

NESTING AND FORAGING CHARACTERISTICS OF THE BLACK
CARPENTER ANT *Camponotus pennsylvanicus* DeGeer
(HYMENOPTERA: FORMICIDAE)

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by
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ABSTRACT

Potential nesting sites of *Camponotus pennsylvanicus* (DeGeer) were investigated in South Carolina to determine if nesting sites features could be characterized by habitat features for black carpenter ant nests. Environmental data from forested plots showed large-scale habitat features such as vegetation density and canopy cover were not useful as indicators for the presence or absence of nests. Small-scale individual nest characteristics such as diameter at breast height of trees, log length, tree defect type or tree species were better indicators of occupied nests. In my study, *C. pennsylvanicus* preferred mature hardwood (*Quercus* spp.) trees approximately 30 cm in diameter and pine logs (*Pinus* spp.) that were approximately 9 m in length. Defects in trees most often associated with nests included tree holes and crotches.

Temperature regulation in nests of *C. pennsylvanicus* is not well understood. Prior studies reported nest temperature passively reflects ambient temperature during winter months. Because *C. pennsylvanicus* inhabits wood, it should benefit from the thermal insulating and buffering properties offered by this unique microhabitat.

To evaluate internal compared to ambient temperature in occupied and unoccupied nests, ten *C. pennsylvanicus* nests were identified in trees on the Clemson University campus. Five of the trees containing *C. pennsylvanicus* nests were injected with a foam containing the non-repellent insecticide Termidor[®], containing the active ingredient fipronil, to induce colony mortality. Nest galleries were located using a microwave emitting detector and a digital infrared camera. HOBO[®] H8 Temp / RH / 2x external channel data loggers were used to record ambient and internal nest temperature

hourly over 52 wks. Comparison of ambient and internal temperature ranges within nest type were significantly different. Ambient temperature range of occupied and unoccupied nests fluctuated approximately 10°C while internal temperature fluctuation was less, around 2°C. Internal nest temperature of occupied nests mirrored unoccupied nests throughout the year and were not statistically significant. These results indicate that internal nest temperature does not fluctuate over as wide a range as does ambient. According to my results, *C. pennsylvanicus* is unable to actively regulate its internal nest environment, but can use the insulative properties of trees to dampen wide temperature fluctuations and provide a more stable nest microclimate.

Since *C. pennsylvanicus* is bound to a central nest, it faces difficulties in foraging that optimize their ability to obtain energy sources. Maximizing net energy yield is one aspect of central-place foraging (CPF) theory. For *C. pennsylvanicus* to adhere to CPF theory, foragers must structure search patterns to collect food of a high caloric value to compensate for the amount of energy needed to obtain it and return to the colony. This selection for higher energy return should be based on colony nutritional requirements and apparent in both carbohydrate and protein foraging.

To determine if *C. pennsylvanicus* forages according to CPF theory, carbohydrate and protein solutions were used to ascertain preference at two fixed distances. Additional data were taken to determine if time spent imbibing, varied with concentration, distance or a combination of the two. Solution concentrations of 5 and 30% casein or sucrose were used for the preference and duration studies and were placed at 1 and 15 m distances from the nest. *Camponotus pennsylvanicus* fed on casein solutions at both distances, with

no difference between higher and lower concentrations. However, *C. pennsylvanicus* selected a higher concentration of sucrose as the distance from a food patch to the nest increased to 15 m. Foragers imbibed sucrose from both concentrations at 1 m with no preference noted between the two solutions. *Camponotus pennsylvanicus* did not adhere to CPF theory, with respect to protein, but did use a CPF strategy with regard to sucrose selection in this study.

Mean feeding durations indicated that foraging black carpenter ants fed differentially on casein solutions, depending on concentration or distance. Overall casein mean feeding time was significant, suggesting *C. pennsylvanicus* feeds longer on 30% casein solution regardless of the distance involved. Additional analysis indicated that the effect of distance on feeding duration was only significant at a 5% solution concentration. Overall mean feeding time was significant, suggesting feeding intervals were greater on 30% casein over both distances.

DEDICATION

I would like to dedicate this dissertation to my wife Marsha who gave me the encouragement to pursue my goals and to my sons Kyle and Ryan in hopes that it will inspire them to follow their dreams. I would also like to dedicate this work in memory of my parents, David and Dawn Oswald. I only wish that they could have seen me finish.

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INTRODUCTION

Within the eastern U.S., the black carpenter ant *Camponotus pennsylvanicus* (DeGeer) is the most common and widely distributed *Camponotus* species (Fowler and Roberts 1982, Hedges 1997). Colony formation usually takes place within a primary nest. Carpenter ants excavate galleries in decayed and sound wood to accommodate increasing numbers within the colony. Primary nests usually contain the foundress, eggs, early instar larvae, and adult workers. In the natural environment, carpenter ants may build their nests in decaying logs and stumps. Live trees also are suitable for nesting, where ants excavate decayed areas through cracks, scars, and knot holes (Hansen and Akre 1990). In urban settings, infestations of carpenter ants are seen as a nuisance and structural pest. Gallery formation in wall voids often can lead to structural damage, necessitating repair.

Most of the previous biological and ecological work on *C. pennsylvanicus* has taken place in Canada, and the northeastern and northwestern sections of the U.S. Aside from the original work on *C. pennsylvanicus* by Pricer (1908), little research has been conducted on this species in the Southeast. No work on this ant species relative to its nesting preferences in the southeastern U.S has been conducted. My initial observations author have echoed previous work by Sanders (1964), Fowler and Parrish (1982), and Klotz et al. (1998) in which *C. pennsylvanicus* nests were found in logs, stumps, and standing trees. Differences may exist in species of trees with respect to South Carolina and the southeastern region. Klotz et al. (1998) listed several *Quercus* spp., *Acer saccharinum* and *Fraxinus americana* containing *C. pennsylvanicus* nests. Tree species diversity was limited to a 0.4-hectare study plot within a managed hardwood forest.

Fowler and Parrish (1982) reported tree species attacked by *C. pennsylvanicus*, but these were tree species in an urban setting that had been selected for their shading ability or aesthetic value. Fowler and Parrish (1982) also reported the association of nests in trees with “mechanical damage”. Their results showed a positive correlation between damage and incidence of infestation of the tree. These results are, however, limited in their scope to urban areas, species diversity in trees, and subjection to artificial pruning. Studies characterizing the habitat associated with nests of *C. pennsylvanicus* would assist in delineating the biology and ecology of this important species from other *Camponotus* species.

Several control strategies are available for carpenter ant management by pest management professionals (PMPs) including the use of baits and residual sprays. However, indiscriminant bait placement or broadcast applications of liquid insecticides are often unsuccessful because sufficient amounts of toxicant fail to reach the reproductive members of the colony to cause colony mortality. An integrated approach including a thorough inspection of the structure and adjacent landscape often provide more complete control. Inspections, often a critical part of integrated pest management, are the most labor intensive and difficult facet of a management program to perform in a time-conscious industry. Characterizing habitats could aid PMPs by focusing their inspections on specific areas, allowing for greater success in nest detection.

Nest-temperature regulation in ant nests is not well known. However, “frost-free” regions were observed in ground-nesting *Formica* spp. and *Lasius* spp. (Steiner 1926, 1929). Temperatures within the nest remained above the metabolic threshold of the ants.

Nest temperatures are thought to passively reflect ambient temperatures (Cannon 1990). Species of ants inhabiting wood should benefit from the thermal insulating and buffering properties offered by this unique microhabitat (Baust and Morrissey 1977). Nest temperatures in overwintering colonies of *C. pennsylvanicus* were recorded by Cannon (1990). Cannon (1990) found that while nest temperatures approached, and in some cases paralleled ambient temperatures, they did not fluctuate in an erratic pattern. Wild fluctuations in ambient temperature were not seen in the nest, possibly due to the buffering properties of the wood (Cannon 1990). Cannon's study covered a nine-week period, January to March, and recorded observations on nests found in logs.

Nutritional selectiveness maximizing net energy yield over increasing distance traveled has been reported for *Pogonomyrmex rugosus* and *Messor pergandei* seed selectivity as a function of distance traveled by the foraging worker (Davidson 1978, Rissing and Pollock 1984). Maximizing net energy yield is one aspect of central-place foraging (CPF) theory. The model contends that the greater the distance traveled to a food source, the more selective the forager should be, opting for a higher nutritional return for a corresponding increase in distance traveled. Generally, the nutritional value of the food item selected should increase with distance traveled to the food item.

Camponotus pennsylvanicus, being an omnivorous feeder, should exhibit this behavior for both carbohydrate and protein foraging, but this theory has yet to be tested with this species. For *C. pennsylvanicus* to adhere to the theory of CPF, a forager must gather higher nutritionally rewarding food with an increase in distance traveled. This selection for higher energy return should be based on colony requirements and apparent in both

carbohydrate and protein foraging. Studies to understand the foraging dynamics of *C. pennsylvanicus* and its nutritional requirements could aid in the development of baits that would be more competitive with natural food sources, thereby increasing the bait's ability to control a pest ant population.

The overall goal of my research was to better understand the interplay of the environment on black carpenter ant distribution in natural settings and internal nest milieu. Secondly, the goal was to determine differences in food selection with regard to concentration and distance traveled. Specifically, the objectives and subsequent hypotheses were:

Objective 1: Characterize nests and associated habitat features for the black carpenter ant, *Camponotus pennsylvanicus* (DeGeer) in western South Carolina.

Hypothesis: Black carpenter ant nests are located in predictable habitats that can be characterized by using environmental features as predictors.

Discussion: Because black carpenter ants are an important economic pest, relevant information concerning their ecology becomes an invaluable tool in contributing to pest management programs designed to eradicate them. Studies have shown correlations with both biotic and abiotic elements, but these are derived in urban habitats. Additional studies have looked at natural settings and associated habitat features in a different species and geographical area. Comparing artificial urban habitats and natural forested areas can highlight similar likely nesting areas of black carpenter ants. This information can assist pest management professionals in finding black carpenter ant nests so that effective treatments can be applied.

Objective 2: Determine if black carpenter ants actively regulate internal nest temperatures year round.

Hypothesis: Black carpenter ant internal nest temperatures in live trees are not significantly different from ambient.

Discussion: Little is known about the internal nest microhabitat of ants with regard to temperature. Other species of Hymenoptera take an active role in controlling nest temperatures by fanning, evaporative cooling, or shivering to either dissipate heat or increase nest temperatures using radiant body heat. Ants, though, are relatively smaller and lack the necessary morphological structures to create excess radiant heat to warm a nest, and no known studies have looked at behavioral adaptations that would suggest that ants either cool or warm their nests. The ability to cope with temperature extremes possibly lies with physiological and behavioral modifications that allow ants to avoid critical thermal maximums and minimums. Other studies reported physiological changes in black carpenter ants in response to overwintering stimuli in addition to the blanketing effect of the nest substrate. Because black carpenter ants lack the morphological structures necessary to actively produce heat to warm their nest, an alternative hypothesis needs to be proposed that centers on the buffering capacity of the selected nest substrate. A long-term study on seasonal temperature changes and fluctuations within black carpenter ant nests should elucidate the role of nest substrate on internal microhabitat.

Objective 3: Determine if foragers are more selective toward higher nutritional-valued food items with increasing distances to a food source.

Hypothesis: Foragers of the black carpenter ant select higher concentrations of carbohydrates with increasing distance traveled to a food source.

Hypothesis: Foragers of the black carpenter ant select higher concentrations of proteins with increasing distance traveled to a food source.

Discussion: Several studies have reported foraging strategies of ants and more specifically black carpenter ants. Ants often select higher quality food items to maximize their energy gain. Maximizing net energy gain plays out more when distance and handling time are considered. Because nutritional requirements for an ant colony differ based on the presence of brood and adults, the question is whether or not quality or availability is more important with regard to food type. In addition to the basic biological questions, is the practical aspect of ‘designing’ acceptable baits for the pest management industry. Baits that offer food sources required by the colony would have a distinct advantage over others to permeate the entire colony.

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CHAPTER I

LITERATURE REVIEW

Classification and Distribution

Ants are among the most numerous organisms on earth and represent approximately half the world's biomass (Hölldobler and Wilson 1994). However, the Formicidae account for only two percent of all described insect species (Hölldobler and Wilson 1994). Currently there are over 12,000 known species of ants encompassing 297 genera (Agosti and Johnson 2005). There could be approximately 20,000 species in 350 genera (Hölldobler and Wilson 1990).

Camponotus contains the most species of any genus in the Formicidae. This ubiquitous genus consists of 54 subgenera, seven of which occur in North America, and approximately 1,000 species worldwide (Brown 1973, Klotz et al. 1996, Hedges 1997). The subgenera *Camponotus*, *Myrmentoma*, *Tanaemyrmex*, *Myrmobrachys*, and *Myrmothrix* contain the structure-infesting species (Hansen 1995). The most economically important species are within the subgenus *Camponotus* (Hansen 1995).

The *Camponotus* genus is widely distributed in the United States, with a mix of structural and nuisance species (Table 1). Ten species of *Camponotus* are found in South Carolina (Sargent et al. 2001). Eight of the ten are considered economically important. These include *C. americanus* Mayr, *C. caryae* (Fitch), *C. castaneus* (Latrielle), *C. decipiens* Emery, *C. discolor* (Buckley), *C. floridanus* (Buckley), *C. nearcticus* Emery and *C. pennsylvanicus* (DeGeer) (Sargent 2001).

Table 1. Regional distribution and pest status of economically important species within the genus *Camponotus*. Compiled from Hansen (1995) and Mackay (unpublished data).

Genus species	Distribution²	Pest status¹
Subgenus Camponotus		
<i>C. americanus</i> Mayr	NE, SC, SE, NC, SW	Nuisance
<i>C. ferrugineus</i> (F.)	NE, SC, SE	Nuisance
<i>C. herculeanus</i> (L.)	NC, NE, NW, SC, SE, SW	Structural
<i>C. laevigatus</i> (Smith)	NW, SW	Nuisance
<i>C. modoc</i> Wheeler	NW	Structural
<i>C. noveboracensis</i> (Fitch)	NE, SC, SW	Nuisance
<i>C. pennsylvanicus</i> (DeGeer)	NE, NC, SC, SE, SW	Structural
Subgenus Myrmentoma		
<i>C. caryae</i> (Fitch)	NE, NC, SC, SE, SW	Nuisance
<i>C. clarithorax</i> Emery	SW	Nuisance
<i>C. decipiens</i> Emery	SE, SW	Nuisance
<i>C. discolor</i> (Buckley)	SE	Nuisance
<i>C. essigi</i> (M.R. Smith)	NW, SW	Nuisance
<i>C. hyatti</i> Emery	NW, SW	Nuisance
<i>C. nearcticus</i> Emery	NE, NC, NW, SC, SE, SW	Nuisance
<i>C. sayi</i> Emery	NW, SW	Nuisance

Table 1 (continued). Regional distribution and pest status of economically important species within the genus *Camponotus*. Compiled from Hansen (1995) and Mackay (unpublished data).

Genus species	Distribution ²	Pest status ¹
Subgenus <i>Myrmobrachys</i>		
<i>C. floridanus</i> (Buckley)	SE	Nuisance
Subgenus <i>Myrmothrix</i>		
<i>C. planatus</i> Roger	SC, SE	Nuisance
Subgenus <i>Tanaemyrmex</i>		
<i>C. acutirostris</i> Wheeler	SW	Structural
<i>C. castaneus</i> (Latreille)	NC, NE, M, SC, SE, SW	Nuisance
<i>C. semitestaceus</i> Emery	NW, SW	Nuisance
<i>C. tortuganus</i> Emery	SE	Nuisance
<i>C. variegatus</i> (Fr. Smith)	NW, Hawaii	Structural
<i>C. vicinus</i> Mayr	NC, NW, SW	Structural

1. Economically important species and pest status according to Hansen (1995).

2. Distributions based on regions as outlined by Mackay (unpublished data).

Regions include:

NE= Northeast. Includes Connecticut, Delaware, Indiana, Maine,

Maryland, Massachusetts, Michigan, New Hampshire, New Jersey, New York, Ohio, Pennsylvania, Rhode Island, Vermont.

SE= Southeast. Includes Alabama, Georgia, Kentucky, North Carolina, South Carolina, Tennessee, Virginia, West Virginia.

NC= Northcentral. Illinois, Iowa, Minnesota, eastern Montana, Nebraska, North Dakota, South Dakota, Wisconsin, Wyoming.

SC= South central. Includes Arkansas, Colorado, Kansas, Louisiana, Mississippi, Missouri, Oklahoma, eastern Texas.

NW= Northwest. Includes northern California, Idaho, western Montana, northern Nevada, Oregon, Washington.

SW= Southwest. Includes Arizona, southern California, western Colorado, Nevada, New Mexico, southern Nevada, western Texas.

Ants within *Camponotus* are known as “carpenter ants.” The carpenter ant name is derived from the galleries excavated in decayed and sound wood for nesting sites by the workers. Within the eastern U.S., the black carpenter ant *C. pennsylvanicus* (DeGeer) is the most common and widely distributed *Camponotus* species (Fowler and Roberts 1982, Hedges 1997).

General Biology of *Camponotus* spp.

Colony founding is initiated when reproductive alates emerge from the nest. Female reproductives are stimulated to swarm in response to a mandibular gland secretion produced by the male reproductives (Hölldobler and Maschwitz 1965). The volatile major compounds of the male mandibular glands were identified by Brand et al. (1973a, b) in *C. herculeanus* as 6-methylsalicylate and 3,4-dihydro-8-hydroxy-3-methylisocoumarin (mellin). These same compounds also are present in secretions of other species, such as *C. pennsylvanicus* and *C. ligniperda*, where they elicit similar behavior (Payne et al. 1975). This suggests the volatile compounds are not species specific (Payne et al. 1975, Hansen and Akre 1990). Female swarms coincide with peak male flight. The ensuing nuptial flight is temperature modulated and occurs on warm days between mid-April and mid-June in late morning or early afternoon (Pricer 1908, Hölldobler and Maschwitz 1965, Hansen and Akre 1993). Sexual reproductives are produced by late summer and overwinter within the nest until the following spring (Pricer 1908, Sanders 1971, Ebeling 1978). Mating is thought to take place while in flight (Pricer 1908), although Goetsch and Kathner (1937) observed mating pairs copulating on the ground. Once mating is completed, the male dies and the inseminated queen selects a

suitable nesting site. This can include small cavities in stumps, logs, or under bark (Hansen and Akre 1985). Akre et al. (1995) state that once nest selection is made, the inseminated queen breaks off her wings. This contradicts observations by Pricer (1908) and those of the author (Oswalt pers. obs.) who have collected *C. pennsylvanicus* dealated queens outside an observable nest. This may be due to species differences. Akre et al. (1995) do not list the species used to characterize their generalized *Camponotus* spp. biology however they often worked with western species of carpenter ants and not with *C. pennsylvanicus*. Sanders (1964) and Fowler (1986) reported inseminated queens of *C. pennsylvanicus* remove their wings shortly after mating and before nest selection is complete.

Newly inseminated *Camponotus* queens produce eggs over several days, which hatch in approximately 2-3 weeks (Mintzer 1979, Hansen and Akre 1985). Nourishment of this first brood is derived from dissolution and metabolism of fat reserves and flight muscles (Hansen and Akre 1990). The larval stage for most *Camponotus* in this first generation lasts 2-3 weeks, as does the pre-pupal and pupal stage. Approximately 4-25 minima workers are produced during the first year (Hansen and Akre 1993). Queen oviposition in the second and subsequent years occurs in two phases when a spring and a summer brood are produced. Eggs laid during the primary phase (spring brood) complete development by late summer or early fall, whereas those laid in the secondary phase (summer brood) enter diapause as first-instar larvae to overwinter (Hölldobler 1961, Dukes 1982, Hansen and Akre 1985). This dual phase oviposition produces a bimodal

emergence pattern, with the primary phase producing workers and alate sexual forms (Fowler 1986).

After emergence of the first brood, nest maintenance and foraging duties are assumed by minima workers. This first generation of workers is small and shows little variations in size (Mintzer 1979, Hansen and Akre 1985). The occurrence of the minima is assumed to be a condition of undernourishment (Smith 1942). This assumption has been supported by Ezhikov (1934) who suggests that polymorphic ants develop castes as a result of below optimum nutrition. Smith (1942) compared the average head capsule width of adult *C. pennsylvanicus* workers produced from well-fed and under-fed larvae. He found that well-fed workers averaged head capsule widths of 47.3-47.5 micrometers, whereas underfed workers averaged 43.8-43.9 micrometers. As successive broods are produced in the second and following years, additional polymorphic (media and major) workers appear (Hansen and Akre 1990). Greater numbers of workers are able to forage for more nutritionally complete food sources (Pricer 1908). Foundresses do not leave their nest chamber and do not consume food during the incubation period of the first brood in natural settings, but do accept food in artificial conditions (Dukes 1982). By remaining within the nest, the queen reduces the chance of predation and limits potential encounters with other biotic and abiotic hazards including exposure to insecticides. Eggs deposited by foundresses hatch within 14-24 days. Once eggs hatch, larvae pass through five instars lasting approximately 21 days (Pricer 1908, Dartigues and Passera 1979a). The pupal stadium lasts for approximately 21 days (Pricer 1908). The life cycle of the first brood is estimated to be completed in approximately 66 days (Pricer 1908). Spring

brood development in colonies, one year and older, averages between 55 and 70 days from egg to adult worker (Hansen and Akre 1990).

Sexual reproductives are produced when the colony has sufficiently matured, usually in 3-6 years, with approximately 2,000 workers (Pricer 1908). Alate females are produced from fertile eggs, whereas males are presumably produced from major workers or founding queens that have depleted their spermatozoa (Sanders 1964, Dartigues and Passera 1979b, Hansen 1996). Non-inseminated queens are readily accepted within the colony where they also may serve as a major reservoir for production of reproductive males (Hansen and Akre 1990). Mature *Camponotus* colonies produce both male and female reproductives throughout the life of the colony, which may be as long as twenty years (Pricer 1908, Sanders 1964, Akre et al. 1995). The proportion of male to female reproductives increases as the colony ages, presumably from the incipient queen's depletion of the spermatozoa and continued production of males by major workers and virgin queens, thereby signaling its eventual colony demise (Pricer 1908).

The colony members, including the queen, workers, alate reproductives and first-instar larvae enter diapause in September or October (Hansen 1985). Activity has been observed as late as November in South Carolina (Oswalt pers. obs.). Hölldobler (1961) demonstrated that the onset of diapause in overwintering colonies of *C. herculeanus* is independent of temperature. This allows the colony to bypass temperature extremes that may potentially be detrimental. Diapause within *Camponotus* spp. is broken in early February and first-instar larvae from the previous summer brood complete development by early spring (Hansen 1985, Hansen and Akre 1990).

