Arboreal Ant Community of a Pine Forest in Northern Florida

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ABSTRACT   The arboreal ant fauna of the longleaf and slash pine forests of the Apalachicola National Forest in northern Florida was studied using baits placed on trunks 1 m above ground level. *Crematogaster ashmeadi* Mayr was by far the most abundant ant attracted to the baits, occurring on ≈50% of all the trees. In addition to *C. ashmeadi*, another 10 species of ants, both ground-nesting and arboreal-nesting, were commonly captured. There was a strong relationship between the identity and abundance of species of ants on pines and the mean tree diameter, indicating that the ant fauna changed as trees grew. In young, recently regenerated stands, baits attracted mostly ground-nesting species of ants. Newly mated *C. ashmeadi* queens colonize the dead branches of pine saplings. As tree size increased, tree occupancy by *C. ashmeadi* rose to a maximum of 60% in middle-sized trees and fell to 50% in the largest trees. Parallel to these changes, the proportion of trees occupied by ground-nesting ants fell from 33% in the smallest pines to ≈15% in the largest, whereas those occupied by arboreal ants other than *C. ashmeadi* rose from 2 to 25%. The data suggested that *C. ashmeadi* is a dominant ant species with which other species do not easily coexist. Coexistence of arboreal ants increased with tree size such that the proportion of trees with >1 species increased steadily from ≈4% in the smallest pines to ≈19% in the largest. The total number of species was about the same in small, medium, and large trees, but the identity of these species changed. As in other ant communities, the assembly of the arboreal ant community in this pine forest is probably an example of the nested-subset phenomenon. That is, the occurrence of species is determined by their ability to coexist with the dominant, aggressive, large-colonied species, in this case, *C. ashmeadi.*

KEY WORDS   *Crematogaster ashmeadi, Pinus palustris, Pinus elliotti,* species diversity, red-cockaded woodpecker, community ecology

ANT COMMUNITIES ARE commonly shaped by competitive interactions among species (Hölldobler and Wilson 1990). Savolainen and Vepsäläinen (1988) divided ant communities into 3 tiers—at the bottom, those species that defend only the nest; in the middle, those that defend the nest and food finds; and at the top, the dominant species with their large colonies and absolute territories. These dominants are able to displace some of the other ant species, determine which other species can coexist with them, where these live, and how they forage (Rosengren 1986).

When there is >1 dominant species in a community, these tend to be mutually exclusive, creating a mosaic distribution of dominants, each with its associated subdominant and subordinate species. Adams (1994) reported on the behaviors that brought about this mutual exclusion in mangrove ants. Arboreal ant mosaics have been described in Ghanaian cacao farms (Room 1971; Leston 1973; Majer 1976a–c; Taylor 1977; Jackson 1984), Brazilian cacao plantations (Leston 1978), Solomon Islands coconut plantations (Greenslade 1971), tropical Australia (Majer and Camer-Pesci 1991, Hölldobler 1983), and Florida Keys mangrove islands (Cole 1983a, b). Terrestrial ant-territory mosaics include semiarid Australia (Greenslade 1982), Australian heath (Fox and Fox 1982), islands on the Baltic Coast of Finland (Pisarki and Vepsäläinen 1981, Rosengren 1986, Savolainen and Vepsäläinen 1988),

English heath and grassland (Brian 1983), and riparian woodland of California (Ward 1987).

The genus *Crematogaster* contains many arboreal species (Hölldobler and Wilson 1990) and is distributed worldwide. In a number of tropical forest ecosystems, such as those of Ghana, species of *Crematogaster* are frequently dominant among arboreal ants (Room 1971). Among the 26 species of ants in the trees of the South African savannas, the 7 most dominant were all species of *Crematogaster* (Grant and Moran 1986). As mentioned above, *Crematogaster ashmeadi* was 1 of 2 dominant ant species on mangrove islands in the Florida keys (Cole 1983a, b).

Crematogaster ashmeadi Mayr is an arboreal ant that commonly nests in pine trees. Although it is probably the most abundant arboreal ant of the coastal plain pine forests of the southeastern United States, very little is known about its life history, distribution, and abundance. The recent confirmation that this species is the dominant food item in the diet of the endangered red-cockaded woodpecker (*Picoides borealis)* (Hess and James 1998) has created an increased interest in the biology of *C. ashmeadi.* In early settlement days (before ≈1800), when open pine forests stretched unbroken from eastern Texas to southern Virginia, the red-cockaded woodpecker was a common bird. Today only ≈30 populations have >10 social units (small family groups of birds), and the bird

continues to decline throughout its range (James 1991, 1995). The largest population of the red-cockaded woodpecker is found on the Apalachicola National Forest southwest of Tallahassee, FL. Understanding the distribution and abundance of its major prey, *C. ashmeadi*, and the ant community to which it belongs may be important to the conservation of the bird. Here, we report on the distribution, abundance, and associated ant species of *C. ashmeadi* in the Apalachicola National Forest in northern Florida.

