ASPECTS OF THE BIOLOGY, BEHAVIOR, AND ECONOMIC IMPORTANCE OF *CAMPONOTUS PENNYSLVANICUS* (DEGEER) AND *CAMPONOTUS FERRUGINEUS* (FABRICIUS) (HYMENOPTERA: FORMICIDAE)

by

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INTRODUCTION

Carpenter ants belong to the genus *Camponotus* (Hymenoptera: Formicidae). They derive their common name from the sandpapered like finish of the galleries of their nests which are built in wood. Although most species nest in wood, they do not feed on wood. The workers tend honeydew excreting insects for the honeydew and will also feed on both dead and live insects. Carpenter ants will nest in both softwoods and hardwoods and nests are usually started in wood that is moist and has already begun to decay (Sanders 1964). Mature colonies can extend their galleries into dry, sound wood (Gregg 1944, Friend and Carlson 1937, Smith 1965)

The genus *Camponotus*, described by Mayr in 1861, is cosmopoliton. Of the many subgenera now recognized as belonging to *Camponotus*, only eight are represented in America north of Mexico (Creighton 1950, Smith 1947). Forty-one species have been described in the U.S. and numerous varieties and subspecies have been recognized (Creighton 1950, Smith 1947). The majority of the species in the U.S. are found in the four subgenera: *Camponotus*, *Tanaemyrmex*, *Myrmentoma*, and *Colobopsis*. The remaining four subgenera: *Myrmothrix*, *Manniela*, *Myrmaphaenus*, and *Myrmobrachys* contain seven species (Smith 1947).

The subgenus *Camponotus* is represented by 29 species in the U.S. and one or more of these species is present in every state (Smith 1947) *Camponotus pennsylvanicus* (DeGeer), the black carpenter ant, is one of the most common species of the subgenus Camponotus. C. ferrugineus (Fabricius), a closely related species which is sympatric with C. pennsylvanicus throughout most of its distribution, is another common member of this subgenus.

Camponotus pennsylvanicus is one of the most widely distributed species in eastern North America. A native species, which ranges from North Dakota to Quebec and Ontario and south to Texas and Florida, was the first North American ant species to be described (Krombein et al. 1979). C. pennsylvanicus is also the most common carpenter ant in the mid-Atlantic states (Fowler and Roberts 1980, Wheeler and Wheeler 1963).

Carpenter ants are among the most common wood-infesting insects in the U.S. Also included are 1) subterranean termites; 2) powder-post beetles; and 3) the old house borer. While considerable research has been devoted to the biology and control of termites, powderpost beetles, and old house borers, little work has been devoted to carpenter ants in the U.S.

Carpenter ants can cause considerable damage to structural timbers (Graham 1918, Friend and Carlson 1937, Dennis 1938) and their within-home foraging can be a source of annoyance to homeowners (Smith 1965). Their importance as structural pests has been noted in a National Pest Control Association (NPCA) report. In the NPCA report (Pinto 1981), carpenter ants were given a rating of 66 (out of 100) in a listing of the relative importance of 70 structural pest species. In the same list, subterranean termites were given a rating of 88 and powderpost beetles were rated 55.

Despite the apparent economic importance of C. pennsylvanicus and the potential economic importance of C. ferrugineus, little work has been done on their biology. Relatively few studies have been made of the ecology or behavior of C. pennsylvanicus since Pricer's publication on its biology in 1908. Fowler and Roberts (1980) published a study of the ecology of this ant in New Jersey and Traniello (1977) examined the role of trail pheromones in worker orientation and recruitment, but these are the first major studies of the ecology and behavior of C. pennsylvanicus since Pricer's (1908) work. No attempts have been made to assess their economic importance, either on a regional or national basis. For these reasons this study was undertaken to further clarify the importance of carpenter ants in the hierarchy of structural insect pests, and to contribute to the understanding of their adaptation to structures in urban environments. The specific objectives of this study were:

1) to observe the seasonal changes in C. pennsylvanicus foraging behavior in an urbanized environment, and to correlate the observed changes with the division of labor among workers and with structure utilization;
2) to test the attractancy of various foods and to correlate this with foraging behavior;
3) to examine aspects of the colony founding behavior of C. pennsylvanicus and C. ferrugineus;
4) to design and execute a survey to obtain data on the economic impact of carpenter ants in Virginia, Maryland, Delaware and Pennsylvania;
5) to examine the division of labor among the polymorphic

workers of *C. ferrugineus* and *C. pennsylvanicus* during nest construction.

LITERATURE REVIEW

The genus Camponotus has been marked by much intricate and confusing taxonomy (Creighton 1950). As a result of the taxonomic confusion, Camponotus pennsylvanicus was considered a subspecies of C. herculeanus (L.) until Creighton's (1950) revision. Before Creighton's work, C. herculeanus was used as a catch-all for any member of the subgenus Camponotus whose exact status was doubtful. The confusion caused by the extensive use of C. herculeanus remains apparent in the carpenter ant literature. Mintzer (1979), cited the work of Pricer (1908) as the study of the biology of C. herculeanus although most current workers cite the work of Pricer as the study of the biology of C. pennsylvanicus. It is doubtful that Pricer worked with C. herculeanus since Urbana, Illinois is far south of the geographic range of this species. To simplify discussion here, any reference to Pricer will assume that he worked with C. pennsylvanicus.

Aspects of the taxonomy of carpenter ants have been reported by Brown (1973), Wheeler (1910), Creighton (1950), Smith (1947), and Emery (1920, 1925). Brown (1973) examined the worldwide distribution of the genus Camponotus and Wheeler (1910) and Smith (1947) examined the North American ants of this genus. Emery (1920, 1925) established the structural criteria of most of the present subgenera, and the North American subgenera of Camponotus were revised by Creighton in 1950. Ross et al. (1971) have included the genus Camponotus in their synopsis of common and economic Illinois ants. Taxonomic characters of the larvae of some Camponotus spp. have been studied by Wheeler and Wheeler (1953).

Camponotus pennsylvanicus

The life history of C. pennsylvanicus was studied by Pricer (1908). He found that colonies are initiated by queens which have overwintered in parental colonies. Nuptial flights by the unmated queens and males take place from May to late July. Folowing mating, a single fertilized female establishes her nest in a self-made, or preformed cavity in wood. After sealing the cavity she lays from 12 to 22 eggs and raises her first brood of workers to maturity by feeding them on salivary secretions (Pricer 1908). During this period she does not gather food from any outside source. The first brood consists entirely of small, minor workers. The next and following broods are all fed by the workers, and as the food supply gradually increases, so does the size of the workers produced. After a number of years, a colony contains workers of various sizes. These are designated as major workers, minor workers, and intermediate workers.

Reproductives are not produced until a colony contains approximately 2,000 or more workers (Pricer 1908). To reach this stage the colony must be at least 3 years old. Once the colony has started to produce reproductives it will continue to do so yearly for an indefinite period. Sanders (1964) indicates that reproductives may not be produced yearly in colonies of C. herculeanus.

The foraging behavior of C. pennsylvanicus was examined by Fowler and Roberts (1980) in New Jersey. They found that workers showed a diel foraging periodicity during the summer, but that patterns changed monthly. In their study Fowler and Roberts found that foraging intensity shifted with the time of day as the months of the summer progressed. Sanders (1972), in a study of seasonal and daily activity patterns of carpenter ant species in northwestern Ontario (Canada), found that C. pennsylvanicus foragers became nocturnal as the seasons progressed during the year.

The observations of these authors indicate that few workers carry visible objects back to the nest. Fowler and Roberts (1980) found that less than 1% of the workers returning to the nest carried insects or spiders. Sanders (1972) observed that 6% or fewer of the ants in his study carried visible objects. Based on these observations, the authors concluded that solid insect or spider tissue is not a major constituent of the colony diet. Based on the nesting habits and behavior of three species of carpenter ants, Sanders (1964) suggested that these ants may feed on fungal mycelia.

Trail-laying behavior of carpenter ants has been studied by Hartwick et al. (1977) and Traniello (1977). They found that C. pennsylvanicus workers concentrate their foraging efforts in the vicinity of a new food source. They also found that workers lay chemical trails which consist of a series of streaks. The trails activate other workers and provide a means of orientation but are nondirectional. The source of the trail substance is the hindgut. Hartwick et al. (1977) found that the ants exhibit less trail fidelity in the presence of a strong direct light. Pricer (1908) found C. pennsylvanicus workers moving from a nest in columns, suggesting that C. pennsylvanicus uses scent trails to orient towards food sources.

Carpenter ants can cause extensive damage to wood with their nesting activities, yet there is very little literature available involving carpenter ant control. Extension publications on carpenter ant control have been written by Akre and Antonelli (1976), Goulding and Capizzi (1976), and Liebherr (1976).

The economic impact of carpenter ants has not been studied extensively. The belief that carpenter ant damage is necessarily preceded by moisture damage, is evident in most of the major works which have been published. Pricer (1908), and Creighton (1950) reported that carpenter ants are incapable of causing extensive damage to dry, sound wood. However, other reports indicate that this is not the case. Brown (1950) and Smith (1965), for example, note that they received reports of sound wood which had been heavily damaged by *C. pennsylvanicus*. Friend and Carlson (1937) reported that *C. pennsylvanicus* caused extensive damage to telephone poles. Sanders (1964) found that several carpenter ant species in New Brunswick were capable of causing significant amounts of damage to standing trees.

Camponotus ferrugineus

Camponotus ferrugineus (Fabricius), the red carpenter ant, was described in 1798, yet its taxonomic status remains unresolved. Creighton's (1950) treatment of the *C. herculeanus pennsylvanicus* (DeGeer) complex retained *C. ferrugineus* as a subspecies of *C. pennsylvanicus* despite the complete sympatry shown by *C. pennsylvanicus* and *C. ferrugineus*. Brown (1950) in a rebuttal of Creighton's revision, stated that *C. ferrugineus* should be granted status as a species due to its marked coloration and ethological traits. Brown (1950) did not provide any other taxonomic characters to separate the species and as a result, other workers may not adhere to the provision of specific status to *C. ferrugineus* without further evidence.

The geographic distribution of *C. ferrugineus* is covered completely by the range of *C. pennsylvanicus*. Though *C. ferrugineus* and *C. pennsylvanicus* occupy much of the same range, *C. ferrugineus* apparently is not as widely distributed as *C. pennsylvanicus*. Morphologically, *C. ferrugineus* is distinguished from *C. pennsylvanicus* only by color (Brown 1950). Workers of *C. ferrugineus* are approximately the same size as those of *C. pennsylvanicus* and are distinguished by the coloration of the thorax, petiole, base of the gaster, and much of the legs. Setae and pubescence on the gaster are more golden yellow than those of *C. pennsylvanicus*. The biology of *C. ferrugineus* is not known, but is assumed to be similar to that of *C. pennsylvanicus*. Furthermore, no information is available concerning the ecology, behavior, food preference, or economic importance of this ant species. Smith (1965) reported that *C. ferrugineus* had been observed in houses, and Graham (1918) reported that considerable damage to standing white cedar in Minnesota had been attributed to infestations of *C. ferrugineus*.

Studies of Other *Camponotus* Species

Some studies have detailed various aspects of the behavior and ecology of other *Camponotus* spp. Mintzer (1979) examined colony foundation and pleometrosis in the *Camponotus* species, *C.* (*T.*) *vicinus*

(Mayr), C. (T.) festinatus (Buckley), C. (C.) modoc (Wheeler), C. (C.) laevigatus (F. Smith), C. (M.) rasilis (Wheeler), and C. (M.) planatus (Roger). Bhatkar and Whitcomb (1975) and Carney (1970) published information on the rearing and laboratory maintenance of carpenter ant colonies of various species.

Markl and Fuchs (1972) examined the function of "rapping" as it refers to alarm reactions in carpenter ant colonies. Rapping refers to the tapping of the mandibles or gaster on the substrate by the workers. Markl and Fuchs (1972) found that rapping fulfills functions of prey-attack and danger-alarm systems. It amplifies the effect of other attack-releasing stimuli. The phenomenon of rapping in carpenter ants may explain the rustling sound often heard when carpenter ant nests are disturbed. Chauvin (1970) reported on the sound receiving organ of the ants of the genus Camponotus.

Barlin et al. (1976) found that the trail pheromone of carpenter ants is not entirely species specific. Caste specific compounds were identified in male carpenter ants by Brand et al. (1973).

Little information is available on the digestive enzymes of carpenter ants. Ayre (1967) compared the enzymes of five ant species, including C. pennsylvanicus and C. herculeanus. Brian (1978) included several species of the genus Camponotus in a list of the enzymes known to be present in six ant genera. The digestive glands in the female castes and the male of C. pennsylvanicus have been examined by Forbes and McFarlane (1961).

Sanders and Baldwin (1969) and Riordan (1960) examined mark-recapture techniques for the study of carpenter ants. Both studies utilized radioactive isotopes to mark the ants. Sanders (1970) reported that colonies of C. herculeanus can cover as much as 830 m^2. Levieux (1971) reported that colonies of C. acvapimensis (Mayr) and C. congolensis (Emery) are composed of about 20 chambers with some peripheric cavities. The nest chambers and cavities of C. acvapimensis and C. congolensis cover a surface of about 15 m^2 and 25 m^2, respectively.

Studies on the genus Camponotus have shown that the workers of a species may form a continuous and gradual series from the smallest to the largest or that they may be distinctly bimodal in size distribution. Smith (1942) found that C. noveboracensis forms a gradual series in which "classes" or workers are not clearly defined. Smith also found that C. pennsylvanicus was not completely gradual in distribution, but neither was it distinctly bimodal. Sanders (1964) found that when head size of C. herculeanus workers was plotted against numbers of ants, the result was a bimodal curve. Pricer (1980), using worker body length, reported a gradual series for C. pennsylvanicus and C. ferrugineus.

While there are few published records of parasites of Camponotus spp., there are references to them in the literature. Carney (1969) observed the behavioral and morphological changes in carpenter ants harboring metacercariae of the Dicrocoeliid liver fluke, Brachylecithum mosquensis (Skrjabin and Isaitschikoff). Van Pelt (1958) reported the parasitism of C. pennsylvanicus by the ascomycete fungus, Cordyceps unilateralis (Tulasne). C. pennsylvanicus is also parasitized by a fly belonging to the family Phoridae, Apocephalus pergandei Coquillett (Smith 1965). The larva of A. pergandei feeds on the inside of the head of a living ant until the ant dies from the attack (Smith 1965)

COLONY FOUNDING IN THE RED CARPENTER ANT,

CAMPONOTUS FERRUGINEUS (FABRICIUS)

(HYMENOPTERA: FORMICIDAE)

INTRODUCTION

Camponotus ferrugineus (Fabricius), the red carpenter ant, is closely related to the black carpenter ant, Camponotus pennsylvanicus. Until Brown's (1950) rebuttal of Creighton's (1950) treatment of the Camponotus herculeanus pennsylvanicus complex, C. ferrugineus was considered a subspecies of C. pennsylvanicus. Brown (1950) suggested that C. ferrugineus be considered a species due to its marked coloration and ethological traits.