Estimates of colony size vary greatly among *Camponotus* species. This variability is attributed to incomplete colony counts. *Camponotus* species are polydomous and exhibit partitioned populations, which may facilitate collection of partial colonies (Hansen and Akre 1993). Population estimates are extremely variable and range from 50,000 and up for *C. modoc*, to 50,000-100,000 individuals for *C. vicinus*. Colony size in *C. pennsylvanicus* is the subject of constant conjecture, but current estimates range from 3,000 - 15,000 (Pricer 1908, Fowler 1982, Gibson 1987, Akre et al. 1994a). However, estimates of 3,000 - 6,000 are typically given for *Camponotus* spp. in general (Fowler 1986).

Colony Otogeny

Most species of *Camponotus* are functionally monogynous. Instances of polygyny in nature, albeit rare, have been recorded in *C. herculeanus*, and *C. ligniperdus* (Pricer 1908, Mintzer 1979, Akre et al. 1994a). According to Hölldobler (1962), these colonies would not be polygynous but oligogynous or functionally monogynous because these queens did not have cooperative brood care and exhibited territoriality within their own area. However, Gadau et al. (1999) located a colony of *C. quercicola* that appeared to be polygynous due to a lack of interspecific aggression. This assumption however, is unproven and might only constitute another example of oligogyny, as reported in *C. herculeanus* and *C. ligniperdus* (Hölldobler 1962, Gadau et al. 1998). Oligogyny in *C. ligniperdus* is documented and suggests that most queens within these types of colonies are not closely related (Gadau et al. 1998). Gadau et al. (1998) further surmised that the formation of oligogynous colonies of *C. ligniperdus* are formed by the adoption of

unrelated queens by orphaned mature colonies. Joint colony founding by multiple queens (pleometrosis) was documented in colonies of *C. vicinus* and *C. vaga* (Stumper 1962, Mintzer 1972, Fowler and Roberts 1983a). Polygyny and colony foundation by budding occur in *C. nawai* and in *C. japonicus* (Satoh 1989, Changlu et al. 1991, Changlu and Jian 1992). Satoh (1991) states that queens within polygynous colonies of *C. nawai* were equally cared for by workers. There was an absence of a hierarchy within the reproductive caste, and no observable intraspecific aggression by workers and reproductives. There are no records of oligynous or polygynous colonies of *C. pennsylvanicus*.

Nesting Sites

Colony formation usually takes place in a primary nest. During colony growth, movement of the primary nest may take place. Black carpenter ants excavate galleries in decayed and sound wood to accommodate increasing numbers in the colony. Galleries are irregular in shape and usually follow the grain in the softer portions of the wood (Krombein et al. 1979, Hansen and Akre 1990). Gallery walls are smooth and have a sandpapered appearance. Workers cut small slit-like openings (windows) in the exterior of the nest to allow for foraging and nest maintenance. The galleries may contain all individuals in a primary nest or, in instances of large colonies, may use secondary or “satellite” nests. In the natural environment, *C. pennsylvanicus* may build their nests in decaying logs and stumps. Live trees also are suitable nesting areas where they excavate decayed areas through cracks, scars and knot holes (Hansen and Akre 1990). In circumstances where secondary nests are used, partitioning of castes may occur. The

main primary nest is usually in a humid area and contains the queen, eggs and early-instar larvae (Hansen and Akre 1990). Satellite nests are usually in a dryer, warmer environment and contain workers, mature larvae, pupae and winged reproductives (Hansen and Akre 1990). Satellite colonies are often perennial and the number of satellite nests varies with species (Hansen and Akre 1990).

Living trees provide the most permanent nesting site for most species of carpenter ants within a natural setting. However, not all species of trees are used (Hansen and Akre 1990). *Camponotus modoc* frequently attacks live trees of Douglas-fir and western red cedar in the Pacific Northwest (Hansen and Akre 1990). Carpenter ant species, including *C. herculeanus* and *C. noveboracensis* in Europe and New Brunswick, Canada, prefer softwoods of the *Abies* and *Picea* genera (Hölldobler 1962, Sanders 1964). Shade trees in urban areas are often attacked. Fowler and Parrish (1982) found that 75% of shade trees sampled in New Jersey were infested with carpenter ants. Silver maples predominated as the host tree, whereas white pine was the least-selected host (Fowler and Parrish 1982). Structural damage to buildings or processed wood from gallery formation is also a serious and costly problem. Damage to chestnut telephone poles was documented in 1910 and represented a serious problem in the eastern U.S. (Snyder 1910).

Polymorphism and Caste

Camponotus polymorphism encompasses four distinct forms of allometry (Hölldobler and Wilson 1990). This ranges from monophasic allometry (bimodal overlapping size frequency distribution) to complete dimorphism, which are two distinct forms (Hölldobler and Wilson 1990). Pricer (1908) found *C. pennsylvanicus* to be

continuously (gradually) polymorphic, or triphasic, where there are three distinct breaks in the allometric regression line resulting in a minor and major caste at the terminal segments and a media caste at the medium segment (Hölldobler and Wilson 1990). Smith (1942), however, could only discern a bimodal distribution in *C. pennsylvanicus*, resembling those of *C. herculeanus*, *C. santosi*, *C. planatus* and *C. inaequalis*, which show strong bi-modality.

There are two functional castes in *C. pennsylvanicus*, reproductive caste and worker caste. The reproductive caste can be further defined by sex discrimination. Reproductive gynes are approximately 16-19 mm in length (Hansen and Akre 1985). Reproductive males are smaller, 10-11 mm in length. The worker caste, which is made up of sterile females, are continuously polymorphic and range in size from 6-13 mm in length (Pricer 1908, Smith and Whitman 2000).

Division of Labor

Division of labor within the worker caste appears to be size based. Smaller minimums or minors and medias serve as foragers, care for brood, and attend to nest maintenance whereas majors serve in colony defense, as protein foragers, and as intermediate transporters or “tankers” of carbohydrates from the smaller foragers or “aphid tenders” to the nest (Pricer 1908, Fowler and Roberts 1980, Tilles and Wood 1986).

Hölldobler and Wilson (1990) found that labor partitioning may not be solely determined by morphology, but also by age, termed temporal polyethism. Buckingham (1911) and Lee (1938) noted in several species of *Camponotus*, the youngest ants were

nurses, slightly older ants were queen attendants, middle-aged workers were foragers and maintained the nest while the oldest ants served as foragers, nest builders, soldiers and transporters during emigration (Fowler and Roberts 1980). Traniello (1977) observed in *C. pennsylvanicus* colonies that 68% of all foraging was performed by older workers.

Foraging

Foraging of many species within the *Camponotus* has been the subject of extensive study. Temperature plays a large part in maximizing foraging activity when food is abundant (Bernstein 1979). However, foraging in *C. modoc* is not directly related to temperature or humidity, but initiation may be triggered once a temperature threshold is obtained (Hansen and Akre 1985).

Within *Camponotus*, foraging periods vary greatly. Sanders (1972) noted in Ontario, activity in *C. herculeanus*, *C. noveboracensis*, and *C. pennsylvanicus* peaked mid-afternoon through early June and shifted to nocturnal activity during the latter portion of the foraging season in Ontario. David and Wood (1980) noted in *C. modoc* a trimodal strategy within the foraging season that initially was diurnal, shifting to nocturnal, then reverting to diurnal. Fowler and Roberts (1980) reported that *C. pennsylvanicus* exhibited a diel foraging periodicity in New Jersey. In general, most species of carpenter ants forage nocturnally with peak intensity occurring prior to midnight (Fowler and Roberts 1980). Nocturnal foraging may be more advantageous in *C. pennsylvanicus* and *C. noveboracensis* to escape daily thermal maxims, reduce competition with other species, and relieve pressure from predation (Fowler and Roberts 1980, Klotz et al. 1996).

Carpenter ants use many sensory and environmental cues to optimize their food gathering and searching abilities. Carpenter ants construct and maintain foraging trails or “trunk lines” to facilitate coordinated food gathering. Foraging trails may be underground in the form of tunnels constructed through soil or duff. Tunnels are usually 1.5-3.0 cm in diameter and 1 cm–1 m deep and may extend 185-200 m from the primary nest (Sanders 1972, David and Wood 1980, Hansen and Akre 1993).

Trunk lines are perennial and are marked with trail pheromones secreted from the hindgut (Hartwick et al. 1977, Traniello 1977, Hansen and Akre 1985). Pheromones are also important for group and mass recruitment (Traniello 1977). Klotz and Reid (1993a) showed that *Camponotus* use visual and tactile cues as “redundant backups” to maintain foraging and orientation. Vision, trail pheromones, crest lines, structural guidelines, natural and artificial light sources (e.g. sun, moon, streetlights) also play important roles in orientation (Klotz et al. 1985, 1996, Klotz and Reid 1992, 1993a).

Ants bound to a central nest face difficulties in foraging that optimize their ability to obtain energy sources (Hölldobler and Wilson 1990). Maximizing net energy yield is one aspect of central-place foraging theory. Maximizing net energy return is achieved by ranking food items by expected net energy content (C) divided by expected handling time (t_H) (Orians and Pearson 1979). Food items included in the optimum set have a higher C/t_H than the value of energy intake if the prey were ignored and the forager sought only food items with a higher C/t_H (Orians and Pearson 1979). It is therefore advantageous to the forager to maximize its net energy gain when distance traveled or handling time is considered. Schoener (1971) suggests that a predator should take a larger prey ($>C$

value), with greater distances traveled and that size limits of prey should decline less and size limit should increase with distance.

For *C. pennsylvanicus* to adhere to the theory of central-place foraging, it must alter its food preference and opt for a higher net return to overcompensate for the distance traversed to a food patch. To simplify the concept, a *C. pennsylvanicus* forager must gather higher nutritionally rewarding food (high *C*) with a corresponding increase in travel time. This selection for higher energy return should be based on colony requirements and apparent in both carbohydrate and protein foraging. In a study with *Camponotus gigas*, Pfeiffer and Linsenmair (1998) reported that within the minors, a physical subcaste of transporters behaved according to central-place foraging theory. Additional studies by Franson (1985) reported that *Formica nitidiventris* (Emery) and *Myrmica americana* (Weber) are non-optimal central place foragers because their foraging territory was not centered with the colony entrance.

Food Preference and Exchange

Carpenter ants are thought to be omnivorous; however, a detailed listing of their food sources is lacking (Cannon 1998). A large portion of the ant diet is carbohydrates in the form of honeydew secreted by many families of homopterans, extra-floral nectaries and fruit (Pricer 1908, Gotwald 1968, Klotz et al. 1996). Foragers are known to scavenge dead insects, arachnids and carcasses of dead vertebrates (Green and Sullivan 1950, Marikovski 1956, Sakamoto and Yamane 1997). Fowler and Roberts (1980) observed *C. pennsylvanicus* attacking disabled insects and spiders, but recorded less than one percent of returning foragers carried discernable body parts. Sakamoto and Yamane (1997)

suggested that a related species, *C. nawai* Ito, imbibes hemolymph as a protein source. *Camponotus* species are also known predators of the jack pine budworm, western spruce budworm, forest tent caterpillar, and blackheaded budworm (Youngs and Campbell 1984).

Food preference shifts during the year to coincide with colony demands. During the spring and early summer proteins are strongly preferred, which corresponds with maximum brood production (Klotz et al. 1996). Carbohydrates make up the significant portion of food during the latter portion of the summer into early fall prior to the onset of diapause (Klotz et al. 1996). Carbohydrates are consumed by adults throughout the year, but mass provisioning before diapause may contribute to overwintering survival (Klotz et al. 1996).

Exchange of food within the nest takes place through stomodeal trophallaxis (Cannon 1998). Replete foragers relieve themselves of their load quickly with a subsequent rapid dissemination to other nestmates. Food dissemination within *Formica* is rapid and can approach complete colony saturation in 30 hours (Wilson and Eisner 1957). Rates of rapid transmission also are recorded in *C. pennsylvanicus* (Traniello 1977). Traniello (1977) reported that a returning forager could transfer up to 98% of her crop contents after returning to the nest, with a subsequent dissemination of the liquid to 62% of the workers within 10 minutes.

While food distribution within the colony may be rapid, partitioning of certain food types may be an important factor to consider when control measures are employed. Observations on *Formica* spp. and *Myrmica rubra* (L.) showed that workers freely

exchanged a sugar syrup, but soluble proteins from prey were passed unidirectionally from foragers to nurses (Lange 1967, Brian and Abbot 1977). Additional studies in *Solenopsis*, *Crematogaster* and *Formica* spp. echoed similar results, but with quantities of food, not types. Honey was equally distributed among workers while larvae and reproductives received proportionally less food (Eisner and Wilson 1958). Additional work showed partitioning of food resources in *S. invicta* Buren. Workers monopolized carbohydrates, queens received proteins and larvae amino acids (Vinson 1968, Howard and Tschinkel 1981, Sorensen and Vinson 1981, Sorensen et al. 1983).

Economic Importance

Ants foraging within a structure are a physical nuisance and may be psychologically stressful for some individuals. Infested goods are often disposed of resulting in monetary loss to the consumer. Ants often trigger strong negative emotions in homeowners who perceive these infestations of their dwelling as caused by unsanitary conditions. Subterranean termites, *Reticulitermes* spp., and carpenter ants, *Camponotus* spp., are recognized as among the most serious structural pests in North America (Levi and Moore 1978). Carpenter ants are recognized as a structurally damaging pest in areas where termites have reached their geographical limits especially in the northeastern and northwestern United States, Canada and Northern Europe (Fowler 1983, Hansen and Akre 1990, Wallin and Schroeder 1994 cited in Hansen 1996). In other sections of North America and Europe, carpenter ants are viewed only as nuisance pests, but this is species dependent (Hansen 1995, 1996, Hansen and Akre 1994). In a survey published by the Environmental Protection Agency, ants were considered to be a more serious pest than

cockroaches and have displaced subterranean termites in public concern (Whitmore et al. 1992). In a recent survey of pest management professionals, nuisance ants continued to rank as the number one urban pest in the United States (Curl pers. comm). Carpenter ant control ranked fourth in total revenue generated by pest management professionals in 2006 (Curl pers comm.).

While ants can mechanically transmit disease-causing pathogens, their capabilities of transmission are not fully understood (Beatson 1972). Carpenter ants are thought to play a role in the transmission of the fungal pathogen *Cryphonectria* (= *Endothia*) *parasitica* (Murrill), the causal agent of Chestnut blight. The pathogen has been isolated from the digestive tract of carpenter ants, though their ability to mechanically transmit the pathogen is unknown (Anagnostakis 1982 cited in Fowler 1986). This is in striking contrast to actual mechanical disease transmitting capabilities and number of disease related organisms potentially carried by cockroaches (Roth and Willis 1957, 1960, Alcamo and Frishman 1980, Rivault et al. 1993, Kopanic et al. 1994, Hedges 1997).

Unlike most species of pest ants, carpenter ant infestations represent a dual problem. As a nuisance pest, carpenter ants forage within structures in search of food and moisture. Carpenter ants are also a potential structural pest causing monetary loss to consumers from structural repairs to wooden timbers damaged during gallery formation by adult workers. The ability of carpenter ants to cause structural damage is well understood, however the actual occurrence of serious structural damage may be overstated (Fowler 1986). Wane and Homer (1969) found only 2.6% of the 2,432 known

carpenter ant infestations treated by pest management professionals in California resulted in wood damage. It is therefore beneficial to educate both pest management professionals and the general public on the biology and actual risks of structural damage posed by carpenter ants (Fowler 1986). No direct monetary losses from repair costs are given or are attributed to carpenter ant structural damage. However, estimates of up to 2.89 m³ of wood volume per hectare are lost to carpenter ant damage in Ontario (Sanders 1964). This accounts for approximately 10% of the merchantable volume of pulpwood for the area (Sanders 1964). The direct annual costs attributed to carpenter ant control with regard to structural pest management in 1982 were estimated at approximately \$25 million for New England alone (Fowler 1986). This figure was estimated to be the amount spent on carpenter ant control using professional pest control services and does not take into consideration the possible amount spent on over-the-counter products purchased by consumers (Fowler 1986). Current estimates of monetary loss from damage are not available however; ant control in 2006 generated an estimated \$1.8 billion in revenue for pest management professionals (Curl pers. comm.). Of that, carpenter ant control represented an estimated 30 % of the total ant control revenue generated by pest management professionals, which translates to \$556 million dollars in 2006 (Curl pers. comm.). Because of the damage potential to structures and subsequent monetary losses, locating and eliminating the colony or colonies becomes very important. Carpenter ant control, albeit difficult, can be managed by adhering to the principles of an integrated pest management program (IPM).

Control

Infestations of carpenter ants are well suited for management practices that include cultural and chemical controls. Black carpenter ants are a nuisance pest and can potentially be a significant structural pest of urban landscapes and suburban areas that adjoin woodlands (Fowler and Parrish 1982, Klotz 1992). The first step in proper carpenter ant management should be correctly identifying the pest species. Correct species identification of carpenter ants allows for greater success in locating nests. Different species inhabit dissimilar niches within the environment; therefore, proper identification is essential to aid the inspection process. *Camponotus pennsylvanicus* is primarily a nocturnal foraging species. Inspections performed during traditional working hours by pest management professionals (PMP's) may not be conducive to locating the source of an infestation. Carpenter ant inspections are extremely laborious and time consuming (Fowler 1986). Performing an inspection during off-peak foraging times can only add to the time and labor involved. Akre et al. (1994b) reported inspection times for locating parent colonies ranged from 15 minutes to two hours. Non-traditional nocturnal inspections during the carpenter ant's peak foraging period could assist the PMP in more easily locating nests, estimating pest density and allowing for precise application of treatment. A thorough inspection of the structure and adjacent property is essential. Inspection is often considered the single most important tool to locate satellite nests. More importantly it is the principal way to find parent colonies, along with determining the location and number of foraging trails to facilitate and gauge control success (Fowler 1986, Hansen and Akre 1993, Hedges 2000, Klotz 2003).

Thorough sanitation should be implemented to reduce available food and water sources and eliminate potential nesting sites (Hedges 1997). Removing vegetation directly touching the structure may impede ants from having direct access to the structure, but more importantly allow for better visual examination of potential points of entry (Hedges 1997). Pruning dense vegetation improves air circulation, thereby reducing available moisture and making the surrounding environment less hospitable to infestations (Hedges 1997). Sealing potential entry points and controlling excess moisture in the structure can eliminate or reduce the incidence and severity of the infestation (Hedges 1997, 2000).

The importance of moisture control is often given as one of the pillars of carpenter ant, as well as general ant, management. Reliance on detecting moisture and its relation to nesting carpenter ants may be overstated. Carpenter ants, especially *C. herculeanus* and *C. pennsylvanicus* cause the most damage in sound wood that has minimal or no fungal decay (Butovitsch 1976). This may relate to the polydomous nature of carpenter ants and the partitioning of castes of certain developmental stages into dryer environments.

Carpenter ant control can be attained with traditional insecticides applied as a remedial or preventative chemical treatment or by the application of toxic baits (Tripp et al. 2000). The use of contact insecticides formulated as dusts, aerosol sprays or liquids are effective as remedial or preventative measures when placed within wall voids or directly in the nest (Tripp et al. 2000). Currently available active ingredients used in commercial and over-the-counter products can be effective in controlling carpenter ants.

Klotz and Reid (1994) reported the susceptibility of *C. pennsylvanicus* to cyfluthrin (as 0.5% Tempo 20WP; Bayer Environmental Science, Kansas City, MO) compared to chlorpyrifos (as 0.5% Dursban LO; Dow Agrosociences, Indianapolis, IN). Cyfluthrin remained 50% effective 28 days after initial treatment, whereas chlorpyrifos was shown to be ineffective even on fresh deposits. Gibson and Scott (1989) performed laboratory bioassays with 13 contact insecticides against *C. noveboracensis* and *C. pennsylvanicus*. Their study showed chlorpyrifos to be highly toxic to both species. This contrasts Tripp et al. (2000) whose data show that chlorpyrifos was significantly less toxic than cyfluthrin in studies using aged panels. The difference between Gibson and Scott (1989) and Tripp et al. (2000) may be experiment design and lethal times based on differing methods of toxicant exposure. The use of repellent liquid insecticidal treatments in conjunction with, or adjacent to, toxic baits is not advisable. Their use can disrupt normal foraging and feeding patterns, thereby inhibiting their performance (Reiersen and Rust 1992). The repellent nature and acute toxicity of synthetic pyrethroids used in a broadcast application can appear to reduce the numbers of foraging ants, but may only reduce a small segment of the entire population since only one to ten percent of the colony may be foraging at any given time (Hansen 2000). Recent introduction of non-repellent, slow-acting classes of insecticides, particularly the fiproles and pyrroles, are gaining acceptance with pest management professionals as direct trail and perimeter band applications (Klotz 2003). Due to the non-repellent nature of these insecticides and low concentrations of finished solutions, the active ingredient can be transferred readily to other nestmates during trophallaxis or social grooming (Klotz 2003).

In contrast to the use of conventional treatments with insecticides, ant baiting provides an additional alternative in situations where insecticides are inappropriate. The use of insecticidal baits for carpenter ant control is the most environmentally friendly method of control because it has the most direct impact on the entire colony while minimizing adverse effects on non-target organisms and ecosystem. Baits are appropriate because they require small amounts of toxicant and they can be placed into protective containers (Klotz et al. 1997). Using baits also requires less labor from inspecting the property because nest locations are not directly treated; therefore, their locations do not have to be ascertained (Klotz et al. 1997). Lastly, baits exploit the social behavior of ants. The act of passing food from one individual to another via trophallaxis disseminates a toxic bait throughout the colony, thereby exposing the colony to a toxicant without the need of direct contact which is important with some chemical treatments (Forschler and Evans 1994, Klotz et al. 1997). However, bait effectiveness is often dependent on species and time of year. Diet preference is often closely correlated with brood production. Proteins are preferred during peak egg production and larval development, while adults primarily consume carbohydrates. This partitioning of food resources may greatly affect toxicant dissemination and localize mortality to one caste or developmental stage.

Baits consist of four components: an attractant consisting of a palatable food matrix or pheromone that is readily accepted by the insect; physical structure in the form of a palatable carrier; a non-repellent and delayed action toxicant, effective over a 10-fold range; and materials such as emulsifiers and antimicrobial agents (Stringer et al. 1964, Perregrine 1973, Cherrett and Lewis 1974). Toxic baits frequently are formulated as

carbohydrates or proteins but often are not as competitive with natural food sources and therefore fail (Akre and Hansen 1990).

Factors affecting the performance of baits include ant species, bait formulation, nutritional requirements of the colony, type of toxicant used and time of year (Rust et al. 2002). One important limitation for the use of baits is the inability to develop one type of bait that will control all pest species of ant. Baits formulated for the control of the red imported fire ant, *Solenopsis invicta* Buren, such as Amdro® (Hydramethylnon; BASF, Research Triangle, NC), which contains a toxicant dissolved in soybean oil and applied to corn grit, are not effective on many honeydew feeding species, including carpenter ants (Wagner 1983, Rust et al. 2002). Food preference within the colony may vary with the form of food taken even if the components are essentially the same. Baker et al. (1985) reported with Argentine ants, a liquid sugar solution was preferred over granulated sugar and a protein food source. An additional factor in acceptance of baits by foraging ant species includes formulation type. Currently, ant baits are formulated as liquids, gels and granules. These formulations differ in their water content, with liquid baits containing the highest concentrations of water and granules containing the least. Liquid baits are preferred because they can be disseminated quickly within the adult worker caste of the colony, without the need of larvae to process solid foods. Adult ant morphology limits food intake to primarily liquids. Food particles ≥ 100 microns are filtered by the hypopharynx, together with the epipharynx, and prevented from entering the alimentary canal (Cannon 1998, Hansen 2002). Particle size may play an important role in acceptability and effectiveness of granular ant baits (Hooper-Bùi et al. 2002).