Materials and Methods

Sites. All sites were managed stands in the Apalachicola National Forest (ANF), southwest of Tallahassee, FL. Approximately 50% of the area of the ANF is pine uplands and 50% wetlands. Most of the upland was originally in longleaf pine (*Pinus palustris*) and was associated with a fire-maintained ground cover dominated by wiregrass (*Aristida stricta*). Slash pine (*Pinus elliotti*) occupied mostly the margins of wetlands and was associated to varying degrees with wetland hardwood species such as titi (*Cliftonia* sp., *Cyrilla* sp.) and gallberry (*Ilex glabra, I. coriacea*). In the last 30 yr, the USDA Forest Service has converted many sites originally occupied by longleaf to slash pine plantations. For the last several decades, pinelands on the ANF have been managed as even-aged stands by a combination of clearcutting and replacement. The sizes of the trees within stands are thus typically clustered around a mean value related to the age of the stand. Nevertheless, older stands always contain smaller trees as a consequence of suppression or reproduction. Although the pinelands are managed with a prescribed-fire rotation of ≈5 yr, there is encroachment of hardwood species in the pine stands. Chief among these species are turkey oak (*Quercus laevis*) on the more xeric sites, gallberry (*Ilex* spp.), runner oak (*Quercus* spp.), palmetto (*Serenoa repens*), and staggerbush (*Lyonia* sp.).

All vegetation surveys and ant baitings were carried out between early July and mid-August 1995. The 74 study sites were chosen to be well distributed throughout the Apalachicola National Forest and to represent the range of the major vegetation types, stand ages, and conditions of both longleaf and slash pine forest. The vegetation of each site was characterized by the methods of James and Shugart (1970). Two 0.04-ha circles were selected within the stand. The number of trees of each species in 8-cm size classes was counted and converted to density in trees per hectare. Ground cover was surveyed using 2 transects of 25 readings each in each stand. These samples were converted to percentage of the ground cover by each of 6 categories of ground cover (wiregrass, gallberry, runner oak, dead leaves, palmetto, and other).

Each of the pines was then baited for ants. Baits consisted of 1-cm-diameter discs of filter paper dipped into a slurry of Alpo's Ocean Whitefish Treat cat food (2 parts) blended with water (1 part) and vegetable oil (0.25 parts). Dipped discs were placed at breast height on the north, west, east, and south sides of each pine tree and on a sample of hardwoods. A total of ≈30 pines was baited at each circle. If there were fewer than 30 pines in the 0.04 ha, the radius was extended until it included 30 or more trees. A total of 4,766 pines was baited. After ≈30–45 min, the number of individuals on each bait was counted, and the species identities were determined by comparison with specimens of each common species glued to a card. Ant species not recognized in the field were collected for identification in the laboratory.

At 1 site, 24 trees on which *C. ashmeadi* had been found on a previous occasion were baited at 1 and 5 m up the trunk. *C. ashmeadi* was found on both baits on 23 of these. In only 1 case were ants found at 1 m level but not at 5 m, and in no case was the reverse true. Presence on baits near the ground was thus a reliable indication of presence of *C. ashmeadi* on the tree.

For each site, data consisted of counts of ants on baits by species of ant and species of tree. Sites usually contained either longleaf pine, or slash pine in even-aged stands, and could thus be characterized by tree species and mean diameter. Mean diameter was related to stand age, soil characteristics, and hydrological conditions, with stand age undoubtedly contributing the most. The mean diameters of stands were distributed as follows: <10 cm, 16%; 10–20 cm, 43%; 20–30 cm, 41%. Mean diameter was used as a surrogate for stand age in this study, but the surrogate measure also included any site-specific effects as well. The sites provided a cross-section of stand ages that could also be interpreted as a successional series. The data were analyzed by regression and analysis of variance (ANOVA), transforming the variables as needed to stabilize the variance. For some analyses, counts were converted to presence (1 or more individuals) or absence on each tree. For other analyses, data were aggregated by tree diameter size-class over all sites.

One caveat that applies to this study is that all the ants were detected on baits near the ground. The representation of species of ants may be different in the crown and branches. In addition, the classification of ants as arboreal and ground-nesting is based necessarily on incomplete information. Finally, the apparent abundance of species depends not only on their actual presence, but also on their recruitment behavior and ability to find and defend baits.

