying and reweighing to obtain a fat-free weight. The difference between the dry weight and the fat free weight gave the fat weight. This procedure was applied to adult workers and worker brood, as well as to adult sexuals and sexual brood. Data analysis showed the seasonality of sexual and worker brood production, and fat content.

Baiting studies

We frequently used baits to detect and quantify ants living in trees. Bait was prepared by blending cat food to a puree, then dipping 1-cm discs of filter paper in the puree and sticking them to the bark of each tree. Usually, we placed one bait paper at breast height at each cardinal compass direction. After approximately one-half hour, we revisited each tree, identified the ants on baits by sight, and counted them. Unfamiliar ants were collected for later identification.

In a modification of this procedure, we tested the consistency and reliability of baiting, and the preference for three different foods. We selected 20 longleaf pine trees of a wide range of sizes at each of 6 flatwoods sites, each in the vicinity of a cluster of trees with red-cockaded woodpecker cavities. This gave a total of 120 trees. Each of three foods (a peanut butter/sugar mixture, pureed cat food and pureed tenebrionid beetle larvae) was applied to a filter paper disc and stuck to the bark in a vertical row on the north and south sides of each tree. The number of ants on each food was counted after 30 min. and used to determine their preference for subsequent baiting studies. The procedure was repeated 6 times during March and April of 1996.

In a second modification of this procedure, sectional Swedish climbing ladders were attached to selected longleaf pines, reaching 15 m up into the crown. Cat food baits were place on the trunk at 1 m intervals to the right and left side of the ladders, beginning at the highest position. Baits were also placed about 0.5 m out on major branches. Baits were checked after one-half hr, beginning at the highest bait. Tree circumference was measured at each bait position. The species and counts of ants on the baits allowed the estimation of "territory size" and the proportion of the tree occupied by ants. This procedure was applied twice during one week in each of spring, summer and fall to 10 to 20 mature pines at each of 3 flatwoods sites.

Archery

As a method for studying ants in the crowns of pines, the ladder method was difficult and time-consuming. In later studies I used a bow and weighted arrows to shoot a light line over dead branches of candidate trees. We then hauled up a heavier rope and broke the branch off by pulling on the rope. Once the branch was in hand, its bark was peeled and it was split open with chisels and hatchets so that the ants within any chambers could be collected.

Long-term baiting study

The stability of ant communities was studied in 6 circular, long-

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term plots 35 m in radius. Five plots were located in the flatwoods and one in the sandhills. All trees on these plots were mapped on polar coordinates and their diameter at breast height measured. During each of 6 summers (1994-1999), a cat food bait (see above) was placed on each cardinal direction of the trunk of each tree at 1 m height. Ants coming to these baits were identified and counted. Baiting was carried out three times during each summer. Presence/absence and abundance of *C. ashmeadi* on each tree were determined from these data and were used to determine spatial and historical patterns.

Colony founding in the laboratory

Founding queens were collected by peeling and splitting dead branches taken from longleaf pine saplings, their preferred nest-founding locale. In the laboratory, nest tubes were made from small test tubes half-filled with water held in by a cotton plug. The queen and her brood occupied the space between this and a second cotton plug that closed the tube. A total of 90 colonies from five collection dates during July and early August were set up and maintained at 27 ^{o} C. All brood stages were counted every 5 to 9 days until most queens had produced minims. Twenty-seven of the 90 nests were randomly chosen for dry weight analysis. These were killed after the last brood check, oven dried at 50 ^{o} C, the brood stages separated and weighed. The remainder of the nests died or were used for other studies.

Data analysis

Data were subjected to regression and analysis of variance, as appropriate, using Statistica 5.0 (Statsoft, Inc.).

Results

Natural history of the nest chambers of C. ashmeadi

Types of chambers used

Crematogaster ashmeadi rarely if ever excavate their own nest cavities in bark or wood of the pines they inhabit. Instead, they occupy the abandoned chambers made by bark-mining caterpillars in the outer bark of the trunk, or the galleries of woodboring beetles in the dead branches, or the galleries of termites in the outer bark at ground level. The nesting biology of *C. ashmeadi* is thus intimately linked to the populations of these three taxa of cavity-forming ecosystem engineers, each of which operates in a different part of the living pine. The most reliable and readily studied of these engineers is a bark mining caterpillar, about which some details follow.

Chamber descriptions and formation

Caterpillars of the cossid moth, *Givira francesca* (Dyar), which are widely distributed in Florida, make the majority of galleries in the bark of pine trunks. A few individuals of a second species, possibly a tortricid or sesiid, were also found, but could not be identified. These caterpillars mine the outer bark just outside the cambium, enlarging the cavity as they grow. Figure 1A shows outlines of representative chambers and Figure 2 shows their distribution in the bark sample areas. The galleries are mostly vertically oriented and elongate, with multiple short side galleries or bays. Typically, they contain frass, probably a mixture of boring dust and fecal material. Many also show shallow pits in the floor, usually at the margins of the galleries and especially in the short side branches or coves.

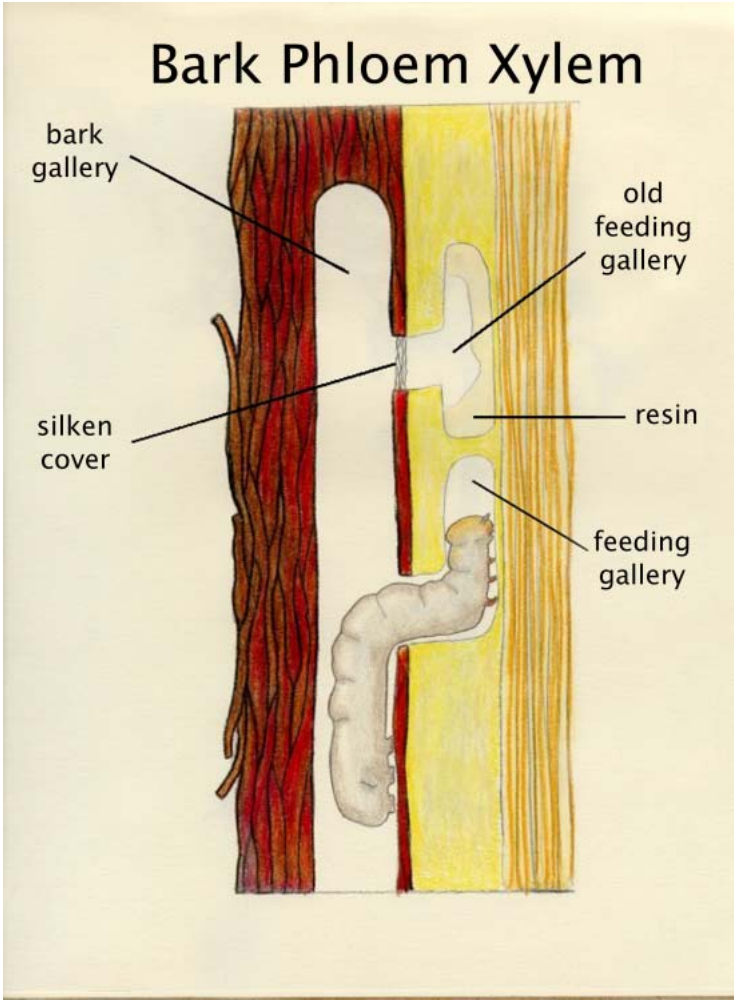


Figure 1 A. Caterpillar of *Givira francesca* (Dyar) (Cossidae) in its gallery, showing the way in which it tunnels into the phloem to feed, then backs out and closes off the hole with a silk door to impede entry of resin into its living space.

Direct observation of caterpillars in their excised galleries with attached phloem gave insight into the origin of these pits. Caterpillars excavate their galleries a mm or less outside the phloem tissue (Fig. 1B). In order to feed, they chew a round hole through the floor of the gallery. Once in the phloem, this feeding gallery makes a right angle turn so that it is oriented vertically in the tree. The caterpillar eats the phloem, then backs out of the feeding gallery and spins a door of silk over its entrance. This silk door presumably prevents the pine's resin, which begins to flow as soon as the caterpillar injures the living phloem, from entering its living space and overwhelming it. The formation of new bark layers later closes the openings, but their locations remain visible as depressions in the floor of the gallery.

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When the caterpillar larva is ready to pupate, it first chews a round, usually downward slanted exit hole, thus solving the problem of the non-chewing adult moth mouthparts.. It then positions itself in its gallery just inside this exit hole, spins a tight silk door to close off the exit, and pupates. The adult emerges from the pupa and ruptures this silk door, leaving the cast pupal cuticle behind in the gallery. Laboratory rearing of adult moths depended on finding pupation-ready larvae and excising their bark home along with attached phloem. The combination of inexactly known timing of emergence and their uncommonness made finding such specimens rare. Careful searching of over 200 pine trunks only discovered 3 live pupae, though recently vacated galleries were also found. A specimen of the adult moth is shown in Fig. 1C.

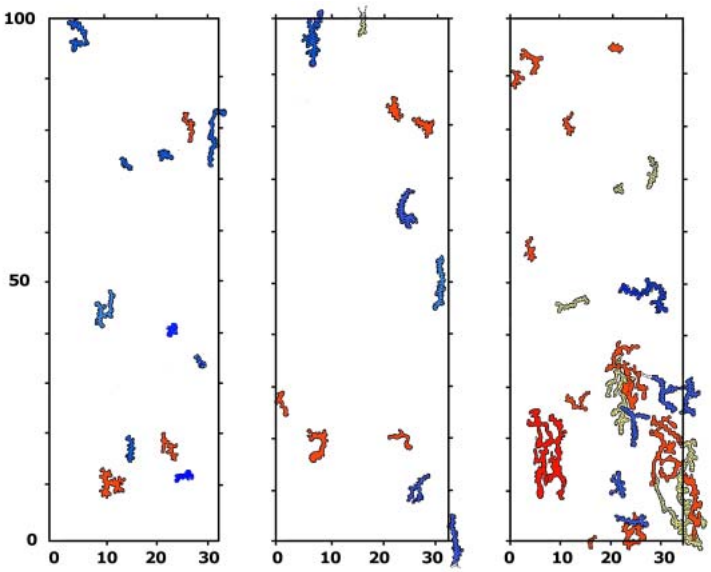


Figure 2.Representative tracings of 3 bark sample areas showing chambers exposed by shaving the bark. The coordinates (cm) of each shaved area are shown. Shading of the chamber tracings indicates the depth of the chamber in the bark (superficial, red; middle, blue; deep, yellow). The large chambers near the bottom of the right panel were made by termites; all the other chambers were made by cossid caterpillars.