C. ferrugineus has been observed in houses (Smith 1965), and has been reported to cause considerable damage to standing white cedar trees in Minnesota (Graham 1918). It is briefly mentioned in Gregg's (1944) study of the ants of the Chicago region and in Dennis' (1938) study of the distribution of ants in Tennessee. Despite the potential economic importance of C. ferrugineus, there are few studies of its biology, habits or ecology. Smith (1965), when attempting to assess the economic importance of C. ferrugineus, noted that he had no record of household foods eaten by this species and could not locate any published information on the subject. Smith's unpublished records indicated that workers, males, and females of C. ferrugineus have been observed in houses.

The objective of the research presented here was to examine colony founding in C. ferrugineus to expand the information currently available on the biology of this species.

MATERIALS AND METHODS

One dealated female of *C. ferrugineus* was collected in Blacksburg, VA. The date of collection was 13 May 1981. The queen was captured in the open, presumably at the conclusion of a mating flight.

The female was housed in a 35 mm plastic petri dish lined with filter paper (Figure 1). Water was supplied continuously by a vial fitted with a sponge wick. The female was not given food until after the eclosion of the first worker. The dish containing the founding female of *C. ferrugineus* was kept in a box to exclude light. Ambient air temperatures ranged from 23 to 28°C during the study.

Eggs laid by the female were counted on a daily basis. The female was observed for at least 30 minutes, four times per day until the eclosion of the first workers. Each day was divided into four equal periods and observations were made at 1:00 a.m., 7:00 a.m., 1:00 p.m., and 7:00 p.m. Eggs, larvae and pupae were counted until the eclosure of the first worker. All observations were made under red light (General Electric incandescent).

RESULTS

Fifty four days were required to rear the first brood to maturity. During colony foundation the queen remained motionless for long periods of time and moved only when grooming herself, laying eggs, or drinking water. The first eggs were produced 3 days after the queen was placed in the petri dish. A total of 31 eggs were laid over 51 days. The eggs were elongate and cylindrical in shape and their color varied from creamy

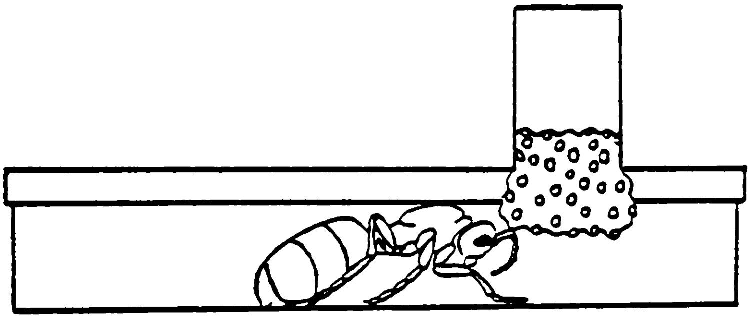

Figure 1. Diagram of the petri dish housing used during colony founding in C. ferrugineus.

white to yellow. Eggs of different age could be readily distinguished by the internal cell movement.

The first eggs hatched in 26 days. The larvae were slightly flattened, cream colored, and setacious. The first larvae to hatch grew rapidly, and most doubled in size in one day. The first-instar larvae were 1.2 mm long and grew to a length of 2.5 mm by the second day of development. The last instar larvae were 5.9 to 6.1 mm long. Seven days were required for development from the first-instar larva to the first pupa, but the number of days required to pupate was variable. For 6 larvae which hatched on the same day, the number of days required to pupate ranged from 7 to 16 days. Most larvae observed entered a one day prepupal stage before spinning a parchment-like cocoon. The larvae which hatched from eggs laid in August remained in the first-instar and did not resume normal growth until March 1982. This first-instar resting stage has also been observed in other species of the genus Camponotus (Pricer 1908, Hölldobler 1961, Mintzer 1979).

Based on the emergence dates of the first 3 workers, the pupal stage lasted for 22 days. Eighteen workers were produced in the first brood, including one intermediate worker. The workers in the first brood did not possess the marked coloration which is characteristic of C. ferrugineus and were visually indistinguishable from first brood workers of C. pennsylvanicus. Voucher specimens have been placed in the collection of the Department of Entomology at Virginia Polytechnic Institute and State University.

The queen continued to share in the care of the brood after the workers eclosed. Newley eclosed workers attempted to hide when the colony was disturbed, but most began to forage within 10 days following emergence. Some recruitment was observed in the colony when food was placed in a foraging arena attached to the colony or when the nest was disturbed. Older workers usually responded to recruiting workers by moving towards the food source or disturbance. Newer workers usually took longer to respond to recruitment towards a food source and attempted to hide when the nest was disturbed.

Although all larvae successfully pupated and pupal mortality was low (5.26%), 12 eggs disappeared and were presumed to have been eaten by the larvae or queen. However, the queen was never observed eating eggs during this study. Egg disappearance was coincidental with the period of rapid larval growth and with the eclosion of the first workers. One pupa failed to develop normally during this study. Appendix 1 provides a more detailed account of first brood development.

DISCUSSION

The time of first brood development in *C. ferrugineus* is similar to the time of development in *C. pennsylvanicus* as reported by Pricer (1908). According to Pricer, the time of development for *C. pennsylvanicus* is 66 days and this is comparable to the 54 days required by *C. ferrugineus*. *Camponotus modoc* (Wheeler) and *C. laevigatus* (F. Smith), also members of the subgenus *Camponotus*, require 55 and 64 days respectively for the development of the first brood (Mintzer 1979). Although the times of development of the species studied by Pricer (1908) and Mintzer (1979) are similar to those found in this study of *C. ferrugineus*, neither Pricer nor Mintzer found evidence of the production of a subcaste other than the minor subcaste in the first brood. One worker of the intermediate subcaste was produced in the first brood of _C. ferrugineus_.

The larvae of _C. ferrugineus_ were similar in shape and size to the larvae of _C. pennsylvanicus_. Wheeler and Wheeler (1953) described the larvae of some members of the subfamily Formicinae, and included several species of the genus _Camponotus_ in their study. The larvae of _C. ferrugineus_ grew at a rate similar to the rate reported for _C. pennsylvanicus_ by Pricer (1908). The last larvae to hatch remained in the first-instar and did not resume normal growth until the following year. The first-instar is a common resting stage during periods of overwintering or food shortages in _Camponotus_ (Hölldobler 1961). Accounts of the first-instar larvae being held back as an overwintering stage have been reported by Pricer (1908), Mintzer (1979), and Sanders (1964).

Queens of the genus _Camponotus_ found colonies independently and do not seek food or prey outside the nest during colony initiation (Pricer 1908, Wilson 1971). The first brood is brought to maturity on a diet of eggs and salivary secretions of the founding queen (Dumpert 1978). _C. ferrugineus_ founds colonies in a similar manner and it appears as if eggs are eaten to provide a source of nutrients for the first brood. Egg eating was thought to occur in _C. pennsylvanicus_ by Pricer (1908), and Mintzer (1979) observed egg eating in _C. laevigatus_ and _C. vicinus_. Egg eating was not observed in this study although 12 eggs disappeared and were presumed to have been eaten.

Previous studies have attributed egg eating to the founding queen (Pricer 1908, Mintzer 1979). However, the eggs and larvae of _C. ferrugineus were maintained in an indiscriminate pile and egg eating may be better explained if attributed to the larvae. In this study, egg disappearance closely coincided with the events of first larval hatching and first worker eclosion. Wheeler and Wheeler (1953) observed larval cannibalism in an artificial nest of C. americanus (Mayr). Egg eating by ant larvae has been reported in Solenopsis invicta (Buren) by Glancey et al. (1973), who found that the larvae of S. invicta can distinguish trophic eggs from embryonated eggs.

Trophic eggs are non-embryonated eggs that "exist only to be eaten" (Wilson 1971). Trophic eggs are produced by some non-social insects, but are most commonly found in the social Hymenoptera. Production of trophic eggs in virgin fire ant queens has been reported by Voss (1981). Wilson (1971) stated that trophic eggs may constitute an important part of the food budget of some social insects and may also play a role in the transfer of information concerning the state of the colony. In S. invicta, as the queen and colony mature, trophic egg production diminishes.

C. ferrugineus is closely related to C. pennsylvanicus (Brown 1950, Creighton 1950) and is separated from C. pennsylvanicus by its coloration. The first brood of C. ferrugineus was indistinguishable from the first brood of C. pennsylvanicus. Brown (1950) stated that C. ferrugineus should be considered a separate species due to the marked coloration while Creighton (1950) retained C. ferrugineus as a subspecies of C. pennsylvanicus because he could not find any taxonomic characters other than color which would separate C. ferrugineus from C. pennsylvanicus. Although this study was based on one founding queen, the lack of the characteristic coloration in the first brood may indicate the need for other taxonomic characters to separate *C. ferrugineus* from *C. pennsylvanicus* at the specific level.

Conditions in the laboratory may have contributed to the success of the founding female used in this study. The queen was protected from adverse conditions and colony founding under natural conditions may extend brood development time. The petri dish satisfied the requirement for a small enclosed cavity during colony initiation, without competition from established colonies and free of attack by predators or parasites in the brood chamber (Dumpert 1978).

The life history of *C. ferrugineus* has been assumed to be similar to that of *C. pennsylvanicus* (Pricer 1908, Dennis 1938, Smith 1965). This study has shown that part of the life histories of *C. ferrugineus* and *C. pennsylvanicus* are similar. Further study of *C. ferrugineus* is necessary to determine the extent of its similarities to *C. pennsylvanicus* or any notable differences which may exist in the biology and habits of these two species.

COLONY FOUNDING IN THE BLACK CARPENTER ANT,

CAMPONOTUS *PENNSYLVANICUS* (DEGEER)

(HYMENOPTERA: FORMICIDAE)

INTRODUCTION

The period of reproductive activity and colony founding is a critical phase in the life cycle of ants. In most ant species, new colonies are established by independent females after a mating flight. The reproductives are subject to predation and affected by climactic conditions during and after the mating flight (Dumpert 1978). The number of suitable sites for colony founding and the adequacy of stored food reserves in the body may be factors which limit the ability of individual females to successfully establish new colonies (Dumpert 1978). Food reserves might be increased by foraging outside of the nest, but foraging by colony foundresses occurs only in a small number of ant taxa studied (Mintzer 1979). In most ant species, females do not forage and rear the first brood on a limited supply of bodily food reserves.

Pricer (1908) studied colony foundation in *Camponotus pennsylvanicus*. He observed that females of *C. pennsylvanicus* found colonies independently in a manner similar to most other ants. Pricer (1908) also noted that females do not seek food or prey outside their nest chamber during colony founding. McCook (1883) also reported that founding queens of *C. pennsylvanicus* initiated colonies independently and did not seek food from sources outside the nest chamber. Mintzer (1979) provided similar accounts of colony foundation in seven species (representing four subgenera) of *Camponotus*.

Colony founding in *C. pennsylvanicus* is examined in this study to extend the data provided by Pricer (1908), and to make it possible to compare the results of this study with the results of Pricer. The following text also examines the effect of ad libitum feeding on founding queens of C. pennsylvanicus.

MATERIALS AND METHODS

Dealate females of C. pennsylvanicus were collected in Blacksburg, VA between 20 May 1981 and 30 June 1981. Most were captured in the open, presumably at the conclusion of mating flights. One female was found when the incipient nest chamber was broken open during field collecting activity.

Seven females of C. pennsylvanicus were housed in 35 mm plastic petri dishes lined with filter paper. Water was supplied to all ants by vials fitted with sponge wicks. Five dishes containing founding females were kept together in a box to exclude light. Two other dishes were kept under a 16L : 8D photophase, beginning at 7:00 a.m. each day. The light-adapted females were labled UL1 (unfed/light) and UL2 to indicate the treatment they received. Ambient air temperatures ranged from 23 to 28°C during colony initiation.

Two of the females of C. pennsylvanicus were kept in dishes which were supplied with a vial of honey and water (50 : 50) in addition to the water vial. These females were labled FD1 (fed/dark) and FD2 to indicate treatment. Three other females of C. pennsylvanicus, UD1 (unfed/dark), UD2 and UD3, were denied access to honeywater until the first workers eclosed. Honeywater and dead insects (i.e., German cockroaches) were given to all colonies within twelve hours after eclosion of the first worker. Both groups of founding females were kept in the box to exclude light. Observations of the dark-adapted colonies were made under red light (General Electric incandescent).

Eggs were counted on a daily basis for each colony. The founding females were observed for at least 30 minutes, four times per day. Colonies were observed at 7:00 a.m., 1:00 p.m., 7:00 p.m., and 1:00 a.m. each day until the emergence of the first workers. After worker eclosion the colonies were moved to plaster nests with plexiglass tops.

Analysis of variance was used to test for differences between treatments of females duirng colony initiation.

RESULTS

Six queens used in this study reared workers to maturity. Forty-two to 50 days were required to rear the first workers from the time the first eggs were laid (Table 1). The number of eggs laid ranged from 12 to 28 for single queens, and the number of workers in the first brood ranged from 4 to 11.

Ad libitum feeding by founding females had no significant effect on the number of eggs laid, the number of eggs eaten, or the duration of the immature stages ($P < 0.05$). Females which did not received an ad libitum feeding of honeywater did not eat a significantly greater number of eggs than females which received food. The queens (FD1 and FD2) which were provided with a constant supply of honeywater were both observed to drink preferentially from the honeywater filled vial rather than the vial filled with water. Both females were observed to feed from the honeywater filled vials approximately 2 times per week during the study. Queen FD1 was observed to drink from the

Table 1. Development of first brood of *C. pennsylvanicus* during colony foundation.

Female	Treatment	Number of eggs laid	Number of eggs presumed eaten	Total workers	Duration of Immature stages (Days) Egg	Larva	Pupa	Total days
FD1	fed/dark	16	4	7	19	11	13	43
FD2	fed/dark	20	1	4	19	14	17	50
UD1	unfed/dark	28	1	5	11	13	25	49
UD2	unfed/dark	13	1	11	22	8	16	46
UL1	unfed/light	28	2	11	20	8	18	46
UL2	unfed/light	12	0	4	13	10	19	42
MEAN:		19.5	1.5	7	17.3	10.7	18	46
STANDARD DEVIATION:		9.10	1.47	3.29	4.32	2.50	4.00	3.51

water vial once a week, and queen FD2 was observed to drink from the water vial 7 times during the study. Feedings lasted from 12 seconds to one minute and 36 seconds, but seldom lasted longer than 45 seconds.