Another factor influencing bait acceptability and effectiveness is contamination of the bait matrix. Benson et al. (2003) reported the adverse effects of several contaminants on commercially available baits used in controlling the red imported fire ant. Baits contaminated by some insecticides, gasoline, and cigarette smoke were significantly less preferred than uncontaminated controls. Hansen (2002) reported the efficacy of several currently available carpenter ant baits over a five-year period on *C. modoc* and *C. vicinus*. Baits showed control rates from 77% to 90%. Liquid baits containing boric acid (variable concentrations) provided 100% control over an average of 11.1 weeks, while hydramethylnon granules (1%, Maxforce; Bayer Environmental Science, Kansas City, MO) achieved the same level of control in approximately 10 weeks (Hansen 2002). Gel and granular bait formulations containing fipronil (0.001%, Maxforce; Bayer Environmental Science, Kansas City, MO) ranged from 76% to 92% control over an average of 5.9 to 6.1 weeks. Hansen (2002) stated that test results were highly variable, depending on site and competition with natural food sources.

Toxicant type is an important aspect considered when developing baits. Metabolic inhibitors, insect growth regulators, and synaptic poisons are efficacious against carpenter ants, as well as other species of pest ants (Hansen 2002, Fowler and Roberts 1983b, Forschler and Evans 1994, Klotz and Moss 1996, Klotz and Reid 1993b, Reid and Klotz 1992, Rust et al. 2002, Vail and Williams 1995, Vail et al. 1996,). Baits containing insect growth regulators are inherently slow-acting and those with metabolic inhibitors may not be sufficiently disseminated within the colony before their lethal effects are realized.

Nutritional requirements of the colony often coincide with brood production, which may peak at differing times of year (Hedges 1997). Bimodal brood production necessitates protein foraging for the developing larvae during late spring and early summer. Late-season brood remain as first-instar larvae and diapause until the following spring when they will complete development. Foraging during the latter half of the summer and fall primarily consists of carbohydrate gathering for immediate consumption by adult workers and storing for use by the colony during the winter. Baits are not always effective because of the shifting nutritional requirements and the competition with natural food sources that

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CHAPTER II

NESTING SITE CHARACTERIZATION OF THE BLACK CARPENTER ANT, *CAMPONOTUS PENNSYLVANICUS* (DEGEER) (HYMENOPTERA: FORMICIDAE), IN SOUTH CAROLINA

Introduction

The black carpenter ant, *Camponotus pennsylvanicus* (DeGeer), is one of the most serious structural pests in North America, especially in the northeastern and northwestern United States (Levi and Moore 1978, Fowler 1983, Hansen and Akre 1990). In a recent survey of pest management professionals, nuisance ants were ranked as the number one urban pest in the United States (G. Curl, pers. comm.). Carpenter ant control ranked fourth in total overall revenue generated by pest management professionals, representing 30% of the total ant control revenue (\$556 million dollars) in 2006 (G. Curl, pers. comm.). Because of their potential to damage structures and the associated monetary losses, locating and eliminating colonies becomes important. An understanding of habitat features that can be associated with *C. pennsylvanicus* nests could be a critical tool in pest management programs.

Animals of a given species do not nest in arbitrarily selected areas within their environment (Brockman 1979). Typically, a narrow spectrum of biological parameters limits nesting to specific locations that maximize reproductive potential (Brockman 1979). This is species dependent, but acceptable ranges can be expected. Within the social Hymenoptera, nest-site selection seems to follow decision making patterns with respect to multiple biotic and abiotic factors. Seeley and Buhrman (2001) reported that swarms of *Apis mellifera* L. collectively chose between acceptable and desirable nest

sites, opting for the desirable site that satisfied colony needs. Common factors in nest-site selection shared by *Sphex ichneumoneus* (L.) and *Halictus rubicundus* (Christ), both ground nesting Hymenoptera, were soil density, conspecific density and resource availability (Brockman 1979, Potts and Willmer 1997). In addition, *H. rubicundus* used thermal gradients generated from solar radiation by selecting southern-facing exposures (Potts and Willmer 1997).

Ants share similar processes in nest-site selection with those of higher social hymenoptera. Mallon et al. (2001) reported that colonies of *Leptothorax albipennis* (Curtis) used both individual and group decision-making processes in nest-site selection. Colony members were able to evaluate two potential artificial nest sites and selected the one more suitable. The optimal site had higher intrinsic qualities (i.e., large cavity area, small nest entrance) based on the value of options available at each site (Mallon et al. 2001). Folgarait et al. (2007) reported that land-use type had a greater impact on colony longevity and spatio-temporal levels in colonies of *Camponotus punctulatus* Emery. Areas of greatest disturbance (abandoned rice fields) were colonized earlier and contained more robust colonies than those in intermediate fields (sown pastures) and fallow grasslands (Folgarait et al. 2007).

Nests of *Camponotus vicinus* Mayr are most often associated with fallen logs with a wide range of diameters. Additionally, Chen et al. (2002) reported a positive correlation between temperature and moisture, as associated with nest presence in *C. vicinus*. Additional important nest-site habitat features included trees, bark duff and a dry soil substrate associated with an open canopy area (Chen et al. 2002). Previous ecological

research on nest-site preference in *C. pennsylvanicus* was undertaken in the northeastern U.S., and southeastern Canada (Sanders 1964). No research has been conducted on this ant species relative to its nesting preferences within the southeastern U.S. My initial observations echoed previous work by Sanders (1964), Fowler and Parrish (1982) and Klotz et al. (1998) in which *C. pennsylvanicus* nests were found in logs, stumps and standing trees. Differences may exist in species and abundance of trees with respect to South Carolina and the southeastern region versus the northeastern U.S. and southern Canada . Klotz et al. (1998) reported that several *Quercus* spp., *Acer saccharinum* and *Fraxinus americana* contain *C. pennsylvanicus* nests. Fowler and Parrish (1982) reported tree species attacked by *C. pennsylvanicus*, but these were in landscaped urban settings and trees were selected for their shading ability or aesthetic value. Fowler and Parrish (1982) reported a positive correlation between “mechanical damage” and infestation of the tree. *Camponotus pennsylvanicus* is often a structural or nuisance pest in residential areas adjacent to forested lands. My study was designed to document habitat features associated with nests of *C. pennsylvanicus* in forested areas in the Piedmont Region of South Carolina. My hypothesis for this project was that *C. pennsylvanicus* ant nests are located in predictable habitats that can be characterized by using environmental features.

Materials and Methods

Study Area and Sampling

The Clemson Experimental Forest was selected as the study site to examine nest-site preference in *C. pennsylvanicus*. The Clemson Experimental Forest is approximately 7,138 hectares located in Anderson, Pickens and Oconee counties within the Piedmont

physiographic region of South Carolina. Elevation ranges from 200 to 300 meters above sea level. Dominant tree species include loblolly pine (*Pinus taeda* L.) and shortleaf pine (*P. echinata* Mill.), with a mixture of oak (*Quercus* spp.) and other hardwoods in both the canopy and understory.

From May to September 2003, areas located at 34° 37.5292 N; 82° 49.8167 W within the forest were sampled for the presence of *C. pennsylvanicus* nests. Elevation of the study area is approximately 228 meters above sea level. Ants were identified using the key by Snelling (1988). Voucher specimens were deposited in the Clemson University Arthropod Collection.

Once a nest was located, a 10 x 10 m plot was established around the nest and habitat data were recorded. Plots of the same dimension in randomly selected adjacent locations without nests were established as a control. A total of 10 sets of nest and control plots were studied. Sampling within each plot included, but was not limited to, examination of live trees, fallen logs and tree stumps for presence/absence of nests. Environmental data were placed in two categories, whole-plot and nest-site specific, to delineate broad areas versus specific potential nest-site characteristics. Whole-plot data included Crown Cover Index (CCI) and Underbrush Density Index (UDI). CCI was estimated using a convex spherical densiometer (Forestry Suppliers, Jackson, MS) at each plot to estimate percent of canopy. UDI was used to numerically classify the density of understory vegetation (Table 1). Additional whole-plot data included the percentage of substrate area covered by cellulose debris, bare ground, leaf litter, herbaceous growth, and grass. Substrate area coverage was visually estimated for each plot.

Table 1. Numerical rating system used to classify the density of understory vegetation.

Number	Description
1	Sparse. Light undergrowth primarily consisting of herbaceous plants and woody ornamentals approximately < 0.5 m in height and > 2m between the bases.
2	Moderate. Undergrowth primarily consisting of herbaceous plants and woody ornamentals approximately ≤ 1 m in height and ≥ 1 m between the bases.
3	Dense. Undergrowth primarily consisting of herbaceous plants and woody ornamentals approximately > 1 m in height and < 1 in between the bases.

Nest-site data within-plots included the presence or absence of occupied nests, type of substrate occupied by the nest (tree, log or stump), type of “defect(s)” on live trees (Table 2), and Diameter at breast height (dbh) of live trees. Additional data included tree species, log or stump, log or stump length and diameter. Logs were identified as any cellulose debris with > 8 cm dm to separate logs from limbs. Fungal decay of logs or stumps was estimated using American Society for Testing and Materials (ASTM 1999) rating of damage by wood-destroying heart rot fungi (genera were not determined) for all samples within the plot (Table 3). Diameter at breast height was taken for each tree, using a metric dbh tape measure (Forestry Suppliers, Jackson, MS). Additionally, log and stump moisture content was measured using a twin pin meter (Delmhorst J 2000, Towaco, NJ).

Table 2. Numerical rating system used to classify defects in hardwood and softwood trees.

Number	Description
0	No visible defects
1	Tree hole
2	Dead limbs
3	Dead tree
4	Toppled crown
5	Broken limbs
6	Crotch
7	Limb scar
8	Attached snag

Table 3. American Society for Testing and Materials rating of damage to logs or stumps by a wood destroying fungus. (Abbreviated list). (ASTM 1999).

Number	Description
1	Complete decay. Approximately 100% of the wood consisted of decay.
5	Moderate decay. Approximately 50% of the wood consisted of decay.
10	Sound wood. No visible signs of decay.

The whole-plot and substrate data were analyzed as a randomized complete block design, with nest and control plots considered the treatments, and the 10 sets considered the blocks. Differences in treatment means for quantitative data were determined using an ANOVA, and differences in treatment percentages for qualitative data were determined using Chi-square analysis. Groups of carpenter ants > 3m apart were counted as separate nests, as outlined in Chen et al. (2002).

Additional analyses of differences for the nest-site specific data within nest-site plots were conducted. Nest-site plots were further divided into substrates with nests present and areas without nests. This additional analysis was performed because most areas within the nest-site plots did not contain *C. pennsylvanicus* nests, and these areas

without nests revealed patterns in means and percentages of the substrate values.

Analyses of the means and percentage differences within nest-site plots followed the same methodology as the original analyses.

All ANOVA calculations were performed using PROC GLM (SAS Institute 2004) and all Chi-square calculations were performed using PROC FREQ (SAS Institute 2004).

Results and Discussion

Whole-Plot Characteristics

Several types of habitats were sampled within the Clemson Experimental Forest ranging from areas of dense undergrowth to open land. Mean percentages of whole-plot data were not significantly different among nest-present and nest-absent plots ($P = 0.1$) for each of the following types of ground cover data: percent cellulose debris, percent bare ground, percent leaf litter, percent herbaceous plants, percent grass and CCI (Table 4). Significant differences in UDI were observed between nest-present and nest-absent plots ($P = 0.1$) (Table 4), suggesting *C. pennsylvanicus* has a propensity for nesting in habitats with sparse undergrowth.

Table 4. Mean (\pm SE) of whole-plot habitat characteristics for *Camponotus pennsylvanicus* (DeGeer) nest-present and nest-absent plots (10 x 10 m).

Category	Plot Type			
	Nest-present		Nest-absent	
	n	Mean	n	Mean
Percent cellulose debris	10	7.7 \pm 0.8 a	10	5.2 \pm 2.3 a
Percent bare ground	10	0.2 \pm 0.2 a	10	0.4 \pm 0.2 a
Percent leaf litter	10	85.2 \pm 1.4 a	10	83.9 \pm 3.3 a
Percent herbaceous	10	6.6 \pm 1.1 a	10	9.7 \pm 3.1 a
Percent grass	10	0.4 \pm 0.1 a	10	0.7 \pm 0.3 a
Underbrush density index	10	1.0 \pm 0.0 b	10	1.3 \pm 0.1 a
Crown cover index	10	89.4 \pm 0.7 a	10	89.7 \pm 1.3 a

* Means followed by the same letter within rows are not significantly different at $\alpha = 0.1$, GLM.

Camponotus punctulatus preferred disturbed habitats over fallow grassland habitats (Folgarait et al. 2007). The assumption is that ground-nesting Formicidae select these habitats based on thermal requirements needed for brood production. Because *C. pennsylvanicus* is primarily an arboreal nester, thermal requirements from a soil-nesting environment would not be advantageous to colony requirements. The relatively sparse undergrowth associated with black carpenter ant nests is probably an artifact of forest tree species. Mature forests containing hardwood tree species have tighter canopies, resulting in less available sunlight reaching the forest floor to support additional plant life.

Substrate Characteristics Within Whole-Plots

Using mean separation analyses to evaluate substrate characteristics, mean differences in tree dbh, log/stump length, log/stump diameter and percent moisture were not significantly different among nest-present and nest-absent sites. ASTM ratings of logs and stumps were significantly different ($P = 0.1$) (Table 5) among nest-present and nest-absent sites. ASTM rating of logs and stumps containing a nest was 6.16 indicating that < 40% of the cellulose was consumed by wood-destroying organisms. Logs and stumps that did not contain a nest had a lower mean ASTM rating of 5.30. Non-nest logs and stumps with a low ASTM rating appeared to be significantly decayed and were easily torn apart for examination. Severely decayed wood appears to be less suitable as a nest substrate. With excessive cellulose loss, the structural integrity is compromised and the log or stump is no longer a viable nesting site. Severely decayed logs and stumps also had prolific infestations of wood-destroying insects that further decreased the suitability of the nesting medium. Cellulose of nest-absent logs and stumps were often thoroughly consumed by other wood-destroying insects such as long horned borers (Cerambycidae), flat head borers (Buprestidae), and subterranean termites (*Reticulitermes* spp.). These insects indirectly compete with *C. pennsylvanicus* for available cellulose and their presence renders the nest substrate unusable by black carpenter ants as a medium for nesting.

Table 5. Mean (\pm SE) of habitat characteristics for *Camponotus pennsylvanicus* (DeGeer) nest-present and nest-absent plots (10 x 10 m).

Category	Plot Type			
	Nest-present		Nest-absent	
	n	Mean	n	Mean
Tree diameter at breast height (cm)	9	11.61 \pm 0.72 a	10	12.25 \pm 1.51 a
Log/stump length (m)	10	5.66 \pm 0.72 a	8	7.07 \pm 2.29 a
Log/stump diameter (cm)	10	12.55 \pm 1.47 a	8	16.05 \pm 3.01 a
ASTM rating	10	6.16 \pm 0.34 a	8	5.30 \pm 0.60 b
% Moisture log/stump	10	35.33 \pm 5.09 a	8	41.25 \pm 10.34 a

* Means followed by the same letter within rows are not significantly different at $\alpha = 0.1$, GLM.

Substrates With Nest Present (NP)

Tree Diameter

Nest-present and nest-absent substrates were not present in all data categories, e.g. treeless plot. This resulted in each category having a different n value for both nest-present and nest-absent substrates. Results of NP substrate data analysis revealed that mean tree dbh was significantly higher compared to nest-absent (NA) substrates ($\alpha = 0.1$) (Table 6). Mean dbh of trees with NP was 37.91 (n = 8) compared with NA trees that averaged 9.90 cm in dbh (n = 130), suggesting *C. pennsylvanicus* typically nest in larger, more mature trees. This observation corroborates the observations of Hansen and Akre (1990) and Chen et al. (2002) who reported the importance of large trees as nesting sites for *Camponotus* spp.

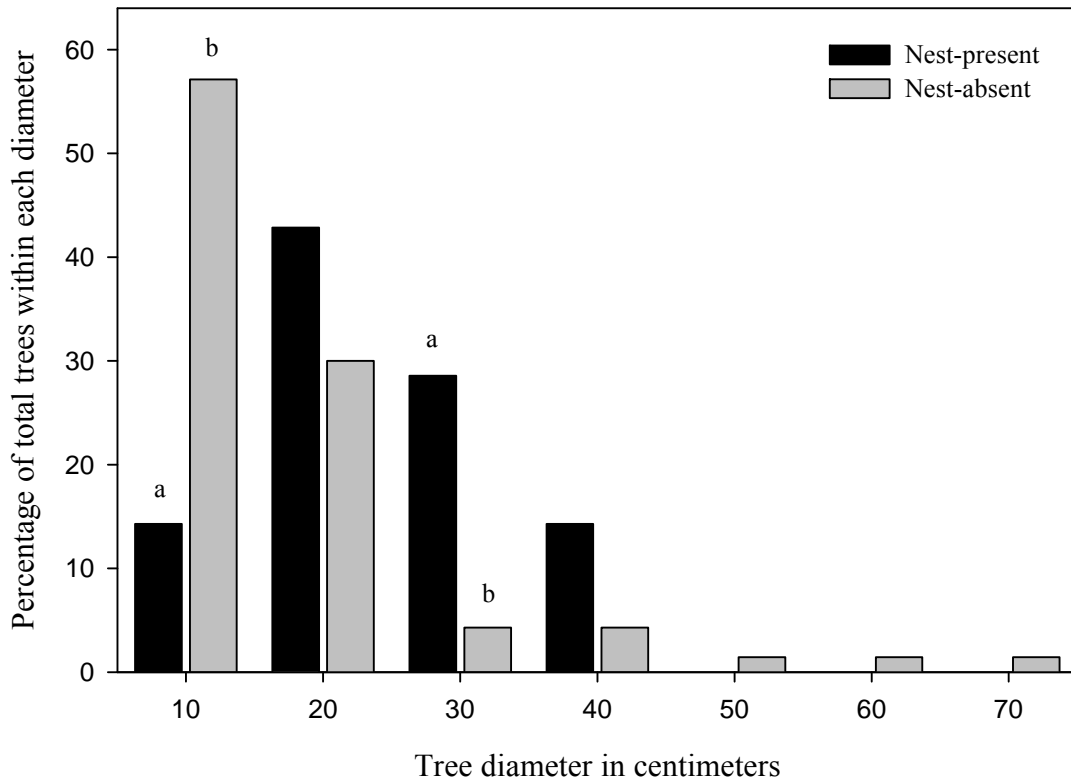
Table 6. Nest-present and nest-absent substrate characteristics for *Camponotus pennsylvanicus* (DeGeer).

Category	Substrate			
	Nest-present		Nest-absent	
	n	Mean	n	Mean
Tree diameter at breast height (cm)	8	37.91 ± 1.54a	130	9.90 ± 3.32 b
Log/stump length (m)	7	9.08 ± 1.77 a	70	4.77 ± 0.61 b
Log/stump diameter	7	18.87 ± 3.22 a	70	12.74 ± 1.27 a
ASTM rating	7	5.42 ± 0.36 a	70	5.75 ± 0.28 a
Percent moisture log/stump	7	29.13 ± 4.48 a	70	40.89 ± 4.24 a

* Means followed by the same letter within rows are not significantly different at $\alpha = 0.1$, GLM.

Nest-absent tree dbh was clustered to the lower diameter ranges (Fig. 1). Trees with nests were grouped in the 10 and 30-cm dbh category (n = 8). Distribution of NA trees decreased curvilinearly (Fig. 1) with a corresponding increase in dbh. The majority of NA trees fell into the 10-cm dbh range. There were significant differences between NP and NA trees at 10 and 30 cm ($\alpha = 0.1$). Nest-present trees in the 10-cm range accounted for only 14.29% of the group while NA trees represented 57.14%. Smaller trees sampled (<10 cm) were usually hardwood saplings with few defects of the types associated with black carpenter ants nesting in mature trees (Fowler and Parrish 1982). Nest-present trees dominated the 30-cm diameter range and accounted for 28.57% of the nests. The 20-cm diameter range accounted for 42.86% of NP trees.

Fig. 1. Distribution of diameter at breast height measurements of *Camponotus pennsylvanicus* (DeGeer) nest-present and nest-absent trees.



* Bars followed by a different letter are significantly different within each diameter class at $P = 0.1$, X^2 (SAS institute).

Log/Stump Length

Logs and stumps of NP sites were significantly longer ($P = 0.1$) (Table 6) compared to NA sites. Mean length of logs and stumps with nests was 9.08 ± 1.77 m ($n = 7$) as opposed to NA logs and stumps that averaged 4.77 ± 0.64 m in length ($n = 70$). Nest-present hardwood logs tended to be trees felled by inclement weather. Infested pine logs usually were felled one to two years previously after succumbing to infestations of southern pine beetles (*Dendroctonus frontalis* Zimmermann). Log age was estimated by visual inspection and sounding. Logs were determined to be one to two years old if they

lacked fungal decay and wood-destroying insects commonly associated with cellulose in an advanced state of decay.