No gallery initiation holes were visible, probably because they are small or hidden under pine bark scales. If the larva fails to pupate, its gallery remains closed and cannot be used by other insects. Successful emergence of *G. francesca* leaves behind a gallery containing a pupal cuticle and much frass, both of which are presumably removed *by C. ashmeadi* workers when they move in.

A small number of large chambers with different morphology were found very low in the 1 m samples. Bark shaving at the very base of the tree, just above ground level revealed more such chambers. They were often complex in form and had several levels with thin floors between levels. Because live termites were occasionally found in them, these galleries were assumed to have been made by termites. This conclusion was reinforced by the frequent presence of fecal speckling, such as produced by termites.

Bark sloughing rate and chamber life span

As described above, chambers originate in the bark layer immediately outside the living phloem. As the tree grows, it continues

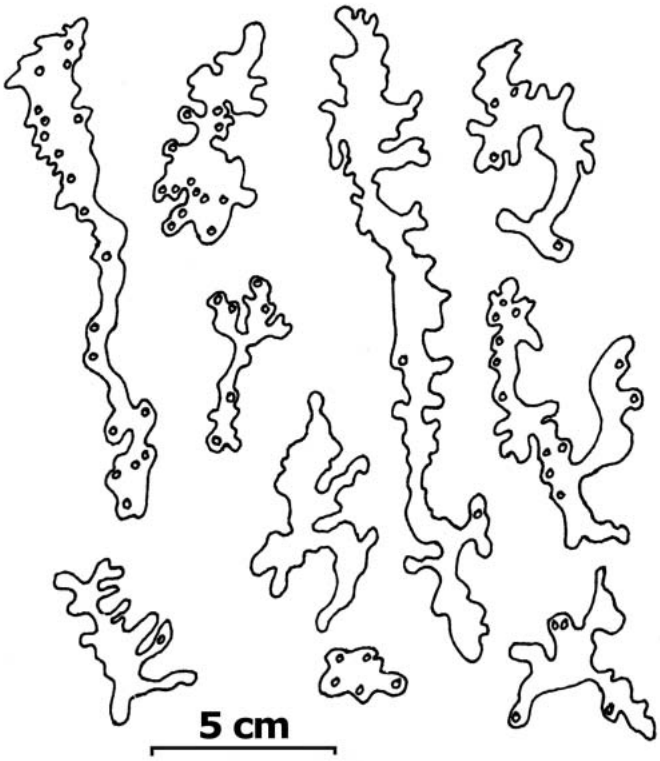


Figure 1B.Outline tracings of representative vacated galleries of *Givira francesca*. Small circles within the galleries are depressions caused by healing of the feeding pits. These probably do not always leave scars, and are not always present in galleries. Scale bar indicates 5 cm.



Figure 1C.*Givira francesca Dyar*, collected in compartment 223 of the Apalachicola National Forest, Leon County, Florida. Reared from pupa collected in its bark chamber, May 19, 1999, emerged June 20, 1999.

to add layers of bark between the chamber and the cambium, and bark sloughs from its outer surface. This gradually moves chambers outward into the bark, until they are exposed to the surface and slough off with the flakes of pine bark. Chambers thus have a life span less than the life of the tree. But what is that life span?

Knowledge of the bark thickness and the sloughing rate allows the calculation of the chamber lifespan. Six trees were chosen at each of the six long-term study plots, two large, two medium and two small trees, for a total of 36 trees. Pairs of flat-bottomed holes were drilled in the bark side-by-side such that one hole ended just outside

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the living cambium (the bottom of the hole was pale brown), and the other ended at the bark/cambium junction (yellow hole bottom). The depth of the second hole served as an estimate of the bark thickness at the beginning of the experiment. The depth of the incomplete hole was measured annually. As bark sloughed off, this hole became shallower. Bark sloughing rate was computed from the depth of this hole over a period of five years. Pairs of holes were placed on the north and south side of each tree at 1 and 5 m height, giving 8 initial holes and 4 that were remeasured for 5 years.

Not surprisingly, bark thickness increased with tree size (diameter), and decreased up the trunk (Fig. 3A). This is because the rate of bark formationexceeded the bark-sloughing rate. For every centimeter increase in diameter, bark thickness increased 0.2 mm (regression with dummy variable for sample height: $F = 55.55$, d.f. = 2, 141, $p < 0.00001$, $R^2 = 43.3\%$). For a given diameter, bark was 2.2 mm thicker at 1 m than at 5 m height. Trees with diameters between 10 and 15 cm had bark between 3 and 10 mm thick, whereas those with diameters between 30 and 40 cm had bark between 7 and 18 mm thick. Bark at 1 m on a tree averaged about twice as thick as at 5 m.

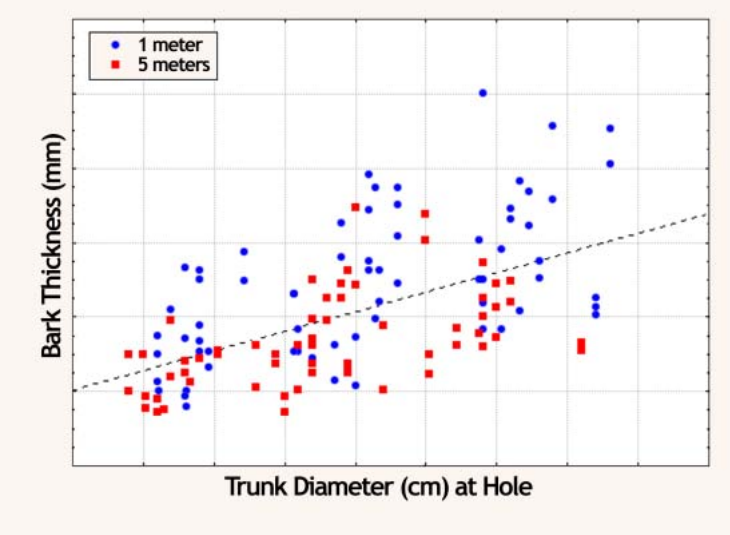


Figure 3A.Thickness of the bark of longleaf pines in relation to the diameter of the tree and the height of the sample on the trunk. Thickness was estimated by drilling flat-bottom holes through the bark (see text).

At 1 m height, the rate of bark sloughing was not significantly related to the thickness of the bark (regression, $F = 2.22$, d.f. = 1, 58, $p > 0.1$, n.s.). At 5 m height, the loss rate increased 0.02 mm per cm of increase in bark thickness ($F = 4.75$, d.f. = 1, 58, $p < 0.05$, $R^2 = 6\%$). The sloughing rate averaged about 0.43 mm/yr with high variability. This was probably because thinning is a step-function, not a gradual process; either a flake of bark is lost or not. The varying thickness of the flakes and the binary nature of flake loss introduced large variation.

Chamber lifespan increased with bark thickness (from which it is calculated). Each mm of bark added an average of 1.8 years to chamber life (regression: $L = 10.6 + 1.8T$; $F = 19.7$; d.f. = 1, 120, $p < 0.0001$; $R^2 = 13\%$; Fig. 3B). The high variation in bark sloughing rate was reflected in the large variation in estimated lifespan. Nevertheless, 80% of the estimates lay between 10 and 50 years, with a mean of 25 years. Presumably, the chambers become useless to the ants as they become exposed at the bark surface.

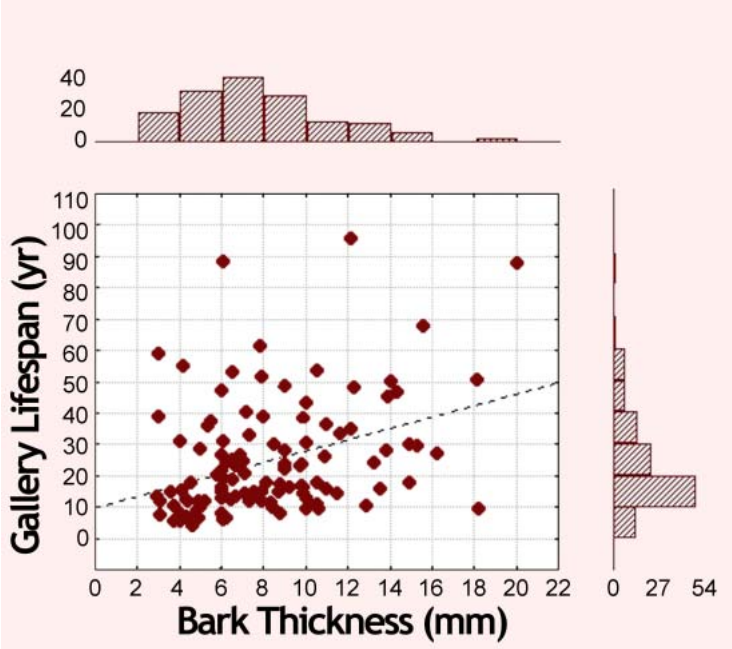


Figure 3B.The lifetime of a cossid gallery in relation to the thickness of the bark in which it was formed. Chambers are formed just outside the cambium and are gradually moved outward by the formation of new bark, eventually sloughing off the outer bark surface in flakes. Eighty percent of estimated lifetimes fall between 10 and 50 yr.

