Trailing the Elusive Carpenter Ant: A Key to Its Control

By
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On any spring day across North America, you may hear radio commercials for pest control companies promising an end to the invasion of “Big Black Ants.” The entomologists among us will recognize this “plague” as the seasonal return of carpenter ants, although the homeowner facing scores of large ants foraging in his home will care little of the taxonomy of Formicidae.

Carpenter ants belong to the globally distributed genus Camponotus, which boasts the largest number of species of all ant genera. Carpenter ants hold a special place in the history of American myrmecology. In 1773, Baron DeGeer described the first North American ant, Formica pennsylvanica, which is now known as Camponotus pennsylvanicus, the black carpenter ant. Twenty-five years passed before the second North American ant species, Formica ferruginea, now Camponotus ferrugineus (red carpenter ant), was described by Fabricius. These large, conspicuous ants are widely distributed in New England so their early recognition is not surprising.

Throughout the United States, carpenter ants are the most important of urban ant pests, even more so than the better-known red imported fire ant, Solenopsis invicta Buren. The economic impact of carpenter ants is greatest in the Pacific Northwest and in the Northeast where millions of dollars are spent each year to control these wood-destroying insects. But carpenter ants are troublesome home invaders across the United States. Even residences in Hawaii are invaded by the imported and poorly studied Hawaiian carpenter ant, Camponotus variegatus (F. Smith).
In their natural habitat, carpenter ants play a significant ecological role as predators of forest defoliators, scavengers of dead arthropods, collectors of honeydew, and contributors to the breakdown of wood, from whence their name is derived. To the distraught homeowner, annoyed by the presence of large ants, the behavioral ecology of carpenter ants holds little interest. However, the average homeowner fails to appreciate that a thorough understanding of the behavioral ecology of carpenter ants holds the secret to effective, long-lived control. Studying the behavioral ecology of two species of carpenter ants has been the central theme of our research.

Our ethological and applied research with carpenter ants began in Kansas, with in-depth studies of home-range orientation of *C. pennsylvanicus*. This work was extended in Indiana, where we investigated the foraging ecology of this species. The story has continued in Florida, with a comparative analysis of the colony dynamics of *C. pennsylvanicus* and *C. abdominalis floridanus* (Buckley), the Florida carpenter ant. Our work has led to an appreciation of the natural history of these two species of carpenter ants and their special adaptations for life in temperate forest and Florida scrub habitats. These studies have provided basic knowledge of carpenter ant behavior and ecology and have formed the foundations upon which we have built an applied research program to successfully control two species of carpenter ants, which are serious structural pests. In this article, we review our contributions to the basic understanding of carpenter ant behavioral ecology and how we use this knowledge to control them.

### Why a Nocturnal Life-Style?

The nocturnal life of *C. pennsylvanicus* may have arisen in response to competition or to avoid predators, or may have resulted from abiotic influences such as temperature and rainfall. In Kansas, *C. pennsylvanicus* and *F. subsericea* share a common woodland habitat and forage for similar resources. We often found *F. subsericea* and *C. pennsylvanicus* collecting honeydew at the same location. However, a clear division of activity rhythms was discovered, with *C. pennsylvanicus* primarily being nocturnal and *F. subsericea* diurnal. Another interesting aspect of the activity rhythm of *C. pennsylvanicus* is the dramatic increase in the number of workers leaving the nest at dusk and the equally dramatic reduction of numbers leaving at daybreak; diurnal foraging continues, but at a reduced level. Furthermore, we found that *C. pennsylvanicus* was able to sustain a higher traveling velocity than *F. subsericea* as temperatures dropped, a clear adaptation to a nocturnal existence. Evidence for interference competition was recorded at foraging sites during the day where major workers of *C. pennsylvanicus* patrolled, attacked, and killed *F. subsericea* foragers. Another advantage of nocturnal foraging is that *C. pennsylvanicus* workers avoid predation. Those that forage during the day become large, conspicuous prey for birds. In fact, in some of our ethology studies of home-range orientation, we had to screen the experimental setup to prevent robins, grackles, and starlings from feeding on these ants.