Log/Stump Diameter

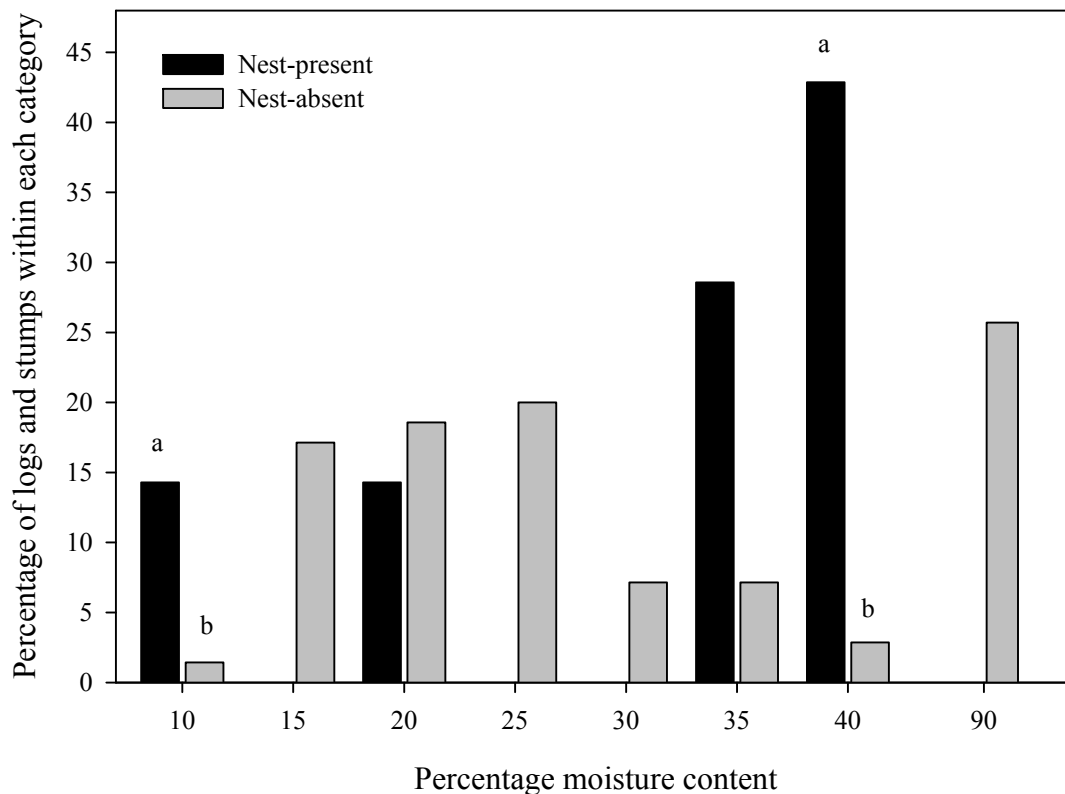
Diameter was not significantly different between NP and NA logs and stumps ($P = 0.1$) (Table 6), perhaps due to data within this category having a high degree of variability. Diameter ranges of logs were extremely variable due to how logs were classified for the purpose of this study. Chi-square analysis failed to delineate significant diameter categories of NP and NA logs and stumps.

Moisture Content of Logs and Stumps

Moisture content was not significantly different between NP and NA logs and stumps ($\alpha = 0.1$) (Table 6). However, χ^2 analysis showed that there were significantly more NP logs and stumps than NA logs and stumps in the 10% and 40% moisture content range (Fig. 2). Nest-absent moisture content ranged from 10% to >40% (Fig. 2) ($n = 70$). The greatest number of NA logs and stumps were within the 15-25% moisture content range and within the 90% range. Samples categorized as in the 90% category had extremely high moisture content that was beyond the mechanical limits of the moisture meter. Logs and stumps in this category were well past the fiber saturation point (approximately 30%) and had significant wood-destroying fungal growth. The lack of active *C. pennsylvanicus* nests in this category is possibly because fungi pathogenic to ants are more likely to be present at higher moisture levels (Clark and Prusso 1986). Nest-present logs and stump moisture content distribution increased curvilinearly, with the 42.86% of NP samples falling within the 40% range (Fig 2) ($n = 7$). The 35%

moisture content range contained the next largest concentration of NP samples with 28.57%. Moisture plays a significant role in nest selection of other species of *Camponotus*. Chen et. al. (2002) reported that *C. vicinus* nested in shaded areas with soil moisture content of 18 - 39%. The majority of *C. pennsylvanicus* nests in logs and stumps also fell within this moisture content range.

Fig. 2. Percentage of nest-present and nest-absent logs and stumps distributed over percentage moisture content.

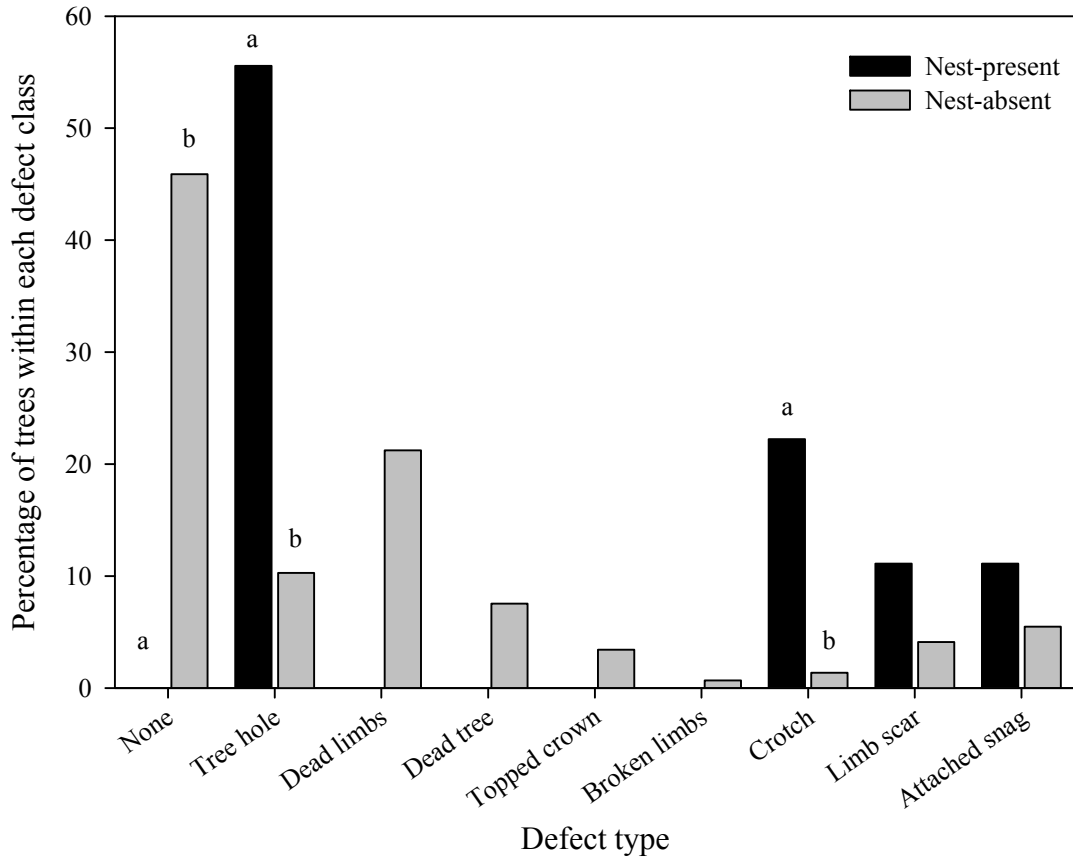


* Bars followed by a different letter are significantly different within each moisture percentage class at $\alpha = 0.1$, X^2 (SAS institute). Moisture contents in the 90% category were beyond the mechanical limits of the moisture meter.

Tree Defect Type

Certain types of tree defects and the presence/absence of *C. pennsylvanicus* nests in trees were positively correlated (Fig. 3). A significantly higher percentage of NA trees had no visible defect. Approximately 45.89% of NA trees (n = 60) were in the no-defect category, whereas trees containing nests were absent from this category. Intuitively, this is reasonable because trees without defects would be healthier and have no internal areas available for ants to nest. Nest-absent trees were present in all defect categories. A significantly more NP trees had tree holes ($P < 0.001$) (n = 4) as opposed to NA (n = 3). Additional tree defects associated with NP trees included limb scars and snags (dead trees that are missing their crown). Fowler and Parrish (1982) reported a positive correlation of *C. pennsylvanicus* nests in trees with 'mechanical damage' from artificial pruning. Tree holes in hardwoods with damage caused by heart rot fungi (species undetermined) allow black carpenter ants to use the tree as a nesting site.

Fig. 3. Distribution of defects in *Camponotus pennsylvanicus* (DeGeer) nest-present and nest-absent trees.



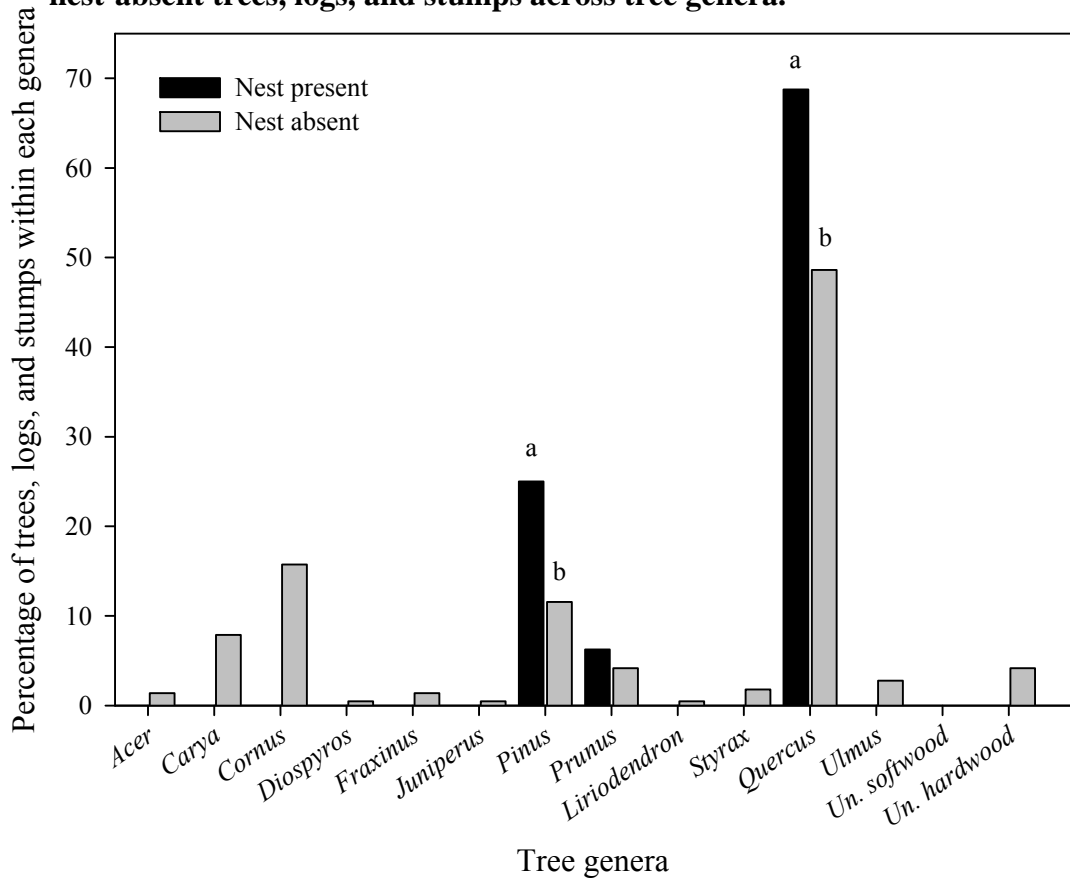
* Bars followed by a different letter are significantly different within each defect class at $P = 0.1$, X^2 (SAS institute).

Tree, Log, or Stump Genera

Twelve tree genera were identified from 138 trees sampled in NP sites (Fig. 4). Species level identification of trees, logs, and stumps was determined, but for the purpose of data analysis, was limited to genera. Nest-absent trees were present in all categories. Nest-present trees were mainly distributed within three genera. Significant differences between NP and NA substrates were observed in *Pinus* spp., and *Quercus* spp. ($P >$

0.001). *Quercus* spp. accounted for 68.75% of the NP substrates (n = 10). *Pinus* spp. accounted for the second largest concentration of NP substrates, with 25% (n = 4).

Fig. 4. Distribution of *Camponotus pennsylvanicus* (DeGeer) nest-present and nest-absent trees, logs, and stumps across tree genera.



* Bars followed by a different letter are significantly different within each genus class at $P = 0.1$, χ^2 (SAS institute).

Camponotus pennsylvanicus nests can be cryptic. To find nest locations, pest management professionals must rely on good inspection techniques as well as have a full understanding of the ant's ecology. Though my study focused on forested areas, similarities between forested and suburban landscapes can be drawn with respect to *C.*

pennsylvanicus nesting sites. I found that *C. pennsylvanicus* nested in areas with relatively sparse undergrowth, which is characteristic of the typical suburban landscape. Additionally, they primarily nested in live trees. Logs and stumps were important as nesting media but played a minor role in my sampled forested habitats. Based on the results of this study, I reject my original hypothesis because habitat features could not be associated with *C. pennsylvanicus* nests. Associations were made only with regard to the nest itself.

Fowler and Parrish (1982) and Klotz et al. (1998) both discuss the importance of trees as a nesting substrate. Tree species was an important factor in locating black carpenter ant nests. Oak trees (*Quercus* spp.) were the dominant genera of tree used by black carpenter ants for a nesting medium. Both Fowler and Parrish (1982) and Klotz et al. (1998) reported similar findings. White oak (*Quercus alba*) was the second most infested species of tree observed by Fowler and Parrish (1982) and also in my study (22%). The primary species of tree infested in my study was the eastern black oak (*Quercus velutina*) (44%).

Logs and stumps that were infested with *C. pennsylvanicus* nests were predominately loblolly pine (*Pinus taeda*) (66%). This may reflect an abundance of material due to Southern pine beetle (*Dendroctonus frontalis* Zimmerman) infestations. White oak (16%) and black oak (16%) were the only other species of logs that contained live black carpenter ant nests.

The predominance of oak trees (*Quercus* spp.) as a preferred nest tree is probably due to several factors. Hardwood cores, in general, represent a stable microhabitat that

can allow for sufficient colony growth and expansion. Because oak trees are highly susceptible to heart rot fungi, this opens up the core of the tree as a protected and stable microclimate. The heart rot fungi are introduced via naturally or mechanically occurring wounds in the tree bark. Fowler and Parrish (1982) reported on the correlation of mechanical wounds to hardwood trees and the incidence of black carpenter ant infestations. Wounds or defects, as illustrated in my study, allow heart rots to establish in oak trees, which in turn aids the establishment of carpenter ant nests in natural and urban landscapes.

Within the scope of this study, my understanding of *C. pennsylvanicus* nest sites in forested situations could be carried over to the urban landscape where similarities exist. Although studies were not performed to test correlations between the two habitats, results of this study and others can be used in *C. pennsylvanicus* management, especially where urban development borders forested areas. Specific recommendations from this study for pest populations of *C. pennsylvanicus* could direct pest management professionals in South Carolina to target their inspections toward areas of minimal undergrowth containing pine logs approximately 9 m in length or mature oak trees at least 20 to 30 cm dbh, containing defects such as tree holes or a crotch.

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CHAPTER III

THERMAL REGULATION AND VARIATION IN NESTS OF *CAMPONOTUS PENNSYLVANICUS*, INFESTING HARDWOOD TREES

Introduction

The ability of an organism to select or maintain an optimal microhabitat is paramount to its survival. Insects usually select nest sites based on several biotic and abiotic factors that optimize egg hatch and maturation. A stable thermal environment can reduce the lethal effects of temperature extremes and provide an optimal microhabitat to maximize growth and development of immatures. An optimal nest microhabitat can be obtained via several mechanisms including architecture, orientation, material decomposition, and thermal inertia of the substrate used as the nest medium (Greaves 1964, Brandt 1980, Coenen-Staß et al. 1980, Korb and Linsenmair 1999, Frouz 2000, Kipyatkov et al. 2004, Frouz and Finer 2007). Several studies involving social insects reported the importance of nest architecture in thermoregulation and gas exchange (Greaves 1964, MacKay and MacKay 1985, Turner 1994, Elmes et al. 1999, Korb and Linsenmair 1999, Frouz and Finer 2007). Turner (1994) reported that *Odontotermes transvaalensis* (Sjöstedt) (Macrotermitinae) mounds are built to aid in nest ventilation but did not play a significant role in regulating colony temperature. Korb and Linsenmair (1999) reported on differences in *Macrotermes bellicosus* (Smeathman) (Macrotermitinae) nest architecture in two differing habitats with respect to both thermoregulation and gas exchange. *M. bellicosus* nests in a forest ecosystem were dome shaped with insulated walls, while those of the savanna were highly structured with

thinner walls (Korb and Linsenmair 1999). Mounds in the forest could withstand cooler temperatures, but gas permeability through the mound decreased. Alternatively, the savanna mounds had greater gas exchangeability but the thin-walled mounds had a lower thermal inertia, limiting their ability to maintain internal nest temperatures (Korb and Linsenmair 1999). Greaves (1964) reported that internal nest temperatures of *Coptotermes acinaciformis* (Froggatt) and *C. frenchi* Hill in trees were significantly higher (13-20°C) than at the center of an uninfested area of the trunk.

The effects of architecture, orientation, moisture, and material decomposition on nest temperatures were reported for several formicid species (Brandt 1980, Coenen-Staß et al. 1980, MacKay and MacKay 1985, Elmes et al. 1999, Frouz 2000, Kipyatkov et al. 2004, Frouz and Finer 2007). Nest temperatures of *Formica polyctena* Först wood ants, increase and remain stable over time due to several factors. Moisture and its effects on decomposition microorganisms were reported to increase nest temperatures over the surrounding soil temperature and subsequent heat loss patterns were observed at night where surface temperatures were significantly warmer than in dry areas (Frouz 2000). Microbial respiration also was implicated as a significant source of heat in moist nests, whereas dry nests relied on ant metabolic heat in conjunction with the insulating properties of the nest material (Coenen-Staß et al. 1980, Frouz 2000). The structure of a *F. polyctera* nest benefits the ant by creating temperature gradients providing optimal temperatures for each developmental stage of the brood (Brandt 1980).

Nest temperature regulation in black carpenter ants (*Camponotus pennsylvanicus* (DeGeer)) is not well known. However, Sanders (1972) reported significant temperature

increases ($\sim 14.9^{\circ}\text{C}$) within the nest as opposed to the surrounding nest material. Frost-free regions also were observed in ground-nesting *Formica* spp. and *Lasius* spp. (Steiner 1926, 1929). Temperatures within the nest remained above the metabolic threshold of the ants. It is generally accepted however, that *C. pennsylvanicus* nest temperatures passively reflect ambient temperatures (Cannon and Fell 1992). Species of ants inhabiting wood should benefit from the thermal insulating and buffering properties offered by this unique microhabitat (Baust and Morrissey 1977). Nest temperatures of overwintering colonies of *C. pennsylvanicus* in logs were recorded by Cannon and Fell (1992). They reported that nest temperatures approached, and in some cases paralleled ambient, provided that temperatures did not fluctuate in an erratic pattern. Wild fluctuations in ambient temperature were not seen in the nest, possibly due to the buffering properties of the wood (Cannon and Fell 1992). However, their study covered only a 9-week period, January to March, and they only observed nests found in logs. The unique thermal buffering property of tree interiors was reported by Greaves (1964) using trees infested with *Coptotermes* spp. Greaves (1964) reported that bark temperatures fluctuated more than 30°C in infested trees while the interior fluctuation was reduced to 1°C . Additional measurements in uninfested trees showed similar temperature buffering capacities (Greaves 1964).

My study examined ambient and internal temperatures of occupied and unoccupied *C. pennsylvanicus* nests in upstate South Carolina. Daily and seasonal differences between nest types were investigated to better understand the relationship between black carpenter ants and the thermal inertia of tree interiors when used as a

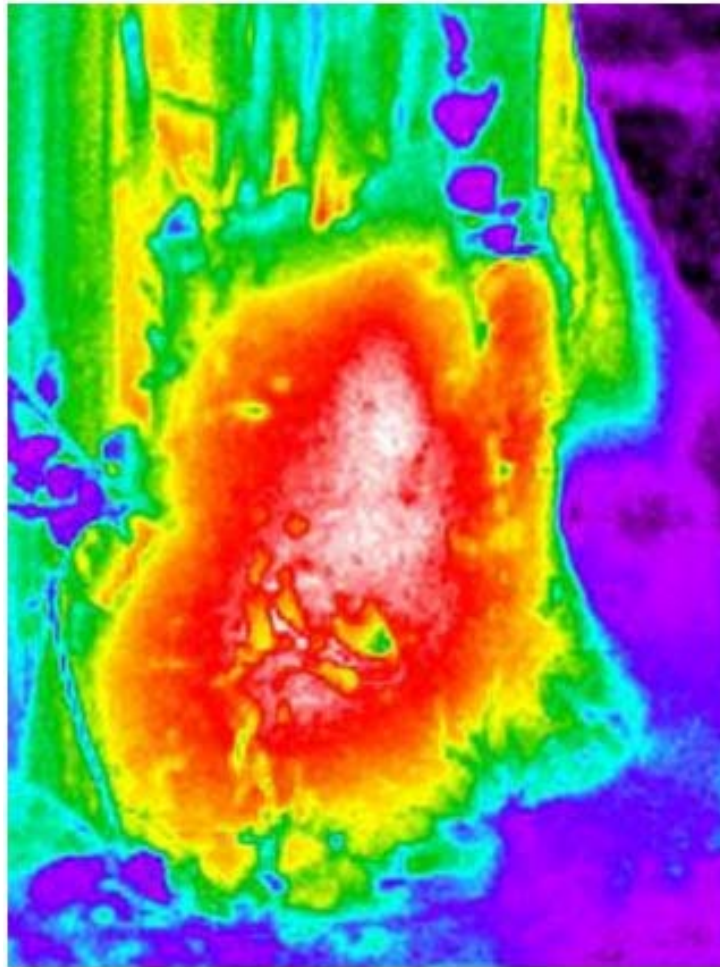
nesting medium. My hypothesis for this project is that *Camponotus pennsylvanicus* internal nest temperatures in live trees are not significantly different from ambient temperatures.

Materials and Methods

Nest Selection

Ten *C. pennsylvanicus* nests were identified in trees at three locations on the Clemson University campus, including six *Fraxinus americana* (White Ash) and four *Quercus alba* (Eastern White Oak). Five of these trees were randomly selected to serve as controls for the experiment. *Camponotus pennsylvanicus* nests in control trees were treated with the non-repellent insecticide Termidor[®] containing fipronil (BASF Corporation, New Jersey, USA). Termidor[®] was injected (as a foam, 25:1 expansion ratio) into galleries and around the nests of control trees to induce colony mortality. Control trees were inspected at 7 and 14d to ensure complete mortality within the nests. Nest galleries were located using a microwave emitting detector (Termatrac[®] Protec industries, Coopers Plains QLD, Australia), and a digital infrared camera (IR 100, Protec industries, Coopers Plains QLD, Australia) (Fig 1). Once the location of the ant nest was determined, a 13-mm hole was drilled into the nest and a borescope (Provision PV 300, CML Innovative Technologies, Inc. Hackensack, NJ) was inserted to visually verify gallery location and activity. Control nests were allowed 14d post-treatment before data collection commenced to prevent inaccurate temperature readings from decomposition of nest contents.

Fig. 1. Colorized image of a *Camponotus pennsylvanicus* (DeGeer) nest, using a digital infrared camera. Yellow – white areas indicate heat produced by the ant nest versus the light blue - green areas of the cooler tree trunk. (IR 100, Protec industries, Coopers Plains QLD, Australia).



Station Design

HOBO[®] H8 Temp / RH / 2x external channel data loggers (Onset Computer Corp. Bourne, Massachusetts) were used to record ambient and internal nest temperatures. Temperature ranges of the data logger are $-20-70^{\circ}\text{C}$. Two external thermocouples (TMC6-HA Onset Computer Corp. Bourne, Massachusetts) were attached to the data

logger and placed approximately 30 cm apart through two holes drilled into the nest galleries to record internal temperature. Temperature ranges of the thermocouples are – 40-100°C. Holes used by the thermocouples through the interior of the tree were sealed using latex caulk to prevent interchange of the ambient and internal nest microclimate. Ambient and internal nest temperatures were recorded hourly over a 52-week period.