It follows directly that the population of galleries on a tree is the work of many generations of caterpillars that accumulates over many years, or even decades. Bark formation rate (which was not measured directly) is higher than bark sloughing rate, so that the bark of pines becomes thicker with age and tree diameter. This is obvious in cross-sections of pines. It also means that chambers formed in the thicker bark of larger, older trees have, on average, a longer lifespan (Fig. 3B). At 1 m height, chamber lifespan increased 1 yr for every 6 cm of trunk diameter ($F_{1,57} = 6.96$; $R^2 = 9.3\%$; $p < 0.01$). Again, variation of this estimate is high because of the nature of the measurements. Actual lifespans are probably much less variable.

Chamber size and distribution

Chamber density was not uniform, but increased with tree diameter and decreased with height on the trunk (ANOVA. Height $F = 69.96$, d.f. = 1, 765, $p < 0.00001$; diameter class, $F = 22.09$, d.f. = 3, 765, $p < 0.00001$). Progressing from trees 10-20 cm diameter to those 20-30 cm and >30 cm, chamber density increased 18% and 46%, respectively, at 1 m height. At 5 m height, the corresponding increases were 59% and 119%. There were almost twice as many chambers at 1 m height than at 5 m (520 vs. 280). Even within the lower sample area, 57% of the chambers were in the lower half and 43% in the upper half of the sample area, a difference that is significant (Kolmogorov-Smirnov test: $d = 0.0797$, $p < 0.01$). This indicates that the chamber density declined sharply from the base up the trunk. The caterpillars that formed the galleries clearly prefer to do so near ground level, perhaps because they prefer the thicker bark in this area. This preference would also explain their greater abundance in larger trees. The longer period of accumulation in thicker bark

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may also contribute to greater abundance. Less than 1 m above ground level, galleries were often constructed by soil-dwelling termites, rather than caterpillars.

The vertical distribution of caterpillar galleries was confirmed by counts of open exit holes in 1-m increments up to 5 m up the trunk of 6 trees varying from 17 to 32 cm in diameter at 1 m. Figure 4 shows the sharp drop in exit hole density with height on the trunk (ANOVA: effect of height on exit density, $F = 7.78$, d.f. = 4, 25, $p < 0.0005$, $R^2 = 55\%$).

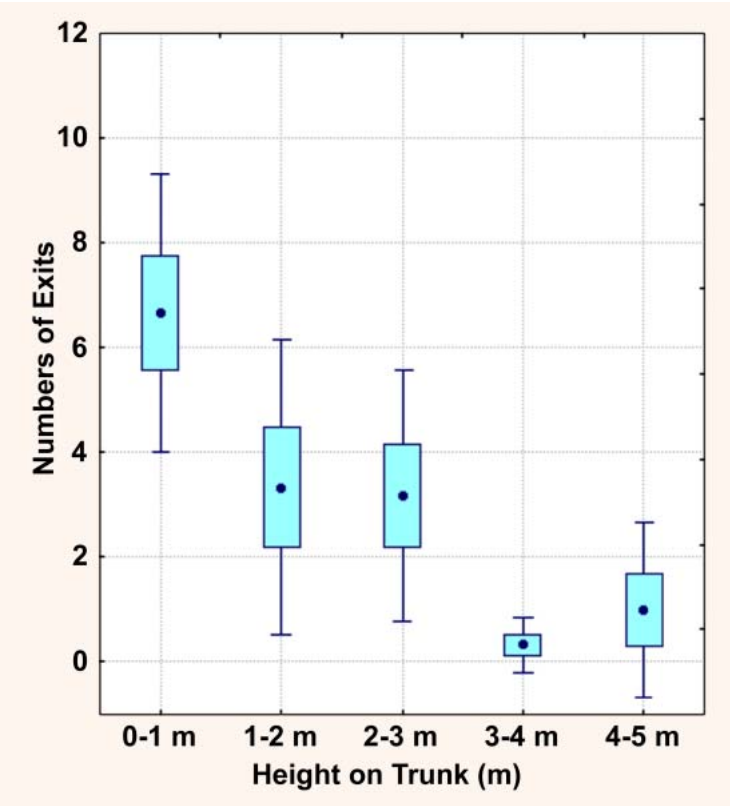


Figure 4.The mean number of cossid gallery exits as a function of height on the trunk, in one-meter increments. Error bars indicate standard deviation and standard error. N = 6, tree diameters 17- 32 cm.

Chamber size and contents

Compared to superficial and middle chambers, deep chambers were smaller (5.98 and 5.24 vs. 3.68 cm^2; ANOVA, effect of depth on size, $F = 6.34$; d.f. = 2, 736, $p < 0.001$) and fewer in number (343 and 261 vs. 135), as might be expected for the zone of formation. However, these zones were not rigorously measured, but merely estimated in the process of bark shaving.

Most galleries were empty (of the 800 chambers exposed, 641 or 83% were empty). The most frequent contents were *C. ashmeadi* workers and brood, but only 42, or 5.4% of the chambers contained them. Another 29 chambers (3.8%) contained living caterpillars, probably *Givira francesca*. Miscellaneous creatures included mealybugs, cavity-nesting wasps, spiders and other insects. Together, these occupied only 30 chambers (3.8%).

The distribution of living contents of chambers was different for the size classes of trees. For both *C. ashmeadi* and caterpillars, the proportion of chambers containing them declined from each size class to the next larger. This may have been the result of the increase in the chamber density with tree size without an increase in insect numbers. *C. ashmeadi* were more likely to use the larger two of four size classes of chambers (Table 1. Pearson Chi-square = 11.328; df=3; $p < 0.01$). As chamber area increased from less than 5 cm^2 to more than 20 cm^2, the proportion of chambers with ants increased from less than 5% to almost 15%. The smaller two size classes had almost the same frequency of occupancy near 4.5%, and the larger were not very different from one another at 12 and 14%.

Chamber Area	0-5 cm^2	5-10 cm^2	10-20 cm^2	>20 cm^2	Row Totals
Total chambers	554	151	74	21	800
No. with *C. ashmeadi*	24	7	9	3	43
% of chambers with *C. ashmeadi*	4.33%	4.64%	12.16%	14.29%	

Table 1.The size distribution of chambers and their occupation by *Crematogaster ashmeadi*. The ants occupied a lower proportion of chambers when these were less than 10 cm^2 in area than when they were larger than this.

Most (705 of the 800, or 88%) chambers had areas less than 10 cm^2 (chambers <10cm will be referred to as small; those >10cm as large). This suggests that the apparent large surplus of chambers available to the ants, while still a surplus, is not as large as it first seemed. If ants also use other criteria to choose chambers, the supply would be restricted even more. One such factor may be depth within the bark. Chambers at mid depth had 9.1% occupancy, while deeper and superficial chambers were less occupied (5% and 1.5% respectively) (Pearson Chi-square = 16.476; d.f. = 2; $p < 0.001$). This might also result in part from the smaller size of the deep chambers.

Combining the ants' preference for chambers larger than 10 cm^2 with the preference for middle depth restricted the acceptable chamber supply to only 54 chambers, or about 7% of the total supply. Ants were found in 43 chambers, of which 10 were preferred large chambers at middle depth. A disproportionate share (56%) of large chambers were found in middle depth, whereas about 34% were superficial and 9.5% were deep. Deep chambers presumably are not acceptable to the ants primarily because they are usually small, and superficial ones because they are exposed. Although there are 7.5 times as many small chambers as large ones, ants occupy only 2.6 times as many small as large ones. Of the 95 large chambers, 12 (13%) were occupied by ants, whereas of the 705 small chambers, only 31 (4.4%) contained ants. Assuming that the ants have "knowledge" of all chambers, proportional occupancy of large chambers (>10 cm^2)was three times higher for those of middle depth than for deep or superficial chambers.

Caterpillars were found in a total of 31 (3.9%) of the 800 chambers. Of these, 24 (5.6%) were found in the winter sample, and 7 (1.9%) in the summer sample, a significant difference (Pearson Chi-square: 7.22; df=1; $p< 0.005$) suggesting that the caterpillars overwinter in the bark, emerge in the spring, and reproduce in the summer. Many of the new generation of caterpillars would then be too small to detect reliably in the summer sample. In the winter, although the frequency of caterpillars in smaller galleries was higher than larger ones, this difference was not significant. In other words, caterpillar ages, sizes and gallery sizes varied greatly. On the other hand, caterpillars occurred with a much higher frequency in deep chambers (15.8%) than in mid-depth (7.7%) or superficial (0.7%) chambers,

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differences that were highly significant (Pearson Chi-square= 14.86; d.f = 2; $p < 0.001$). This confirms that the caterpillars make their galleries close to the cambium and phloem tissues on which they feed. In the summer there was no significant relationship between caterpillars and depth, probably because of the small number found. They were also as likely to be found at 5 m as at 1 m on the trunk.

The low occurrence of caterpillars in our samples is interesting. A large fraction of the chambers found were clearly created by caterpillars, and bore characteristic outlines and feeding pits. If we assume that the sample fairly represents the average standing caterpillar population, and that chambers are occupied for about a year and never re-used, then the 800 chambers found took 25 years to accumulate (800/31). This corresponds exactly with the average life expectancy of chambers, from formation to sloughing (see above). This reemphasizes that the abundant galleries were the products of a rather uncommon insect accumulated over a long period of time.

When queens of *Crematogaster ashmeadi* were found, they were frequently in termite galleries at ground level or below. Other living contents in the galleries were too rare to test for patterns.