Two females successfully reared their first brood under artificial light, although both delayed the laying of the first eggs for a number of days. Queens UL1 and UL2 did not lay their first eggs until 18 and 21 days after being placed in their respective culture dishes. Queen UL1 began to lay eggs only after she had formed a nest beneath the filter paper lining of the petri dish. The nest was formed with filter paper removed from the lining of the petri dish. Queen UL1 left her nest chamber only for water from the water vial on her dish. No significant differences ($P < 0.05$) in the number of eggs laid, the number of eggs eaten, or the duration of the immature stages were detected between light-adapted queens and the dark-adapted queens.

Egg eating was not observed among any of the queens used in this study, although unaccounted egg loss was noted in all but one dish. None of the eggs of queen UL2 disappeared during the study. Egg disappearance was most notable during the period when the first larvae to hatch exhibited their most rapid growth. The first larvae to hatch frequently doubled in size in one day, growing from a first-instar length of 1.2 mm to a length of 2.5 mm by the second day of development. Final larval length was 6.2 to 6.4 mm. Larvae which hatched later exhibited more gradual growth.

One queen failed to lay any eggs during the study although she survived throughout the entire study. Two additional queens were caught near the end of this study, but attempts to induce colony founding under artificial light failed and both died without laying any eggs.

DISCUSSION

In this study, founding queens usually began to lay eggs 3 to 5 days after installation in culture dishes. Eggs were laid at a rate of 2 or 3 eggs per day but the queens did not lay eggs as continuously as those observed by Pricer (1908). Most of the queens observed in this study laid eggs for 2 or 3 days and rested for 1 day before egg laying resumed. As reported by Pricer, the number of eggs laid during the first year of colony foundation was highly variable.

Although egg eating was not observed during the study, most of the queens lost 1 or more eggs. Pricer (1908) also noted the unexplained disappearance of eggs in his study, Mintzer (1979 observed egg eating among queens of C. vicinus and C. laevigatus in his study of colony founding in seven species of Camponotus. The absence of observations of egg eating by queens of C. pennsylvanicus in this study and Pricer's (1908) study suggests the possibility of another explanation for egg disappearance in this species. The eggs, larvae, and pupae of C. pennsylvanicus are maintained in an indiscriminate pile and the first larvae to hatch develop much more rapidly than larvae which appear later in the new colony. Pricer (1908) also noted this mode of development among the first brood larvae of C. pennsylvanicus. Egg disappearance in this study always corresponded with the period of rapid larval growth and may be more adequately explained if attributed to egg eating by the larvae. Egg eating by ant larvae has been reported in *Solenopsis invicta* by Glancey et al. (1973), who found that the larvae of *S. invicta* can distinguish trophic eggs from embryonated eggs.

Trophic eggs are non-embryonated eggs that "exist only to be eaten" (Wilson 1971). Trophic eggs are produced by some non-social insects, but are most commonly found in the social Hymenoptera. In many insect societies, these eggs constitute an important part of the food budget and may also play a role in the transfer of information concerning the state of the colony (Wilson 1971). In *S. invicta*, as the queen and colony mature, trophic egg production diminishes (Glancey et al. 1973). Trophic egg production has been reported in a wide diversity of both primitive and advanced ant genera (Wilson 1971).

The time of development of the first brood of workers in this study was considerably less than that reported by Pricer (1908). The 6 queens observed in this study required an average of 46 days to produce the first workers from the first eggs laid. Pricer reported that the queen observed in his study required 66 days to produce the first workers from the first eggs in his study. As in Pricer's study, the duration of the immature stages was taken as the average of the time required to produce the first 2 workers. The differences in the times of development may be due to laboratory conditions, the number of females observed, or the dates on which the females were collected. Pricer observed one queen which was captured July 10, 1906, while the 6 queens observed in this study were collected between May 20 and June 30, 1981.

The light-adapted queens did not lay eggs as quickly as the dark-adapted queens, however the duration of the immature stages did not increase. The data suggest that C. pennsylvanicus can be reared successfully in the light although some difficulties may be encountered. The queens which were kept under lighted conditions seemed to be disturbed by their inability to escape the light and frequently exhibited extreme agitation for periods of 30 minutes or more during days before the day the first eggs were laid. After the first eggs were laid the pattern of queen behavior was similar to that observed in the dark-adapted colonies, and to that observed by Pricer (1908) and Mintzer (1979).

The reasons for the deaths of the two queens which were captured late in the study are unknown. However, both females exhibited extreme agitation during the days following their placement in the culture dishes. The day of their deaths was marked by symptoms which resembled insecticide poisoning. Death was preceded by extreme hyperactivity, cleaning and antennal grooming, convulsions, ataxia, and prostration. Both died 3 days after they were placed in the petri dishes.

The last larvae to hatch remained in the first-instar and did not resume normal growth during the study period. The first-instar has been reported to be a common resting stage during periods of overwintering or food shortages (Hölldobler 1961, Mintzer 1979). Pricer (1908) also noted the occurence of a first-instar resting stage in C. pennsylvanicus.

All workers produced in the first broods of the queens in this study belonged to the minor subcaste. Similar results were reported by Pricer (1908) and Mintzer (1979). Although the genus Camponotus is characterized by a polymorphic worker caste, no noticeable differences were present among the workers produced by any of the queens used in this study.

In summary, considerably fewer days (20) were required to produce the first brood of workers when the results of this study are compared to the results of Pricer (1908). Differences in laboratory conditions, dates of collection, and the number of queens observed may have contributed to the observed differences between the studies. Egg disappearance may be attributable to larval egg eating rather than to egg eating by founding queens. C. pennsylvanicus can be induced to found colonies under artificial light although it may be difficult to do so. Although queens of C. pennsylvanicus will accept ad libitum feedings under laboratory conditions, such feedings have no apparent effect on the ability of founding queens to successfully rear first brood workers and do not increase brood size in any appreciable manner. Ad libitum feedings might produce a noticeable difference if a wider range of foods were made available. The data of Ayre (1967) suggest that C. pennsylvanicus is capable of utilizing a variety of food sources. Although founding queens of C. pennsylvanicus do not forage outside the new nest for food, laboratory colonies may make it possible to assess the long term effects of supplemental feedings on colony founding and development.

ECONOMIC IMPORTANCE OF CARPENTER ANTS IN THE MID-ATLANTIC STATES

INTRODUCTION

Carpenter ants are members of the wood-infesting insect complex which includes termites, powderpost beetles, carpenter bees and the old house borer. All ants belonging to the genus Camponotus are called carpenter ants, and most of the North American species are almost exclusively wood-nesting forms. Nests are usually formed in moisture-damaged wood, but mature colonies can extend their galleries into dry, sound wood (Dennis 1938, Gregg 1944). The wood-nesting habits of carpenter ants and their foraging activities in and around houses, make carpenter ants serious pests yet relatively little is known about them.

Robinson (1980a) found that extension agents in Virginia, Pennsylvania, Maryland, and Delaware have an adequate knowledge of the biology, habits and damage of carpenter ants. In a subsequent study, Robinson (1980b) found that Virginia homeowners lack adequate knowledge of the habits and damage caused by these ants. Barrows (1980) reported on the cost of carpenter bee control (regional basis), and Ebeling (1968) estimated the cost of termite damage (national basis). There is little information on the economic importance of carpenter ants, powderpost beetles or old house borer.

In a recent NPCA report (Pinto, 1981), carpenter ants were given a rating of 66 (out of 100) in a listing of the relative importance of structural pest species. In the NPCA list, subterranean termites were given a rating of 88 and powderpost beetles were rated 55. Smith (1965) attempted to assess the biology, taxonomy and economic importance of house-infesting ants of the eastern United States. His assessment included eight carpenter ant species, but he did not attempt to determine their economic importance quantitatively. The lack of information on the economic importance of carpenter ants makes a more detailed and accurate assessment of the economic impact of carpenter ants necessary.

A survey of professional pest control operators in Virginia, Maryland, Pennsylvania, and Delaware was conducted to determine the economic importance of carpenter ants. The results and evaluation of that survey are presented here.

METHODS

The economic importance of carpenter ants was evaluated by a questionnaire consisting of 12 questions. Three questions provided information on the age, education, and years experience of the survey respondents. The other questions dealt with the number of and average cost of carpenter ant control work, the relationship between infestations and actual damage, the average age of houses treated, and the frequency of callbacks.

A total of 1414 questionnaires, along with a cover letter explaining the purpose of the study, were sent to professional pest control operators in Virginia (631), Maryland (536), Pennsylvania (159), and Delaware (88). The results presented here are based on a 33% return on the questionnaires.

A number of factors must be considered when interpreting the percentages reported. These factors include specialization within the industry, age size and reputation of the individual business, ability of the pest control operator to perform carpenter ant control, and the location of the business within the geographic distribution of carpenter ants.

RESULTS

The questions are not presented in the sequence they occurred on the survey form, but are grouped by topic to provide easier discussion of the results.

Pest Control Operator Profile

The pest control operators participating in the survey were approximately 40 years of age, had a high school education, and had approximately 13 years experience in the pest control business.

Importance of Carpenter Ants

Q. What percentage of your business is devoted to carpenter ant control?

A. 74%	0 - 5%	4%	16%-20%
13%	6%-10%	2%	21%-25%
5%	11%-15%	2%	More than 25%

Q. How many carpenter ant control jobs did you perform in 1980?*

A. 38%	0 - 10	6%	31 - 40
19%	11 - 20	8%	41 - 50
12%	21 - 30	12%	More than 50

*5% reported no carpenter ant work or did not respond.

A majority (74%) of the pest control operators reported that carpenter ant control represented less than 6% of their business. Only 4% of the PCO's questioned reported that carpenter ant control represented more than 20% of their business.

A majority (62%) of the pest control operators performed more than 10 carpenter ant jobs in 1980. Only 5% reported that they performed none. The number of carpenter ant control jobs performed by individual businesses ranged as high as 2,000. Twelve percent of the pest control operators who performed carpenter ant control during 1980, performed more than 50 control jobs.

Q. At what time(s) of the year do you receive the most requests for carpenter ant control?

A. 1) 0.6% Winter (Dec., Jan., Feb.)

2) 26% Spring (Mar., Apr., May)

3) 53% Summer (June, July, Aug.)

4) 16% Fall (Sept., Oct., Nov)

Q. Are return visits usually required to give complete treatment?

49.5% Yes 50.5% No If yes, what is the average number of return visits required?

A. 68% one

21% two

7% three

1% four

0 five

3% more than five.

Less than one percent (0.6%) of the respondents received requests for carpenter ant control during the winter months. The percentages rose in the spring (26%) and summer (53%) and declined to 16% during the fall.

The percentages indicate that carpenter ants can remain active within the home throughout the year. The relatively low (26%) spring percentage may reflect the differences in the climates of the states included in the survey. The warmer weather and longer days of spring trigger outdoor foraging and swarming. This behavior is indicated by the data of Dukes (see section on Seasonal Foraging Patterns of *Camponotus pennsylvanicus*). Outdoor foraging and swarming activity can reduce the visibility of carpenter ants in infested homes and produce a corresponding reduction in requests for control.

To give complete treatment of carpenter ants, return visits were required in about one half of the treatments (49.5%). Of those that required return visits, the majority (68%) required one return visit. Twenty-one percent required two return visits and 4% required four or more return visits to give complete control. Return visits indicate the difficulty encountered by pest control operators who contract for carpenter ant control. The most important factor in carpenter ant control is the location of the colony (Truman et al. 1976). Control where the nest is not destroyed is only temporary at best (Truman et al. 1976), and callbacks are an indication of the trouble in locating carpenter ant nests.

Rising chemical, fuel, and labor costs make callbacks increasingly cost ineffective. Thus, control of the number of callbacks required to give complete control of carpenter ants is important to the pest control operator.

Age of Infested Structure and Damage Association

Q. Were the carpenter ant infestations you treated in houses:

A. 11% generally less than 10 years old

50% generally more than 10 years old

29% about equal

10% don't know

Q. What percentage of the carpenter ant infestations you treated were associated with actual damage to structural wood?

A. 79% 0 -25% | 4% 51%-75%

13% 26%-50% | 4% 76%-100%

Fifty percent of the pest control operators reported that carpenter ant infestations were in houses more than 10 years old. A significant percentage (29%) found infestations to be equally prevalent in older and newer homes, and 11% treated infestations in houses that were less than 10 years old.

The percentage of newer homes (less than 10 years old) that were treated provides evidence of the susceptibility of new homes to carpenter ant infestation. More houses are being built in suburban areas. These suburbs displace the wooded areas inhabited by carpenter ants.

When asked about the extent of carpenter ants associated with actual damage to structural wood, 79% of the pest control operators reported a 25% or less association with actual structural damage. Only 8% reported a greater than 50% association with damage.

Carpenter ant nests are often difficult to locate and this problem is compounded by brick and block construction. These ants are opportunistic and will nest in wall voids, ceilings and insulation.

Pest control operators often drill wall voids and forcibly inject chemicals when treating carpenter ant infestations. This method precludes the removal of a suspect portion of a wall. As a result of the drill and inject method, accurate assessments of structural damage may not be possible.

Economic Impact

Q. What was the average cost to the customer for a carpenter ant control job you performed in 1980?

A. 10% 0-$25 | 20% $76-$100

16% $26-$50 | 11% $101-$125

24% $51-$75 | 19% More than $125

Q. What was the lowest cost (to the customer) for a carpenter ant control job you performed in 1980? (Reported here as averages)

A. $64.00 Range: 0-$490

Q. the highest?

A. $219.00 Range: $10-$3000

(12% greater than $300 and 70% greater than $100)

When asked to provide their average cost to the customer for carpenter ant control in 1980, 50% of the respondents reported an average cost of greater than $75. Only 10% reported an average of $25 or less and 19% reported an average of more than $125. Forty-three pest control operators provided their 1980 averages, and these averaged $206.

The lowest cost to customers in 1980 averaged $64 and ranged from 0 to $490. The highest cost to customers in 1980 averaged $218 and ranged from $10 to $3,000. Seventy percent of the prices in the high cost range were greater than $100 and 12% cost more than $300.

The importance of the reported average costs to the customer for carpenter ant control is highlighted by the apparent low level of carpenter ant association with structural damage. Although most pest control operators (79%) reported a 25% or less association with structural damage, only 26% of their customers paid less than $50 for carpenter ant control in 1980.

Two factors may be responsible for the cost of carpenter ant control: customer desire to rid their home of carpenter ants, even in the absence of apparent structural damage, and the difficult nature of locating and treating carpenter ant nests makes it necessary to charge enough to defray the costs of callbacks.