Results

Crematogaster ashmeadi was by far the most abundant ant attracted to the baits and was found on ≈50% of all the pine trees (total $n = 4766$). In addition to *C. ashmeadi*, a number of other species of ants, both ground-nesting and arboreal-nesting, were commonly taken on the baits. For purposes of analysis, the ants were grouped into *C. ashmeadi*, other arboreal-nesting species (*Solenopsis picta* Emery, *Leptothorax wheeleri* M. R. Smith, *Camponotus nearcticus* Emery) and ground-nesting species (*Solenopsis geminata* F., *S. invicta* Buren, *Brachymyrmex obscurior* Forel, *Forelius humilis* Mayr, *Pheidole dentata* Mayr, *P. moerens* Wheeler, *P. anastasii, P. metallescens* Emery, *Campono-*

tus floridanus (Buckley), *Monomorium viridum* Brown). Inclusion of *P. anastasii* with the ground-nesting group is perhaps debatable because it usually nests in the flaking bark of pines at or just below ground level (Naves 1985) and forages on the ground as well as on tree trunks. We interpret this habit as more ground-nesting than arboreal. Similarly, *M. viridum* seems capable of nesting terrestrially as well as arboreally, and we have included it with the ground-nesting group.

Unlike trees, baits were almost never shared among species. However, because 4 baits were placed on each tree, >1 species of ant could be detected on a tree. The proportion of trees and the proportion of baits occupied by a species were often not identical. Species that recruited weakly to food were often found on 1 or 2 baits, whereas strong recruiters tended to dominate all 4 baits on a tree. Proportions based on trees can thus be either higher or lower than those based on baits.

For each site, we calculated the mean diameter of the pine trees and the proportion of trees that contained ants of each type. There was a strong relationship between the presence of ants on pines and the mean tree diameter (Figs. 1–3). In young, recently regenerated stands, the ant species present on trees were largely ground-nesting (Fig. 1A), the most abundant being *S. invicta, Forelius pruinosus, B. obscurior,* and *P. anastasii* in declining abundance. These and other ground-nesting ants became less frequent as tree diameter increased. A regression of the proportion of trees with ground-nesting ants (log-transformed to stabilize the variance and normalize the residuals) on the mean pine diameter accounted for 31% of the variation in the proportion ($\log_{10}$ prop. $= -0.0065$ d $+ 0.182$; $F = 34.23$; df $= 1, 73$; $P < 0.000001$).

Young longleaf pines are colonized by *C. ashmeadi* queens when the trees are large enough (≈ 3–5 m tall) to have 1 or more dead lower branches. The queens establish their new colonies in abandoned beetle galleries in these dead branches (Hahn and Tschinkel 1997). Thus, as pine trees grow, they are increasingly likely to be occupied by *C. ashmeadi*. When the stand's mean diameter had increased to 12–18 cm, 50–90% of the trees contained colonies of *C. ashmeadi* (Fig. 1B). The rise in the presence of *C. ashmeadi* was accompanied by a fall in the frequency of ground-nesting ants on trees (Fig. 1A). Most of this decrease in ground-nesting species was probably the result of yielding of baits to *C. ashmeadi*, rather than their disappearance from the sites. In many stands with mid-sized trees, *C. ashmeadi* was almost the only ant on baits. In a quadratic regression, mean pine diameter explained 36% of the variation in proportion of trees with *C. ashmeadi* (prop. $= -0.605 + 0.15$ d-0.0043 d^2; all terms were significantly different from zero (*t*-test), with $P < 0.0001$ in all cases).