Reproductive history of C. ashmeadi

Seasonality of brood production and fat content

The production of sexuals was highly seasonal (Fig. 5A). Sexual larvae began appearing in early May, with pupae following in mid-May so that sexual brood peaked during the second half of May. Sexual adults, both male and female, began appearing in late May and peaked in June. Mating flights began to deplete the sexual adults in the chambers in June, so that by mid-July, very few nests still contained sexual adults. These patterns are consistent with the presence of sexuals in dead branches and bark chambers sampled in other parts of this study.

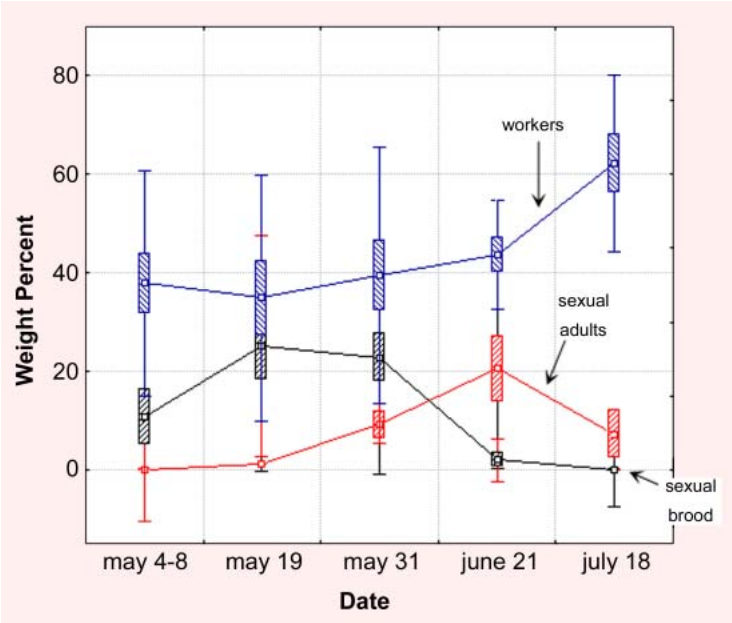


Figure 5A.Seasonality of *Crematogaster ashmeadi* brood production as a percent of total weight. Sexual brood peaks mid-to-late May, and adult sexuals appear in mid-June, and are depleted by mid-July.

The percent fat (based on changes in dry weight) varied greatly among the different types of ants and brood stages (Fig. 5B). Workers averaged slightly less than 20% fat, with worker pupae and larvae in the mid-to-high 20s. Sexual brood ranged from about 13% fat for larvae to 29% for female pupae. As expected, male adult sexuals were very low in fat, as are many male ants, and female adult sexuals were very high (near 50%) in keeping with their function in independent colony founding.

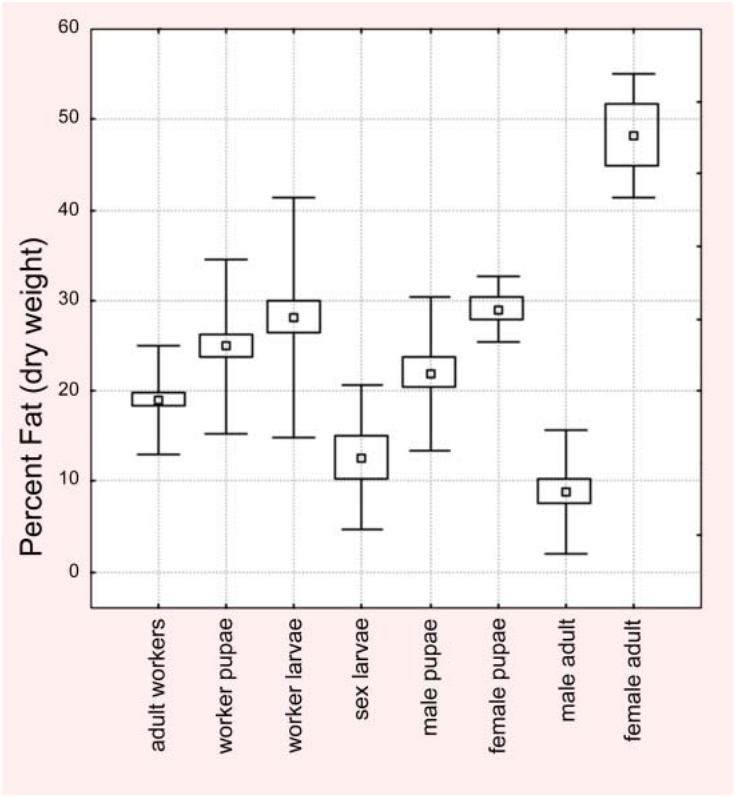


Figure 5B.Percent fat of the various *Crematogaster ashmeadi* castes and life stages. Female adults ready for their mating flights are by far the most fat-rich.

Based on their composition, the energy content of the stages and types of ants is given in Table 2. The value of 18.87 J/mg was used for the energy content of lean weight, and 39.33 J/mg for fat (Peakin, 1972). Adult female sexuals have a very high energy content because they are both large and fat. A woodpecker would have to eat 19 adult workers to gain as much energy as provided by a single adult female sexual.

Reproduction and colony size

It is nearly impossible to make direct estimates of the sizes of colonies dispersed among dozens or hundreds of chambers scattered over an entire 30 or 40 meter-tall pine tree. Indirect methods of estimation such as one based on the queen's egg-laying rate must therefore be used. . The vast majority of eggs laid by an ant queen develop into workers that merely replace those that died. Knowledge of worker longevity (or assumptions about longevity) allows the estimation of how large a colony an observed egg-laying rate can sustain.

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Type & stage	N	Mean	Std. Dev.	Worker equivalents
Adult worker	107	6.58	1.19	1.00
Worker larva	89	5.87	3.17	---
Worker pupa	79	5.50	1.09	0.83
Sexual larva	12	61.78	8.17	9.39
Male pupa	44	7.67	1.60	1.17
Female pupa	10	66.05	4.08	10.0
Male adult	45	6.02	2.00	0.91
Female adult	5	126.2	37.7	19.2

Table 2. The energy content of types and stages of ants in joules/individual and in worker-equivalents. Energy content was calculated from the fat and lean weight of *Crematogaster ashmeadi* ants, using 18.87 J/mg for lean weight, and 39.33 J/mg for fat. Energetic investment in adult females far exceeds any other. A worker-equivalent value for worker larvae was not calculated because these were mixed instars.

Queens of mature *C. ashmeadi* colonies were captured during the summer by opening chambers near the ground with a chisel, and aspirating the queen. The presence of clumps of eggs in chambers usually predicted the presence of a nearby queen. Queens were placed in a test tube with moist cotton and a few of their workers, and immediately returned to the laboratory, where they were kept at 28 °C. Eggs were counted after 4 to 6 hr, and again after 14 to 18 hr. Dividing the elapsed time into the number of eggs laid gave two estimates of egg-laying rate (eggs/hr) for the two time intervals. Because queens were attended by only a few workers, and probably did not feed much, the second rate in 6 of the 8 queens was lower than the first. Overall, the rate during the second interval averaged 85% of the rate in the first. Only the initial rate was used for the following calculations. Over the entire period, queens lost an average of 0.03 mg (SD= 0.007) for every egg they laid. Of course, this is more than simply the weight of the egg. By direct measurement, eggs weigh about 0.023 mg.

The maximum colony size sustainable by each queen's observed egg-laying rate was estimated by multiplying the eggs/day times the assumed worker lifespan. Because the life span of workers is not known, two values were used in the range typical of other ant workers of similar size, 90 and 180 days (Calabi and Porter, 1989). For worker lifespans of 90 days, these queens could sustain colonies ranging from 15,000 to over 40,000 workers. If the worker lifespan is 180 days, colonies of about 30,000 to 80,000 workers could be sustained (Fig. 6). These calculations apply to constant conditions, but the ants are highly seasonal in their reproduction, and temperature varied as well. However, changes in the reproductive season and temperature-induced variation in egg-laying rate would bear a linear relationship to the colony size estimate. If the queen lays eggs for half the year, size estimates would be half as large. Crude as these estimates are, they give a rough indication of colony sizes. There seems little doubt that colony sizes range in the tens of thousands of ants. Until adequate direct estimation methods are developed, we will have to be satisfied with these indirect ones.

Reproductive characteristics of queens

At capture, queen live weight ranged from 12.6 mg to 17.8 mg (n= 8). A queen with minimally developed ovaries and minimum body

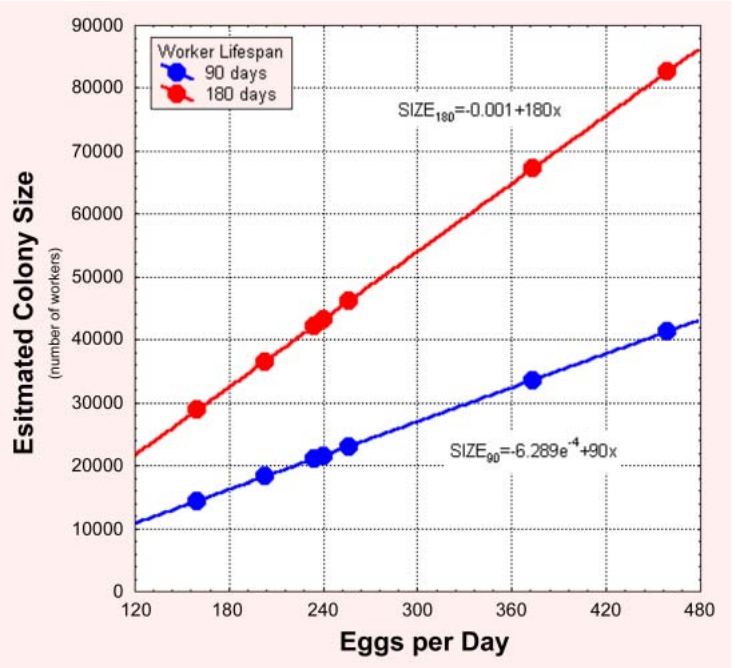


Figure 6. Estimated *Crematogaster ashmeadi* colony size as a function of the queen's egg-laying rate, assuming worker longevity to average 90 or 180 days.

reserves, such as occurs at the end of the founding period, weighed about 3 to 5 mg. The excess over this weight in queens of established colonies therefore represents the functional weight of the reproductive tissues;ovaries, fat body and digestive system. The ovaries of an actively ovipositing queen have 45 to 60 active ovarioles, 2 to 9 inactive ovarioles and 120 to 600 vitellogenic oocytes. Queen weight increased as this tissue increased in production rate, and was therefore positively related to the egg-laying rate (Fig. 7). Every mg increase in body weight resulted in an average increase of 37 eggs per day (regression: Eggs/d = 37W - 254; $F = 17.0$, d.f. = 1, 5; $p < 0.01$, $R^2 = 73\%$). Backwards extrapolation suggests that queens of less than 7 or 8 mg body weight do not lay eggs. This boundary agrees well with the weights of founding queens (mean = 7.25 mg) that lay a modest batch of eggs during the first few days of the claustral period. It is also in line with post-founding queens, that have a live weight of about 3 to 5 mg (1.2 to 2.7 mg dry) and lay eggs at very low rates.