SUMMARY

Carpenter ants are considered a serious problem by homeowners. Although a low damage-association value is apparent, customers are willing to pay considerable amounts of money for carpenter ant control. The presence of detectable damage is not the definitive factor in the homeowners decision to request control.

Pest control operators do not devote a large percentage of their business to carpenter ant control, but nearly all (95%) of the pest control operators in this sample performed some carpenter ant jobs. Carpenter ants generate requests for control year round and pest control operators often have trouble providing complete control. The difficulty in providing complete control contributes to the cost to the customer and only 10% of the customers can expect to pay $25 or less when they request control.

As more homes are built in the suburbs, the incidence of infestations will probably increase. Brick and block construction makes the location of carpenter ant nests difficult, and accurate assessments of damage are often impossible in such structures. This set of circum-

stances indicates the need for further study of carpenter ants and their relationships with man.

Questionnaires which gather information in one geographic region cannot be considered representative or define trends for the country as a whole. The species and problems caused by carpenter ants vary in intensity and type from one area to another. The states included in this survey represent a geographic region which has in common many wood-infesting insects and related problems. However, the conclusions drawn here are applicable to this region only.

FOOD PREFERENCE STUDIES OF

CAMPONOTUS PENNSYLVANICUS AND C. FERRUGINEUS

(HYMENOPTERA: FORMICIDAE)

INTRODUCTION

Carpenter ants are considered serious pests (Pinto 1981, Ascerno 1981) and can damage structural timber during their nesting activities (Akre and Antonelli 1976, Friend and Carlson 1937). A number of *Camponotus* species, including *C. pennsylvanicus* and *C. ferrugineus*, are known to infest houses in the U.S. Eight house-infesting species in the eastern U.S. have been reported by Smith (1965).

Camponotus pennsylvanicus is the most destructive of the U.S. carpenter ants (Wheeler and Wheeler 1963) and is an important house-infesting species (Krombein et al. 1979) It is known to feed on household foods, and apparently prefers sweets (Smith 1965). *C. pennsylvanicus* has been reported to feed on honey, syrup, sugar, jam, raw and cooked meats, fruits, melons, cakes, and boiled eggs (Smith 1965). Due to its nesting habits and because it feeds on household foods, *C. pennsylvanicus* can detract from the quality of life in a home.

Camponotus ferrugineus is closely related to *C. pennsylvanicus* and is found throughout most of the distributional range of *C. pennsylvanicus* (Creighton 1950). Though it is not as common as *C. pennsylvanicus*, it is considered an important pest species and has been reported as a house-infesting species (Smith 1965, Krombein et al. 1979). *C. ferrugineus* has been found to feed on small insects, the juice of fruits, the sap of plants, and honeydew excreted by aphids and other honeydew-excreting insects. Although it has been observed in houses, there are no reports of household foods eaten by this ant.

Both C. pennsylvanicus and C. ferrugineus are known to tend aphids and other honeydew-excreting insects. Honeydew is an important source of colony nutrients, and solid foods are apparently not major constituents in the diet of a number of Camponotus spp. (Fowler and Roberts 1980, Sanders 1972). The subject of ant-Homopteran commensalism has been reviewed extensively by Way (1963). The chemical composition of honeydew has been examined by Auclair (1963) and Maurizio (1975).

There is little information published on the digestive enzymes of ants. Ayre (1967) included two species of Camponotus in his study of the digestive enzymes of five ant species. He reported that tests for digestive enzymes can be used to determine the feeding habits of ants. The results of Ayre (1967) indicate that C. pennsylvanicus and C. herculeanus are capable of utilizing sugars of a higher molecular weight than monosaccharides and that they may feed on carbohydrate sources other than honeydew.

House-infesting colonies of carpenter ants are apparently able to utilize household foods as a source of colony nutrients, yet no studies have attempted to examine the household foods eaten by carpenter ants. The purpose of this study was to examine food preference in the carpenter ants, C. pennsylvanicus and C. ferrugineus. A number of potential food materials were examined for attractancy to these carpenter ant species.

MATERIALS AND METHODS

Two colonies of *C. pennsylvanicus* and one colony of *C. ferrugineus* were used to examine the attractancy of various substances to worker ants. Colonies were maintained in modified hive bodies used for keeping bees. The hive bodies could be attached to a "Y" shaped choice box by tygon tubing. All colonies received honeywater and various insects, including adult German cockroaches and various Lepidoptera and Coleoptera larvae, during the study. Colonies did not receive supplemental feedings when involved in feeding trials.

Prior to the presentation of food in the choice box, colonies were attached to the empty choice box to test for random entrance into the box. Thirty replicates of this procedure were performed to ensure randomness. To test for orientation towards a food source, honey:water (50 : 50) was placed in one of the arms of the choice box. A table of random numbers was used to determine the placement of the honeywater, and this procedure was replicated 20 times.

The remaining tests involved direct comparisons of various substances. These substances were chosen based on their availability and to provide a range of food types for comparisons. Boiled oatmeal, insects, artificial honeydew with different sugar concentrations, processed meat, boiled raisins, boiled and fermented raisins, and Nu-Lure (Miller Chemical and Fertilizer Corp.) were all examined against honeywater (standard) and in various combinations. The artificial honeydew was formulated according to specifications determined by Dr. Donald G. Cochran of the department of Entomology, Virginia Polytechnic Institute and State University. The sugar concentrations used in this test were 0.1% and 10.0% (by weight). Specifications for the artificial honeydew are listed in Table 2. Twenty replicates of each combination were performed.

The sampling method employed during this study involved counting the number of ants feeding on a food during a 30 minute observation period. One count was taken each minute, and the number of ants at each feeding station was determined. The number of ants feeding at each station during a test was summed over the observation period and the sums were converted to percentages of ants feeding during a trial before comparisons were made. The sampling method was modified for the comparisons of the artificial honeydew concentrations. Fifteen-minute observation periods were employed and the number of replicates performed was increased to 40. The Students T test was used to examine the comparisons for preference.

RESULTS

When the colonies were first attached to the choice box the ants were reluctant to enter the foraging area, although they readily entered the tygon tube pathway attached to the nest box. The first ants to enter the choice box displayed the body vibrations and searching behavior typical of disturbed or aggressive ants (Hartwick et al. 1977, Markl and Fuchs 1972). After a short period of exploration the ants began to drag their abdomen on the floor of the choice box in the manner described by Hartwick et al. (1977) and Traniello (1977). Preliminary tests of the choice box indicated that when no food was

Table 2. Formulation of Artificial Honeydew.

Amino Acids at 0.05% each (by Weight)	Sugars at 10.0% or 0.1% each (by Weight)
Lysine	Sucrose
Glutamic acid	Glucose
Aspartic acid	
Alanine	
Valine	
Arginine	
Glycine	
Isoleucine	
Proline	
Threonine	
Tyrosine	
Mold Inhibitor (Carolina Biological Supply)	

present, the ants exhibited no preference for either arm of the choice box ($P < 0.995$).

When honeywater was tested against water, the ants quickly demonstrated preference for the food baited arm of the choice box. Ants which located and fed upon the honeywater usually fed until their gasters became distended and then exhibited trail-laying behavior as they returned to the colony box. When met by unfed workers entering the foraging area, gorged workers readily engaged in trophallactic food exchange with unfed workers. Fed workers frequently engaged in food exchange with more than one unfed worker, often exchanging food with 2 to 5 workers at one time. Although group food exchange was most common when the first workers to feed returned to the nest box, it was observed during most trials. Many workers became disoriented when food was placed in an arm other than the arm where food had previously been located, but most chose the food baited section after a 30 to 50 second orientation period. When the ants returned to the arm in which food had previously been present, they exhibited searching behavior characterized by a series of fast runs and self-grooming.

Within the nest boxes, unfed workers responded to recruitment rapidly when gorged workers returned to the colony. Some gorged workers appeared to tap the bottom of the nest box with the tip of their gasters upon returning to the colony. Unfed workers appeared to respond to the "rapping" behavior of these gorged workers even in the absence of actual contact with the recruiting workers. The rapping of the gorged workers produced a response of general excitement among the potential recruitments. Food exchange and a series of fast runs followed the response to rapping.

When honeywater was tested against boiled oatmeal the ants preferred the honey to the oatmeal ($P < 0.005$), and few ants collected the oatmeal. Seven ants were observed to carry oatmeal back to the nest from the choice box during the twenty trials. The oatmeal could be made more attractive with the addition of honey or sugar at a ratio of 1 : 1. However, the attractancy of the honey or sugar sweetened oatmeal was not enhanced sufficiently to stimulate prolonged feeding in the presence of honey or honeywater.

Against Nu-Lure (Miller Chemical & Fertilizer Corp.), honeywater was still preferred as a food. Nu-Lure did stimulate prolonged feeding by 20.8% of the ants feeding over the first 7 repetitions of the comparisons. After 7 trials, most of the ants entering the choice box during the Nu-Lure comparisons appeared to recognize Nu-Lure as an unacceptable food. Most of the ants which chose the arm containing the Nu-Lure would approach the food container slowly, test the food with their labial palpi or antennae, and then back away from the container before displaying body vibrations indicative of disturbance or aggressiveness. This sequence of behaviors was not interpreted as recruitment towards the food source since other workers which encountered the agitated worker ran away from the food rather than towards it. The attractancy of Nu-Lure was enhanced by the addition of honey, but long term feeding was not increased significantly. Honeywater was preferred to the Nu-Lure or the Nu-Lure/honey (50:50:) combination at the $P < 0.005$ level of significance.

Both colonies exhibited a sudden shift in food preference in mid July and for the next month (July 17 to Aug 21, 1981), the foraging workers did not accept honey or honeywater. The shift in food preference was preceded by a number of important colony functions. Male and female reproductives started to swarm periodically from June 18 to July 6, 1981. As many as 19 male and female reproductives emerged from the colonies in an apparent attempt to swarm. Most climbed to the top of the colony box or to the tops of the nest sections in the box, where they would attemp to fly. Upon failing to gain flight, most repeated the action several times and continued to do so until they were dragged back into the nest by workers. Swarming activity was most frequently observed in the late afternoon (approximately 5:00 p.m. until 7:30 p.m.). On June 26 workers began to place pupal cocoons on the refuse pile within the nest box. Both colonies began to remove cocoons on the same date, and the workers continued to do so for 9 and 11 days, respectively, for colonies 1 and 2. Workers in colony 1 began to remove wood from the nest section in the nest box on June 30 and continued to do so until September 4, 1981. A total of 110.5g of wood was removed.

Comparisons of honeywater and artificial honeydew were made during and after the shift of food preference (Figure 2). Comparisons of honeywater and honeydew indicated a marked preference for artificial honeydew from July 18 to August 20, 1981 ($P < 0.005$). From August 21 to August 27 no preference was shown for either honeydew or honeywater. After August 27 the ants resumed honey and honeywater acceptance and subsequent comparisons between honey and the artificial honeydew showed significant preference for honeywater at the $P < 0.005$ level of

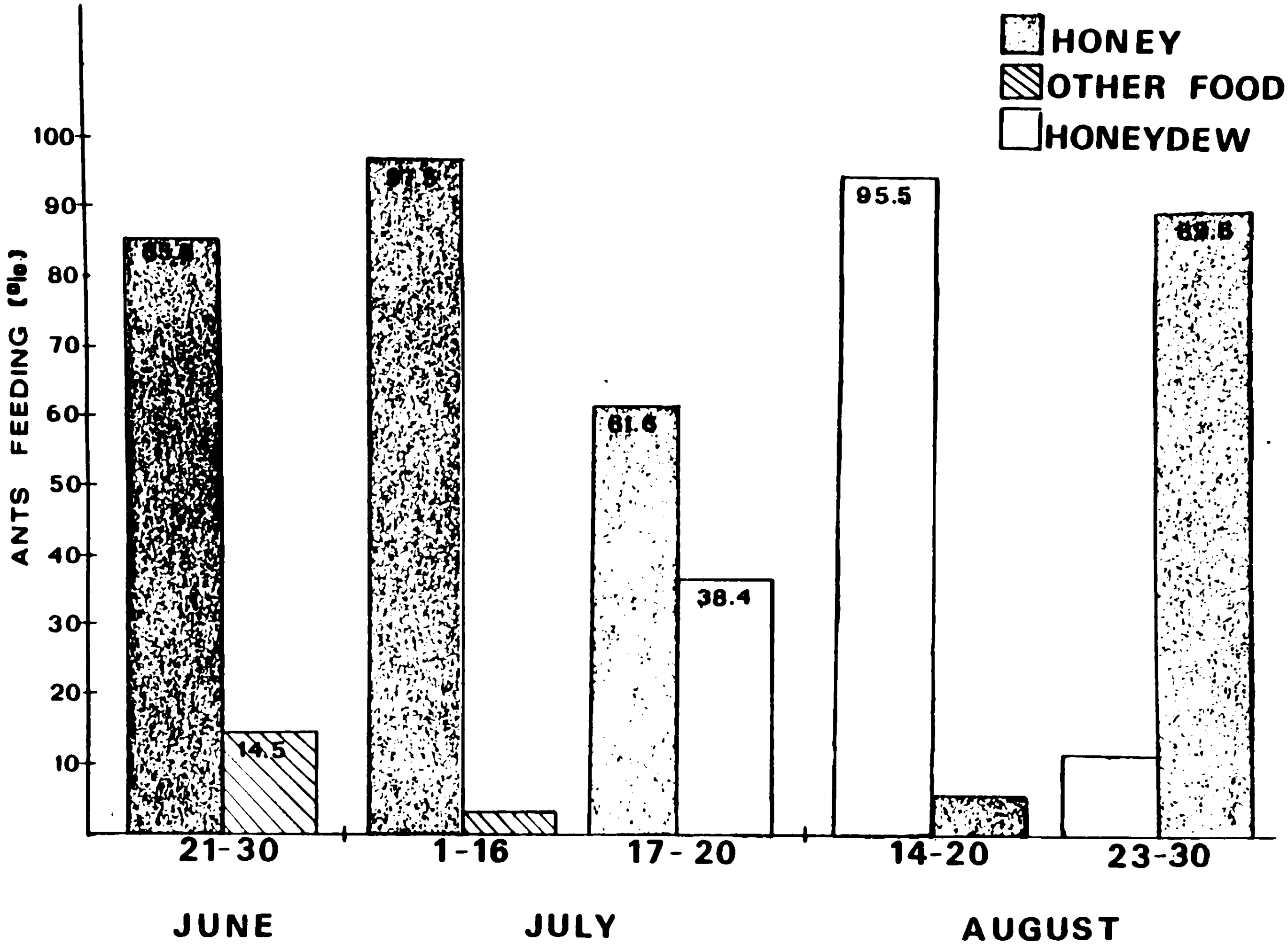

Figure 1. Graph of food preference in Camponotus pennsylvanicus

significance. During the shift, 94% of the ants feeding preferred the artificial honeydew to honeywater. After the shift the percentage of ants feeding on honeywater rose to 93.4% and the ants would accept the artificial honeydew only after the colony had not been fed for several days.