As mean pine tree diameter increased still further, the presence of other arboreal species on the baits increased (Fig. 1 B and C). This was partly the result of a 10% decrease in trees with *C. ashmeadi* in these mature stands, as compared to the 2 middle-sized classes. A linear regression of proportion with arboreal
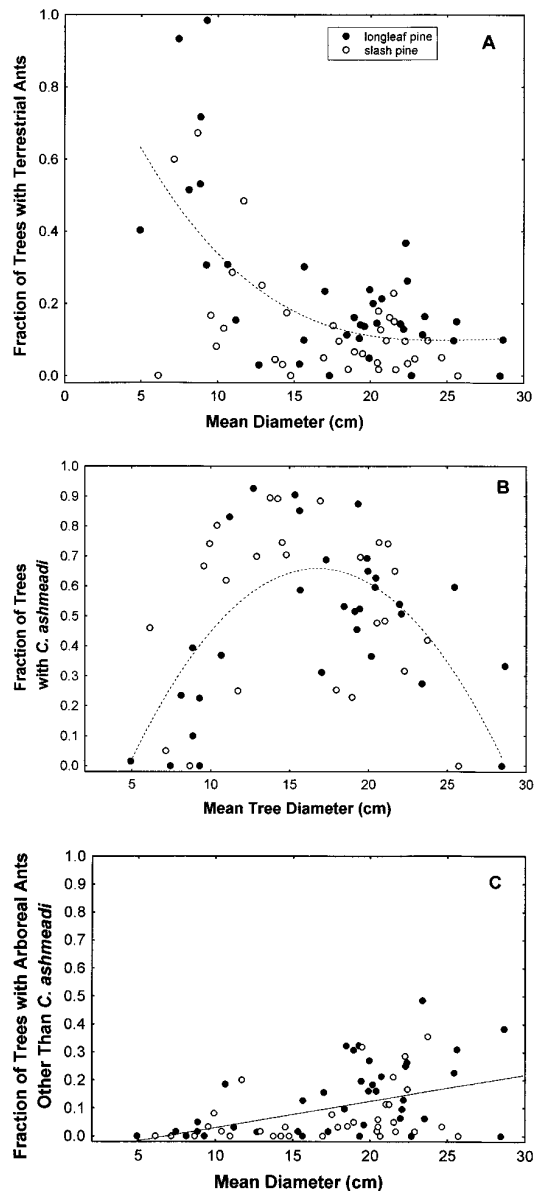

Fig. 1. (A) Proportion of pines with ground-nesting ant species on baits in relation to the mean diameter of the trees in that stand. Stands were even-aged. Each point represents 1 site (stand). Longleaf and slash pines are shown as different symbols, but there was no significant difference in the presence of terrestrial ants on these 2 pine species. The fitted line is a quadratic function. (B) Proportion of pines with *C. ashmeadi* in relation to the mean diameter of the pines at that site. *C. ashmeadi* were significantly more likely to occur on longleaf pine. The fitted line is a quadratic function. (C) Proportion of pines with species of arboreal ants other than *C. ashmeadi*, in relation to the mean pine diameter. There was no significant difference in the proportion on sites with slash or longleaf pines.

ants (log-transformed) on mean diameter explained 20% of the variation (Log prop. $= 0.023 + 0.0036$ d; $F = 19.29$; df $= 1, 73$; $P < 0.00004$).
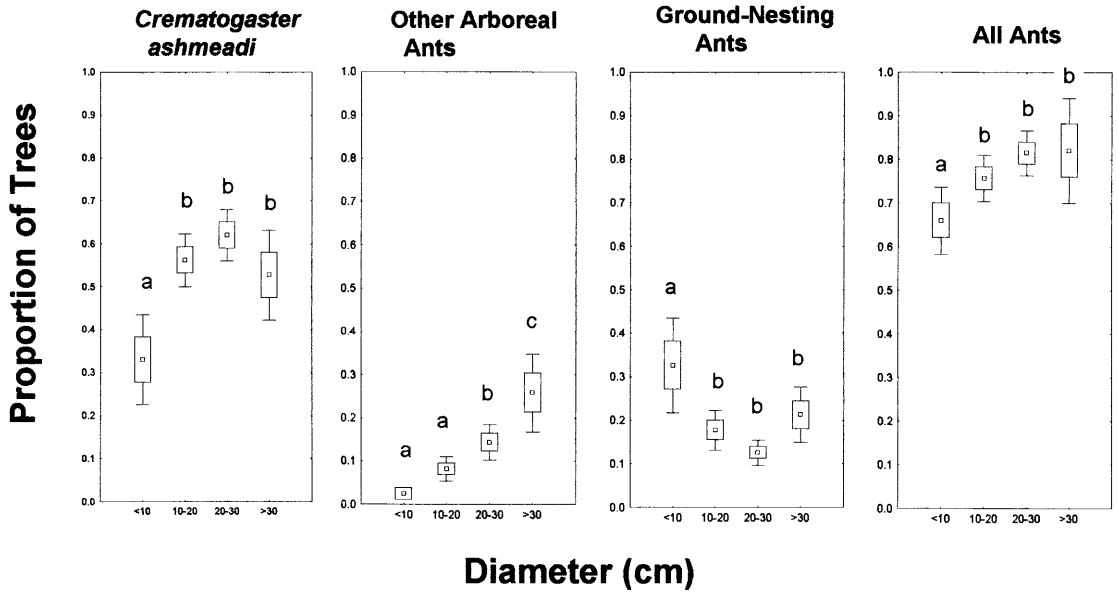
Fig. 2. Proportion of trees (longleaf and slash pine only) containing (a) *C. ashmeadi,* (b) other arboreal ants, (c) ground-nesting ants, and (d) all ants in relation to diameter of the trees. Trees were grouped by diameter, ignoring site. Points indicate means, boxes standard error, and error bars 1.96 SE. Significantly different means (Duncan test) are indicated by different letters.