To protect data loggers from environmental extremes and locate them adjacent to the *C. pennsylvanicus* nest, weatherproof stations were constructed (Fig. 2). Ten-millimeter diameter polyvinyl chloride (pvc) pipe caps (Charlotte Pipe and Foundry, Charlotte, NC) were used for the main housing of the station. A 2.5-cm bolt was placed through the top center of the station as a point of attachment. Clear acrylic sheeting was cut to the same diameter as the pvc cap and secured in place with silicone sealant (Dap Inc., Baltimore, MD). The acrylic sheeting served as an attachment point for the data logger. Data loggers were held to the acrylic sheeting with Velcro[®] tape (Velcro USA Inc., Manchester, NH). To prevent tampering and data logger damage, a 100-mm diameter round drainage grate (NDS Inc., Lindsay, CA) was fitted inside the pipe cap. Camouflage tape (Realtree[®] Hardwoods HD Duck[®] Tape, Henkel Consumer Adhesives, Düsseldorf, Germany) was placed on the outside of the pvc station to reduce incidences of human tampering, because stations often were located in popular campus recreation areas. Two, 6-mm diameter holes were drilled through the pipe cap parallel to the acrylic sheeting to allow thermocouples to be attached to the data logger. The station was attached to the tree, using a 7.62-cm elbow bracket and screws.

Fig. 2. Weatherproof station (A) on a tree with thermocouples (B) inserted in *Camponotus pennsylvanicus* (DeGeer) nest galleries. Wooden dowel (C) inserted into tree hole was used for accessing galleries to verify nest activity with a borescope.



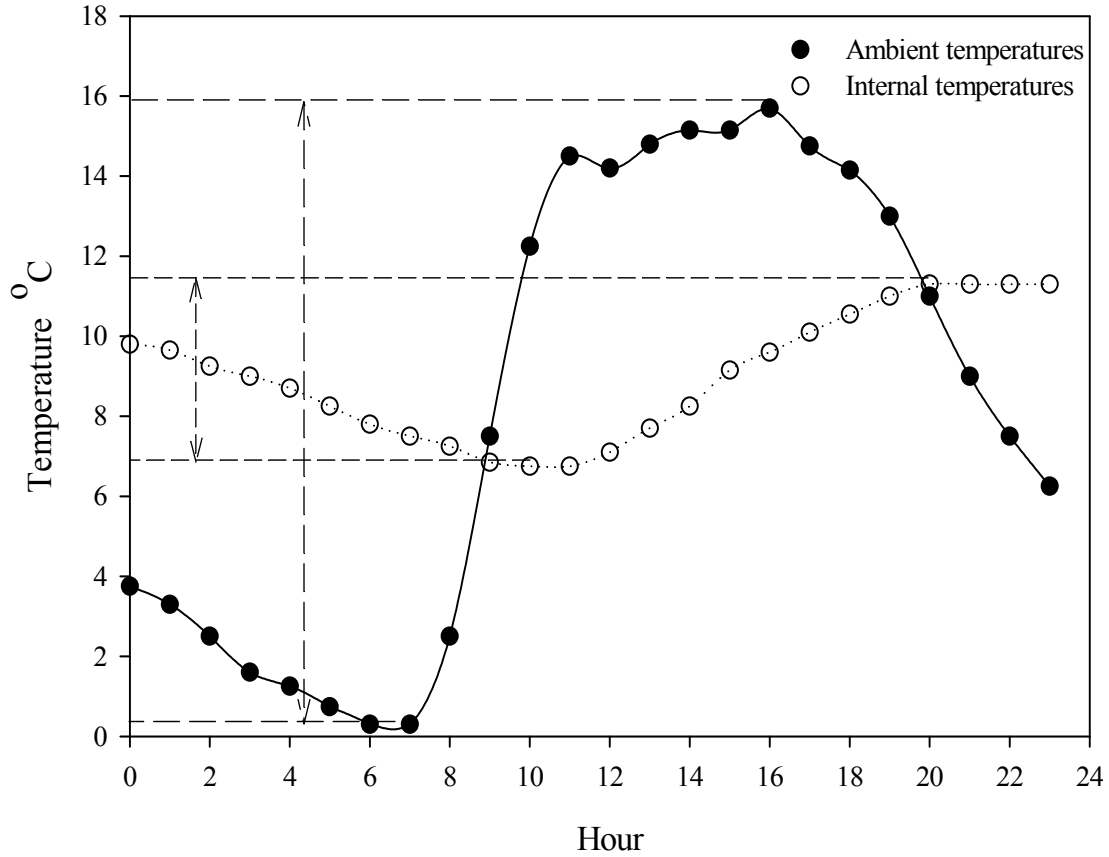
Trees with a nest were treatments (n=5), whereas trees without nests were controls (n=5). A completely randomized design (CRD) with repeated measures was used for this experiment, with treatments blocked by nest type (n=10). Ambient and internal nest temperature range was calculated by taking the difference of daily temperature maximums and minimums (Fig. 3). Raw data were used to calculate temperature range to reflect maximum and minimum variability. Range was used to evaluate the relationship between the internal and ambient microhabitat.

Range difference was calculated using the following formula.

$$\text{Range}_{\text{diff}} = (A_{\text{max}} - A_{\text{min}}) - (I_{\text{max}} - I_{\text{min}})$$

Where A is ambient temperature and I is internal temperature. Ambient and internal temperature range differences were compared between nest types using ANOVA (PROC GLM, SAS Institute 2004) and Fisher's LSD (Proc Mixed, SAS Institute 2004).

Fig. 3. Example of ambient and internal nest temperatures of a *Camponotus pennsylvanicus* (DeGeer) nest during a 24 hr period. Dashed lines represent areas of the temperature curve used to calculate range.



Results and Discussion

Comparison of Ambient and Internal Nest Temperature

The ambient temperature range in both occupied and unoccupied nests were significantly different ($P = <0.0001$) (Table 1). Occupied nest ambient temperature range was lower (10.62°C) than unoccupied (11.20°C). While statistically significant, their importance is relatively minor within the context of this study. Several factors are plausible to explain the difference between the two nest types. The largest concentration of nests was adjacent to a recreational field that was bordered by a small lake. This horseshoe-shaped tree line was exposed to differing amounts of sunlight throughout the diurnal phase. Stations were not placed in a standard location on the tree due to tree shape, but were generally placed within 30 cm of the nest. Stations also were placed to limit human tampering. Eastern exposure to sunlight was greater than western. The internal nest temperature range was not significantly different from each other (Table 1) with respect to nest type. Internal temperatures ranged from 2.27 to 2.35°C for unoccupied and occupied nests.

Table 1. Comparison of ambient and internal nest temperature range (°C) in occupied and unoccupied nests of *Camponotus pennsylvanicus* (DeGeer) for 52 wks.

ANOVA for type by condition effect			
Type	Condition	n	Mean (\pm SE)*
Occupied	Ambient	365	10.62 \pm 0.15a
	Internal	365	2.35 \pm 0.15b
Unoccupied	Ambient	365	11.20 \pm 0.15c
	Internal	365	2.27 \pm 0.15b

* Means within columns followed by the same letter are not significantly different based on Fisher's LSD test at $P = 0.05$. $F = 5.62$, $df = 728$, $P = <0.0001$, $R^2 = 0.87$.

Comparisons of ambient and internal temperature range within nest type were significantly different ($P = <0.0001$) (Table 1). Ambient temperature range of occupied nests fluctuated 10.62°C while internal temperature ranged only 2.35°C. This calculates to a temperature swing of 8.27°C. Unoccupied nests showed similar results of 11.2°C ambient range versus a 2.27°C internal range, which equates to an 8.93°C difference. These results show that internal nest temperature does not fluctuate over as wide a range as ambient. Cannon and Fell (1992) reported in their study that internal nest temperature was within 3°C of ambient. My data support their original conclusion that cellulose acts as an insulator from extreme fluctuations in ambient temperature. Experimental differences between their and my study may account for temperature range differences between the two. Cannon and Fell (1992) recorded nest temperature in logs, my study measured temperatures in live trees. Live trees have a higher thermal inertia and lower thermal conductivity because their cellular structure is intact. Logs are typically in a state

of decay (Oswalt pers obs.), which would have an inverse effect on thermal inertia and conductivity. Geographic differences also exist between the two studies and also may account for some difference. Greaves (1964) reported small diurnal fluctuations in the nurseries of *C. acinaciformis* nested in *Eucalyptus pilularis*. He surmised that the tree provided a thermal buffer between the internal microclimate of the nursery and unstable ambient temperatures. Brandt (1980) reported similar beneficial thermal conductivity properties of cellulose nest material in *F. polyctera* nests where temperature fluctuations within the nest were muted versus the surrounding sand.

Seasonal Comparison of Nests

Temperature ranges of occupied and unoccupied nests were made to compare seasonal differences versus nest type. The seasons were defined as Winter = 31 December– 19 March, Spring = 20 March – 20 June, Summer = 21 June – 22 September, Fall = 22 September – 30 December. Ranges of ambient and internal nest temperatures were significantly different ($P = <0.0001$) for each season (Table 2 and 3). For each season, the ambient temperature range was distinctly higher, reflecting normal air temperature patterns for their respective time frame. Winter and spring seasons had the highest ambient fluctuations of 12 –13°C in both occupied and unoccupied nests. Internal ranges mirrored ambient with a temperature range increase, but only by about 2 –3°C. Conversely, fall and summer each had the lowest seasonal temperature fluctuations for both internal and ambient temperatures (Table 2 and 3). Examples of seasonal temperature patterns in both occupied and unoccupied nests over a 24-hr period are in the appendix (Figs. 1-8).

Table 2. Differences in internal and ambient temperature ranges (condition) of occupied *Camponotus pennsylvanicus* (DeGeer) nests categorized by season.

Season	n	Ambient	n	Internal	<i>t</i> -test for condition effect		
		Mean (\pm SE)*		Mean (\pm SE)*	<i>t</i>	df	<i>P</i>
Fall	90	8.96 \pm 0.27a	90	1.92 \pm 0.27b	20.81	178	<0.0001
Winter	90	12.26 \pm 0.33a	90	2.70 \pm 0.33b	21.50	178	<0.0001
Spring	90	12.49 \pm 0.33a	90	3.03 \pm 0.33b	21.60	178	<0.0001
Summer	95	8.89 \pm 0.19a	95	1.76 \pm 0.19b	29.30	188	<0.0001

* Means within rows followed by the same letter are not significantly different based on Fisher's LSD test at $P = 0.05$.

Table 3. Differences in internal and ambient temperature ranges (condition) of unoccupied *Camponotus pennsylvanicus* (DeGeer) nests categorized by season.

Season	n	Ambient	n	Internal	<i>t</i> -test for condition effect		
		Mean (\pm SE)*		Mean (\pm SE)*	<i>t</i>	df	<i>P</i>
Fall	90	9.73 \pm 0.27a	90	1.85 \pm 0.27b	20.81	178	<0.0001
Winter	90	12.73 \pm 0.33a	90	2.67 \pm 0.33b	21.50	178	<0.0001
Spring	90	13.08 \pm 0.33a	90	2.98 \pm 0.33b	21.60	178	<0.0001
Summer	95	9.37 \pm 0.19a	95	1.44 \pm 0.19b	29.30	188	<0.0001

* Means within rows followed by the same letter are not significantly different based on Fisher's LSD test at $P = 0.05$.

The relationship of internal nest temperature to ambient in occupied and unoccupied nests is illustrated in Figs. 4 and 5. Temperatures are averaged by day in 10-day blocks over a 365-day sampling period. Regression curves show the overall trend in temperature range data over a 52-week period. Internal ranges in Figs. 4 and 5 show little

variation when compared to ambient for the same time frame in both occupied and unoccupied nests.

Fig. 4. Scatter plot of daily ambient and internal temperature ranges in a *Camponotus pennsylvanicus* (DeGeer) occupied nest over 52 wks. Each dot represents the range as calculated by $\text{Range}_{\text{diff}} = (A_{\text{max}} - A_{\text{min}}) - (I_{\text{max}} - I_{\text{min}})$. Regression curves illustrate trends in the temperature ranges over 52 wks.

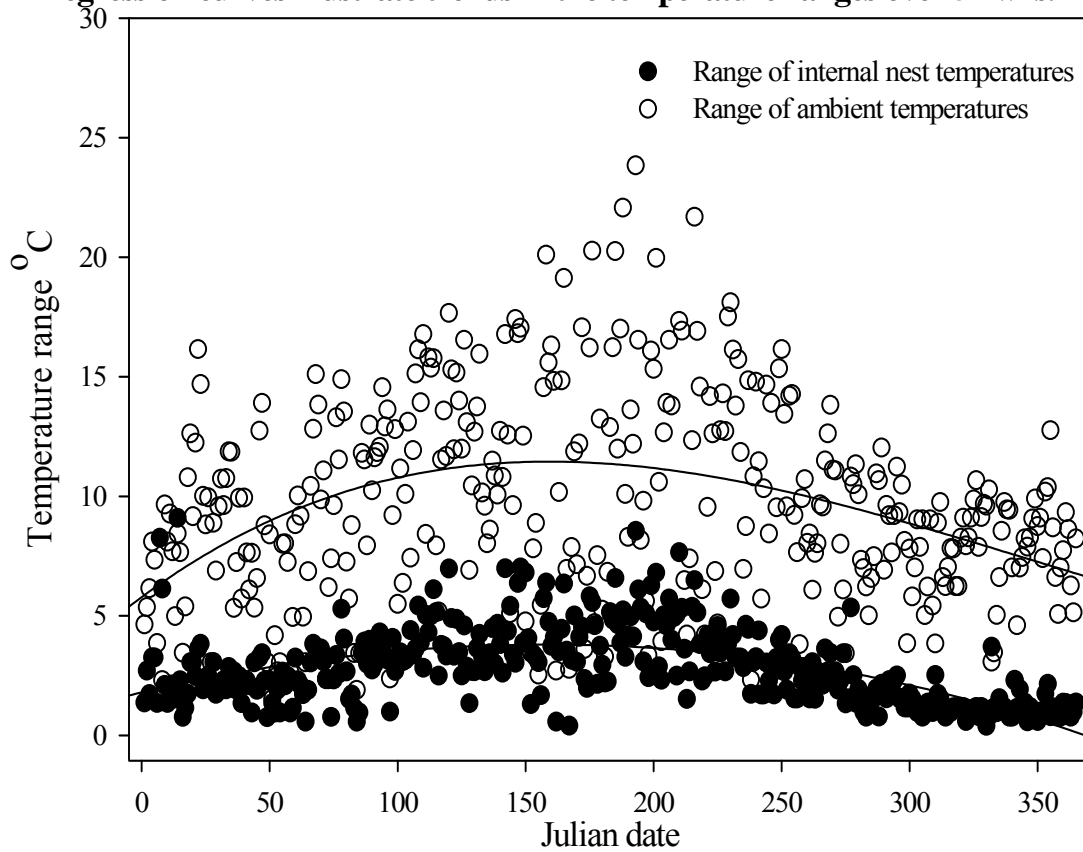
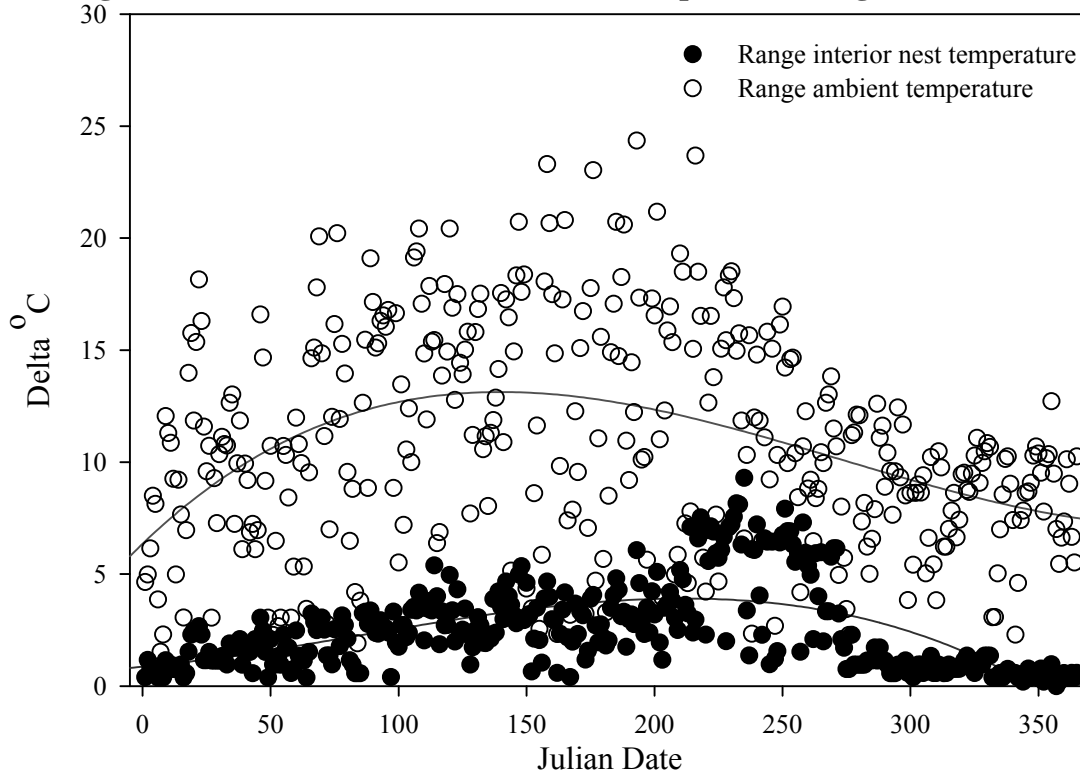


Fig. 5. Scatter plot of daily ambient and internal temperature ranges in an unoccupied *Camponotus pennsylvanicus* (DeGeer) nest over 52 wks. Each dot represents the range as calculated by $\text{Range}_{\text{diff}} = (A_{\text{max}} - A_{\text{min}}) - (I_{\text{max}} - I_{\text{min}})$. Regression curves illustrate trends in the temperature ranges over 52 wks.



Seasonal Comparison of Internal Temperature Ranges

Seasonal differences of internal temperature ranges in both nest types were not significantly different (Table 4). Internal nest temperatures of occupied nests mirrored unoccupied within the same season. Winter and spring seasons had the highest range fluctuation, with spring being the highest for both nest types 2.98 – 3.03°C. This is probably due to the thermal conductivity of the cellulose and fluctuations of ambient temperatures.

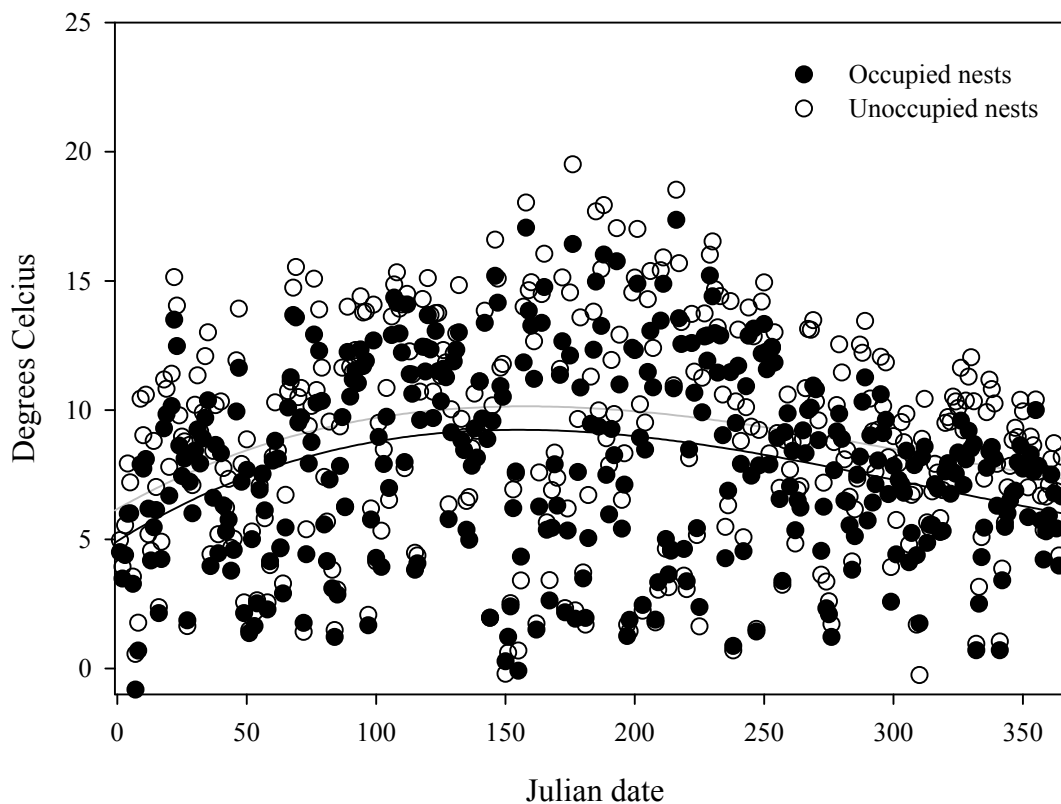
Table 4. Internal temperature range differences as calculated by $\text{Range}_{\text{diff}} = (A_{\text{max}} - A_{\text{min}}) - (I_{\text{max}} - I_{\text{min}})$ in occupied vs. unoccupied *Camponotus pennsylvanicus* (DeGeer) nests by season.

Season	Occupied		Unoccupied		<u>t-test for nest type effect</u>		
	n	Mean (\pm SE)*	n	Mean (\pm SE)*	t	df	P
Fall	90	1.92 \pm 0.27a	90	1.85 \pm 0.27a	.18	178	.8584
Winter	90	2.70 \pm 0.33a	90	2.68 \pm 0.33a	.11	178	.9115
Spring	90	3.03 \pm 0.33a	90	2.98 \pm 0.33a	0.05	178	.9584
Summer	95	1.76 \pm 0.19a	95	1.44 \pm 0.19a	1.19	188	.2366

* Means within rows followed by the same letter are not significantly different based on Fisher's LSD test at $P = 0.05$.

Cannon and Fell (1992) reported similar findings and noted no evidence of thermoregulation during their study period. The relationship of internal nest temperatures in occupied and unoccupied nests are illustrated in Fig. 6. Regression curves show similar trends in internal temperature ranges throughout the study period. Seasonal breakdowns of internal nest temperature ranges of occupied and unoccupied nests are available in appendix A (Figs. 9 - 12). Greaves (1964) reported that winter nest temperatures were approximately 9°C above the surrounding wood. No comparisons were made using ambient temperature, so direct correlations cannot be made. Fall and summer temperature ranges were lower (Table 4) for both occupied and unoccupied nests. This is possibly due to the lower temperature fluctuations from a diurnal to nocturnal time period rather than a biological mechanism.