Comparisons between the 10% and 0.1% honeydew showed a significant preference for the 10% honeydew at the $P < 0.005$ level. These comparisons were made during the shift in food preference and neither concentration stimulated prolonged feeding after the ants resumed the honeywater feeding preference they had demonstrated during the year.

The ants were given choices of other foods including boiled raisins, boiled and fermented raisins, processed meat, German cockroaches, and plums. The ants fed on the juices of the boiled, fermented raisins during the period when honey was not accepted. Attempts to induce feeding after the initial trial comparisons failed. Boiled raisins were not accepted. Processed meat was an unacceptable food and the ants ignored its presence after a short period of time. Plums with broken skins stimulated some feeding on the juices present on the wound. When dead German cockroaches were placed in the choice box in comparison with honeywater, the ants demonstrated a short term reversal in their feeding behavior. The presence of the cockroaches stimulated strong recruitment toward the choice box arm containing the cockroaches. Recruitment of workers toward the cockroaches remained intense until the cockroaches were transported to the nest. Although recruitment toward the cockroaches was notable, it was not complete and many ants continued to feed on the honeywater even when the cockroaches were present.

Replicated comparisons of foods were not performed for _C_. _ferrugineus_, but all of the substances which were examined with _C_. _pennsylvanicus_ were presented to _C_. _ferrugineus_ during pretrials. _C_. _ferrugineus_ is apparently similar in its food preferences. When honeywater was compared to Nu-Lure, 89% of the ants feeding chose the honeywater, and most ants which fed on Nu-Lure did not exhibit prolonged feeding. Subsequent comparisons of the liquid and particulate fractions indicated that the liquid fraction was preferred over the particulate fraction. Although most ants entering the choice box did not feed on either fraction (93.5%), 6% chose the liquid fraction over the particulate fraction.

When no other food was present, workers of _C_. _ferrugineus_ would accept boiled, fermented raisins, and 10% artificial honeydew. The average number of ants observed feeding on boiled, fermented raisins and 10% artificial honeydew were 34 and 47 ants, respectively. These averages were based on 10 observations each.

Insects accepted by _C_. _ferrugineus_ included German cockroaches, eastern tent caterpillars and various other Lepidoptera and Coleoptera larvae. No preferences were tested for when these insects were given to the ants. The German cockroaches were always taken back to the nest by the worker ants. The larger insects such as the tent caterpillars and beetle larvae were usually eaten where they were found. The ants would ingest most of the body fluids before attempting to tear the insect into smaller pieces which they could transport to the nest. The head capsules were always carried back to the nest and would reappear on the refuse pile one or two days later.

The ants were incapable of subduing healthy insects, and most of the insects had to be disabled before they were placed in the foraging area. Once an insect was disabled, the ants were effective scavengers and were found capable of tearing apart adult Japanese beetles.

DISCUSSION

Although both *C. pennsylvanicus* and *C. ferrugineus* are known to eat dead or live insects, a number of workers have reported that they seem to feed preferentially on the honeydew produced by aphids and other honeydew-producing insects (Pricer 1908, Smith 1965, Sanders 1972). They have also been reported to feed on plant sap and the juices of fruits (Smith 1965). Similar preferences have been noted in *C. noveboracensis* (Fitch) (Gotwald 1968). This study also indicates that liquid foods, particularly sweet liquids, are preferred by *C. pennsylvanicus*. Although *C. ferrugineus* was not tested as thoroughly as *C. pennsylvanicus*, its food preferences appeared to be similar in the limited tests that were performed. Sanders (1964) suggested that several species of *Camponotus* may feed on fungal mycelia. Ayre (1967) provides evidence that *C. pennsylvanicus* and *C. herculeanus* have the digestive enzymes necessary to utilize fungal mycelia as a source of nutrients.

Ayre (1963) reported that *C. herculeanus*, a species closely related to *C. pennsylvanicus* and *C. ferrugineus*, was found to be an effective predator during laboratory experiments. Myers and Campbell

(1976) reported that a species of *Camponotus* was found to be an effective deterrent to the spread of Cinnabar moth, *Tyria jacobaeae* (L.) in Linn County, Oregon. However, neither *C. pennsylvanicus* nor *C. ferrugineus* were found to be effective predators against healthy Lepidoptera larvae or adult German cockroaches. Workers of both species were able to subdue unhealthy or partially disabled insects. In a manner similar to that described by Pricer (1908), the ants usually ingested the liquid portions of the insects before returning to the nest. The head capsules were usually removed and taken to the nest. They were always placed on the refuse pile within two days after they were carried into the nest. Pricer speculated that the head capsules of insect prey contain a preferred nutrient which is reserved for some special member of the colony, or that a special skill is needed to extract the nutrient from the head capsule. The head capsule may be carried back to the nest due to the time required to extract the nutrients present rather than for the purpose of reserving the nutrients present for a special member of the colony. Studies by Fowler and Roberts (1980) and Sanders (1972) indicate that solid foods are apparently not major constituents in the diet of a number of *Camponotus* spp. including *C. pennsylvanicus*. The observations of these authors do not support the belief that some special member of the colony derives a significant amount of its nutrients from the head capsules of insect prey.

Though honeywater was the preferred food throughout most of the study, a notable shift in food preference was observed during this study. Figure 2 shows the feeding preference of *C. pennsylvanicus* before and after this shift. Honeydew has been observed to be a preferred food source for many species of the genus Camponotus (Smith 1965, Gotwald 1968, Pricer 1908). Honeydew is a nitrogen rich food source and may be a more complete food (Auclair 1963, Maurizio 1975). Although the ants used in this study preferred honeywater to most other foods during most of this study, the sudden shift in preference indicates that honeywater did not supply all of the nutrients required for complete colony nutrition. While honeydew usually contains 0.2 to 1.8% nitrogen compounds, 70-90% of which are amino acids (Maurizio 1975, Auclair 1963), honey contains only trace amounts of amino acids (Crane 1980). The shift to artificial honeydew may have been related to a need for foods with a higher nitrogen content during brood production or to meet the nutritional demands of new workers in the colony. Abbott (1978) reported that differential food exchange in several ant genera determines the distribution of carbohydrates, proteins, and lipids among colony members. The continued presence of mature reproductives within the confines of the nest box would place an additional demand for nutrients on the colony and may have contributed to the shift in preference. The events which preceded the shift provide evidence of the possibility of the change in food preference being related to major colony events such as swarming, brood production, or preparation for hibernation during the late fall and winter. Sudden shifts in food preference have been reported in other ant genera by Way (1963). The return to honey feeding may be related to preparation for winter and the higher carbohydrate content of honey. The honey used in this study was slightly diluted with water and the final sugar concentration was between 40 and 43%

sugar while the honeydew which was preferred by the ants contained 10% sugar by weight. The preference of the 10% honeydew over the 0.1% honeydew indicates the ants preference for foods with higher sugar contents. Brian (1973) observed that workers of Myrmica rubra (L.) frequently took no more sugar than was necessary for their own basal metabolism, and that increased supplies of sugar improved the assimilation of protein in this ant.

In general, both C. ferrugineus and C. pennsylvanicus preferred sweet foods as indicated by the decided preference for honey and honeydew with 10% sugar. Few of the household foods used were competitive with honey although some were accepted when no other food was present. The ability to eat some household foods may be important when outdoor food sources are limited or when weather limits outdoor foraging. Rainfall has been shown to be a limiting factor in the foraging activity of C. pennsylvanicus by Fowler and Roberts (1980). Although the data of Ayre (1967) show that C. pennsylvanicus may be able to utilize a range of food sources, it is not known if carpenter ants can successfully rear brood to maturity or maintain proper colony nutrition on a diet composed solely of household foods. A more detailed study will be necessary to determine the contributions of household foods to colony nutrition.

SEASONAL FORAGING PATTERNS OF *CAMPONOTUS PENNSYLVANICUS* IN URBAN HOUSING IN BLACKSBURG, VA

INTRODUCTION

Camponotus pennsylvanicus is a common and important house-infesting ant (Krombein et al. 1979). It is rated as the most destructive carpenter ant species in the U.S. and is the most common member of the genus *Camponotus* in the north Atlantic and Mid-Western states (Wheeler and Wheeler 1963).

Despite the economic importance of *C. pennsylvanicus*, relatively little work has been done on its biology or behavior. The biology of *C. pennsylvanicus* was examined by Pricer (1908) and McCook (1883). Hartwick et al. (1977) and Traniello (1977) examined the role of trail pheromones in worker orientation and recruitment. Sanders (1964, 1972) reported on *C. pennsylvanicus* in his studies of Canadian carpenter ants.

Sanders and Baldwin (1969) and Riordan (1960) examined the use of radioactive isotopes as markers for foraging workers of *Camponotus* spp. The foraging behavior of *C. pennsylvanicus* in New jersey was recently examined by Fowler and Roberts (1980). In their study, the role of the microenvironment on foraging intensity, forager specialization, and forager constancy were examined. Sanders (1972) included a colony of *C. pennsylvanicus* in his study of seasonal and daily activity patterns of *Camponotus* spp. in Ontario, Canada. However, no studies have examined foraging patterns and structure utilization in an urbanized environment.

The purpose of this study was to examine the foraging patterns of *C. pennsylvanicus* in a man-made structure. How the structure was used, worker task constancy, worker subcaste composition, and seasonal changes in foraging intensity were examined.

MATERIALS AND METHODS

One colony of C. pennsylvanicus was selected for detailed study of its foraging patterns in an urbanized environment. The colony was located in a three-unit apartment building in Blacksburg, VA. Each apartment unit contained two bedrooms and a bathroom upstairs; a kitchen, dining area, and living room downstairs. The seasonal foraging patterns of workers were studied from January 1981 to January 1982. Additional observations were made from the end of January 1982 until the end of April 1982.

Bait stations baited with honey were placed in all rooms of each unit for a total of 6 bait stations per apartment. Each station was placed in an area frequented by foraging ants. The number of ants feeding at the bait stations and the number of ants foraging within a room were included in the number of ants counted during a sampling period. Sample counts were taken at least 3 times per week, and a total of 12 samples were taken per month. Each weekly sample included 2 fixed sampling days and at least one randomly selected day. Counts were taken between 6:30 p.m. and 10:00 p.m. Outdoor temperature was recorded each sample time.

Seasonal changes in worker composition were also examined. During each sampling period, workers were visually graded as major, minor, or intermediate workers based on head capsule size and body size. The number of ants belonging to each subcaste was counted, and the task being performed by each was recorded.

Movement within an apartment, between apartments, and outside the apartment building were examined by mark-recapture techniques. Individual workers were marked on the upper surface of the gaster and/or thorax with typewriter correction fluid (Wite-Out Products Inc.). Four colors were used to mark ants captured in different areas. During a sampling period, all marked ants sighted were captured and the location of capture and the task being performed by each was recorded. All recaptured ants were released at the point of capture after the completion of a sampling period.

Pearson product-moment correlations were used to examine the effects of rainfall and outdoor temperature on indoor foraging intensity. Chi square goodness of fit tests were used to examine foraging intensity with respect to month. Worker subcaste composition was examined by analysis of variance.

RESULTS

Foraging workers were present during every month of 1981, although the number of ants observed varied from month to month (Table 3). A total of 1,117 ants were counted during this study. A total of 157 ants were marked. Of the 765 ants which were observed during indoor foraging, 760 (99.5%) were observed in a single apartment. This apartment was determined to be the "focus" apartment due to the extremely low levels of foraging observed in the remaining apartments.

Pearson product-moment correlations indicated that although indoor foraging was independent of rainfall and outdoor temperature during most

Table 3. Monthly totals of ants observed during the study of seasonal foraging behavior.

	Total Foragers Observed		Indoor Subcaste Summary		
Month	Indoors	Outdoors	Major	Intermediate	Minor
January	31	0	0	15	16
February	16	0	0	6	10
March	175	0	24	93	58
April	143	151	10	82	51
May	87	144	4	28	55
June	83	57	3	44	36
July	84	0	0	36	48
August	80	0	3	26	51
September	46	0	0	25	21
October	10	0	1	5	4
November	6	0	0	2	4
December	4	0	0	3	1
TOTALS:	765	352	45	365	355

months, some correlations did exist during some months. Positive correlations between forager intensity and rainfall were observed during the months of April, June, July, and November. A positive correlation between rainfall and the number of foragers present, indicates that as rainfall increased, the number of foragers observed indoors increased. A negative correlation between rainfall and foragers during May indicates that as rainfall increased, the number of ants present decreased. Although no positive correlations were found between foraging intensity and outdoor temperatures, negative correlations were found for these parameters during June and October. A negative correlation between outdoor temperature and foragers indicates that as outdoor temperatures increased, the number of ants observed inside decreased. Pearson product-moment correlation coefficients of indoor foraging and outdoor environmental measures are listed in Table 4.

Observations of outdoor foraging indicate that workers did not forage outdoors on days when it rained. This has been reported by Fowler and Roberts (1980). Outdoor foraging was first observed on April 23, 1981 when 34 foraging workers were seen. The outdoor temperature at the time when the first outdoor foraging was observed was 11.6°C. Outdoor foraging was observed until June 24, 1981. During this time, 352 ants were counted during observations of outdoor foraging. Most of the ants observed outdoors were major and intermediate workers and the number of minor workers appearing outdoors did not increase noticeably until the first aphids appeared on a *Spiraea* sp. shrub located at the corner of the focus apartment. After the appearance of the first aphids (*Aphis spiraecola* Patch) on the *Spiraea*, the

Table 4. Correlation coefficients (Monthly) of Camponotus pennsylvanicus indoor foraging and outdoor environmental measures (ants versus temperature and rainfall).

	Ants (No. Foragers)					
	April	May	June	July	October	November
Temperature (alpha level)	0.37420 (0.2308)	0.43704 (0.124)	-0.61476* (0.0334)	0.00429 (0.9895)	-0.65801* (0.0200)	-0.35616 (0.2558)
Rainfall (alpha level)	0.53200 (0.0750)	-0.64148 (0.246)	0.66601* (0.0181)	0.79360* (0.0021)	-0.31435 (0.3197)	0.70065* (0.0111)

* Coefficients followed by * are statistically significant ($P < 0.05$).

percentage of the minor workers observed during outdoor foraging rose from an average of 33.3% to an average of 63.6% of the total number of foragers counted during each observation period. The Spiraea supported a large population of Aphis spiraecola from May 14 until May 21, 1981. The number of ants observed during outdoor foraging decreased form a total of 129 ants counted between May 5 and May 20, to a total of 64 ants counted between May 21 and June 10, 1981. The aphid population on the Spiraea began to decline on May 21 after several days of rain (1.58 inches) and the decrease in observable foragers was most notable at this time.