### Home-Range Orientation

Everyday, we face the challenge of moving through our complex environment. However, humans possess the sensory tools and cognitive skills to relegate such a daunting obstacle to an unconscious task. However, when our vision is withheld, this simple activity becomes impossible. The spatial orientation of *C. pennsylvanicus* is a fascinating subject precisely because it has adapted to a nocturnal existence. The adaptations that facilitate this behavior are the focus of many of our experiments.

*Camponotus pennsylvanicus* is well adapted to its nocturnal lifestyle as shown by our investigation of the cues it uses for topographic orientation. Olfactory cues, in the form of odor trails, are of primary importance. *C. pennsylvanicus* in the process of laying odor trails is easily recognized as they drag the
tips of their abdomens across the substrate. Drawing a finger across the trail of *C. pennsylvaniaicus* workers will quickly disrupt their trailing behavior. Unlike the ephemeral trails of *S. invicta* that last for seconds, *C. pennsylvaniaicus* workers deposit chemicals from their hindgut that last for several hours. Heavy deposits build-up over time to form trunk routes, which guide foragers to stable food sources. This pheromone trail functions to recruit cohorts to newly discovered food resources. Olfactory cues in the odor trail clearly are important because of the low light conditions under which these nocturnally active ants must forage. However, an individual forager eventually must deviate from the trunk trail in search of resources and it is here that tactile and visual cues become important.

*Camponotus pennsylvaniaicus* workers exploit structural features in their environment when foraging. This behavior, which we have termed structural guideline orientation, is an important cue for ant orientation. Unlike the chemicals in the odor trails, structural guidelines are tactile stimuli in the form of edges, grooves, or crestlines provided by tree bark, vines, branches, or roots on the forest floor. These guidelines provide routes for traversing territory that otherwise might impede the progress of the ant. A foraging ant follows the path of least resistance and thus conserves energy. Tactile stimuli such as structural guidelines were hierarchically the lowest cue that we investigated. When placed in total darkness, *C. pennsylvaniaicus* workers no longer negotiate shortcuts by using visual cues rather they orient their path along structural guidelines to reach food. However, if total darkness is interrupted momentarily by an overhead view of the forest canopy or another visual cue, they switch from structural guideline orientation to landmark orientation. *C. pennsylvaniaicus* uses the forest canopy for orientation under low light conditions of the night sky. Because this species nests within trees, the use of canopy landmarks as cues may be an adaptation to increase the likelihood of workers returning to the nest tree after foraging.

*Camponotus pennsylvaniaicus* workers show a strong orientation response to an incandescent light at night. This suggested to us that the moon might be used by *C. pennsylvaniaicus* as a directional cue. In experiments...
modeled after those of Santschi in 1911, where he demonstrated sun compass orientation in *Messor barbarus* (L.), we performed a mirror experiment at night and were able to reverse the direction of foraging ants in response to a change in the apparent position of the moon.

Within this assembly of orientation cues there is a built-in redundancy. Foraging ants rely on more than one orientation cue, e.g., a forager may use an odor guideline as well as a light source. As a consequence, this assemblage of cues provides the ants a series of back-up cues with which they can continue to orient in the absence of any one particular cue. This arrangement provides *C. pennsylvanicus* with the ability to forage in woodlands under darkening skies as well as in total darkness.

### Vision

The reliance of *C. pennsylvanicus* on terrestrial landmarks and light sources during spatial orientation requires the compound eyes of these ants to detect diverse light cues. In terms of visual acuity, *C. pennsylvanicus* falls somewhere between blind army ants and highly alert ants like *Gigantiops* (Roger) with large eyes. By counting the number of corneal facets in the compound eyes of *C. pennsylvanicus*, we discovered a positive correlation between the size of a worker and the number of facets. The counts ranged from 375 to 658 facets over a smooth and continuous range of head sizes from very small, minor workers to the larger, major workers. These size differences in eyes raise many questions concerning specific worker tasks that may be related to visual acuity, and thus, the foraging efficiency of specific worker castes. For example, smaller workers, which are usually aphid guardians, collect honeydew and pass it to larger workers, who transport it back to the nest.