Fig. 6. Scatter plot of mean differences in internal temperature ranges for occupied and unoccupied *Camponotus pennsylvanicus* (DeGeer) nests over 52 wks. Regression curves illustrate overall trends in the data.



Several factors could explain the lack of thermoregulation in *C. pennsylvanicus* nests. Large colonies can split into one or more satellite nests. The primary nest is usually in a humid area and contains the queen, eggs and early instar larvae (Hansen and Akre 1990). Satellite nests are usually in a drier, warmer environment and contain workers, mature larvae, pupae and winged reproductives (Hansen and Akre 1990). Satellite nests break up the colony population, potentially reducing its size and metabolic output because larvae are essentially separated into two groups. Overall, *C. pennsylvanicus* has fewer colony members than *C. herculeanus* (L.), *C. modoc* Wheeler, and *C. vicinus*

Mayr, so the metabolic heat generated by these larger colonies, if placed in the same nesting material, could generate enough metabolic heat to alter the internal nest microhabitat. Because South Carolina is at the southern end of the black carpenter ant's range, geographic studies using the same experimental parameters may yield different results. Climactic differences coupled with larger colony sizes in the northern range could show results similar to those reported by Sanders (1972).

According to my results, *C. pennsylvanicus* is unable to actively regulate its internal nest environment. Therefore, I accept my original hypothesis that *C. pennsylvanicus* nest temperature is not significantly different from ambient. My conclusion corroborates that of Cannon and Fell (1992), that the wood itself acts as a temperature buffer and reduces erratic fluctuations in the nest. *Camponotus pennsylvanicus* in South Carolina does not appear to possess the ability to actively alter the nest microclimate. However, this should not be taken as a blanket statement for other geographic regions the black carpenter inhabits. Because South Carolina is at the southern extent of its range, behavioral differences may exist in northern areas where it is found. Future research should explore the possibilities of regional effects on nest temperature because areas of the northern U.S. and southern Canada have drastically different weather extremes than the southern U.S. Because black carpenter ants have larger colonies and more satellite nests in its northern range, one could speculate that they may have behavioral modifications working in concert with physiological adaptations in other regions to cope with extreme cold that are not needed in its southern range. Additional areas of focus could include expanding this study to investigate three areas of

temperature comparisons: tree, nest, and ambient. Comparing all three areas could provide a clearer picture of nest microclimate, especially if nests in multiple regions were included in the experimental model.

Applied aspects of my research are less tangible than the ecological ones. While nests temperatures are not directly related to insecticide efficacy or monitoring, there are indirect uses of the inspection methods used to locate nests that can be useful to pest management professionals. Technological improvements to the inspection process have seen introductions of infrared cameras, borescopes, and microwave emitting detectors. All of these tools have useful benefits but cannot replace a thorough inspection with the human eye. Using an infrared camera for finding carpenter ant nests in trees has limited applicability and a low success rate. The water jacket surrounding the tree masks any significant heat signatures emanating from the nest. The infrared picture included in this chapter was a unique find, but was the only one located using a camera. To find nests in trees, a greater level of success was obtained using visual inspections, then pinpointing possible galleries with the microwave-emitting detector, followed by internal verification using a borescope.

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CHAPTER IV

IMPACT OF FORAGING DISTANCE ON NUTRIENT SELECTION BY THE BLACK CARPENTER ANT, *CAMPONOTUS PENNSYLVANICUS* (DEGEER)

Introduction

One of the most important aspects of a eusocial insect society is the ability to locate and gather large quantities of food. Foraging strategies used by ants are the subject of significant conjecture and are extensively reported in the literature. Food resources encountered, in part, are selected based on forager age, caste and prior experience (Traniello 1989). Additional selection parameters may be thermal stress on the forager, resource quality and quantity, physical properties of the food particle, and the colonies current nutritional requirements (Hooper-Bùi et al. 2002, O'Brien and Hopper-Bùi 2005, Traniello 1989). Inherent problems with labeling foraging patterns are that ants maybe pigeon-holed into one type of foraging strategy based on the parameters of a given experiment. In reality, multiple factors may control colony and individual foraging dynamics, especially over time (Bristow and Yanity 1999, Traniello 1989).

Ants bound to a central nest face difficulties in foraging that optimize their ability to obtain energy sources (Hölldobler and Wilson 1990). Maximizing net energy yield is one aspect of central-place foraging (CPF) theory. Within social insects, energy costs can be spread by communication of the spatial distribution of food items to a large number of foragers (Hölldobler and Wilson 1990). The theory assumes that individual fitness increases if the net rate of energy is maximized while foraging (Schoener 1971, Orians and Pearson 1979). Applying CPF to social insects should assume that colony fitness

increases by maximizing net rate of energy intake during foraging. Maximizing net energy intake should be important to ants because large numbers of “energy packets” are produced in the form of nonreproductive workers (Hölldobler and Wilson 1990). The expense of nonreproductive workers also may increase overall fitness through cooperative foraging, allowing reproductives to maximize net energy intake for the purposes of egg production instead of diverting energy and time into costly foraging (Oster and Wilson 1978).

Maximizing net energy return is achieved by ranking food items by expected net energy content (C) divided by expected handling time (t_H) (Orians and Pearson 1979). Handling time includes pursuit, capture, consumption, and any mandatory post-consumption pauses (Orians and Pearson 1979). Food items included in the optimum set have a higher C/t_H than the value of energy intake if the prey were ignored and the forager sought only food items with a higher C/t_H (Orians and Pearson 1979). The basic consideration in CPF theory is the round trip, consisting of (a) an outbound trip to a food patch (b) a foraging period, and lastly (c) a return trip (Orians and Pearson 1979). Energy is expended in all three trips but is higher in the return trip considering a load cost from prey handling (Orians and Pearson 1979). Load costs increase if the forager has ingested part of the food item for its own use. This may be necessary because returning to the central place without a food item is not advantageous and the nutritional requirements of the forager must be met (Orians and Pearson 1979). It is therefore advantageous to the forager to maximize its net energy gain when distance traveled or handling time is considered. However, assuming large metabolic costs of the forager during its round trip

may lend credence to factors that are of lesser importance. Fewell (1988) reported that metabolic costs for *Pogonomyrmex occidentalis* (Cresson), western harvester ant, were less than 0.1% of the caloric content of the average seed collected. But, specific foraging patterns with respect to longer distances (>10 m) and spatial heterogeneity of food patches make blanket metabolic costs appear inaccurate. Schoener (1971) suggests that a predator should take a larger prey (>*C* value) with greater distances traveled and that size limits of prey should decline less and size limit should increase with distance. The model proposed by Orians and Pearson (1979) predicts that a predator (forager) would be least selective (choose from a broader range of food items) at intermediate distances, while Schoener's model (1971) predicts increased selectivity with increased distance (Elliott 1988).

For *Camponotus pennsylvanicus* (DeGeer) to adhere to the theory of CPF it must alter its food preference and opt for a higher net return to compensate for the distance traversed to a food patch. To simplify the concept, a *C. pennsylvanicus* forager must gather higher nutritionally rewarding food (high *C*) with a corresponding increase in travel time. This selection for higher energy return should be based on colony requirements and apparent in both carbohydrate and protein foraging. Davidson (1978) reported that *Pogonomyrmex rugosus* Emery, rough harvester ant, took a narrower range of barley seeds as distance to the food patch increased. Foragers consistently overlooked the smaller seeds for larger ones, presumably based on caloric value (Davidson 1978). In a similar study by Rissing and Pollock (1984), *Messor* (= *Veromessor*) *pergandei* (Mayr) was reported to generally increase their search time with increased distance traveled;

however, no difference in seed selectivity could be determined. In a study with *Camponotus gigas* (Latreille), Pfeiffer and Linsenmair (1998) reported that within the minors, a physical subcaste of transporters behaved according to CPF theory. Franson (1985) reported that *Formica nitidiventris* (Emery) and *Myrmica americana* (Weber) are non-optimal central place foragers because their foraging territory was not centered with the colony entrance. Adler and Gordon (2003) reported that alterations in foraging patterns and selectivity at the individual and colony level could be attributed, in part, to resource depletion and costs associated with conflict.

Feeding duration, using liquid food sources, in ants is not well studied. Several studies have looked at carbohydrates and amino acid (protein) foods, or a combination of both, only with regard to preference (Hooper-Bùi et al. 2002, Lanza 1988, 1991, Lanza et al. 1993, Sakamoto and Yamane 1997, Kay 2002, 2004, Bristow and Yanity 1999). However, a directly related aspect was reported by O'Brien and Hooper-Bùi (2005), regarding liquid viscosity and crop filling. Their results showed that in red imported fire ants, *Solenopsis invicta* Buren, as viscosity of a sucrose solution increased, crop loads decreased. O'Brien and Hooper-Bùi (2005) surmised that a more viscous liquid ant bait would take longer to permeate the colony in its entirety. This may also tie in with load costs; because viscous liquids are denser and thereby cost the forager more with respect to metabolic energy usage.

The objective of this study was to examine the relationship of foraging distance to nutrient selection of *C. pennsylvanicus*, the black carpenter ant, in Upstate South Carolina. Differences between low and high concentrations of carbohydrate and protein

solutions were investigated at two distances to better understand foraging strategies used by this ant. Comparisons of feeding duration were also examined to determine if time spent imbibing a liquid source increased with a corresponding increase in distance to a food patch. I hypothesized that *C. pennsylvanicus* foragers select higher concentrations of carbohydrates/proteins with increasing distance to a food source.

Materials and Methods

Protein And Sucrose Preference

Prior to the experiment, preliminary tests were conducted to determine nutrient palatability and concentration to be tested. Two nutrient sources, carbohydrates and proteins, were selected as the nutritional base. Refined sugar was used as the sole carbohydrate source because it is a standard used in most experiments involving formicids (Greenberg et al. 2006). Nutritional studies using pure protein baits are conspicuously absent from the literature. Multiple studies have reported using other protein sources, e.g. peanut butter or macerated crickets, as a bait. These protein sources are not pure and contain other nutrients such as carbohydrates and lipids that increase variability for this study. Casein hydrolysate, enzymatic digest (USB Corp., Cleveland, Ohio) was selected as a pure protein source based on research by Kay (2002, 2004). Kay (2002) found casein was highly palatable to multiple species of Formicidae.

Multiple concentrations of sucrose and casein were evaluated to establish experimental minimum and maximum concentrations to be tested. Solutions of 1 – 30% w/v sucrose (in 5 % increments) and casein in dH₂O were evaluated in a preliminary field test for acceptance by *C. pennsylvanicus*. Casein concentration was capped at 30%

because higher concentration solutions were unstable. Sucrose concentrations were capped to match those of the casein. *Camponotus pennsylvanicus* foragers' readily accepted 30% sucrose/casein solutions. Minimum concentration was set at 5% since foragers failed to accept lower levels.

Nest Selection

Black carpenter ant nests were located in trees at two locations on the Clemson University campus. Selection criteria for nests used in this study were that two separate foraging trails extended from the nest, and that a sufficient distance was maintained by the foraging trail as set by experimental parameters. Counts of adult foragers at a fixed point in the foraging trail were made approximately 30 min after sunset. Nests were then broken into three categories of low (≤ 50), medium (50 – 149), and high (≥ 150) populations based on the number of foragers counted during a five-minute period. Six nests ($n = 6$) with high populations of foragers with two foraging trails were used for this study. Nests were selected from two areas of the Clemson University campus ($34^{\circ} 40'38.15''$ N and $82^{\circ} 51'5.20''$ W) separated by 1.6 km.

Station Design and Arrangement

Feeding stations (Fig. 1) were constructed to hold liquid sucrose and casein solutions adjacent to black carpenter ant foraging trails. Stations were constructed of 100 x 15 mm Petri dish lids with a 9 mm hole drilled through the center to accommodate a 8 mm x 13 cm eyebolt. Two 3.8 cm diameter fender washers and nuts were placed on both sides of the Petri dish for stability. The eyebolt tip was ground to a point so that it could be inserted into the soil to anchor the station to the substrate. Filter paper was placed in

the station to use as a feeding substrate. Six feeding stations were placed adjacent to foraging trails at 1 and 15 m from the nest.

Fig. 1 Bait station constructed to hold liquid protein and carbohydrate solutions. Stations were designed to be secured into a soil substrate.



Fig. 2. Arrangement of liquid bait stations flanking a foraging trail of *Camponotus pennsylvanicus* (DeGeer). Stations were partially embedded into the soil to allow foragers easy access to station contents.



Concentration Preference Study

Feeding stations were placed 1hr prior to sunset at 1 and 15 m distances. Ten ml of solution was applied to the filter papered dishes 30 min prior to sunset to allow solutions adequate time to acclimate to ambient temperatures. Solution concentrations used for this test were, 5 and 30%, with dH₂O as a control. Sucrose and casein solutions were tested separately. Casein, was used in its pure form with no preservatives. Test concentrations were made daily and kept refrigerated until needed. Experiments were repeated three times (n = 3) over a 3 d period, with 7 d between nutrient types. Data were recorded every 10 minutes for a 2 h duration between 2100 and 2300 h. Numbers of ants

in stations imbibing liquid and encountering the food source (discovery, but no sustained uptake of liquid > 2 seconds) were counted at 10 min intervals for two hours.

A split plot in time with repeated measures design was used for this experiment. Distance was used as the whole plot treatment, while solution concentration was used as the split plot treatment. Data were analyzed using ANOVA (PROC GLM, SAS Institute 2004) for the split plot and means were compared using Fisher's LSD (Proc Mixed, SAS Institute 2004).

Feeding Duration Study

Six nests were randomly selected to test feeding duration at each concentration for sucrose and casein. Data were collected in conjunction with the preference study.

Carpenter ants were recorded (Handycam Vision, Sony Corp. Tokyo, Japan) at one nest per night at 1 and 15 m using the infrared feature of the camera. Feeding duration (time) was recorded for each ant feeding at each station. The experiment design was a split plot in time with repeated measures. Distance was used as the whole plot treatment while solution concentration was used as the split plot treatment. Data were analyzed using ANOVA (PROC GLM, SAS Institute 2004) for the split plot and means were compared using Fisher's LSD (Proc Mixed, SAS Institute 2004).

Results and Discussion

Comparison of Protein Concentrations

Mean number of black carpenter ants foraging at the 1 m casein food patch were significantly higher at the 30% concentration than the control at 1 m (Table 1). However, differences were not noted between 0 and 5% nor between 5% and 30%. More foragers

($\bar{x} = 21.83$) were observed at 30% casein than 5% ($\bar{x} = 8.15$). There were no significant differences at the 15 m distance for any casein concentration. Mean separation of casein at both distances when averaged together yielded similar levels of significance as those at the 1 m interval. Significance was only observed between 30% and 0% casein solutions.

Table 1. Selection of three concentrations of casein hydrolysate (0, 5 and 30%) in water by *Camponotus pennsylvanicus* (DeGeer) foragers (mean number \pm SE; n = 3)* over two distances (1, 15 m) during a two hour period.

Distance (m)	Percent Casein Hydrolysate			Distance Mean Averages
	0	5	30	
1	1.06 \pm 7.96 a	8.15 \pm 7.96 ab	21.83 \pm 7.96 b	10.35 \pm 5.71 A
15	0.56 \pm 7.96 a	16.40 \pm 7.96 ab	20.22 \pm 7.96 ab	12.39 \pm 5.71 A
Casein Mean Averages	0.81 \pm 6.76 A	12.28 \pm 6.76 AB	21.03 \pm 6.76 B	

* Mean comparisons based on Fisher's Protected LSD test at $\alpha = 0.1$, $df = 2$. Distance means followed by the same style capital letters are not significantly different. Casein means followed by the same style capital letters are not significantly different. Distance and casein means followed by the same style lower case letters are not significantly different.

In addition to within-distance comparisons mean separation was used to analyze differences in both 1 and 15 m distances within the same concentration (Table 1). Analysis showed distance was not significant for the mean number of ants feeding at each concentration. The mean distance averages for all concentrations were insignificant.

Black carpenter ants, based on these results, do not appear to adhere to CPF theory with respect to protein selection. Nor does their foraging resemble an optimal foraging model where food selection is based on optimizing calorie intake. To support the

original theory of CPF, the black carpenter ant should have optimized travel time and metabolic costs by selecting the 30% casein solution at the 15 m distance. However, because there were no significant differences between the high and low concentrations at either distance, alternate foraging theories may be considered. Observations of foragers while recording data showed that once foragers contacted either concentration of casein, all efforts were focused on exploiting that single resource. Intuitively, one would expect foragers, once the food source had been encountered, to recruit more individuals to search this food patch whereby the higher concentration solution or one of the additional low concentrations of casein could have been discovered because they were in relatively close proximity to the each other. This in turn would suggest an increased number of foragers recruited to the area to exploit this new food patch. This, however, was not observed. Another plausible explanation is that a 5% solution of casein has a sufficient amount of amino acids to meet the colonies protein requirements; therefore searching for a more nutritionally rewarding protein source would not be necessary. While this explanation of protein foraging is conceivable, it is probably the least likely because *C. pennsylvanicus* foragers are known to forage on live insect and other prey that would have a higher protein content than 5%. Several species of ants including *Camponotus* spp., feed on secretions from plant nectaries and homopteran honeydews (Bristow and Yanity 1999, Lanza et al. 1993, Sakamoto and Yamane 1997). These secretions are composed of carbohydrates, amino acids and lipids in varying concentrations, and ingredient components that are species and seasonally dependent (Bristow and Yanity 1999). Artificial honeydews modeled after secretions of homopteran plant feeders

contained between 1% and 4% amino acid concentrations, with only three constituent parts (Bristow and Yanity 1999). While these concentrations are present in natural sources, my preliminary study showed that *C. pennsylvanicus* did not feed on casein concentrations lower than 5%. In regard to protein foraging in black carpenter ants, I speculate that colony nutritional requirements (ie. brood, reproductive castes) cause foragers to exploit most nutritionally viable protein sources discovered because they are a limited resource and once discovered is used regardless of the inherent caloric value versus metabolic costs to the forager.

Comparison of Sucrose Concentrations

Mean number of foragers at each solution concentration at the 1 m distance was not significant (Table 2). Mean number of ants foraging at 5% sucrose was 9.24 while at 30% the mean was 23.06. Even though larger numbers of foragers were noted at the higher concentration, experimental variability was large enough to overshadow the effects. The data trend indicates that foragers did not prefer a higher concentration of sucrose at 1 m even though foragers sampled both solutions. Solution concentration at 15 m was significant. While there was no significant difference between 0 and 5% sucrose concentrations, there was a significant difference between forager numbers at the control (0) and low concentration sucrose ($\bar{x} = 1.53$) versus the higher 30% solution ($\bar{x} = 61.11$), suggesting that foraging carpenter ants selected the higher concentration at the greater distance. Mean separation of sucrose across both distances within the same concentration was significant for only the 30% casein solution. This seems apparent

because foragers fed almost exclusively on the 30% solution at 15 m; whereas both solutions were fed on at the 1m distance.

Table 2. Selection of three concentrations of sucrose (0, 5 and 30%) in water by *Camponotus pennsylvanicus* (DeGeer) foragers (mean number \pm SE; n = 3)* over two distances (1, 15 m) during a two hour period.

Distance (m)	Percent Sucrose			Distance Mean Averages
	0	5	30	
1	0.06 \pm 8.32 a	9.24 \pm 8.32 a	23.06 \pm 8.32 a	10.78 \pm 4.89 A
15	0.00 \pm 8.32 a	1.53 \pm 8.32 a	61.11 \pm 8.32 b	12.39 \pm 4.89 A
Sucrose Mean Averages	0.03 \pm 5.93 A	5.38 \pm 5.93 A	42.08 \pm 5.93 B	

* Mean comparisons based on Fisher's Protected LSD test at $\alpha = 0.1$, $df = 2$. Distance means followed by the same style capital letters are not significantly different. Sucrose means followed by the same style capital letters are not significantly different. Distance and Sucrose means followed by the same style lower case letters are not significantly different.

Camponotus pennsylvanicus appears to use a CPF strategy with regard to sucrose selection. For carpenter ants to adhere to the model, there should be no preference between the low and high concentration of sucrose at 1m. The data in this study support the CPF model. Additionally, as distance to a food patch increases, so should the selection criteria used by the forager. As my data indicate, *C. pennsylvanicus* selected a higher concentration of sucrose as the distance from a food patch to the nest increased to 15 m. These data also corroborate visual observations made during my data collection. Ants were routinely observed testing several dishes at 15 m before selecting the 30% concentration. Once a forager had located the highest concentration, recruitment to the dish was rapid and involved a large number of nestmates.

Casein Feeding Duration

Mean feeding duration indicated that foraging black carpenter ants fed differentially on casein solutions, depending on concentration or distance. At 1 m there was a significant difference observed between mean feeding duration between the 5 and 30% casein concentrations (Table 3). Feeding time at 5% casein was approximately 47.76 s with an average time of 60.48 s at the higher concentration. Similar results were noted at the 15 m distance where the mean time spent feeding at the 5% solution was significantly shorter (53.30 s) than mean time spent at 30% (58.40 s). However, the time interval had increased with the corresponding increase in distance and was approaching the mean time of the higher solution. Overall casein mean feeding time was significant, suggesting black carpenter ants feed longer on 30% casein solution regardless of the distance involved. Additional analysis showed that the effect of distance on feeding duration was only significant at a 5% solution concentration.

Table 3. Feeding times (sec.) of three concentrations of casein (0, 5 and 30%) in water by *Camponotus pennsylvanicus* (DeGeer) foragers (mean seconds \pm SE; n = 3)* over two distances (1, 15 m) during a two hour period.

Distance (m)	Concentration		Distance Mean Time
	5	30	
1	a 47.76 \pm 1.92 a	a 60.48 \pm 1.92 b	a 54.12 \pm 1.43
15	b 53.30 \pm 1.92 a	a 58.40 \pm 1.92 b	a 55.85 \pm 1.43
Casein Mean Time	50.53 \pm 1.43 a	59.44 \pm 1.43 b	

* Means within *columns* or rows followed by the same style letter are not significantly different based on Fisher's Protected LSD test at $\alpha = 0.1$, $df = 6$.

Sucrose Feeding Duration

Similar results were found in relation to mean time spent feeding on two different solutions of sucrose as were found in casein (Table 4). Feeding duration at 1 m was significantly different at a 5% concentration (8.15 s.) than at 30% (31.28 s). Mean time at 15 m also was significant, with foragers imbibing 30% sucrose (46.04 s) longer than 5% (9.13 s). Overall mean feeding time was also significant, suggesting feeding interval was greater on 30% over both distances. Feeding durations within concentrations across distances was significant for only 30% sucrose. One-meter feeding times were shorter, with a mean of 31.28 s versus the 46.04 s observed at the highest concentration.

Table 4. Feeding times (s) of three concentrations of sucrose (0, 5 and 30%) in water by *Camponotus pennsylvanicus* (DeGeer) foragers (mean seconds \pm SE; n = 3)* over two distances (1, 15 m) during a two hour period.