Chi square goodness of fit tests indicated that the number of foragers indoors varied significantly with respect to month at the $P < 0.005$ level. The months from March to August were the months during which foraging activity was greatest. March and April were the months during which indoor foraging intensity was greatest during 1981. Although the number of workers in each subcaste also varied significantly with respect to month, no significant differences were noted between intermediate and minor worker composition during the study. Intermediate and minor workers represented 47.7% and 46.4% of the observed indoor foragers, while the major workers represented only 5.9% of the sample during the year. Major workers were seldom seen foraging indoors, and were not observed among the foraging workers until March. Major workers were seen from March through June and then in August and October. The maximum number of major workers (24) foraging indoors was observed in March.

Most of the foraging workers (99%) were observed to forage in the kitchen of the focus apartment during this study. Of the remaining ants, 0.8% were seen in the bathroom, while the other 0.2% were found in rooms adjacent to the bathroom or kitchen. A number of areas in the kitchen appeared to be preferred foraging sites.

Mark-recapture studies indicated that a dishwasher in the kitchen, the trashcan in the kitchen, the kitchen counters, and the kitchen cabinets were preferred foraging sites. One group of 14 minor and intermediate workers maintained a temporary 'resting' site in a box of confectioner's sugar for 2 weeks. These workers participated in foraging with other workers and mixed with the population of 64 workers which frequented the dishwasher. Trashcan foragers and floor foragers dis not exhibit any extremes of preference and appeared to mix freely with the 'dishwasher' population. During the periods of outdoor foraging, the 'floor' and 'trashcan' foragers were the first to appear outdoors. All of these foragers were intermediate workers. The dishwasher foragers exhibited the greatest foraging site fidelity with 87.6% of the recaptured workers found foraging in the same area during the study. Cabinet foragers, composed largely of workers from the confectioner's sugar rest site, exhibited a foraging site fidelity of 74.2%. Trashcan and floor foragers had the lowest level of foraging site fidelity and 58.0% were recaptured while foraging in the same area.

Throughout the study, few ants were observed to carry solid matter. Only 12 ants were found attempting to carry solid food particles back to the nest. One ant was observed attempting to tear a piece off one leaf of celery for 35 minutes, while most of the others carried crumbs which they had removed from the kitchen counter top. Although food particles were often available in the kitchen sink, the ants were never observed to eat any of the food or to attempt to carry any of it back to the nest. Most of the foods eaten by the ants appeared to be liquids. The ants were observed feeding on ice cream drippings, honey, soda, and sugar sweetened beverages such as tea.

The residents of the focus apartment moved out of their apartment in mid-April 1982. Several days after they moved, the residents of the apartment next to the focus apartment (adjacent apartment), began to notice foraging worker ants in their apartment. In 10 observation periods performed after the focus apartment was vacated, 69 ants were counted during the remainder of April. The number of ants counted during May rose to 274 in the adjacent apartment. Five marked ants were among those counted in the adjacent apartment after the tenants of the focus apartment moved, indicating that the ants will readily shift foraging areas. Only 8 ants were observed in the focus apartment from the date the ants began to appear in the adjacent apartment until the end of May. Most of the foraging activity was confined to the kitchen with the exception of a few workers appearing in the bathroom upstairs. The residents of the third apartment also reported that the number of ants observed in their apartment increased, although this number was small (4 per week).

DISCUSSION

When compared with other studies of the seasonal foraging behavior of *C. pennsylvanicus*, the results of this study demonstrate the adaptability of this ant. The studies of Fowler and Roberts (1980) and Sanders (1972) indicate that there is an apparent lack of correlation between foraging intensity and temperature. Sanders (1972) observed that the start of seasonal activity apparently depended on temperature, but that cessation of activity in the fall occured before threshold temperatures were reached again, indicating that cessation of activity was regulated by some other factor. Temperature did not appear to be the definitive regulating factor during this study, but several interesting correlations were found between foraging intensity and temperature.

During June, there was a significant negative correlation between foraging and temperature. As outdoor temperatures increased, the number of ants foraging indoors decreased. This relationship is probably due to the increased outdoor foraging which was observed from April through June. As shown by the mark-recapture portion of the study, foraging workers do not limit their foraging activities to the indoors. A negative temperature-foraging correlation was also observed during October, although the reduction in the number of indoor foragers cannot be attributed to outdoor foraging. As noted by Sanders (1972), the cessation of fall foraging activities is probably due to some factor other than temperature. Although the ants continued to forage at low levels during the fall and winter months, the levels of foraging were probably too low to support most members of the colony. Low level foraging may be attributable to the absence of actively growing larvae during the fall and winter months. The larvae of Camponotus spp. usually enter a first-instar "resting stage" (Pricer 1908, Holldobler 1961, Mintzer 1979), thus the colony would not require high levels of food. Low level foraging year-round indicates an adaptation by workers of this species and is probably best explained by the nutritional needs of the adult members of the colony.

Fowler and Roberts (1980) noted that C. pennsylvanicus did not exhibit any visible foraging activity on days when it rained, and that rainfall was apparently a limiting factor on foraging activity. The results of this study suggest that C. pennsylvanicus may alter its behavior patterns to allow it to more adequately use man-made structures. During most months when statistical significance was shown, there was a positive correlation between rainfall and indoor foraging intensity. This indicates that when rainfall limits outdoor foraging activity, the ants increase indoor foraging to ensure or supplement colony nutrition during months when the colony contains growing larvae and reproductives.

C. pennsylvanicus has been reported to tend aphids (Pricer 1908, Smith 1965, Fowler and Roberts 1980). Although the colony of C. pennsylvanicus observed during this study was adapted to a man-made structure, the ants exhibited a preference for honeydew. The number of foraging workers tending aphids on the Spiraea shrub outside the focus apartment increased rapidly once the aphids had been located by the first workers. The relative number of workers feeding on honeydew and foraging outdoors grew rapidly from April to June and is indicative of the importance of honeydew in the diet of these ants. As in the studies of Sanders (1972) and Fowler and Roberts (1980), few ants (1.57%) were observed to carry solid objects back to the nest, thus indicating the lack of importance of solid matter in colony nutrition. Most of the observations of feeding ants indicated that C. pennsylvanicus prefers sweet foods as has been reported by Pricer (1908) and Smith (1965).

Although there was no significant subcaste variation with respect to the proportion of intermediate workers to minor workers, the proportion of major workers participating in foraging was minimal. Pricer (1908) noted the lack of major worker involvement in foraging activities and concluded that the major workers were "housekeepers" for the colony. The number of major workers participating in foraging increased noticeably during the spring but most did not appear to be very active in foraging. As observed by Pricer (1908) and Fowler and Roberts (1980), the major workers appeared to act as "transporters" for the honeydew which the smaller workers collected from aphids on the Spiraea shrub. A waiting station was established at one of the entrances used by the ants in their return to the building, and the larger workers waited in this area until a foraging worker returned to the station. Upon reaching the station the smaller worker was approached by a larger worker and the two ants would then exchange food. The larger worker would then return to the station until another gorged worker appeared. The smaller worker would usually leave the station and then return to the Spiraea to collect more honeydew.

Task constancy in Camponotus has been reported by Fowler and Roberts (1980). Task constancy, as evidenced by foraging site fidelity, was also observed in this study. The data of Traniello (1977) suggest that older workers become task constant, and orient to their sites of activity by visual cues, while younger workers comprise a recruitment force. The floor and trashcan foragers of this study probably correspond to the ground foragers noted in the study of Fowler and Roberts (1980) as indicated by the relatively lower level of task fidelity.

Most of the foraging workers were observed in one apartment. Of the 765 ants observed during indoor foraging, 760 (99.5%) were observed in the focus apartment. Although some movement between apartments was observed, the low level of movement indicates that foraging workers hunt in restricted areas of their potential hunting area. Levieux (1971) reported that workers of Camponotus acvapimensis and C. congolensis prospect about 10% of their potential hunting area and that workers of C. acvapimensis can hunt within a radius of twelve meters around the nest.

C. pennsylvanicus appears to have developed a number of important adaptations to man-made structures. The results of this study show that although house-infesting colonies of C. pennsylvanicus retain a number of behaviors observed in naturally occuring colonies, they have adapted to man-made structures in a way which probably enhances their success. They are not restricted to indoor foraging or outdoor foraging and can maintain some level of activity throughout the year. Further study will be required to adequately determine the extent of the adaptation to man-made structures by this ant.

DIVISION OF LABOR AMONG WORKERS OF *CAMPONOTUS PENNSYLVANICUS* AND *C. FERRUGINEUS* (HYMENOPTERA: FORMICIDAE)

INTRODUCTION

The genus *Camponotus* is the largest and one of the most important living ant genera (Brown 1973). All ants in this genus are commonly called carpenter ants because of their habit of nesting in wood (Krombein et al. 1979). Eight subgenera, including the most important subgenus, *Camponotus*, are found in the U.S. (Smith 1947). The nest forming activities of carpenter ants can cause considerable damage to structural timber and standing trees (Graham 1918, Friend and Carlson 1937, Dennis 1938), yet little is known about their nest-forming behavior.

Polymorphism in ants has been examined by Wilson (1953, 1971) and Smith (1942). The genus *Camponotus* is characterized by a polymorphic worker caste, consisting of major, minor, and intermediate workers. Fowler and Roberts (1980) examined the role of subcaste variation in the foraging behavior of workers of *C. pennsylvanicus*. In their study, Fowler and Roberts found that minor workers showed significantly greater task fidelity than major workers. Traniello (1977) briefly examined the role of worker age in foraging. Sanders (1964) has examined polymorphism in *C. herculeanus* and Gotwald (1968) examined the role of worker size in the food gathering behavior of *C. noveboracensis*. No studies have addressed the role of polymorphism in the nest-forming activities of these wood-nesting ants.

The purpose of this study was to examine the role of polymorphism in the nest-forming activities of carpenter ants. Two species of the subgenus *Camponotus*: *C. pennsylvanicus* and *C. ferrugineus*, were examined for a division of labor during nest-forming activities.

MATERIALS AND METHODS

Workers from 1 laboratory colony each, of *C. pennyslvanicus* and *C. ferrugineus*, were used in this study. Workers of the major and minor subcastes were visually differentiated and selected for use in the study. The ages of the colonies of *C. pennsylvanicus* and *C. ferrugineus* were estimated to be 3 years and 6 (or more) years, respectively. Individual workers were selected at random with the aid of a table of random numbers. Forty workers of each subcaste were selected from each colony for a total sample of 80 workers per colony.

The head capsule of each worker was removed and the width across the occiput and the height of the head (excluding the mandibles) were measured with an ocular micrometer (Figure 3). These measurements were used to calculate a cephalic index according to the formula, CI= head width across the occiput x 100/ head height. The mandibles of each worker were removed and the amount of mandible wear was graded according to the scale 1, 3, 5, or 7, where a grade of 1 demonstrates no noticeable wear. Figures 4 through 5 show the wear patterns associated with each grade of mandible wear.

Tests for correlation between cephalic index and mindible wear were used to examine the division of labor among worker subcastes during next forming activities. High levels of mandible wear were considered an indication of extensive woodworking activities.

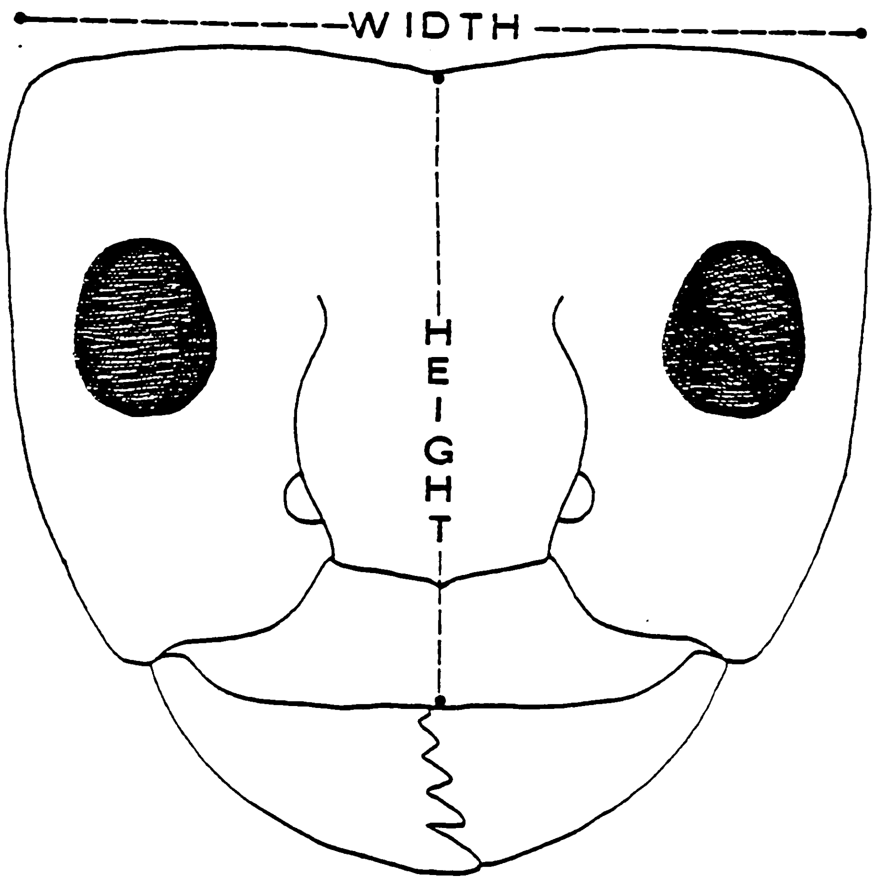

Figure 3. Measurements used for calculation of the cephalic index

Table 5. Legend for Figures 4 and 5. (Photographs of the mandible wear patterns associated with the mandible wear grades 1, 3, 5, and 7.)