### Other Aspects of Foraging Behavior

*C. pennsylvanicus* workers are omnivorous. As with many ants, they gather honeydew from aphids and other homopteran plant-sucking insects. Extrafloral nectaries and fruits provide another carbohydrate source. The workers scavenge dead arthropods and prey on live arthropods to acquire proteins. *C. pennsylvanicus* has a distinctive cycle of food preferences. During the spring and early summer, when brood production is maximal, the ants have a strong preference for proteins, which are fed to the developing larvae. Freshly diced mealworms offered during many of our experiments are mobbed by workers from May through mid-July, but are less attractive when offered in August and September. Conversely, the ants will recruit slowly to simple sugar or honey baits in the spring, but any carbohydrate source is depleted rapidly from July through the end of colony activity at the time of approaching winter. Carbohydrates are used as an energy source by adults throughout the year, but the mass provisioning in the fall—before the onset of the obligatory diapause—may contribute to overwintering survival.

Foraging theory suggests that animals conserve energy during foraging. One prediction of foraging theory is that as the distance between the nest and a food source increases, foragers will become more selective in their diet. In economic terms, the ants must maximize caloric revenue to compensate for increased expenditures incurred by foraging at greater distances from the nest. To test this prediction, a colony of *C. pennsylvanicus* was trained to travel on a garden hose to forage on a platform containing four concentrations of sucrose. As the platform was moved from 1 to 15 meters from the nest, the proportion of ants gathering the lower (0.1 molar) versus the higher concentration (0.5 molar) baits decreased as the distance traveled increased.

Another prediction of foraging theory is the optimization of travel time. The central nest of social insects forces them to travel out to secure resources and return to store them. Thus, travel time is likely to have been subject to selection pressure. In addition to this theoretical premise, we were drawn to this question after repeatedly seeing foragers of *C. pennsylvanicus* following elaborate detours along branches or sidewalks rather than following a straight line from the nest to a resource. Why were the ants not going directly between points A and B? We set about testing our field observations with experiments. We trained colonies of *C. pennsylvanicus* to follow a garden hose set parallel to their existing, straight trail on the ground between two trees. We then began to lengthen the garden hose incrementally and thus the foraging trail along branches or sidewalks rather than following a straight line from the nest to a resource. Why were the ants not going directly between points A and B? We set about testing our field observations with experiments. We trained colonies of *C. pennsylvanicus* to follow a garden hose set parallel to their existing, straight trail on the ground between two trees. We then began to lengthen the garden hose incrementally and thus the foraging trail by displacing the midsection of the hose sideways while maintaining contact to both trees. In these experiments, as well as in field measurements on the naturally occurring examples, we found that the velocity of foragers was always greater when traveling along the structural guideline than it was along the nat-
ural trail on the ground. The movement of the ants was more efficient on these smooth, uncluttered guidelines when compared with the existing trail on the soil where the turf and surface features imposed numerous impediments to travel. The benefit of these detours was the shortening of overall trip time.

Through these studies, we have found that *C. pennsylvanicus* foragers follow the optimal foraging theory in various ways; they will maximize energy gains by selectively feeding among different resources, and they minimize time traveling, and thus, save energy, by orienting to structural guidelines.

**Colony Size and Structure**

We compared colony characteristics of two species that live in different habitats. In Kansas and Indiana, *C. pennsylvanicus* is found in temperate, hardwood forest ecosystems. In Florida, we studied *Camponotus abdominalis floridanus* in a subtropical sandhill habitat. We discovered significant differences in the adaptations of these two species to their respective environments.