The data for the above analyses were mean diameters of the trees sampled in each of the 74 stands and the proportion of all these trees that contained ants of each type. These results suggested that the size of each individual tree was a determinant of the presence of the species of ants, regardless of the mean diameter of the trees in its stand. As a result of suppression or reproduction, mature stands usually contained trees whose diameter was much less than the average, and whose ant fauna might be expected to be more similar to trees in younger stands. The data were therefore further analyzed by aggregating trees within stands into four 10-cm-diameter classes and computing the proportions of occupancy by class within stand. Proportions derived from samples of fewer than 10 trees were not used.

Within the same stands, the occupation rates of diameter classes by *C. ashmeadi* were positively correlated to each other (r between 0.62 and 0.94). In other words, a high rate of occupancy in 1 diameter class was likely to be associated with high rates in all classes. This was true even when the diameter class represented only a small fraction of the trees in the stand and contributed little to the stand-wide average. Thus, when *C. ashmeadi* occupation rates in minor diameter classes (those making up <25% of the total trees in the stand, with $n > 9$) were regressed against the diameter, using stand-wide occupancy as a covariate, the stand-wide rate explained 74% of the variation in occupancy rate in these minor size classes ($F = 58.1$; df = 3, 39; $P < 0.0001$). The actual diameter of the minor class added only ≈11% more to the explained variation ($F = 25.32$; df = 3, 39; $P < 0.001$). The occupancy of all but the smallest size class increased

at nearly the same rate as the stand-wide rate (slopes 1.0–1.1) even though each made up a minority of the stand. In other words, the relationship of individual tree diameter to occupation held within stands, but the absolute values of occupation were mostly determined by the stand's mean diameter. The size distribution of trees in a stand is therefore unlikely to add much to the 36% of variation explained by mean tree diameter (Fig. 1B). Other stand characteristics must determine the majority of the occupation rate, which is then reflected in trees of all sizes.

The occupancy rates by diameter-class were calculated without regard to stand to reveal the relationship of tree size to bait occupation (Fig. 2). This analysis showed that, as trees grew, the proportion with *C. ashmeadi* increased significantly from 32% in trees <10 cm in diameter, to ≈60% in those 10–30 cm and dropped significantly to 52% in trees >30 cm diameter (One-way ANOVA: $F = 8.13$; df = 3, 160; $P < 0.00001$; the Tukey honestly significant difference (HSD) test, $P < 0.05$). Terrestrial ants were present on about ⅓ of the small trees and dropped to 10–15% in the larger trees (ANOVA: $F = 6.93$; df = 3, 160; $P < 0.0002$). Simultaneously, trees with arboreal ants other than *C. ashmeadi* increased steadily from 2 to 25% (ANOVA: $F = 13.6$; df = 3, 160; $P < 0.00001$). Overall, the proportion of trees with ants of any type increased with age, from ≈65 to 75–78% (Fig. 2).

When the number of individual ants on the baits was taken into consideration, *C. ashmeadi* made up 80–90% of the total on the 3 larger size classes of trees, and 45% on the smallest, emphasizing the numerical dominance of this species. Across all size classes, no other

arboreal species ever made up >4% of the total number of individuals.

Effects of Vegetation Composition. Although some mixed stands occurred, sites were mostly either longleaf pine or slash pine. On sites subjected to more frequent prescribed fire, the ground cover was mainly wiregrass (*Aristida stricta*) and its associated herbaceous species. On less frequently burned sites, or those burned only during the dormant season for plant growth, ground cover was dominated by various low, woody shrubs, especially gallberry (*Ilex glabra, I. coriacea*), runner oak (*Quercus pumila, Q. minima*), several species of huckleberry (*Vaccinium* spp.), fetterbush (*Lyonia* spp.), and others. Because this gradient is correlated with several indicators of the reproductive health of the red-cockaded woodpecker population (James et al. 1997), we tested whether vegetational composition might also be associated with the distribution and abundance of the ants.

The effect of tree species on the occurrence of ants was tested by adding a dummy variable for pine species to the regressions of proportion occupied trees on mean tree diameter. *C. ashmeadi* was not significantly more likely to occur on 1 species of tree or the other. However, slash pines were significantly less likely to have ground-nesting ants than were longleaf pines ($t = 2.83$, df = 72, $P < 0.01$). This effect was reduced ($t = 2.34$, df = 71, $P < 0.05$) when the percentage of wiregrass was added to the regression (see below) because wiregrass was associated more with longleaf pine. Arboreal ants in general were more likely to occur on longleaf than slash pine ($t = 2.21$, df = 73, $P < 0.05$), but this effect disappeared when percentage of wiregrass was added to the regression (see below).