Figure Code	Subcaste	Mandible Wear Grade
A	Minor	1
B	Minor	1
C	Minor	3
D	Minor	3
E	Minor	3 (range)
F	Minor	5 (range)
G	Minor	7 (range)
H	Major	1
I	Major	3
J	Major	3
K	Major	5
L	Major	5
M	Major	7
N	Major	7

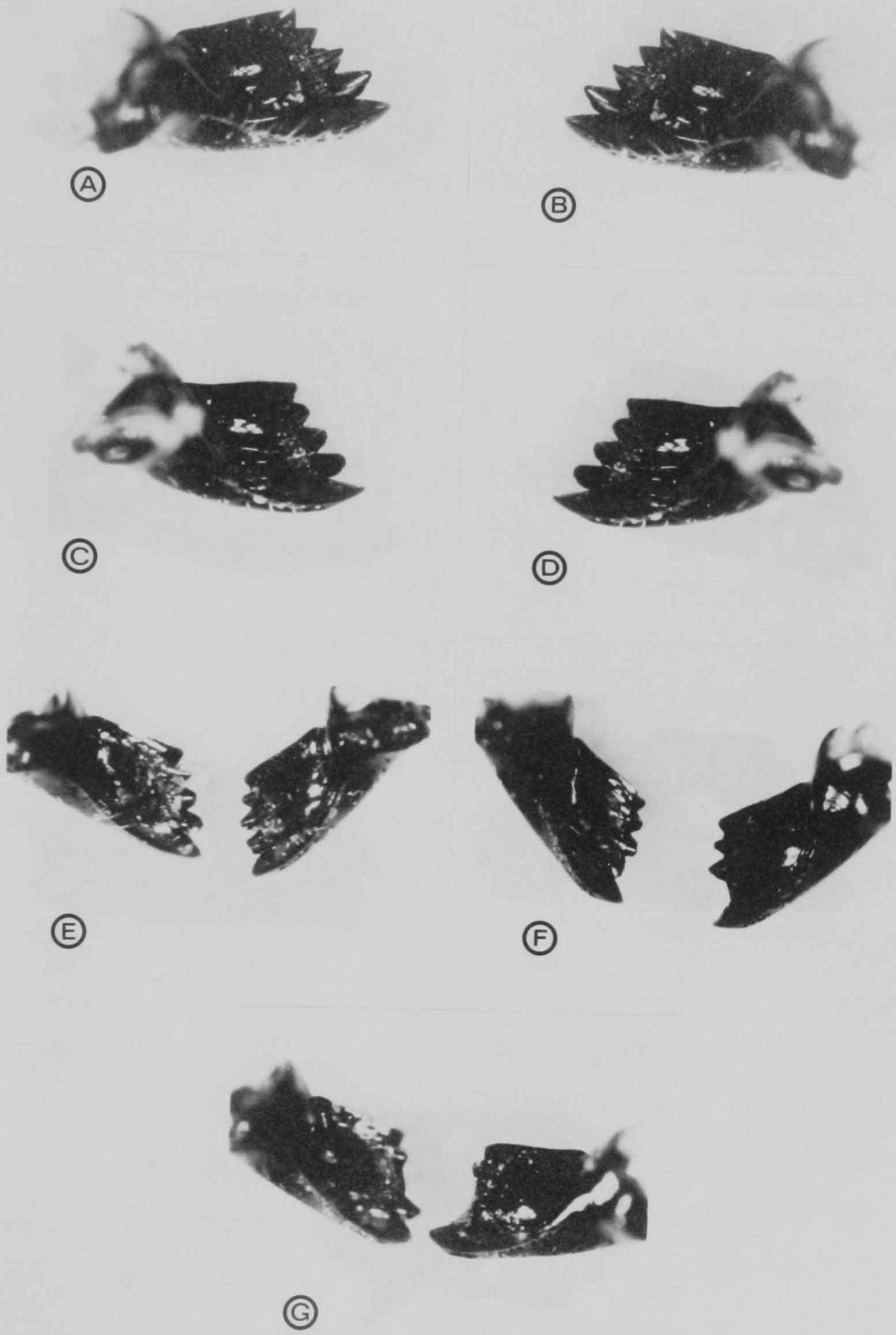

Figure 4. Photograph of mandible wear patterns (Minor workers).

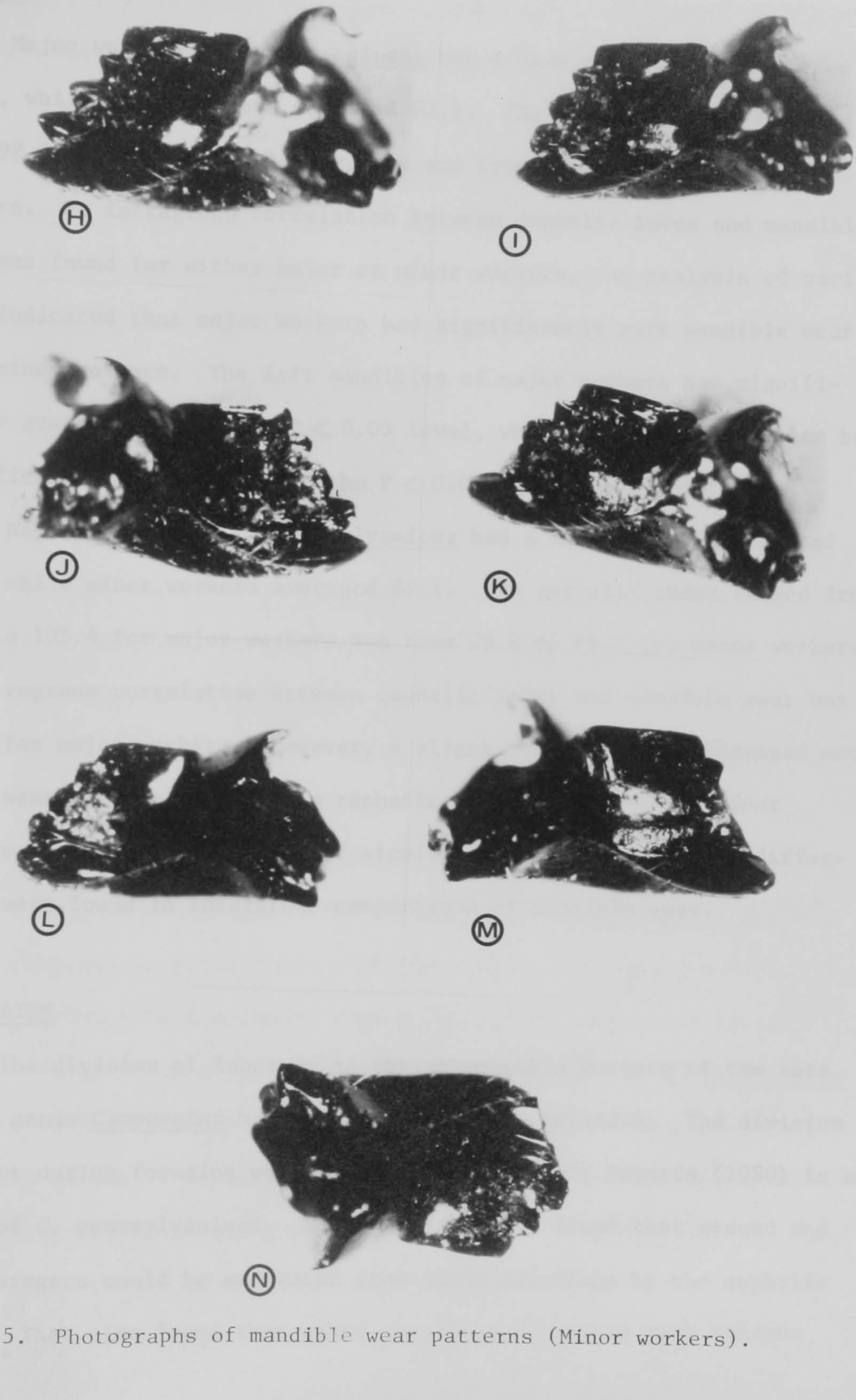

Figure 5. Photographs of mandible wear patterns (Minor workers).

RESULTS

Major workers of *C. ferrugineus* had a mean cephalic index of 106.9, while minor workers averaged 83.6. The cephalic index ranged from 97.0 to 126.4 for major workers and from 77.0 to 90.7 for minor workers. No intragroup correlation between cephalic index and mandible wear was found for either major or minor workers. An analysis of variance indicated that major workers had significantly more mandible wear than minor workers. The left mandibles of major workers had significantly greater wear at the $P < 0.05$ level, while the right mandibles had significantly greater wear at the $P < 0.001$ level of significance.

Major workers of *C. pennsylvanicus* had a mean cephalic index of 99.2, while minor workers averaged 84.1. The cephalic index ranged from 94.2 to 105.4 for major workers and from 79.0 to 89.7 for minor workers. No intragroup correlation between cephalic index and mandible wear was found for major workers. However, a slight trend towards increased mandible wear with an increase in cephalic index was found for minor workers at the $P < 0.10$ level of significance. No significant differences were found in intergroup comparisons of mandible wear.

DISCUSSION

The division of labor among the polymorphic workers of the ants of the genus *Camponotus* has been an area of speculation. The division of labor during foraging was examined by Fowler and Roberts (1980) in a study of C. pennsylvanicus. Fowler and Roberts found that ground and tree foragers could be separated from aphid guardians by the cephalic index. They also found that aphid guardians exhibited much greater task fidelity than ground foragers. Pricer (1908) indicated that the smallest and largest workers were housekeepers, and that the largest workers seemed to take no part in the work of gathering food for the colony. Pricer further speculated that the largest workers in the colony might be the true carpenter ants due to the immense mandibles of the major workers. Sanders (1964) reported that minor workers of C. herculeanus were associated with the larvae to a greater extent than were the major workers. The significant difference between mandible wear in the major and minor workers of C. ferrugineus examined in this study supports the possibility of a division of labor during nest construction based on worker size. However, the data provided by the examination of C. pennsylvanicus indicates the need to examine a number of important factors before conclusions can be made.

The colony of C. pennsylvanicus used in this study was a small colony relative to the size of the colony of C. ferrugineus. The colony of C. pennsylvanicus contained approximately 215 ants and the partial colony of C. ferrugineus, contained approximately 850 workers and 49 reproductive females. The colony of C. pennsylvanicus did not contain any reproductive forms with the exception of the founding queen. Although both colonies were in wood, the difference in the relative stage of decay was significant. The colony of C. ferrugineus was in wood that was dry and sound, having a moisture content between 14 and 18 percent. The moisture content of this wood was measured with a hand-held moisture meter. The colony of C. pennsylvanicus was in oak which was in an advanced stage of decay. The colony of C. ferrugineus had formed extensive galleries in the wood in which they lived, while the colony of C. pennsylvanicus had not yet begun to form extensive galleries, although some new galleries had been formed. According to Pricer's (1908) collections of natural colonies of C. pennsylvanicus and C. ferrugineus, the colonies used in this study were approximately 3 years old and 6 (or more) years old, respectively. The time required for a complete division of labor among worker subcastes with respect to nest construction activities, may require longer than three years to become evident. Additionally, the length of time required for mandible wear to become visually determinable may be longer when the wood is in a more advanced stage of decay.

Although the trend towards an increase in mandible wear as the size of the head increased among minor workers of C. pennsylvanicus was not statistically significant at a high level of confidence, it does provide evidence of the overlap in the duties of the workers. Pricer (1908) found that the first workers produced by the founding queen of C. pennsylvanicus all belong to the minor subcaste. He also reported that major workers are probably not produced until after the colony is 3 years old or older. Therefore, until the third year or later, colony enlargement would necessarily be performed by workers of a subcaste other than the major subcaste. The colony of C. pennsylvanicus which was used for this study was a relatively young colony with few major workers and little difference between the largest and the smallest workers in the colony. The largest workers in the colony were probably among the youngest of the workers in the colony, and would not exhibit signs of extreme mandible wear even if the major workers were responsible for all nest enlargement.

The work of Fowler and Roberts (1980), Traniello (1977) Gotwald (1968), Sanders (1964), and Pricer (1908) provide evidence that a division of labor according to subcaste does occur in the genus Camponotus. However, the work of these authors does not address the possibility of division of labor during nest-construction activities. The data presented in this study suggest that a division of labor based on subcaste, may exist during nest-building activities as well as during foraging. The determination of the existence of such a division of labor may be of considerable importance to persons engaged in the control of house-infesting carpenter ants. Further study is necessary to extend the usefulness of the data presented here.

CONCLUSIONS

Colony founding in *C. ferrugineus*

Colony founding in *C. ferrugineus* is similar to colony founding in *C. pennsylvanicus*. Although the time of development might be increased under more natural conditions, the developmental time for the first brood was 54 days. Egg eating was not observed in this study, but 12 eggs were presumed to have been eaten. Egg disappearance coincided with the period of rapid growth exhibited by the first larvae to hatch and with the emergence of the first adult worker. Thus egg disappearance may be better explained if attributed to egg eating by the larvae rather than to egg eating by the queen. Workers of the intermediate subcaste may be produced in the first brood.

Colony Founding in *C. pennsylvanicus*

Queens of *C. pennsylvanicus* can be induced to rear their first brood under artificial light although some difficulties may be encountered. Ad libitum feeding had no effect on the number of eggs presumed to have been eaten or the duration of the immature stages. The queens observed in this study required considerably fewer days to produce the first workers (20 fewer) than the queen observed in the study of Pricer (1908). Differences in laboratory rearing conditions may have contributed to the observed differences.

Economic Importance of Carpenter Ants

Carpenter ants are considered a serious problem by homeowners. Although a low damage-association value was apparent, customers were willing to pay considerable amounts of money for carpenter ant control, even in the absence of detectable damage. Most pest control operators did not devote a large percentage of their business to carpenter ant control, but the majority of pest control operators in this sample performed some carpenter ant control jobs in 1980. Carpenter ant infestations were most often associated with houses older than 10 years old, but a significant number of pest control operators indicated that newer houses were also infested. The trend towards more infestations associated with newer houses will probably continue to grow as more houses are built in suburban areas.

Food Preference Studies In *C. pennsylvanicus* and *C. ferrugineus*

Both *C. pennsylvanicus* and *C. ferrugineus* preferred sweet foods during this study. Although both species ate all insects that were given to them, neither species was effective at subduing healthy insects. Their relative ineffectiveness against healthy insects indicates that neither *C. pennsylvanicus* nor *C. ferrugineus* are important predators under natural conditions. A shift in food preference during the study indicated that although honey was preferred to other foods during most of the study, it apparently did not supply all the necessary nutrients for proper colony nutrition. The shift in food preference was particularly obvious before colony reproduction (swarming). These ants will eat household foods, but it is doubtful that household foods compete effectively with natural foods such as honeydew.

Seasonal Foraging Patterns of C. pennsylvanicus in Urban Housing

House-infesting colonies of C. pennsylvanicus have developed a series of adaptations to man-made structures which allow them to exploit both the outdoor and indoor foraging areas of their habitat. Though some foraging workers are present year-round, foraging intensity decreases during the fall and this decrease in activity appears to be related to some parameter other than temperature.

Division of Labor Among Workers of C. ferrugineus and C. pennsylvanicus

Fowler and Roberts (1980), Traniello (1977), and Gotwald (1968), have provided evidence that division of labor according to subcaste occurs in the genus Camponotus. A division of labor may also occur during nest construction. The data indicate that a division of labor during nest construction may develop as a colony approaches maturity, but that overlap of duties may exist in younger colonies. The major workers appear to be the true carpenters in the colony, perhaps as shown by the excessive mandible wear exhibited by the major workers of C. ferrugineus. The data also suggest that the larger workers of the minor subcaste may be responsible for nest construction until the intermediate and major workers are produced.