Nest sites of carpenter ants, their colony size, and the dimensions of their home range, were determined for both *C. pennsylvanicus* and *C. abdominalis floridanus*. In Florida, we systematically searched a 1.2-acre tract of sandhill populated by *C. abdominalis floridanus* to determine the number of nests and estimate the number of ants in each nest. To do this, every nest was vacuumed up and brought to the laboratory, where we counted the number of adults and brood from each nest. These individual nests were then kept separate and reared in the laboratory for future tests. *C. abdominalis floridanus* workers are aggressive towards nonnestmates, so we exploited this behavior in agonistic tests to group various nests and, were able to estimate the territory they occupied.

Twenty nests were located in the sandhill. Seven of these were unrelated to other nests and thus constituted individual colonies. Worker populations in these colonies ranged from 150 to 2,400. An eighth colony consisted of three nests, with a worker population size of 2,700, occupying a territory some 16 meters in diameter. The ninth colony, a *super colony* residing in 10 distinct nest sites, was populated by 8,100 workers and was spread over an area measuring 43 meters across. Only 7 of the 20 nests were located in natural sites, such as beneath logs or in hollow tree stumps. The remaining 13 nests were literally in trash. The site was being used as an illegal dump, and the ants established nests in the ready-made cavities afforded by siding, floor coverings, lumber, and plastics scattered across the site. In fact, all 10 of the nests constituting the super colony were found in this trash.

An area of similar size in Indiana was a one-acre cemetery plot, bounded on all sides by a road. A thorough survey of the site found *C. pennsylvanicus* active in or on 22 of the 29 trees in the plot and these represented 6 distinct colonies. These colonies occupied from two to six trees (average 3.8 per colony), spread over an area 6 to 28 meters across (average 16.3 meters per territory). All of the colonies in the Indiana site were nesting within hollows of standing trees.

The black carpenter ant gets its name from its color and nesting habits. While the heavily sclerotized mandibles of the workers are capable of excavating sound wood, colonies of *C. pennsylvanicus* may begin life within a preexisting cavity (e.g., lightning scars, knot holes, open root crowns) and expand into rotting and sound wood around these injuries.

This feature of nesting in preexisting cavities accounts for the ants propensity to nest within wall voids and similar cavities in manmade structures. *C. abdominalis floridanus* readily nests in these sites. *C. pennsylvanicus*, too, will exploit structural voids, but these are frequently smaller satellite nests that have split off from the principal brood or parent nest. Knowing the colony and territorial size of *C. pennsylvanicus* and *C. abdominalis floridanus* can help us design management strategies that are based on sound biological principles.

An arena test to determine which of eight different food types are most attractive to carpenter ants.
Interface of Biology with Control

Urban myrmecology, a subdiscipline of urban pest management, deals with protecting human health and property from ants through the use of techniques that are environmentally sound, effective, and economical. Camponotus spp. are the most difficult of all ants that pest control operators are called upon to control. They are common pests because of the spread of suburban housing developments into picturesque, woodland areas that are the natural habitats of these ants. Unfortunately, pest control operators find it difficult to locate their nests, which is a necessary prerequisite for effective treatment. A primary goal of our applied research has been to address this difficulty.

We have approached our applied program with two themes: (1) the development of toxic baits effective against C. pennsylvanicus and C. abdominalis floridanus, and (2) the integration of detailed knowledge of the behavioral ecology of these two species into a sensible, rational management program. In doing so, we have strived to coordinate our basic research closely with the needs of the applied program. This approach has been a successful model to develop management programs for a variety of insect pests.

Colony Size and Structure. From our home range studies, we became adept at tracking ants and finding their nests. This kind of practical knowledge from basic research was helpful when we began formulating control strategies for infestations of C. pennsylvanicus. Based on our research findings, we recommended to pest control operators that they search for these ants at night and, when found, that they be fed and followed back to their nests. These two recommendations take advantage of the circadian rhythm of this species and their basic instinct for homing. For control, this approach can mean the difference between success or failure, which in the pest control business is measured by the frequency of callbacks from dissatisfied customers.