The effect of ground cover composition was tested by adding a term for each vegetation type to the nonlinear regression of the fraction of trees with *C. ashmeadi* on mean stand diameter. Ground cover variables included percentage of wiregrass, gallberry, runner oak, palmetto, dead material, and combinations of gallberry, oak, and palmetto. None of the vegetation types had a significant effect on the frequency of *C. ashmeadi*.

The proportion of trees with arboreal ants increased significantly with % wiregrass ($t = 2.77$, df = 72, $P < 0.01$). Part of this effect was the result of the association of wiregrass and mature longleaf pine stands, so that when tree species was added to the regression, the effect of wiregrass on arboreal ants was weakened ($t = 2.23$, df = 71, $P < 0.05$).

These vegetational effects can be interpreted as follows. Although none of the effects was large, factors that favor wiregrass, such as the increased frequency of fire, also favor arboreal ant species other than *C. ashmeadi*.

Relative Abundance of Ant Species in Relation to Tree Size. For the purpose of analyzing the species composition of ants on individual trees, we used baits, rather than trees as the units. Ants almost always excluded other species of ants from baits and many species recruited nestmates to these baits. The number of individuals on a bait varied with species-specific recruiting behavior. Using the simple presence/absence of a species on a bait eliminated these differences among species.

Trees were grouped by diameter class without regard to site. Species composition was determined on the basis of occupied baits, which were almost never shared between species. Overall, as tree diameter increased, the relative abundance of arboreal ants other than *C. ashmeadi* rose from 2.6% of occupied baits to ≈17% (25% of trees), whereas those with ground-nesting ants fell from 46% (33% of trees) to ≈15% (Fig. 3). The proportion of baits occupied by *C. ashmeadi* rose from ≈50 to 80% and then fell again to 67% (Fig. 3). As a result of these changes, the relative abundance of several species on baits changed with increasing tree diameter. Early successional, opportunistic, species, such as *Solenopsis invicta* (Tschinkel 1987) and *B. obscurior*, dropped steadily in relative abundance as tree diameter increased (Fig. 3). *P. anastasii*, which nest in pine bark at ground level, dropped from 5th to 9th rank. Some species were stable in rank: *F. pruinosus, C. floridanus*, and *M. viridum*. However, the arboreal specialists, *C. nearcticus* and *L. wheeleri* were relatively rare on the smallest trees, but increased steadily to 3rd and 4th rank. Another arboreal nester, *S. picta*, shifted irregularly between 8th and 11th place. This species often nests in hollow branches. Therefore basal baits may underestimate its prevalence. Finally, *C. ashmeadi* remained the most abundant species throughout tree growth.

The proportion of trees with >1 species increased steadily from ≈4 to ≈19% as tree diameter increased. The dominance and exclusiveness of *C. ashmeadi* was illustrated by the pattern of tree-sharing with other species. Trees were aggregated within diameter class into the following categories: no ants, *C. ashmeadi* only, other species only, and other species sharing with *C. ashmeadi* (Table 1).

The observed pattern of tree-sharing indicated that *C. ashmeadi* rarely occurred with other ants. The observed frequency of trees shared by *C. ashmeadi* and other ant species was much lower than the expected frequency in all diameter classes (chi-square test; Table 1). Both categories of ants tended to occur by themselves on trees more frequently than expected. However, the ratio of expected to observed frequency of sharing increased from 0.11 in the smallest trees to 0.4 in the largest, indicating that, although still much lower than expected, the share-rate increased with tree size. Altogether, these calculations, in combination with *C. ashmeadi* biology, support the idea that *C. ashmeadi* is a dominant ant species with which other species are unlikely to coexist.