Sperm counts were made on queen of established colonies and on newly mated queens by dissecting out the spermatheca, dispersing the sperm in 0.5M NaCl, and counting the sperm in a hemocytometer (Tschinkel, 1987b). Sperm counts of queens captured from mature colonies ranged from 330,000 to 1.75 million (mean = 1.06 million, SD = 0.55 million). This contrasted with a mean sperm count of 2.64 million (SD = 0.31 million) for newly mated queens, which presumably represents the starting value at the outset of reproductive life. The difference between these counts is sperm depletion resulting from sperm-use for producing female offspring (workers and female sexuals). If the sperm use efficiency is similar to that of the fire ant, *Solenopsis invicta* (3 sperm per adult female produced), this implies that the average queen has produced about 0.5 million workers beforecapture. Assuming queens began life with the average count, the maximum and minimum number of workers produced would be 0.8 million and 0.3 million. Such numbers suggest either large colonies or long queen life spans, or both.

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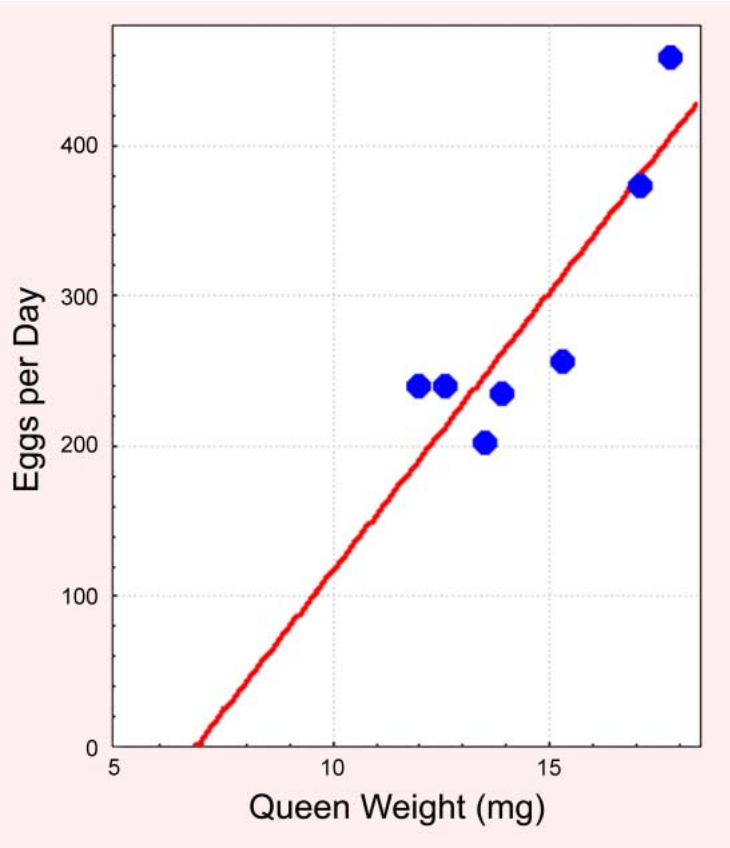


Figure 7. Egg-laying rate of *Crematogaster ashmeadi* queens taken directly from field colonies in relation to their body weight at capture. One outlier was deleted. Regression: Eggs/day = 37W - 254; F= 17.0, d.f. = 1, 5; p< 0.01, R^2 = 73%.

Colony dynamics

Food preference and reliability of baiting

The 6 repetitions of the baiting study showed that *C. ashmeadi* strongly prefer cat food over peanut butter (mean 13.5 vs. 3.8 ants/ bait), and slightly prefer it over beetle larvae (mean 13.5 vs. 10.0 ants/bait). They also come in higher numbers to baits on the shady north side of the tree compared to the south side (means 10.7 vs. 7.5 ants/bait). One of the repetitions was also significantly higher than the rest. All these factors had a significant effect on the number of ants on baits (ANOVA: F =7.51, p < 0.00001; orientation: F = 63.8, d.f. = 1, 4284; p < 0.00001; food type: F =208.5, d.f. = 1, 4284; p < 0.00001; food x orientation interaction, F =4.04, d.f. = 1, 4284; p < 0.05).

Of greater interest was the likelihood of detection or non-detection when ants were present on trees, in other words, the consistency of detection. This was estimated separately for each of the three foods as the number of 6 baitings that ants were present on the bait. When the food was peanut butter, ants were detected in more than half the trials on 57 of the 120 trees, and were never detected on 22 of them. When the food was pureed beetle larvae, 78 trees drew ants more than half the time, and 10 never did. When the bait was cat food, these numbers were 77 and 13. Cat food and beetle larvae were equally reliable in detecting ants, although cat food attracted larger numbers of ants. We used only cat food in all subsequent baiting studies, and placed baits on all four cardinal compass points.

There was a strong relationship between the mean number of ants on baits and the number of times (of 6 trials) in which ants were detected (Fig. 8). Colonies that fielded only small numbers of ants to baits went undetected more frequently than those fielding large numbers. In other words, colonies were consistent in the number of foragers coming to the baits, and therefore in their detectability on the tree. Colonies that were detected 5 to 6 times in the 6 trials averaged 15 to 50 workers on baits, whereas those that went undetected 1 to 4 times averaged fewer than 6 workers when they did come to baits. Colonies rarely fielded a few workers in one trial and a large number in another. With a single exception, all colonies that sent 50 or more workers to a bait in at least one of the six trials were detected in all six trials. The only exception was a colony sending more than 50 in a single trial and 0 in another.

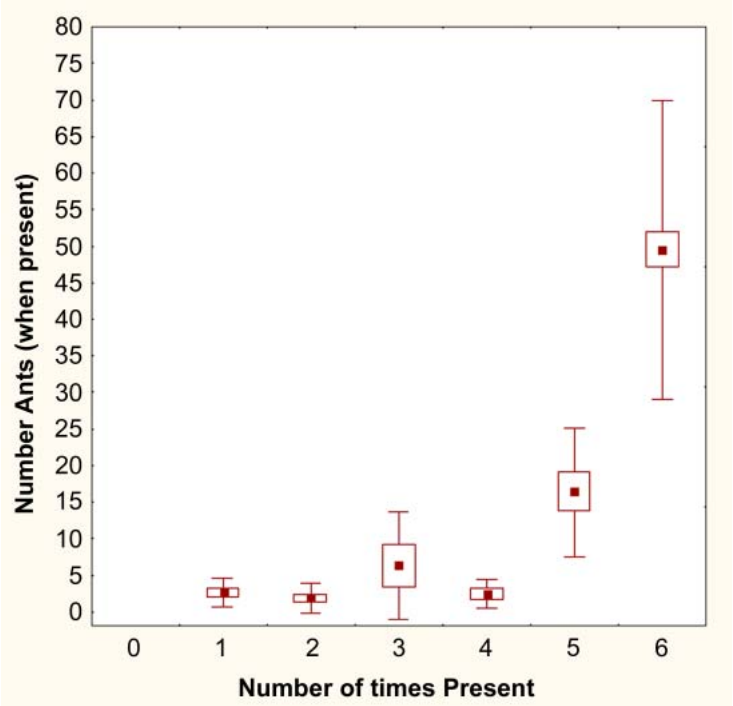


Figure 8. The mean number of times *Crematogaster ashmeadi* colonies were detected in 6 baiting trials in relationship to the number of workers on baits. Only baits with workers present were used to calculate the statistics. Error bars show standard deviation and standard error.

On 13 (11%) of the 120 trees, *C. ashmeadi* were never detected and can be presumed to have been absent, at least from the lower trunk. To the extent that large numbers of workers on baits indicate the presence of a vigorous colony, about 60% of the trees were occupied by substantial, readily detectable colonies of *C. ashmeadi*. An additional 29% of trees harbored colonies that did not consistently come to baits (4 or fewer trials), and thus might be missed in a single baiting. When a colony was detected 3 or fewer times in 6 trials, there was a 50% or lower chance of detecting it in a single baiting. About 25% of the colonies fell into this category. When all trials were included, *C. ashmeadi* was detected on almost 90% of the 120 trees, a rate much higher than the mean of 55% occupancy found in extensive surveys using a single baiting per tree (Tschinkel and Hess, 1999). It seems likely that the difference consists of small colonies that field very low numbers of workers to baits, and are therefore likely to go undetected in single baitings. It follows that single-baiting studies underestimate the number of trees occupied by *C. ashmeadi* by a substantial amount.