Distance (m)	Concentration		Mean Time
	5	30	
1	<i>a</i> 8.15 \pm 5.05 <i>a</i>	<i>a</i> 31.28 \pm 5.05 <i>b</i>	<i>a</i> 19.72 \pm 3.94
15	<i>a</i> 9.13 \pm 5.05 <i>a</i>	<i>b</i> 46.04 \pm 5.05 <i>b</i>	<i>a</i> 27.58 \pm 3.94
Sucrose Mean Time	8.64 \pm 3.94 <i>a</i>	38.66 \pm 3.94 <i>b</i>	

* Means within *columns* or rows followed by the same style letter are not significantly different based on Fisher's Protected LSD test at $\alpha = 0.1$, $df = 6$.

Drawing on the results of these data, feeding durations vary with distance and concentration. While I am not aware of any model that predicts feeding times based on distance or solution concentrations, duration may be, in part, related to concentration selection. Foragers contacting casein failed to select the higher concentration at greatest

distance tested however, feeding time was higher at both distance intervals suggesting that density of the solution may affect the ability of the forager to quickly imbibe the higher concentration. At the lower concentration of casein, the feeding duration increased. Because there would be no physical differences between these solutions the distance factor must play into a decision for the forager. Therefore, a greater amount of solution should be taken to account for the increased amount of distance, even though the protein food source is of a lower nutritional value.

The distance and concentration interplay of solutions is also interesting, suggesting a dual modality of behaviors used by *C. pennsylvanicus* foragers. At 1 m, there was no difference in sucrose selection by foragers, but there was a difference in the amount of time spent feeding on the solution. The functionality of this at the shorter distance may indicate there is an inherent solution density difference in uptake rate because metabolic load costs to the forager would be equal if the amount of intake into the crop were the same. Distance effects show up at 15 m, but only with 30% sucrose, because like casein, the physical attributes of the same solution are identical with the only difference being distance. The data indicate that foragers spend a greater amount of time feeding on 30% sucrose at 15 m than at 1 m. It appears that the increased feeding time is due to the forager maximizing the amount of material uptake into the crop because the metabolic load cost has increased.

Conclusions

Foraging in black carpenter ants cannot be placed under a single strategy type. Preference studies often use a single food type, most often sucrose, to explain foraging

patterns observed in a laboratory setting. The results are extrapolated so that inferences are drawn to broadly explain behaviors in natural settings. The inherent dangers are that a colony nutritional requirements are extremely dynamic and should be factored into an overall model to explain foraging strategies. My results indicate that black carpenter ants use multiple foraging strategies, depending on the type of food that may be required by the colony. While *C. pennsylvanicus* foraging on sucrose adheres to a CPF model, protein foraging does not. Therefore, I reject my hypothesis with regard to *C. pennsylvanicus* using CPF when gathering sources of protein, but accept it in relevance to sucrose foraging.

The value of this research as a tool in pest management should be applied to increasing the efficacy of existing carpenter ant bait products. Currently available commercial ant bait products, aside from fire ant baits, overwhelmingly use carbohydrates as the single food attractant. Protein matrices are often overlooked because they are more expensive to produce and have a shorter shelf-life than carbohydrate baits. Once powdered casein is brought into solution, it will denature within a few hours. Maintaining laboratory colonies of black carpenter ants on casein was possible by adding preservatives commonly found in most published Lepidoptera larval diets (Raulston Lingren. 1972). Preservatives added to casein allowed the solutions to remain palatable for 7 days at room temperature. Commercial production of viable protein bait, like casein, would give pest management professionals a valuable tool to use in conjunction with carbohydrates for control of *C. pennsylvanicus*.

In addition to recognizing the value of protein baits, a better understanding of foraging strategies for both types of food sources could enhance existing bait placement strategies. Multiple bait placements should be made at intervals along a column of foraging carpenter ants. Placing high carbohydrate concentrated baits close to the nest may not evoke a foraging response. Carbohydrate based baits should be placed farther away from the nest where active foraging is observed.

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SUMMARY AND DISCUSSION

Nest Site Preference Of Black Carpenter Ants In Forested Habitats

Nesting sites of *Camponotus pennsylvanicus* (DeGeer) in natural settings are cryptic and may use several types of cellulose-based substrates in which to nest. The dominant nest substrate used by *C. pennsylvanicus* in my study was hardwood trees in the genus *Quercus*. *Pinus* spp. logs and *Quercus* spp. stumps also served as suitable nesting substrates, but in lower abundance. Data taken of broad habitat features, often observed in association with nests of *C. pennsylvanicus*, were not positively correlated with nest presence.

Analysis of individual nests yielded identification of several characteristics of nesting medium. *Camponotus pennsylvanicus* nests were in logs and stumps where < 40% of the cellulose was consumed by wood destroying fungi. Non-nest logs and stumps often had higher percentages of decay and were easily torn apart for examination. The structural integrity of these nest-absent substrates was severely compromised, limiting long-term viability as a stable nesting medium. Log length was important in nest selection, where nest-present logs averaged over 9 m in length.

Nest-present substrates were invariably in trees that contained the nest prior to felling, as with *Quercus* spp. in which mature nests were often documented. Nests in pine logs, *Pinus* spp., were often small founding colonies or satellite nests that occupied the substrate after tree decline and fall.

Several features made standing trees with active nests discernable from those without nests. Hardwood trees containing nests were a larger diameter than trees without

a nest. Diameter directly relates to maturity indicating larger older trees had a higher likelihood of containing a nest than did smaller, younger trees.

Some defects and the presence/absence of *C. pennsylvanicus* nests in trees were positively correlated. For *C. pennsylvanicus* to infest a standing hardwood tree, an injury must exist to allow the ants to circumvent the tree's defensive mechanisms. Injuries allow fungi to invade and destroy the heartwood of the tree, which *C. pennsylvanicus* excavates as a nest site. The most common type of defect found in conjunction with *C. pennsylvanicus* nests were tree holes. Holes are a visible sign of damage to the tree core and one that foragers use as a point of entry and egress from the nest. Another defect associated with nests is a crotch. Tree crotches are areas where two or more main areas of the trunk split off, or at the apex of the trunk where multiple main branches form an attachment. This area collects water and detritus that can facilitate entry of fungi into the tree.

Temperature Regulation of Black Carpenter Ant Nests

The ability to alter habitat microclimate is a unique characteristic found in some species of eusocial formicidae. Studies have shown that internal nest temperatures of *C. pennsylvanicus* are warmer than the surrounding tree but track ambient temperature in a similar, but less variable pattern during periods of wide temperature ranges. My study investigated internal and ambient temperatures in both occupied and unoccupied nests to determine if *C. pennsylvanicus* could regulate nest microclimate.

The results indicate that internal temperature range is less than ambient temperature range in both occupied and unoccupied nests. Temperatures inside the nest

of both occupied and unoccupied nests mirrored mean ambient temperature, but fluctuated by only 2 –3°C regardless of season. Mean ambient temperature had a larger temperature range of approximately 9 – 13°C over 52 wks. When the data were analyzed by season, summer temperature range was the narrowest, regardless of nest activity, while spring temperature range was the widest. In addition, internal temperature ranges of occupied and unoccupied nests were not statistically different. If *C. pennsylvanicus* actively regulated nest temperature, my data would indicate elevated temperatures during cold periods, possibly emanating from metabolic heat. Because internal temperature differences did not exist between occupied and unoccupied nests, *C. pennsylvanicus* in trees in this study relied on the nest substrate, which is often large oak trees, *Quercus* spp., to dampen temperature extremes.

Distance Effects on Nutrient Selection of Black Carpenter Ants

The ability of *C. pennsylvanicus* to locate, gather, and distribute large quantities of food is important to its survival. Food selection in *C. pennsylvanicus* is dynamic and based on nutrient requirements of various castes within the colony. Individual foragers must obtain food in an efficient manner, optimizing effort.

Foraging strategy in *C. pennsylvanicus* cannot be explained under one model because foraging behavior is modified in response to food selection, colony nutritional requirements, and distance traversed. *Camponotus pennsylvanicus*' response to a 5% and 30% sucrose solution after traversing either 1 or 15 m indicated that as distance increased to the food patch, foragers became more selective and opted for the highest sucrose solution (30%), even when it was less abundant. However, at 1 m foragers fed from both

5 and 30% solutions equally without discrimination. This selectivity has been theorized to maximize the caloric intake to compensate the forager for increased travel time and metabolic load costs. With regard to carbohydrate selection in my study, *C. pennsylvanicus* foraging adhered to a central place foraging model.

Forager response to varying concentrations of casein (protein) was not as clear as their response to sucrose. The 1 or 15 m traveled had no observable effect on protein concentration selection by foragers. Both 5 and 30% casein solutions were readily imbibed and were heavily recruited to by nestmates once discovered. No additional behaviors were observed that suggested foragers were actively searching for additional protein sources after the original discovery, nor did recruitment shift to the higher concentration if it was discovered. *Camponotus pennsylvanicus*' response to different concentrations of protein is complex and attributed to the CPF model based on this study.

Discussion

Pest management professionals (PMP) are called upon daily to safely and effectively control a variety of household and structural insect pests. To be successful, PMPs must have a sound knowledge of a pest's biology to achieve control. Annually carpenter ant control is a multimillion dollar business in the U. S. Successful PMPs use many tactics to control *Camponotus* spp., including toxic baits, residual insecticides, and physical removal and exclusion. No single control method can manage or eliminate all pest colonies of *Camponotus* spp. Multiple tactics are needed in conjunction with extensive inspections to achieve an acceptable level of control. Increasing our knowledge

base on nesting and foraging behavior will lead to improved methods of carpenter ant control.

Little information is available on the nesting behavior of *Camponotus spp.*, and even less on *C. pennsylvanicus*. My research provided ecological information on the nest characteristics of *C. pennsylvanicus* colonies. In general, the current literature regarding *C. pennsylvanicus* biology and behavior is an amalgamation from several species across vastly different climactic regions. What was known regarding nesting behavior was that *C. pennsylvanicus* infests logs, stumps, and trees. Infested tree species were documented but this, too, was region-specific with little information regarding the southeastern range of this important pest. In South Carolina, according to my data, *C. pennsylvanicus* primarily nests in oak trees. (*Quercus spp.*). However, other tree species also were documented. I have observed *C. pennsylvanicus* nests in varying species of hardwood trees including *Fraxinus americana* (white ash), *Cornus florida* (flowering dogwood), *Betula nigra* (river birch), and *Prunus serotina*, (black cherry). While oak trees are dominant in the areas surveyed during this research project, I feel that this is of lesser importance than in almost every instance of *C. pennsylvanicus* nesting in trees suffering from heart rot fungi. This also applied to diameter at breast height (dbh) data. *Camponotus pennsylvanicus* may infest smaller trees, but more often, black carpenter ants nest in older mature trees. Large mature trees are prone to heart rot fungi indicating the relationship is one of a fungi/ant association rather than simply tree dimensions. Research to determine if *C. pennsylvanicus* can mechanically transmit the fungi commonly associated with heart rots could delineate this relationship and evaluate if this

is a primary vector able to introduce fungal spores into otherwise healthy hardwood trees. Previous research has documented that *C. pennsylvanicus* can mechanically transmit chestnut blight, *Cryphonectria* (= *Endothia*) *parasitica* (Murrill).

One area of the original data set that perplexed me was the lack of correlation between nests and vegetation density. After several years of locating nests, I never observed black carpenter ant nests in areas with dense undergrowth. My opinion is that it is an artifact of the predominately hardwood forest habitat. Because *C. pennsylvanicus* nests in hardwood trees, this type of dominant habitat has sparse undergrowth due to low amounts of sunlight available at the forest floor. A more extensive survey using larger plots might reveal a correlation between sparse vegetation and nest occurrence.

My results should help PMPs when inspecting for *C. pennsylvanicus* nests. One problem that PMPs face is not the inability to control a pest, but rather the time required to perform a thorough inspection. Inspections for *C. pennsylvanicus* in the Piedmont region of South Carolina should focus on large hardwood trees with visible signs of heart rot damage. These are evident by the presence of sometimes large holes and fungal bodies on the trunk of the tree. Logs approximately 9 m in length, also too should be inspected.

Because *C. pennsylvanicus* nests in hardwood trees, a question one may ask is, “Why”. Does the tree convey any benefit to the ant or is it the simple use of an unused niche? Studies with tree-nesting termites and another using *C. pennsylvanicus* report significantly warmer temperatures inside the nest than in the surrounding uninfested tree trunk. This implies active mechanisms are used to modify the internal nest temperature.

However, because the core of the tree is not alive, measurable metabolic activity should not be observed. I found no active means of nest thermoregulation by *C. pennsylvanicus*. This corroborates the study by Cannon and Fell (1992) characterizing *C. pennsylvanicus* nests in logs. Soil-nesting formicids use nest architecture, decomposition products, and other factors to artificially warm their nest to create optimal brood-rearing temperatures. I speculate this is in part to overcome the variable nature of soil-temperature fluctuations. By nesting inside a tree cavity, *C. pennsylvanicus* can use the buffering capacity of the tree and not waste vital resources to artificially control the internal nest microclimate. Ideally, there would be complementary mechanical or physiological mechanisms in place allowing the ants to maintain a constant nest temperature instead of reflecting ambient temperatures. My study should be expanded to include northern areas of the *C. pennsylvanicus* range, where tree species are different and winter temperatures are much colder than in South Carolina. Expanding the original study to include ambient, internal, and sound areas of the trunk could also be more informative in regard to heat loss or gain in nests. A regional study might show behavioral adaptations specific for the local climate and may show a gradation of mechanisms employed by *C. pennsylvanicus* within distinct geographies.

My foraging study of *C. pennsylvanicus* created more questions than it answered. My original assumption was that *C. pennsylvanicus* gathered food according to a central place foraging model (CPF). According to my data, this was true for sucrose solutions but not casein solutions. I suggest that foragers reacted to the sucrose solutions, following the CPF model because carbohydrates are a resource quickly disseminated within their own

caste. Metabolic costs from travel time and searching would necessitate maximizing nutrient selection by foragers because a large portion of the colony population feeds predominately on carbohydrates.

Protein foraging in *C. pennsylvanicus* in my study does not fit the CPF model because caloric intake is not maximized as distance to a food patch increases. If protein foraging fit the model, *C. pennsylvanicus* should have chosen the 30% at 15 m. Instead, foragers showed no preference and readily fed on 5% and 30% casein. Because my original hypothesis, in part, was not accepted, alternate hypotheses should be explored to help characterize protein foraging. Future research projects should explore the protein requirements needed for colony growth and spatial heterogeneity of protein sources. Nutritional requirements of a *C. pennsylvanicus* colony may not require high concentrations of protein although this does not adequately explain ants feeding on both 5 and 30% casein. Investigating the spatial heterogeneity of protein sources may reveal that naturally occurring prey are inconsistent and when encountered illicit a strong foraging response to maximize uptake.

Based on my results, feeding durations vary with distance and concentration. Whether or not those times lengthened due to increased liquid uptake or as a response to the solution's density or viscosity cannot be answered within the limitations of my study. While solution density and viscosity were not evaluated in this experiment, similar inferences could be drawn from other studies to explain the data in part. If a solution's density or viscosity is increased, uptake of fluid likely would lengthen and might

decrease the volume imbibed because the density of the solution might deceive the forager that it has a full crop when it is not.

The results of my foraging study has the most potential importance for the pest management of *C. pennsylvanicus*. During my observations of *C. pennsylvanicus* foraging on casein solutions, recruitment of other foragers was swift and continuous until the casein solution was depleted. The sucrose solution was readily fed on by foragers but they lacked the intensity at which they fed on the casein solutions. Commercial protein baits using casein are viable if simple preservatives are used to keep them from becoming rancid. Carbohydrate-based food baits are readily available but primarily affect the foraging caste, with varying degrees of control, because it is their dominant source of nutrition. Protein baits offered jointly with carbohydrate baits would have a greater ability to affect both brood and foragers, causing colony collapse.

LITERATURE CITED

Cannon, C. A., and R. D. Fell. 1992. Cold hardiness of the overwintering black carpenter ant. *Physiol. Entomol.* 17: 121-126.

APPENDIX

Fig. 1. Fall season (22 September - 31 December) ambient and internal temperatures ($^{\circ}\text{C}$) during a 24 h period in an occupied *Camponotus pennsylvanicus* (DeGeer) nest.

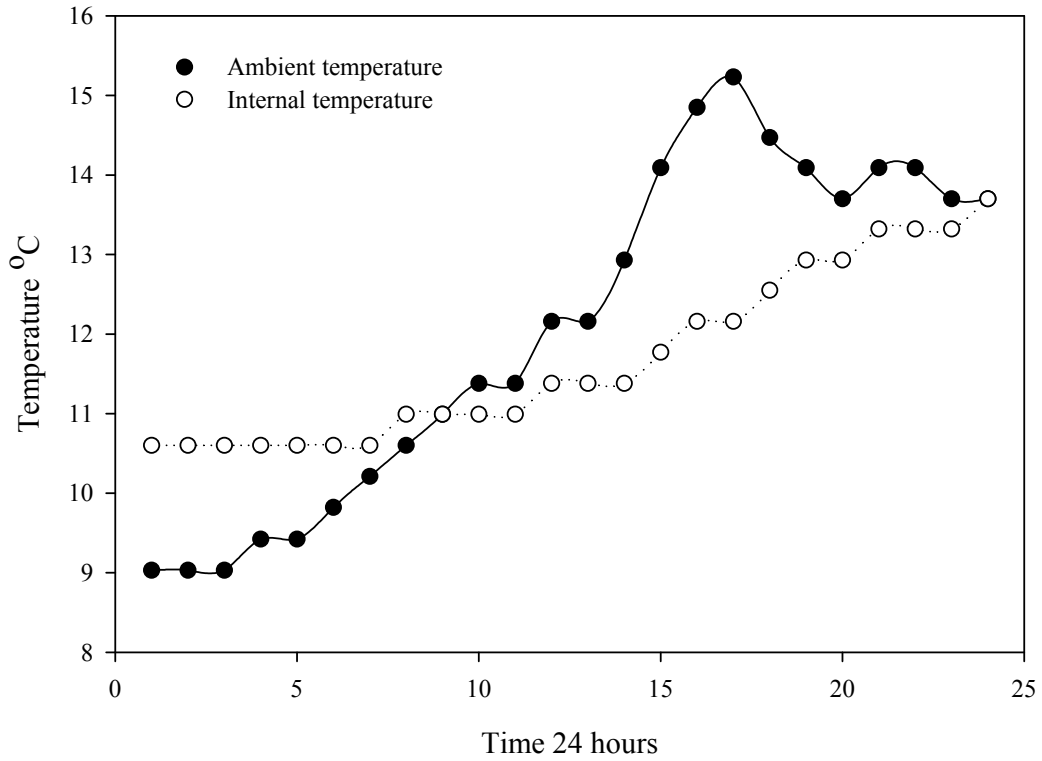


Fig. 2. Fall season (22 September - 31 December) ambient and internal temperatures (°C) during a 24 h period in an unoccupied *Camponotus pennsylvanicus* (DeGeer) nest.

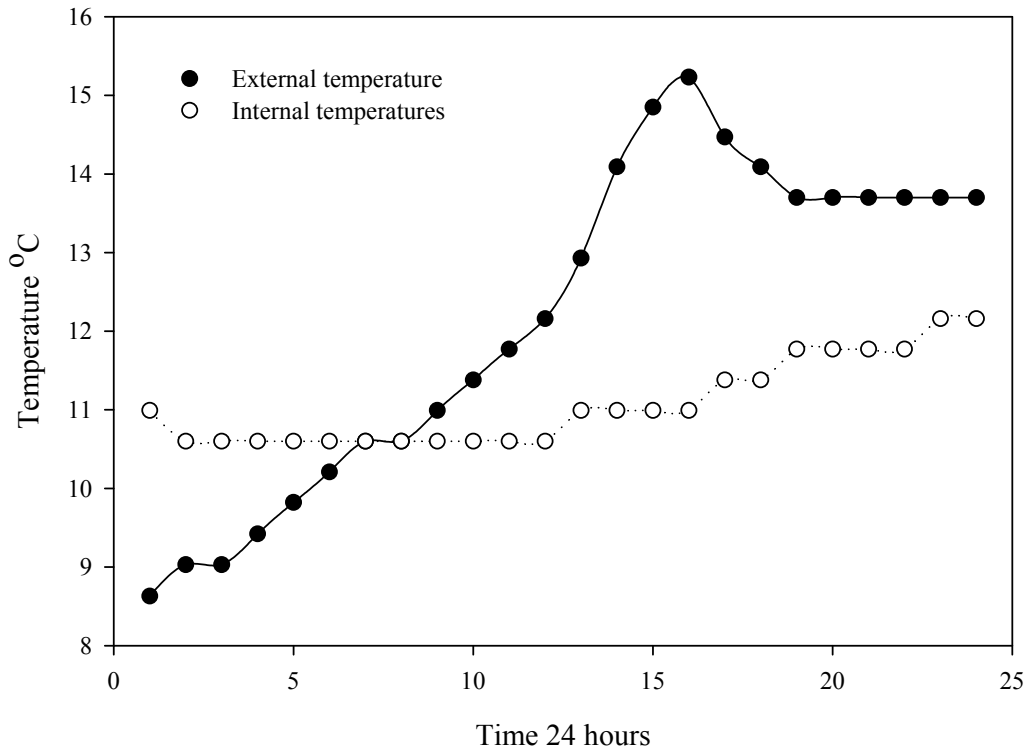


Fig. 3. Winter season (31 December- 20 March) ambient and internal temperatures ($^{\circ}\text{C}$) during a 24 h period in an occupied *Camponotus pennsylvanicus* (DeGeer) nest.

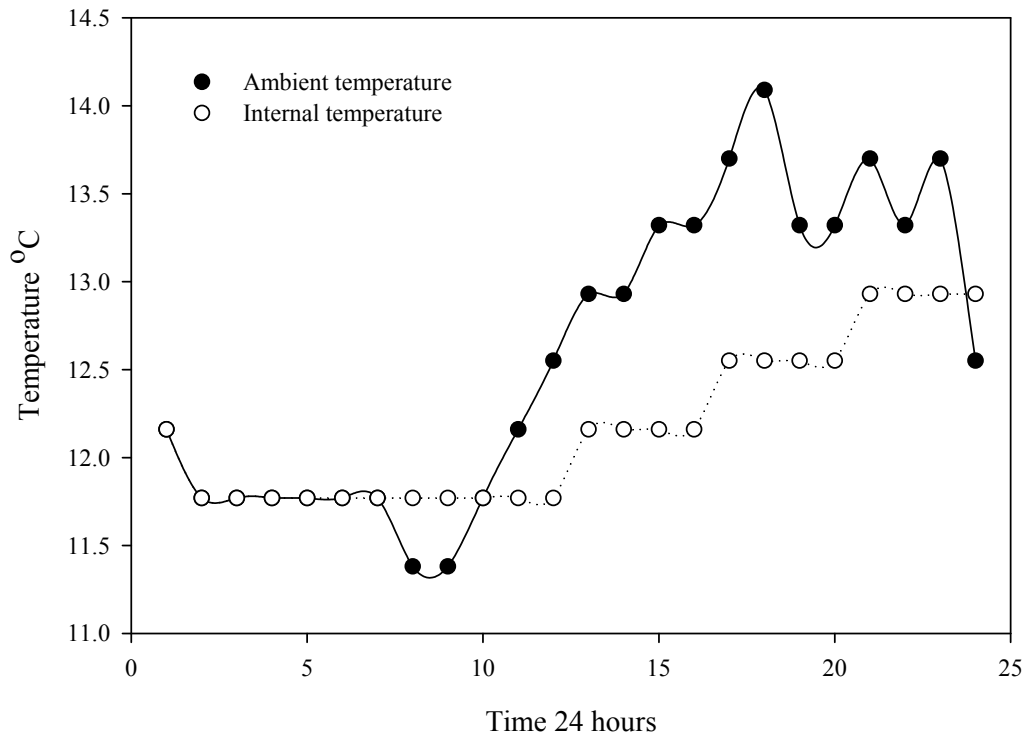


Fig. 4. Winter season (31 December- 20 March) ambient and internal temperatures ($^{\circ}\text{C}$) during a 24 h period in an unoccupied *Camponotus pennsylvanicus* (DeGeer) nest.