Discussion

The most obvious finding of these surveys is that *C. ashmeadi* is an exceedingly common ant, by far the most abundant arboreal ant in the pine forests of the Apalachicola National Forest. It dominated all but the youngest pine saplings, occupying most of the baits in some stands of middle-sized trees. Even when the
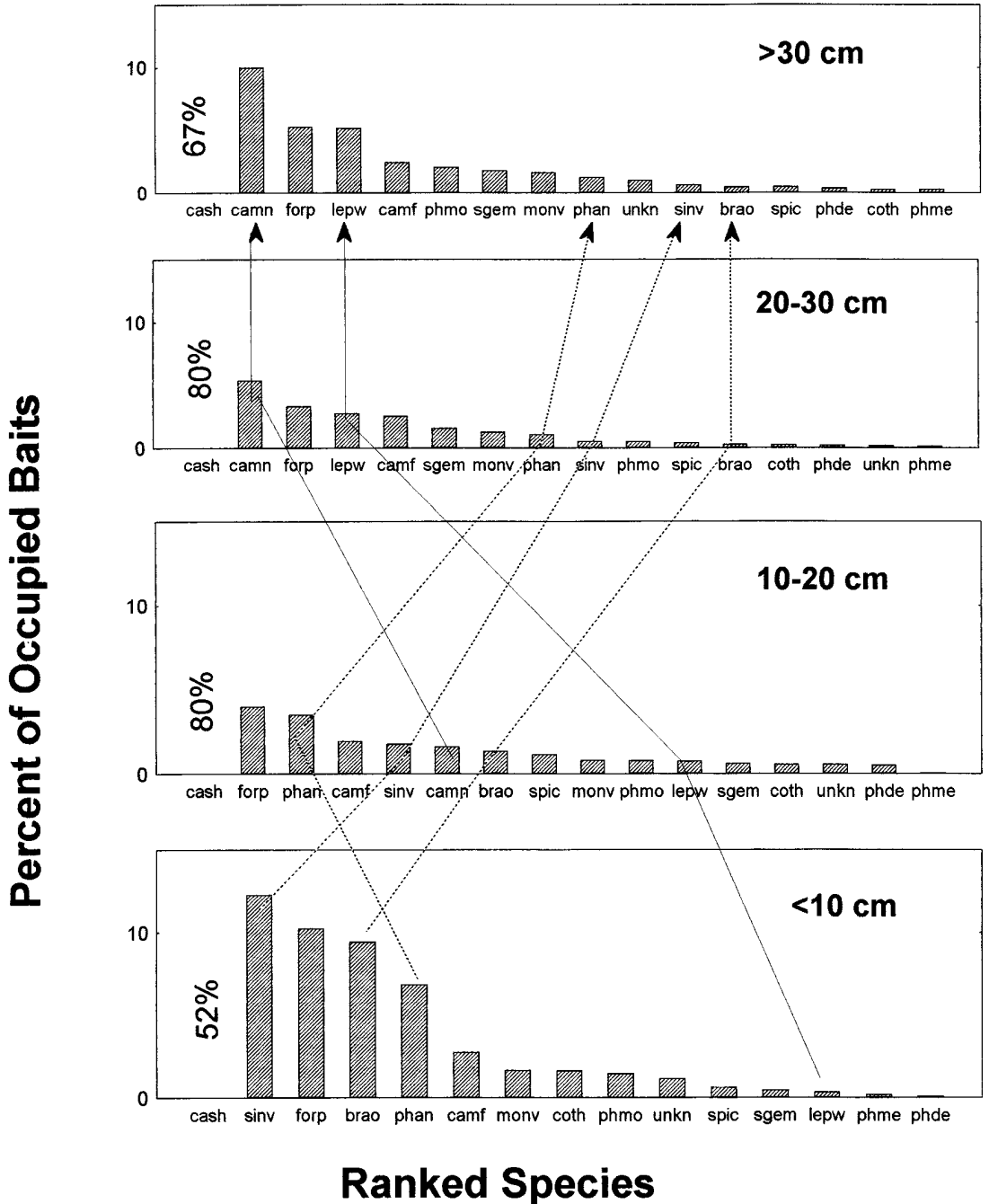
Fig. 3. Ranked proportions of occupied baits held by each species within pine diameter class. Except for *C. ashmeadi*, the rank of many species changed with tree diameter. Arrows trace significant changes of rank, with solid arrows identifying arboreal-nesting species, and dashed arrows ground-nesting species. As pines increased in size, ground-nesting ant species decrease in relative abundance, whereas arboreal ant species (other than *C. ashmeadi*) increased. Species codes: CASH, *C. ashmeadi*; SINV, *S. invicta*; FORP, *F. pruinosus*; BRAO, *B. obscuripes*; PHAN, *P. anastasii*; CAMF, *C. floridanus*; MONV, *M. viridum*; OTHR, other spp; PHMO, *P. moerens*; UNKN, unknown spp.; SPIC, *S. picta*; SGEM, *S. geminata*; LEPW, *L. wheeleri*; PHME, *P. metallescens*; PHDE, *P. dentata*; CAMN, *C. nearticus*.

other 3 common arboreal species were present in a stand, *C. ashmeadi* was by far the most abundant ant. Eighty percent of the individual ants coming to baits in this study belonged to this single species. The next 3 most abundant species each supplied only ≈5% of the total individuals.