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Occupancy of trees

Baits near the ground attract ants in a large fraction of cases. However, the upper trunks and crowns of trees are not readily accessible to investigation, so it remained to be determined if *C. ashmeadi* used only the base or the entire tree. In a preliminary study, baits were placed at 1 m and at 5 m on the trunk of 24 trees known from previous baiting at 1 m to harbor *C. ashmeadi*. In all but one case, workers were found on both baits, suggesting that they occupied at least the lower half of the trunk. Two different methods were then used to test entire trees; climbing trees with ladders to bait far up into the crown, and archery to retrieve dead branches.

When a pine was inhabited by *C. ashmeadi*, workers recruited to baits at all levels in the tree, from the ground into the crown and branches. The proportion of the baits occupied did not differ between the trunk and branches, suggesting that *C. ashmeadi* nested in these in similar proportions.

These results were corroborated through the use of archery. Four baits were placed 1 m above ground level on the trunk of each tree. After half an hour, the workers coming to the baits were counted and chambers in the base were opened with a chisel. Each tree was checked four times every 2 days in mid-May 1996. Once the presence of ants was established, a bow-shot line was used to break one or more dead branches from the tree. These dead branches were peeled and split and the number of any *C. ashmeadi* workers, brood and sometimes sexuals in them was estimated. This procedure was carried out in one sandhills site and 3 flatwoods sites.

Of the 60 trees checked at the sandhills site, 33 contained ants that came to baits low on their trunks. In these 33 trees, *C. ashmeadi* nest chambers were found in the dead limbs of 19 (58%) of them. Because only 1 to 3 dead limbs were sampled, and other potential nesting sites in the crown were not checked, this is surely an undercount. It is likely that most of the occupied trees were entirely occupied. In only one case did was *C. ashmeadi* found in dead limbs but not on the lower trunk. Ground level nest chambers were rare at this site; only 2 of the 33 occupied trees had ants in ground level chambers.

At the three flatwoods sites, of the 21 trees on which *C. ashmeadi* came to baits low on the trunk, 15 also had *C. ashmeadi* in dead branches. Of the 17 trees on the 3 sites that were checked for them, 7 had occupied ground level chambers, much higher than the sandhills site. This rate of occurrence is more in line with my general collecting experience. Why the sandhills site is low in ground-level occupied chambers is unknown.

C. ashmeadi regularly shares the pine forest habitat with 3 other arboreal ant species, but is much more common than any of them. *C. ashmeadi* were detected on almost 90% of the censused trees at least once. *Camponotus nearcticus* occurred on almost 20% of trees, and *Leptothorax wheeleri* on about 8%. About 12% of trees were occupied by multiple species. When *C. ashmeadi* was present with the other two species, it usually dominated most of the baits. *Solenopsis picta* was not found in this study, but is known to occur regularly. Some aspects of the structure of this arboreal ant community have been published (Tschinkel and Hess, 1999), and more details will follow elsewhere.

One colony per tree?

C. ashmeadi from different colonies are very aggressive towards one another, and attack intruders very quickly, pinning and holding them for nestmates to kill. This aggressive response was used to determine if a single colony occupied an entire pine tree by bringing workers from different parts of a single tree together. A lack of aggressive response indicated that the workers were all from the same colony. Initially, we used tree-climbing ladders to place baits at intervals on the trunk and main branches of the crown, as described above. Ants that came to these baits were carried to adjacent baits or more distant baits and allowed to encounter workers there. The 4 longleaf pines that were surveyed this way all contained a single colony each. There was no aggression in any of the encounters within trees.

This laborious and time-consuming method was later supplanted by the archery method described above. Workers from nest chambers in dead branches in the crown were made to encounter workers coming to baits or taken from chambers opened with a chisel at the base of the same tree. Again, lack of aggression indicated that the workers belonged to the same colony. This procedure was carried out in June and July, 1999 on 24 trees located in 4 widely separated flatwoods sites in the Apalachicola National Forest. Occasionally, workers were tested against those from other trees to make sure that the aggressive response resulted.

Of the 14 trees in which workers were found in dead branches in the crown and on baits or in chambers at the base of the tree, all were occupied by a single colony. We never observed aggression in encounters between these workers. In contrast, pitting workers from different trees against one another invariably resulted in immediate attack.

Do colonies occupy more than one tree?

Worker ants coming to baits were carried to other nearby trees and made to encounter workers on bait there. An aggressive response against the intruder indicated that the intruder was from a different colony. At one site, workers from each of 40 occupied trees were tested against workers from all nearby occupied trees. The great majority of inhabited pairs of trees contained different colonies. However, in 7 cases, neighboring trees were occupied by the same colony. The mean distance between these trees was 1.25 m (SD = 0.65, n=8), whereas that between trees with different colonies was 4.95 m (SD = 2.10; n=56). Of 14 pairs of occupied trees that were 2 m or less apart, 8 pairs were occupied by the same colony, and 6 by different ones. . One colony occupied 3 trees. When pairs of trees were separated by more than 2 m, none were occupied by the same colony. These results are in line with the observation that baits placed on the ground near occupied trees rarely drew workers, and when they did, they never ventured more than a meter or two from their

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tree. A second tree closer than 2 m enabled colonies to occupy both trees, but it did not assure that they would do so

Activity rhythms of foraging

Ten trees in the climb-and-bait study were baited and censused during the summer at 7 a.m., 1 p.m., 7 p.m. and 1 a.m. This was repeated for 3 days. *C. ashmeadi* came to baits in large numbers (mean = 13; SD =7) during all but the 7 a.m.sample at when foragers on baits averaged less than 1.0.

Colony founding in the field and laboratory

Newly mated queens of *C. ashmeadi* seek out abandoned galleries of woodboring beetles in the dead branches of pine saplings to establish nests (Hahn and Tschinkel, 1997). Although several founding queens might be found in a single branch, they never shared a founding chamber. Each queen reared her own brood. The exact date of mating was not known, but small numbers of eggs and the absence of larvae were taken as signs that the queen had flown and mated less than a week before.

The reproductive season begins with the appearance of sexual larvae in late April and early May. Adult sexuals appear during late June and peak sometime before late July (see above). Mating flights are probably cued by rain, and most likely begin about early July. By late July, sexuals of all forms are no longer abundant in mature colonies. These dates agree reasonably well with the dates on which founding queens were collected, between July 14 and August 2, 1994. It seems likely that few flights take place during August.

The progress of brood production during colony founding in the laboratory is shown in Figure 9. The number of eggs peaked at about 15 days, then dropped to a minimum at about 30 days. This was probably the result of the combined effect of egg-hatch and the eating of trophic eggs by larvae. The number of larvae peaked at about the same time as eggs reached their minimum (30 days). Pupae began to appear at about 30 days and peaked at about 40 days. The first substantial numbers of minims appeared on day 36. Minims accumulated through the end of the experiment on day 64. With the appearance of the minims, the claustral period is usually considered ended. The claustral period is thus probably 40 to 50 days long. The amount of variation introduced by environmental temperature regimes is unknown.

Weight and production relationships were as follows. When first collected, queens averaged 8.11 mg live weight (SD = 1.3; n= 24), and 3.1 mg dry (SD = 1.2; n= 6). By the end of the experiment, their dry weight had dropped to 1.67 mg (SD .= 0.53; n= 18), a mean loss of 46% of their dry weight. This weight loss of 1.43 mg was accompanied by the production of a mean of 0.89 mg (SD = 0.43; n= 18) of brood, a conversion efficiency of 62%. At termination, the brood consisted of 0.34 mg worker brood, and 0.55 mg adult minim workers. These minim workers averaged 0.099 mg in weight (SD = 0.018; n= 18 colonies).

There was a strong relationship between the initial queen live weight

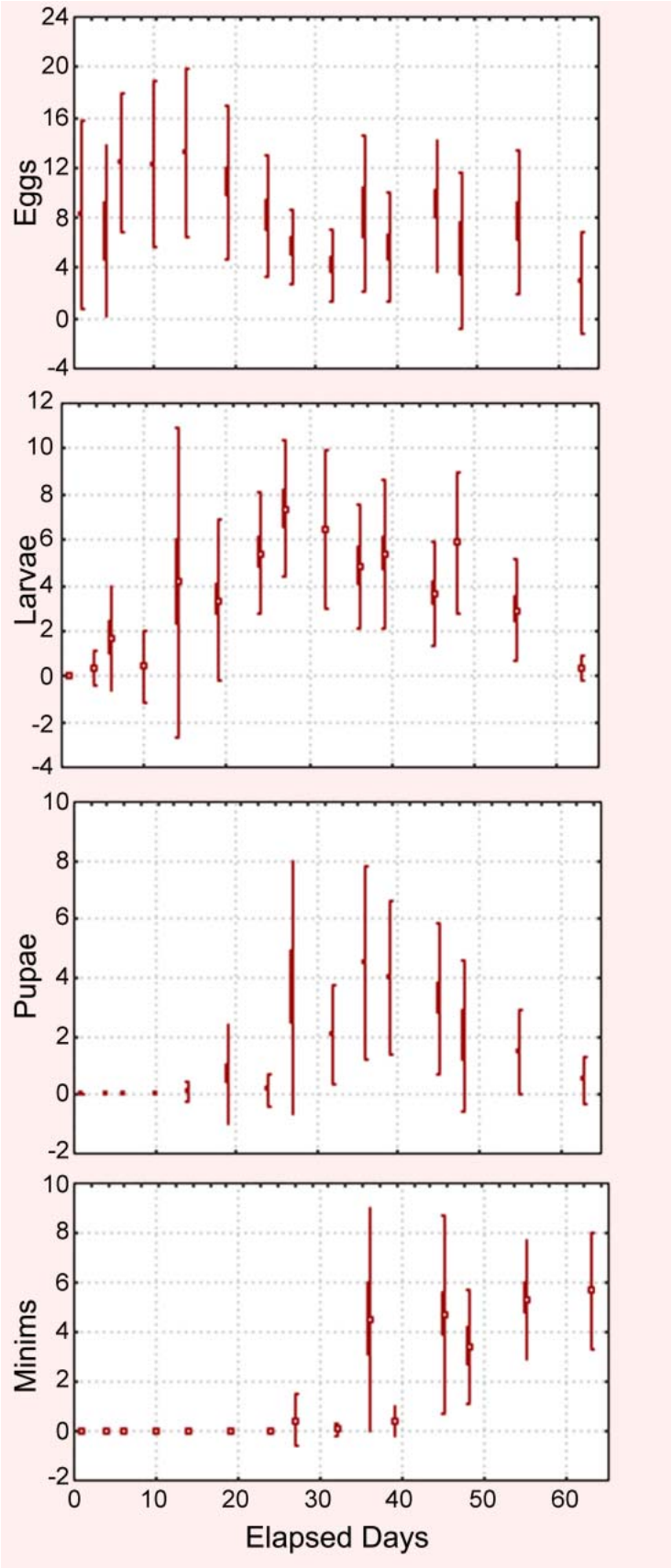


Figure 9. The course of brood production during colony founding in 27 nests by *Crematogaster ashmeadi* held in the laboratory. The mean number of eggs, larvae, pupae and minim workers is shown beginning at the time of capture. Only queens captured with few or no eggs were used for this study, and most had probably mated less than a week previously. Error bars show standard deviation and standard error.