Differences in nesting biology between carpenter ant species may have important implications for infestations. For example, C. pennsylvanicus is known to cause significant damage to structural timbers. In comparison, C. abdominalis floridanus is more of a nuisance pest, causing only minor damage to wood. As we noted previously, these two species' natural preferences for nest sites are very different. C. pennsylvanicus nests are found primarily in wood, whereas nest sites of C. abdominalis are highly variable. These differences may be one reason for the controversy in the pest control industry as to whether carpenter ants damage structures. The anecdotal reports from different parts of the country that appear contradictory may only reflect a difference in the species of Camponotus involved.

Trail Orientation. During an inspection, pest control operators should pay particular attention to ants that are trailing because trails often can lead to the nest. When Camponotus spp. establish a satellite nest, or locate a stable food source, they create permanent trails on which workers travel. These trails are usually straight when crossing open surfaces, except when interrupted by a sidewalk or other structural feature that the ants may use as a guideline. To use workers to find the nest(s), the pest control operator should first locate foraging ants around the structure and then note the direction they are walking. The nest can be found by fixing the location of several ants over a distance of about three feet. Then, the pest control operator can extend a straight line from the positions of the ants and look into the distance for a tree, stump, or other likely nest site.

Trails also may indicate where ants are getting into or onto a structure. A tree limb touching a roof is a good physical trailway for ants to crawl onto a structure. Trimming vegetation away from a structure eliminates this potential problem. Frequently, ants enter a structure by following utility lines. Sealing the points where these lines enter the structure closes these entrance holes. The above are examples of habitat modification—a non-chemical measure that can be taken to help control or prevent carpenter ant infestations.

Foraging Ecology. In chemical pest control, baits are becoming increasingly more important, especially for social insects, such as ants, where they have proven to be particularly useful. To be effective, a bait must be attractive. Our studies on foraging ecology have shown that the diet of a colony of C. pennsylvanicus changes over the active season. In spring, they prefer protein, while in late summer they prefer carbohydrates. A good bait for C. pennsylvanicus should attract ants any time of the year. Therefore, the bait should contain both proteins and carbohydrates or there should be two different kinds of bait, one containing protein for the beginning of the season and one containing sugar for later in the season.
From previous work by others with delayed-action toxicants on leaf-cutter and red imported fire ants, we know the importance of using these slow-acting poisons. A successful delayed-action toxin will allow time for the ants to share their food and spread the poison throughout the colony before it begins to kill them. We have found a number of potentially good toxicants, including boric acid, which at very low concentrations is slow acting and effective.

Proper placement of baits is critical for success. For maximum effect, baits should be placed where ants are likely to encounter them, such as where utility lines enter a structure or along pheromone trails that the ants are using to and from their nest. *Camponotus* spp. commonly infest structures in disrepair or with maintenance problems where the ants enter through cracks along window casings or wall joints. Repairing and sealing these areas will contribute to pest prevention. Hypothetically, if a pest control operator could seal up all entryways into a structure, the structure would be pest-proofed.

Finally, from our studies of colony dynamics, we learned that the nest organization of *C. pennsylvanicus* and *C. abdominalis floridanus* consists of parent and satellite nests. This makes it mandatory for pest control operators to perform thorough inspections and surveys of an area to locate all of the potential sources of infestation, both inside and outside the structure. Frequently, the source of infestation is a parent nest located outside, which must be eliminated to prevent future infestations by foraging ants or satellite colonies.

In summary, this behavioral approach to ant control can serve as a model for future research on other pest ants. Our goal is an integrated approach to ant control based on habitat modification and minimal use of insecticide. Following this approach will enable us to safeguard ourselves as well as the environment.

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**Suggested Reading**


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