Table 1. Number of trees shared or not shared between *C. ashmeadi* and other species, within tree size classes

Diam. Class	Trees with *C. ashmeadi* only	Tree with other species of ants only	Trees without ants	Total trees	Observed occurrences of sharing with *C. ashmeadi*	Expected occurrences of sharing with *C. ashmeadi*	Yates chi-square	P-value	Ratio: obs/exp
<10 cm	270	331	371	983	11	97.8	165.4	<0.0001	0.11
10–20 cm	1,048	400	389	1,906	69	274.3	491.6	<0.0001	0.25
20–30 cm	724	294	242	1,325	65	154.3	348.7	<0.0001	0.42
>30 cm	234	206	86	578	52	133.7	158.2	<0.0001	0.39

Expected fraction sharing was calculated as the product of the fraction of trees with *C. ashmeadi* and the fraction with other species. All observed occurrences of sharing were significantly different from the expected values, as indicated by the chi-square test. All chi-square tests have df = 1, and an expected chi-square value = 1.0. *P* values were multiplied by 4 in each diameter class to adjust for multiple tests.

Crematogaster ashmeadi has several characteristics of a highest-level dominant species. It has large colonies and is aggressively territorial toward other colonies of its own species or toward other species. On several occasions, *C. ashmeadi* was seen attacking other species, a behavior that probably contributes to the relatively low rate of co-occupation of trees with other species. The reduction of ground-nesting species on baits as trees grow may be evidence of the aggressive exclusion of which *C. ashmeadi* is capable. Its abundance and aggressiveness is probably crucial to the determination of the species of ants on pine trees in the southeastern United States.

When ants colonize small units of habitat, such as islands, the species tend to form nested sets with larger islands adding subdominant species not present on smaller ones (Hölldobler and Wilson 1990, p. 420). The assembly of the ant fauna on pine trees is similar to that of small mangrove islands (Cole 1983a, b). In both cases, the smallest inhabitable unit is first colonized by a dominant species (aside from the opportunistic foraging on these trees by ground-nesting species), with subordinate species appearing only as the unit (pine tree or mangrove island) grows. In mangroves, removal of the dominants allows colonization and indefinite persistence by subdominants, even on very small islands (Cole 1983a, b). In pines, other arboreal species are infrequent in the smaller trees, but gradually increase as the trees grow to maturity. In both pines and mangroves, *C. ashmeadi* is a dominant species (There is also a possibility that our *C. ashmeadi* and Cole's are different species. Cole's prefers mangrove and is polygyne, whereas ours prefers pines and is monogyne). Pines, like mangroves, are island-like to *C. ashmeadi* (and other arboreal species) because the ants cannot persist between the pines. Both are usually colonized by newly mated queens that alight after a dispersal flight, rather than by movement on the ground or over water.

There are differences, of course. As mangroves reproduce, they form ever larger island groves with closed canopies. The branches of pines do not usually touch those of neighboring trees, limiting most colonies to a single tree. The forest is thus an archipelago of trees to the ants. Pines are not true, oceanic islands, but more akin to habitat islands. Travel on the ground between trees is possible, and probably easier than

travel across water, although it seems to occur rarely. Mangrove saplings are devoid of ants, whereas pine saplings are the foraging domain of ground-nesting ants.

Excluding species that forage on trees but nest in the ground, pines in the Apalachicola National Forest are inhabited by only 4 nonrare, truly arboreal species. The dominance of *C. ashmeadi* would seem to be another example of the pattern noted by Hölldobler and Wilson (1990) that "the fewer the ant species in a local community, the more likely the community is to be dominated behaviorally by one or a few species with large, aggressive colonies that maintain absolute territories."

There remains much unexplained variation in the proportion of trees housing each type of ant. Some of this variation is probably the result of differences among sites, but does not seem to be correlated with differences in ground-cover vegetation. There are probably site-wide characteristics that affect the ant fauna independently of the size of individual trees. These might include, but not be limited to, colonization rate from neighboring sites and distances to source populations.

It is unclear whether managing pine forests for arboreal ants would have any impact on the populations of red-cockaded woodpecker. Under current forest conditions, *C. ashmeadi* is so abundant that its simple numbers seem unlikely to be limiting to the red-cockaded woodpecker populations, nor do the birds seem to forage preferentially on pines that harbor *C. ashmeadi* colonies. Factors other than food are more likely to limit woodpecker success (James 1995). However, it is not possible to rule out that more specific dependencies of the birds on the ants are indeed critical. For example, availability of the fat-rich sexual brood during the bird's breeding season may be important to nesting success. It is also the case that when *C. ashmeadi* is absent from trees, the other arboreal ants that take its place are much less numerous, almost certainly resulting in a reduction of ant biomass available to the woodpeckers. Thus, if the populations of *C. ashmeadi* were to decline drastically, other arboreal ants would be unlikely to fill the food void in the woodpeckers' diet.

Acknowledgments

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