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and the total dry weight of progeny she produced (Fig. 10; regression of progeny vs. queen weight, P= 0.35W - 2.05; F = 50.0, d.f. = 1, 16, p< 0.00001, R^2 = 74%). Every mg increase in initial live weight was accompanied by an increase of 0.35 mg of dry progeny weight. Queens of less than 5.9 mg produced no progeny. Progeny production was also positively related to weight loss (not shown). Assuming queens to be 41% dry weight, weight loss was calculated as Loss = 0.41 (initial queen live weight) – final queen dry weight. Every mg of dry weight loss was accompanied by 0.46 mg more of dry progeny weight, a conversion efficiency of 46%, higher than the above estimate but not significantly so (regression of progeny weight vs. queen weight loss, P= 0.46L + 0.076; F = 14.2, d.f. = 1, 16, p< 0.005, R^2 = 44%).

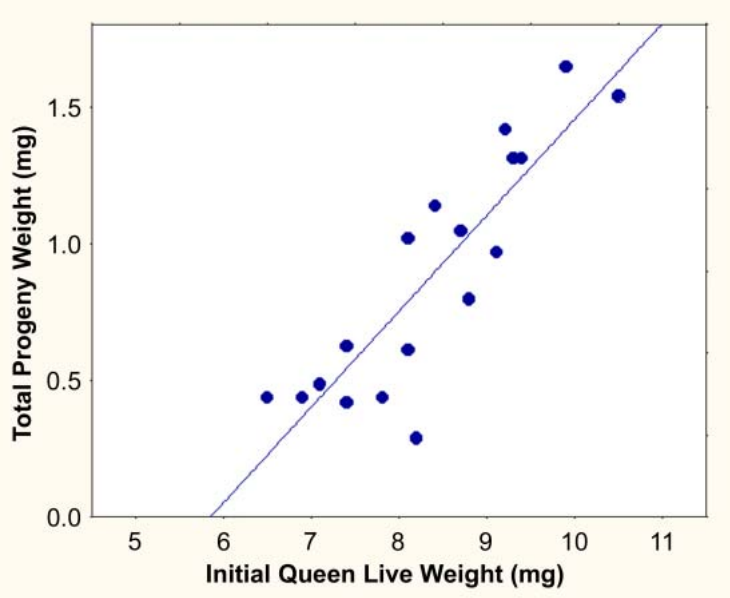


Figure 10. The total weight of progeny produced by *Crematogaster ashmeadi* founding queens in relationship to their initial live weight. Heavier queens produced more progeny. Regression: P= 0.35W - 2.05.

Colony longevity and turnover (mapped plots)

If one makes certain assumptions, one can estimate the average colony lifespan from the long-term studies of the six mapped forest plots. If a tree harbored a vigorous colony of *C. ashmeadi* for several years, and then none, it seems likely that the colony has died, especially if a "weak" colony appears after a gap of one or more years. In our first baiting study, about 25% of colonies were detected in half or fewer baitings. These "weak" colonies may be immature colonies that do not yet occupy the entire tree, or whose worker force is too small to find and exploit most of the baits. The existence of such colonies is consistent with the replacement of dead mature colonies with newly founded ones. An alternate, not mutually exclusive interpretation is that the queen of "weak" colonies had died, and the colony gradually becomes smaller as workers die and are not replaced. In either case, an occupancy gap of one or more years can be interpreted as colony turnover. Laboratory colony growth rates suggest that full occupancy of a vacated tree cannot be achieved in one year. From this turnover rate, we can calculate a mean colony longevity, as follows.

Considering the six years in sequential pairs, there are three kinds of year-to-year sequences:
(1) a colony was detected on baits both years of a pair (P-P, colony survival)
(2) a colony was detected in the first year of a sequential pair but not the next (P-A, colony death)
(3) a colony was not detected in the first year of a pair, but was in the next (A-P, new colony).

There are 5 such pairs in the 6-year record of baiting. Let X= the observed number of P-P pairs (persistence), Y_1 = the number of P-A pairs (deaths), and Y_2 = the number of A-P pairs (new colonies). The longer-lived the colonies, the more X will predominate over the other two. In a stable population the chance of a new colony starting is equal to the chance of an old colony dying. This means that the average of the two rates, $(Y_1+Y_2)/2$, corrected for continuity by adding 1, provides a better estimate of the chance of dying. Therefore

The average colony lifetime = $1 + [2X/(Y_1+Y_2)]$

This computation was applied separately to each of the six plots, and the estimates used to calculate an overall mean and standard error. Use of the entire data set resulted in a mean lifespan estimate of 6.72 yr. Inspection of the data shows that 38% of the colonies were detected in all six years (that is, had 5 P-P transitions), and that about 75% of the colonies alive in 1994 were still alive in 1999. This suggests that the post-juvenile lifespan is considerably greater than 6 yr.

There is a positive relationship between the mean number of workers recruited to baits and the number of years during which a colony was detected (Fig. 11). Colonies present all six years averaged about ten times as many workers on baits as colonies present one or two years. An index was created by combining the number of annual detections with the number of workers recruited. This index showed essentially the same pattern against years present as in Fig. 11. These patterns are consistent with the claim that colonies detected only in one or two years were probably mostly young, small colonies that subsequently failed, and can be regarded as juvenile mortality. The full data set includes 16% of colonies that were never detected two years in a row and another 9% present two years in a row only once. Calculations of mean lifespan are heavily affected by high juvenile mortality. In such cases, the longevity of individuals (colonies) that survive the juvenile period often greatly exceeds the mean lifespan. Leaving out the juvenile mortality by using only colonies detected at least two years in a row, the mean lifespan estimate increased to 10.4 yr. Specifying detection at least 3 years in a row boosted the lifespan estimate to 15.4 yr.

The combination of egg-laying rate and spermathecal sperm count can also be used to estimate the "effective" queen lifespan. Assuming an average of 300 eggs/day (see above), a sperm efficiency of 3 sperm/adult female (estimated in *Solenopsis invicta;* Tschinkel and Porter, 1988) and an egg-laying season of 6 months, we find that a queen uses 165,000 sperm/yr. Dividing this use-rate into the spermathecal sperm count of newly mated queens (2.64×10^6) indicates that the average queen will run out of sperm in 16 yr (incorrect guesses about egg-rate, sperm efficiency and reproductive

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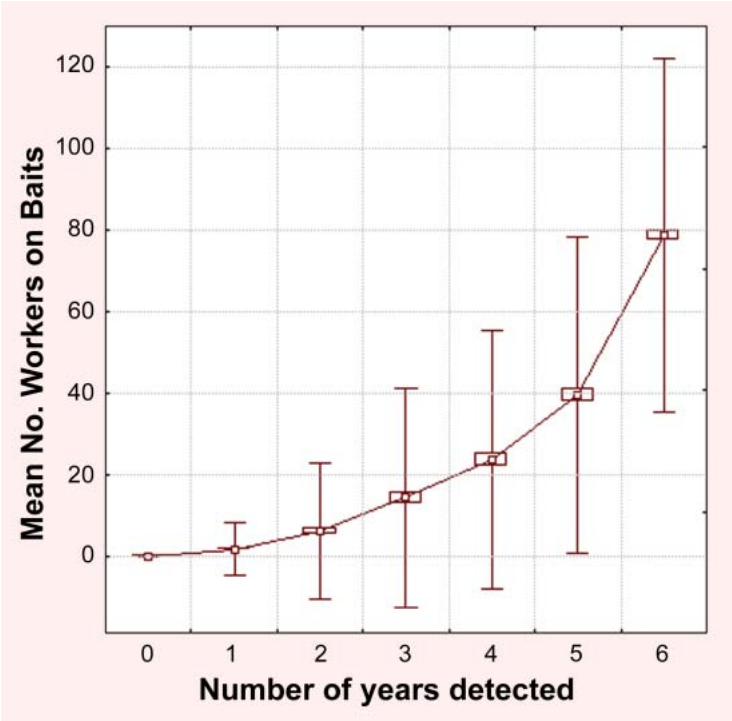


Figure 11. The mean number of *Crematogaster ashmeadi* workers on occupied baits in relation to the number of years out of six that a colony was detected on a tree. Colonies fielding many workers were detected more consistently over the years. The pattern may be the result of higher mortality among smaller colonies (those that field fewer workers to baits).

season will affect this estimate in a linear fashion). Without sperm, she cannot produce workers to sustain her colony. This is her maximum lifespan, excluding extrinsic sources of mortality, and should be greater than the realized lifespan calculated from the data. Crude as the sperm-based estimate is, it agrees well with the estimate based on colonies present at least three years, i.e. mature colonies.