LITERATURE CITED

Abbott, A. 1978. Nutrient dynamics of ants. In: M.V. Brian, editor. Production ecology of ants and termites. Cambridge University Press. Cambridge, London, New York, Melbourne. pp 233-244.

Akre, R.D. and A.L. Antonelli. 1976. Carpenter ants, their biology and control. Washington State University, Cooperative Extension Service. EM 4040. 3 pp.

Ascerno, M.E. 1981. Diagnostic clinics: more than a public service. Bull. Entomol. Soc. Amer. 27: 97-101.

Auclair, J.L. 1963. Aphid feeding and nutrition. Annual Rev. Entomol. 8: 439-490.

Ayre, G.L. 1963. Laboratory studies on the feeding habits of seven species of ants (Hymenoptera: Formicidae) in Ontario. Can. Entomol. 95: 712-715.

__________. 1967. Enzymes in five species of ants (Hymenoptera: Formicidae). Can. Entomol. 99: 408-411.

Barlin, M.R., M.S. Blum and J.M. Brand. 1976. Species specificity studies on the trail pheromone of the carpenter ant *Camponotus pennsylvanicus*. J. Ga. Entomol. Soc. 11: 157-162.

Barrows, E.O. 1980. Results of a survey of damage caused by the carpenter bee *Xylocopa virginica* (Hymenoptera: Anthophoridae). Proc. Entomol. Soc. Wash. 82: 44-47.

Bhaktar, A.P. and W.H. Whitcomb. 1975. Rearing arboreal ants in glass tubing. Fla. Entomol. 58: 58-63.

Brand, J.M., R.M. Duffield, J.G. MacConnell, and M.S. Blum. 1973. Caste-specific compounds in male carpenter ants. Science 179: 388-389.

Brian, M.V. 1973. Feeding and growth in the ant Myrmica. J. Anim. Ecol. 42: 37-53.

__________. 1978. Production ecology of ants and termites. Cambridge University Press. Cambridge, London, New York, Melbourne. 409 pp.

Brown, W.L. 1950. The status of two common North American carpenter ants. Entomol. News 61: 157-160.

__________. 1973. A Comparison of the Hylean and Congo-West African Rain Forest Ant Faunas. In: B.J. Meggers, E.S. Ayensu, and B.J. Duckworth, editors. Tropical Forest Ecosystems in Africa and South America. pp. 161-185.

Carney, W.P. 1969. Behavioral and morphological changes in carpenter ants harboring Dicrocoeliid metacercariae. Amer. Midland Nat. 82: 605-610.

__________. 1970. Laboratory maintenance of carpenter ants. Ann. Entomol. Soc. Amer. 63: 332-334.

Chauvin, R. 1970. The world of ants, translated by G. Ordish. Hill and Wang. New York. 216 pp.

Crane, E. 1980. A book of honey. Charles Scribner's sons. New York. 193 pp.

Creighton, W.S. 1950. The ants of North America. Harvard Univ. Mus. Comp. Zool. Bull. 104: 1-585.

Dennis, C.A. 1938. The distribution of ant species in Tennessee with reference to ecological factors. Ann. Entomol. Soc. Amer. 31: 267-308.

Dumpert, K. 1978. The social biology of ants. Pitman Publishing Inc. Marshfield, Massachusetts. 298 pp.

Emery, C. 1920. Le genre Camponotus Mayr, nouvel essai de sa subdivision en sous genres. Rev. Zool. Afr. 8: 16-19.

__________. 1925. Formicinae. In: Wytsman, editor. Genera Insectorum, Fasc. 183. 302 pp.

Forbes, J. and A.M. McFarlane. 1961. The comparative anatomy of digestive glands in the female castes and the male of Camponotus pennsylvanicus DeGeer. N.Y. Ent. Soc. Jour. 69: 92-103.

Fowler, H.G. and R.B. Roberts. 1980. Foraging behavior of the carpenter ant Camponotus pennsylvanicus, (Hymenoptera: Formicidae) in New Jersey. J. Kansas Entomol. Soc. 53: 295-304.

Friend, R.B. and A.B. Carlson. 1937. The control of ants in telephone poles. Bull. Conn. Agric. Exp. Sta. 403: 913-929.

Glancey, M.B., C.E. Stringer, and P.M. Bishop. 1973. Trophic egg production in the imported fire ant, Solenopsis invicta. J. Ga. Entomol. Soc. 8: 217-220.

Gotwald, W.H., Jr. 1968. Food gathering behavior of the ant, Camponotus noveboracensis (Fitch). J. N.Y. Entomol. Soc. 76: 278-296.

Goulding, R.L. and J. Capizzi. 1976. Carpenter ant control. Oregon State University, Extension Service. Circ. 627. 6 pp.

Graham, S.A. 1918. The carpenter ant as a destroyer of sound wood. Minn. State Ent. Rpt. 17: 32-40.

Gregg, R.E. 1944. The ants of the Chicago region. Ann. Entomol. Soc. Amer. 37: 447-480.

Hartwick, E.B., W.G. Friend, and C.E. Atwood. 1977. Trail laying behavior of the carpenter ant Camponotus pennsylvanicus. Can. Entomol. 109: 129-136.

Hölldobler, B. 1961. Temperaturabhängige rhythmische erscheinungen bei rossameisenkolonien (Camponotus ligniperda Latr. und Camponotus herculeanus L.). (Hymenoptera: Formicidae). Insectes sociaux 8: 13-22.

Krombein, K.V., P.D. Hurd, Jr., D.R. Smith, and B.D. Burks. 1979. Catalog of the Hymenoptera in America north of Mexico, Vol. 2. Smithsonian Institution Press. Washington D.C. 1010 pp.

Levieux, J. 1971. Mise en évidence de la structure des nids et de l'implantation des zones de chasse de deux espèces de Camponotus (Hym. Form) a l'aide de radio-isotopes. Insectes sociaux 18: 29-48.

Liebherr, J. 1976. Wood damaging insects in the home. Michigan State University, Cooperative Extension Service. E-497. 8 pp.

Markl, H. and S. Fuchs. 1972. Alarm by rapping in carpenter ants (Camponotus: hymenoptera: Formicidae). Z. Vergl. Physiol. 76: 204-225.

Maurizio, A. 1975. How bees make honey. In: Eva Crane, editor. Honey, a comprehensive survey. Crane, Russack and Co., Inc. New York. pp. 77-105.

McCook, H.C. 1883. How a carpenter ant queen founds a formicary. Proc. Acad. Nat. Sci. Phila. 35: 303-307.

Mintzer, A. 1979. Colony foundation and plemetrosis in Camponotus (Hymenoptera: Formicidae). Pan-Pac. Entomol. 55: 81-89.

Myers, J.H. and B.H. Campbell. 1976. Predation by carpenter ants: a deterrent to the spread of Cinnabar moth. J. Entomol. Soc. Brit. Columbia 73: 7-9.

Pinto, L.J. 1981. The structural pest control industry: description and impact on the nation. National Pest Control Association, Inc. Vienna, VA. 36 pp.

Pricer, J.L. 1908. The life history of the carpenter ant. Biol. Bull. 14: 177-218.

Riordan, D.F. 1960. The location of nests of carpenter ants (Camponotus spp.) by means of a radioactive isotope. Insectes sociaux 7: 353-355.

Robinson, W.H. 1980a. Extension agents knowledge of wood-infesting insect pests. Melsheimer Entomol. Ser. 29: 28-34.

__________. 1980b. Homeowner knowledge of wood-infesting insects. Melsheimer Entomol. Ser. 29: 48-52.

Ross, H., G. Rotramel, and W. LaBerge. 1971. A synopsis of common and economic Illinois ants, with keys to genera (Hymenoptera: Formicidae). Illinois Natural History Survey. Urbana, Illinois. 22 pp.

Sanders, C.J. 1964. The biology of carpenter ants in New Brunswick. Can. Entomol. 96: 894-909.

__________. 1970. The distribution of carpenter ant colonies in the spruce-fir forests of northwestern Ontario. Ecology 51: 865-873.

__________. 1972. Seasonal and daily activity patterns of carpenter ants (Camponotus spp.) in northwestern Ontario. Can. Entomol. 104: 1681-1687.

Sanders, C.J. and W.F. Baldwin. 1969. Iridium-192 as a tag for carpenter ants of the genus Camponotus (Hymenoptera: Formicidae). Can. Entomol. 101: 416-418.

Smith, F. 1942. Polymorphism in Camponotus. Tenn. Acad. Sci. Jour. 17: 367-373.

Smith, M.R. 1947. A generic and subgeneric synopsis of the United States ants, based on the workers. Amer. Museum of Natural History Bull. 45: 631-710.

__________. 1965. House-infesting ants of the eastern United States: Their recognition, biology, and economic importance. U.S. Dept. Agr. Tech. Bull. 1326. 105 pp.

Traniello, F.A. 1977. Recruitment behavior, orientation and the organization of foraging in the carpenter ant Camponotus pennsylvanicus Degeer (Hymenoptera: Formicidae). Behav. Ecol. Sociobiol. 2: 61-79.

Truman, L.C., G.W. Bennett, and W.L. Butts. 1976. Scientific guide to pest control operations, third edition. Harvest Publishing Company. Cleveland, Ohio. 276 pp.

Van Pelt, A.F., Jr. 1958. Parasitism of Camponotus pennsylvanicus by a fungus. Tenn. Acad. Sci. Jour. 33: 120-122.

Voss, S.H. 1981. Trophic egg production in virgin fire ant queens. J. Ga. Entomol. Soc. 16: 437-440.

Way, M.J. 1963. Mutualism between ants and honeydew-producing Homoptera. Annu. Rev. Entomol. 8: 307-344.

Wheeler, W.M. 1910. The North American ants of the genus Camponotus Mayr. N.Y. Acad. Sci. Ann. 20: 295-354.

Wheeler, G.C. and J. Wheeler. 1953. The ants of North Dakota. University of North Dakota Press. Grand Forks, North Dakota. 326 pp.

Wilson, E.O. 1953. The origin and evolution of polymorphism in ants. Quart. Rev. Biol. 28: 136-156.

__________. 1971. The insect societies. Belknap/Harvard Univ. Press. Cambridge, Massachusetts. 548 pp.

APPENDIX I

SUMMARY OF FIRST BROOD DEVELOPMENT IN *Camponotus ferrugineus*

Queen collected in Blacksburg, VA: 13-V-81

Date	Number of Eggs Laid	Number of Larvae Hatched	Number of Pupae Formed	Number of New workers
16-V-81	2	--	--	--
17-V-81	2	--	--	--
19-V-81	3	--	--	--
23-V-81	2	--	--	--
24-V-81	1	--	--	--
25-V-81	2	--	--	--
26-V-81	2	--	--	--
28-V-81	1	--	--	--
30-V-81	2	--	--	--
1-VI-81	2	--	--	--
2-VI-81	1	--	--	--
4-VI-81	2	--	--	--
11-VI-81	-	6	--	--
12-VI-81	2	--	--	--
13-VI-81	-	3	--	--
14-VI-81	1	3	--	--
15-VI-81	-	2	--	--
16-VI-81	-	2	--	--
17-VI-81	-	--	--	--
18-VI-81	-	--	2	--
19-VI-81	-	--	2	--
20-VI-81	-	--	1	--
21-VI-81	-	--	2	--
22-VI-81	-	--	--	--
23-VI-81	-	1	2	--
24-VI-81	1	--	1	--
25-VI-81	2	--	1	--
27-VI-81	-	--	2	--
28-VI-81	-	--	2	--
29-VI-81	1	--	3	--
5-VII-81	2	--	--	--
6-VII-81	-	--	--	--
8-VII-81	-	--	--	1
9-VII-81	-	--	--	--
10-VII-81	-	--	1	--
12-VII-81	-	--	--	2
13-VII-81	-	--	--	2
15-VII-81	-	2	--	1
17-VII-81	-	--	--	2
18-VII-81	-	--	--	3

Date	Number of Eggs Laid	Number of Larvae Hatched	Number of Pupae Formed	Number of New Workers
19-VII-81	-	--	--	4
21-VII-81	-	--	--	1
24-VII-81	-	--	--	1
31-VII-81	-	--	--	1
TOTALS	31	19	19	18

ADDITIONAL EGGS AND LARVAE APPEARED AS FOLLOWS:

9-VIII-81	1	--
11-VIII-81	2	--
13-VIII-81	2	--
15-VIII-81	3	--
2-IX-81	-	1*
5-IX-81	-	1*
6-IX-81	-	2*
8-IX-81	-	2*
9-IX-81	-	2*

* These larvae remained in the first instar and did not resume normal growth during this study.

SUMMARY:

Number of eggs eaten: 12
First egg to first larvae: 26 days
First larvae to first pupae: 7 days
Total number of workers in the first brood: 18
Number of days from first egg to first worker: 54 days

VITA

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ASPECTS OF THE BIOLOGY, BEHAVIOR, AND ECONOMIC IMPORTANCE OF CAMPONOTUS PENNSYLVANICUS (DEGEER) AND CAMPONOTUS FERRUGINEUS (FABRICIUS) (HYMENOPTERA: FORMICIDAE)

by

John Dukes, III

(ABSTRACT)

Aspects of the behavior, biology, and economic importance of carpenter ants were examined. The overall objectives of this study were to determine the economic importance of carpenter ants, and to extend the data currently available on two of the most common and economically important species in the U.S.

A survey for the economic importance of carpenter ants indicated that carpenter ants are considered a serious pest by homeowners. The results show that 90% of the homeowners who requested control for carpenter ants during 1980, paid more than $25 for carpenter ant control. The presence of detectable damage was not the definitive factor in the decision to request control.

Camponotus ferrugineus and C. pennsylvanicus are similar in their colony foundation and biology. C. ferrugineus required 54 days to produce the first brood and there were 18 workers, including one intermediate worker, in the first brood. Queens of C. pennsylvanicus required an average of 46 days to rear the first brood. Ad libitum feeding did not have a significant effect on colony founding in C. pennsylvanicus. Two queens reared their first brood under artificial

light.

Food preference studies of _C_. _pennsylvanicus_ and _C_. _ferrugineus_ indicated that these two species have similar food preferences. Although honey was preferred to most foods tested, it may not supply sufficient nutrients to ensure proper colony nutrition.

_C_. _pennsylvanicus_ has become well adapted to man-made structures. Some foraging ants are present year round. _C_. _pennsylvanicus_ optimizes its foraging by exploiting indoor and outdoor foraging sites.

The division of labor during nest construction may be based on subcaste. Major workers appear to be responsible for most nest-building in mature colonies.