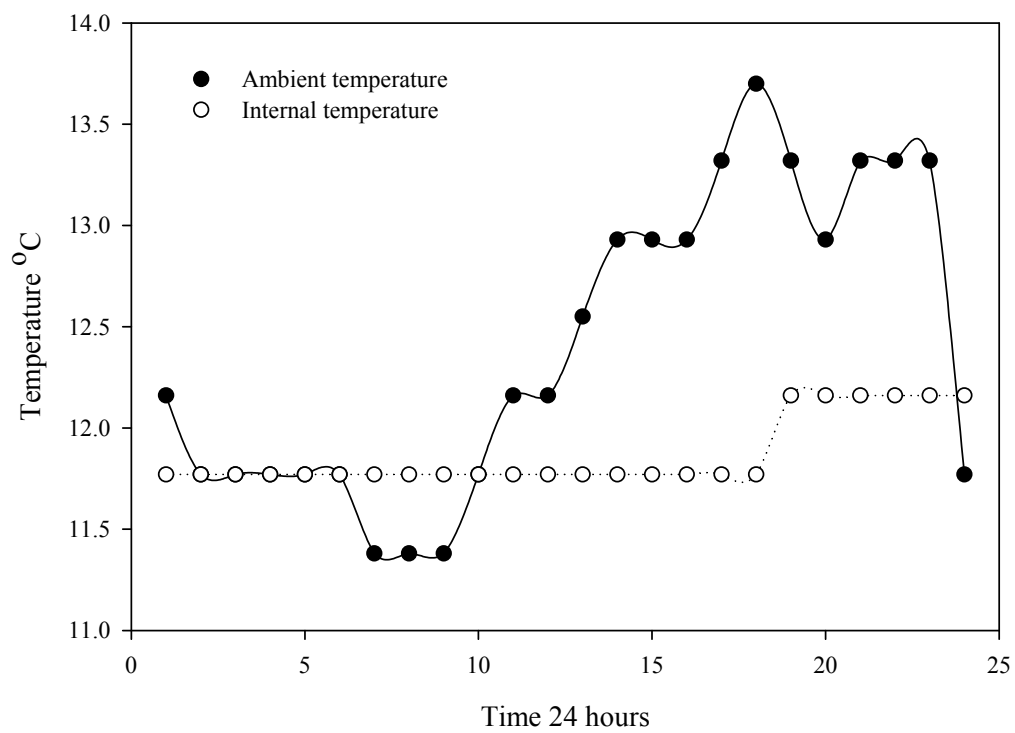


Fig. 5. Spring season (20 March - 21 June) ambient and internal temperatures ($^{\circ}\text{C}$) during a 24h period in an occupied *Camponotus pennsylvanicus* (DeGeer) nest.

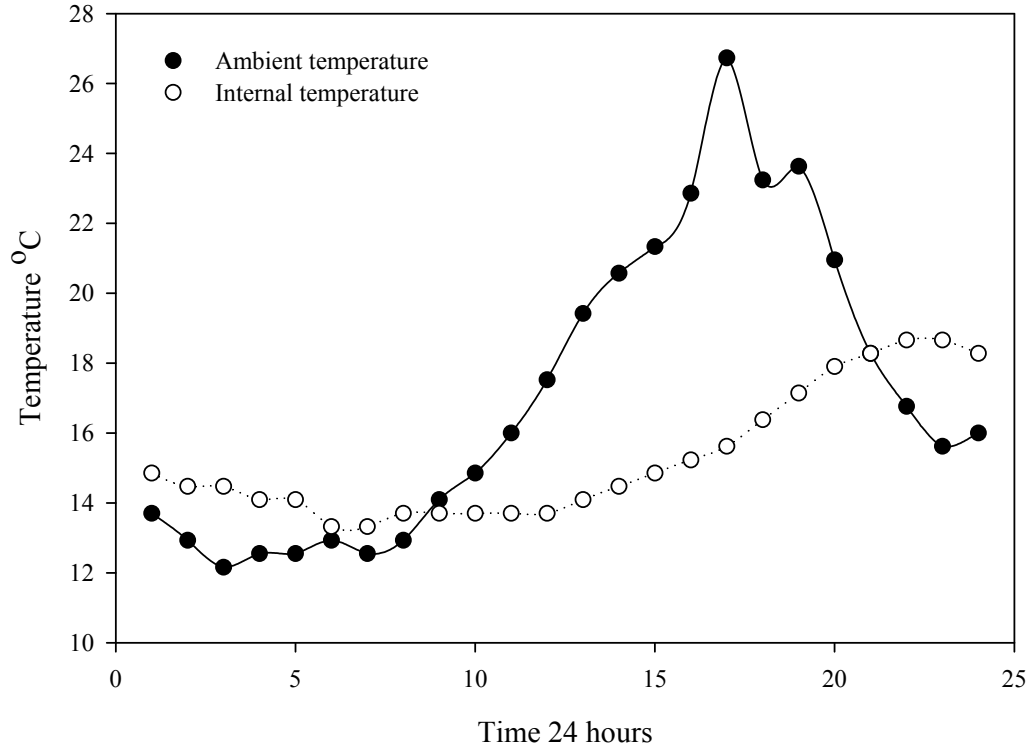


Fig. 6. Spring season (20 March - 21 June) ambient and internal temperatures ($^{\circ}\text{C}$) during a 24 h period in an unoccupied *Camponotus pennsylvanicus* (DeGeer) nest.

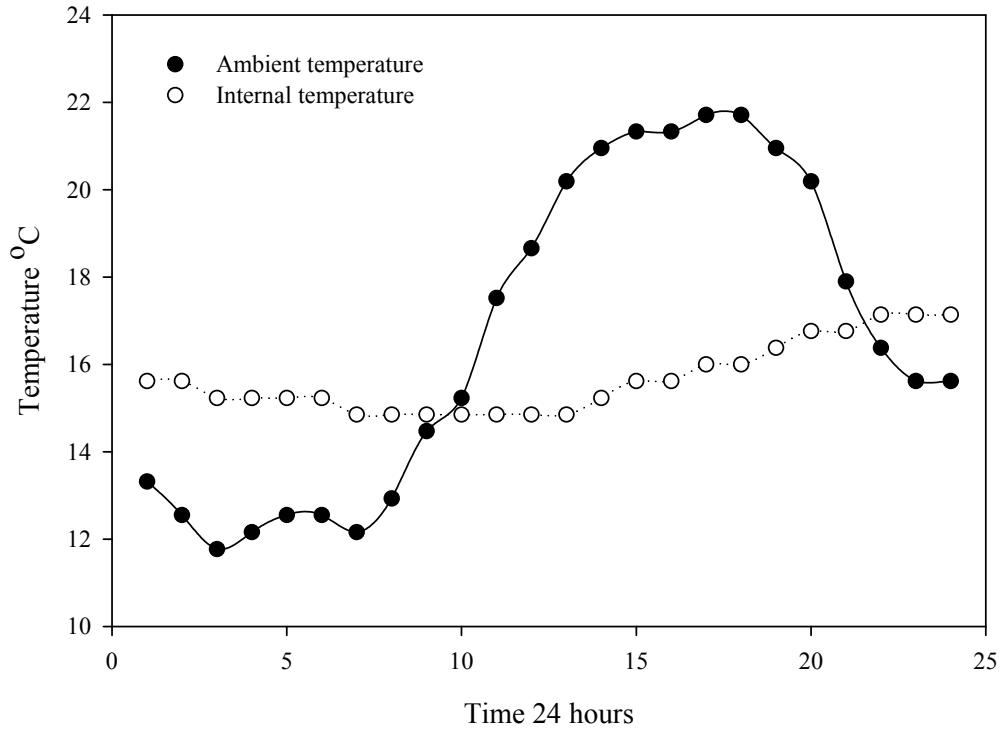


Fig. 7. Summer season (21 Jun - 22 September) ambient and internal temperatures ($^{\circ}\text{C}$) during a 24h period in an occupied *Camponotus pennsylvanicus* (DeGeer) nest.

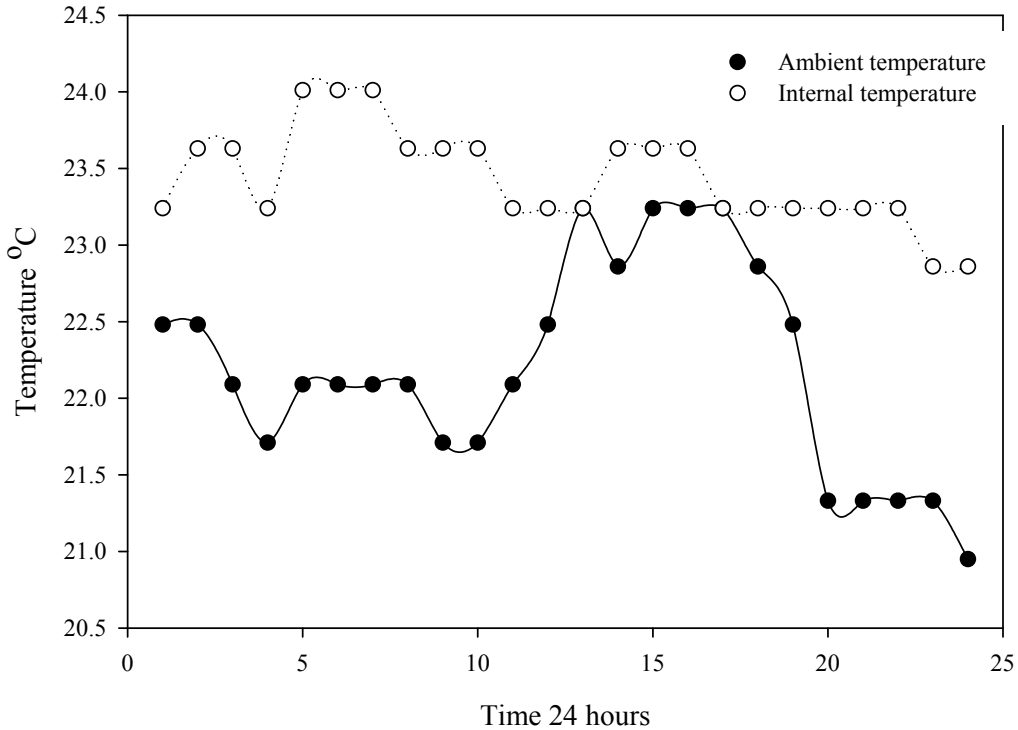


Fig. 8. Summer season (21 Jun - 22 September) ambient and internal temperatures ($^{\circ}\text{C}$) during a 24 h period in an unoccupied *Camponotus pennsylvanicus* (DeGeer) nest.

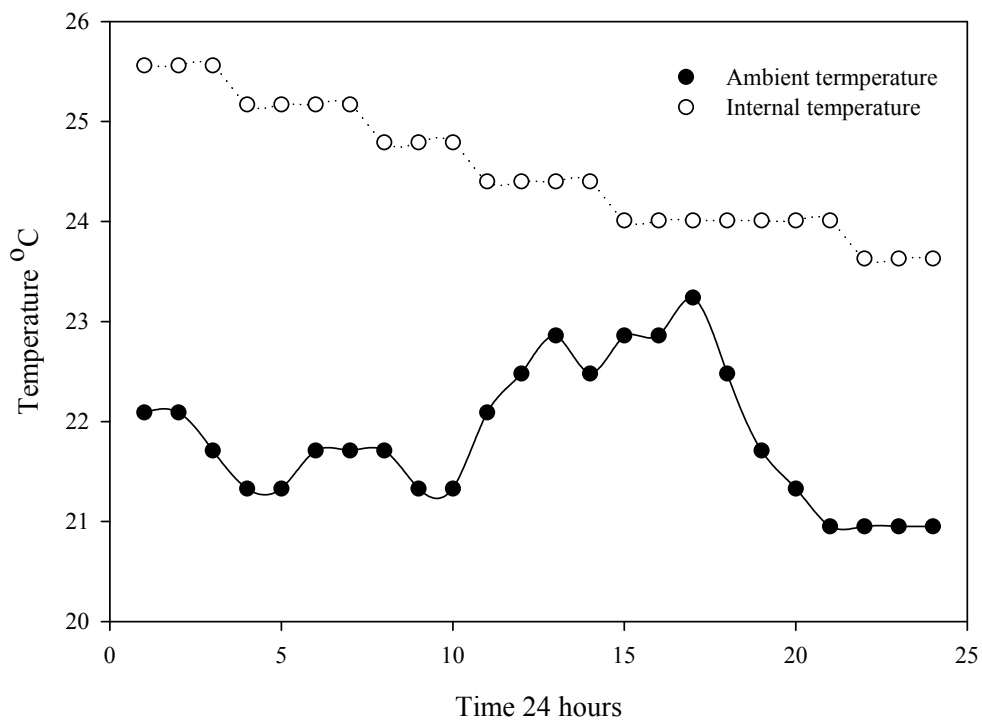


Fig. 9. Mean differences in internal temperature ranges for occupied and unoccupied *Camponotus pennsylvanicus* (DeGeer) nests during the fall season.

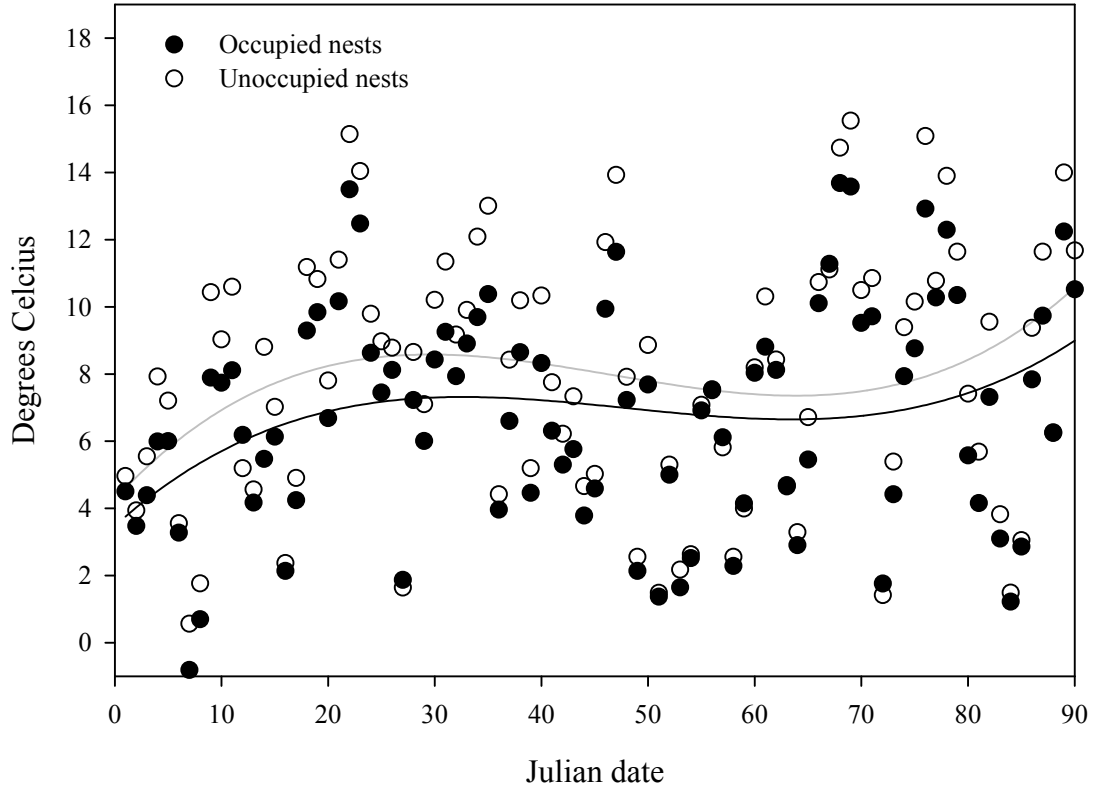


Fig. 10. Mean differences in internal temperature ranges for occupied and unoccupied *Camponotus pennsylvanicus* (DeGeer) nests during the winter season.

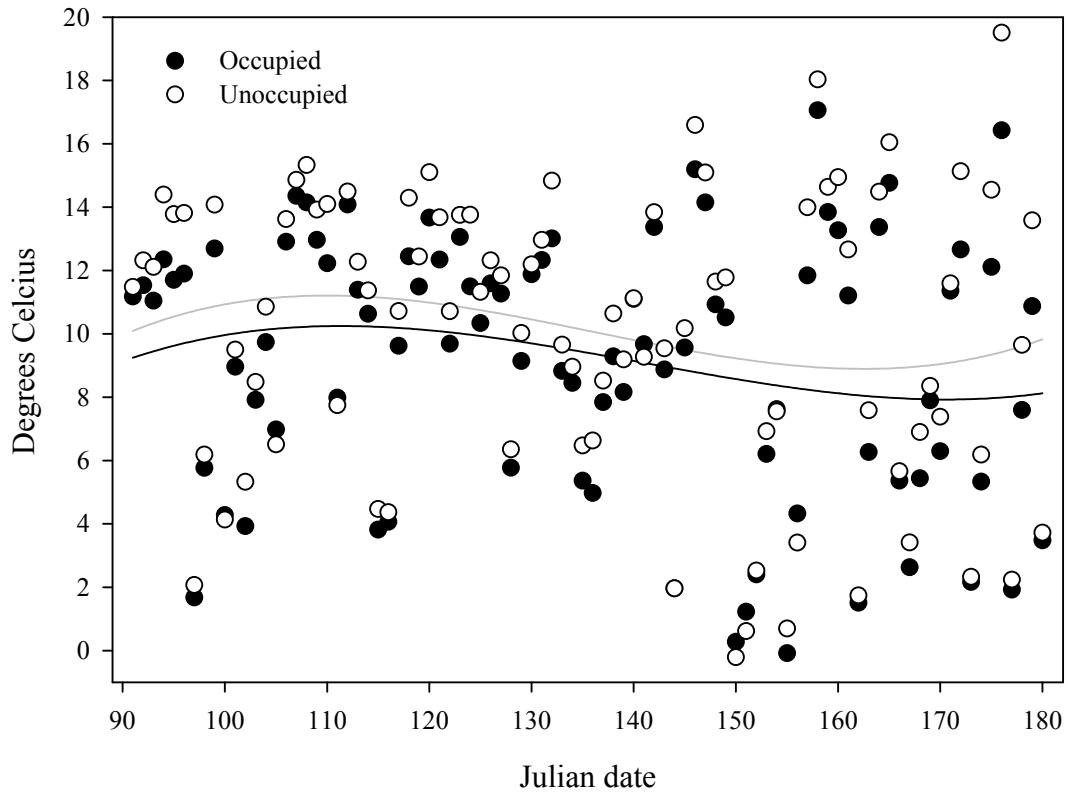


Fig. 11. Mean differences in internal temperature ranges for occupied and unoccupied *Camponotus pennsylvanicus* (DeGeer) nests during the spring season.

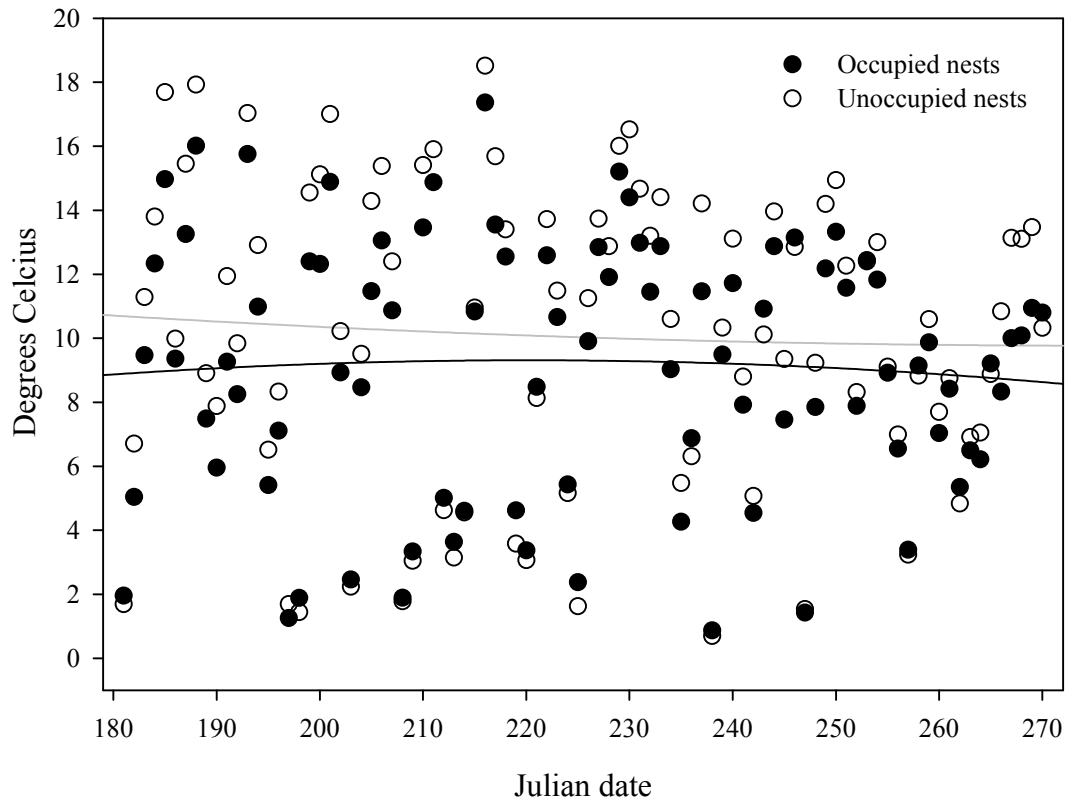


Fig. 12. Mean differences in internal temperature ranges for occupied and unoccupied *Camponotus pennsylvanicus* (DeGeer) nests during the summer season.