Colony size can also be estimated from the demographic data and the initial spermathecal sperm counts: Colony size = 2.64×10^6 sperm/3 sperm per worker/ 15.4 yr = 60,000 workers/yr. Assuming a mean worker lifespan of 90 days, this yields a standing colony size of 15,000. For 180 days, it is 30,000. Using the less extreme estimate of demographic lifespan (detection at least two sequential years, 10.4 yr), results in colony sizes of 20,000 and 40,000. All these estimates are somewhat lower than those derived from egg-laying rates.

Discussion

C. ashmeadi is by far the most abundant arboreal ant in the longleaf and slash pine forest of the coastal plains of Florida. The majority of pine trees harbor a colony, and each mature colony occupies at least an entire tree. At all stages of their life cycle, populations of *C. ashmeadi* are linked to populations of woodboring insects who create cavities later used by the ants. Newly mated queens seek out the abandoned galleries of cerambicid and buprestid beetles in the first dead branches that form on longleaf pine saplings (Hahn and Tschinkel, 1997). Under natural forest conditions, longleaf pine saplings therefore acquire a colony of *C. ashmeadi* very early in life. As the tree grows, the bark of its trunk becomes host to several species of bark-mining caterpillars, most commonly the cossid, *Givira francesca*. The successful emergence of these caterpillars leaves behind vacant chambers that, after some minor renovation and cleaning, can be occupied by colonies of *C. ashmeadi*. Colonies of this ant therefore exist as groups of workers and brood, and sometimes sexuals, dispersed among many chambers. Because the caterpillars prefer the thicker bark at the tree base, their abandoned galleries are much denser low on the trunk. Near ground level, large galleries made by ground-nesting termites supplement them. As a result, the center of gravity of *C. ashmeadi* colonies is typically low on the trunk, with queens located in ex-termite galleries at or below ground level in about one-third of the cases. In spite of this higher chamber density low on the tree, a single colony typically occupies an entire mature pine tree. In the branches, they readily use as nest chambers the abandoned galleries of cerambicid and buprestid beetles. *C. ashmeadi* foragers therefore forage over most of the tree, including at least the larger branches. Whether they forage on the twigs and foliage is unknown, but likely.

There are many organisms whose activities create habitats for others, a phenomenon often referred to as ecological engineering. From the ponds created by beavers to leaf-tying caterpillars or the holes made by woodboring beetles, these habitats can be critical to the animals dependent on them (Laland, et al. 1999; Wilby et al., 2001). Because *C. ashmeadi* seems not to excavate its own chambers, it appears to be completely reliant on the activity of the wood and bark-mining engineers for the provision of nest chambers. This dependence raises the question of whether the availability of chambers is limiting to *C. ashmeadi*. Would a decline in the populations of woodboring insects bring about a decline of *C. ashmeadi* populations through a decrease in nesting opportunities? In the natural longleaf pine forests of the Gulf Coastal Plain, chambers seem in great excess, and empty chambers are the norm. However, the ants show a clear preference for larger chambers in the middle depths of the bark, greatly reducing the apparent excess of high-quality chambers. Other choice-factors may reduce the supply further. The ants do nest in smaller, suboptimal chambers, but whether this exacts a cost in performance is not known. On urban loblolly and shortleaf pines in Florida, woodboring beetles and bark-mining caterpillars are much less abundant, and so are *C. ashmeadi* colonies (personal observation). Whether this correlation is also causal is unknown, but it is interesting.

When it comes to opportunities for colony founding, limitation by the abundance of woodboring beetles seems clear. Longleaf pine saplings are never colonized by newly mated queens before they have at least one dead branch with beetle-made cavities. Slash pine saplings are rarely colonized until they are older because their thin, almost pith-less branches do not support as many suitable beetle galleries. The supply of founding opportunities therefore depends on the abundance of longleaf pine saplings and woodboring beetles. It seems likely that the beetles are not specific to saplings, but mine any dead pine branches, including those on mature pines. However, searches of large numbers of dead branches from mature trees found no newly mated queens or young colonies (unpublished data). Perhaps newly mated queens prefer saplings because these are unlikely to be occupied by a mature colony of *C. ashmeadi* or other

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competitor ants. Or perhaps newly mated queens are quickly eliminated by mature colonies, or there are so many dead branches with galleries to choose among that finding one with a newly mated queen is unlikely. On rare occasions, I have discovered, quite by accident, founding queens in galleries on the trunk. Obviously, pines are much longer-lived than *C. ashmeadi* colonies. Because old pines also harbor these ants, the ants must start new colonies on mature trees, even if the founding queens are rarely discovered.

Whether or not pre-formed insect galleries are ever limiting to *C. ashmeadi*, dependence on them and the ecosystem engineers that produce them is clear. This ties the ant to a habitat resource with a finite useful life, and creates a dynamic system in which new chambers are continuously formed while old ones decay, slough off or break off. Bark chambers formed by cossid caterpillars have a remarkably long life of about 25 years before they slough off the bark surface. The large number of these chambers in the bark of mature pines has therefore accumulated over decades. The commonness of the chambers belies the relative rarity of the cossids forming them. Only 4% of the chambers contained living caterpillars, in good agreement with the average chamber lifespan of 25 years.

C. ashmeadi occurs throughout the geographic range of the red-cockaded woodpecker. , *Givira francesca*, which occurs widely in Florida and has been recorded as far west as Louisiana. Another, somewhat larger species, *G. anna*, occurs from the pine barrens of southeastern New Jersey south to Florida and west to Missouri and Arkansas (Covell, 1984). The larvae of *G. anna* are also reported to bore in pine trunks. If the abandoned chambers of this species are also acceptable to *C. ashmeadi*, then the moths, ants and red-cockaded woodpeckers are all more or less coextensive in range.

The seasonal production of sexuals during the spring and early summer is typical of the majority of ants (Hölldobler and Wilson, 1990), and therefore unremarkable. Judging from the decline of adult sexuals in colonies and the appearance of newly mated queens in their preferred founding sites, mating flights take place mostly during June and July. As in other ants, flights are likely to be associated with rain, but actual mating flights have not been observed.

Colony founding is claustral, that is, sealed in a chamber. The course of founding is similar to that of many ant species (Hölldobler and Wilson, 1990). Founding queens lay an initial batch of eggs, some of which are trophic eggs, and over the course of about one to one and a half months, produce a small number of very small minim (or nanitic) workers. They do this without feeding by drawing on stored metabolic reserves that include an initial fat content of about 50%. Such a fat content is typical for ant species whose queens found new colonies independently, that is, unassisted by workers (Keller and Passera, 1989). During colony founding, the *C. ashmeadi* queen loses about half her body weight, converting it into progeny with an efficiency about 50 to 60%. Body weight predicts the amount of brood a queen produces, something which is not always true in ant species (Tschinkel, 1993). Once produced, the minims take over brood rearing and foraging as the colony begins to grow. How fast or how long colonies grow is not known, but the fact that about a quarter of colonies were "weak" suggests that the growth phase occupies a small proportion of the life cycle, most of which is spent in the mature stage.

Indirect estimation of mature colony size suggests that it is typically in the tens of thousands of workers. It would hardly seem possible for a colony to occupy entire 30-m tall pines with fewer workers than this. Among ant species, colony sizes in the hundreds of workers are probably the norm (Hölldobler and Wilson, 1990), so *C. ashmeadi* ranks among species with large colonies. Combining large colony size with occurrence on a majority of pine trees confirms what woodpeckers have known for millions of years, namely, that *C. ashmeadi* is an extremely abundant ant and therefore an important component of the forest ecosystem.

A colony lifespan of 10 to 15 years, once the juvenile period has been weathered, is probably not unusual for ants with large colonies. Of the 20 queen longevity records compiled by Hölldobler and Wilson (1990), most fell between 4 and 30 years. Almost half lived from 5 to 10 years, only 1 less than 5 years, and only 3 more than 20 years. The 10 to 15-year lifespan of *C. ashmeadi* colonies is not out of line with these. It should be cautioned, however, that only the estimates for *S. invicta* (Tschinkel, 1987a) and *Pogonomyrmex owyheei* (Porter and Jorgensen, 1988) were made on field populations. Almost all other estimates resulted from single laboratory colonies.

A number of fundamental questions about the biology of *C. ashmeadi* remain, the most important of which is diet. Although foragers readily come to baits stuck to pine bark, foraging trails and food traffic generally can be observed for only a few cm before they vanish under the overlapping scales of pine bark. It is likely that the ants are general scavenger/predators like most ants, but what they eat is currently unknown. Pines are home to many species of arthropods, some of which make their living by eating pine tissue or sucking sap, others merely shelter there and some of are incidental "tourists". The scaly bark of smaller pine branches harbors a diverse community of about 20 species of mites, psocids, collembola, beetle larvae, mealybugs and caterpillar larvae (unpublished data). Some of these live off the pine's production, others eat the abundant fungus, lichen and pollen which collects on or under the scales. A few prey on the others. Whether or not *C. ashmeadi* crop this bark-scale community is unknown. What does seem clear is that it makes its entire livelihood on the tree, for it very rarely forages on the ground.

The dispersion of groups of workers in chambers scattered over as much as 30 m of tree must be a challenge to colony control and integration. Social and regulatory effects of such dispersal of queenless colony fragments have been documented (Herbers, 1989), but the effects of this nest subdivision in *C. ashmeadi* colonies is unknown. The existence of effective regulation is suggested by an incidental observation that when workers were brought into the laboratory in queenless nests, they soon developed active ovaries and began to lay eggs. But how does a single queen inhibit egg laying by workers dispersed up and down a 30 m-tall pine tree? Is there sufficient traffic among chambers to maintain queen control? No trails of workers moving up and down the tree are ever seen, but if these moved under the overlapping bark scales, they would not

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be visible to the human observer.

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