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Life History and Natural Enemies of Parthenolecanium spp. in Four Southeastern States

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LIFE HISTORY AND NATURAL ENEMIES OF *PARTHENOLECANIUM* SPP.
IN FOUR SOUTHEASTERN STATES

A Dissertation
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy
Entomology

by
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May 2015

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ABSTRACT

Soft scales (Hemiptera: Coccidae) are some of the most prevalent and difficult to control arthropod pests in urban landscapes of the southern United States. European fruit lecanium, *Parthenolecanium corni* (Bouché), and oak lecanium, *Parthenolecanium quercifex* (Fitch), are commonly found in mixed populations as pests of oak trees (*Quercus* spp.) in the region. The phenology and natural enemies of the two species are poorly understood, which in turn hinders pest managers' ability to develop an integrated management program against these species. This research project aims to fill the information gaps concerning the life history and natural enemies of *P. corni* and *P. quercifex*.

The first study sought to better understand the life history of *P. corni* and *P. quercifex* in South Carolina, and to develop predictive models (based on degree-day and plant phenological indicators) for crawler emergence in Georgia, North Carolina, South Carolina and Virginia. The scale insects were found to be univoltine. Eggs hatched between mid-April and early June, second instars began to occur in October, and third instars and adults in mid-March to early April. Each parthenogenetic female produced 177 to 2,398 eggs. Fecundity was found to be proportional to weight of females (including eggs) and body length, width and height. Gross reproductive rate (*GRR*) was $695.98 \pm 79.34 \text{ ♀/♀}$, net reproductive rate (R_o) was $126.36 \pm 19.03 \text{ ♀/♀}$, mean generation time (T_G) was 52.61 ± 0.05 weeks, intrinsic rate of increase (r_m) was 0.04

♀/♀/week, and finite rate of increase (λ) was 1.04 times per week. Crawler emergence in Georgia, North Carolina, South Carolina and Virginia occurred when 229 degree-day units (DDC) had been accumulated with the simple-average method at a base temperature of 12.8°C (55°F), and at the first bloom of the southern magnolia, *Magnolia grandiflora* L.

The second study documented and compared the species composition, seasonal activity and impacts of parasitoids and predators of *Parthenolecanium* spp. in Georgia, North Carolina, South Carolina and Virginia. Twenty-one parasitoid species and twelve predator species were found associated with the lecanium scales. Based on results of species diversity (Shannon, effective number of species, and Gini-Simpson indexes) and community similarity (Chao-Jaccard index) analyses, the parasitoid community in Georgia was different from those of the other states and the predator communities were different among the four states. Parasitism rates were 27-92% in South Carolina. Five main parasitoid species (*Blastothrix* sp. 1, *Coccophagus lycimnia* (Walker), *Encyrtus* sp. 1, *Eunotus* sp. and *Pachyneuron* sp.) emerged from adults and parasitism by these species reduced the fecundity of the scales. *Coccophagus lycimnia* was the only parasitoid species that emerged from immature scales. In the southeastern U.S. about 90% of the total abundance of the population is reached from late March to late August for parasitoids, and between late April and late October for predators.

The third study evaluated the potential of *Parthenolecanium* spp.-infested willow oaks (*Q. phellos* L.) as banker plants for *C. lycimnia* that might attack other scale insect

pest populations (such as the Florida wax scale, *Ceroplastes floridensis* Comstock) in the landscape. Parasitism rates by *C. lycimnia* were not significantly different between the exposed and unexposed hollies. The lack of significant difference was most likely due to failures in the experimental design and the time of exposure to parasitism. The potential of scale-infested willow oaks as banker plants in the landscape remains to be assessed.

DEDICATION

To my mother, for her unconditional love, support, and spiritual guidance throughout this unique learning experience.

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CHAPTER ONE
LITERATURE REVIEW AND INTRODUCTION
SOFT SCALE INSECTS AND THEIR MANAGEMENT

Economic Importance

Among the scale insects (Hemiptera: Coccoidea), members of three families – Coccidae (the soft scales), Diaspididae (the armored scales) and Pseudococcidae (the mealybugs) - are the most common and serious pest species around the world (Ben-Dov et al. 2015). Scale insects cause an estimated \$5 billion in annual damage to agricultural and horticultural crop production worldwide (Kosztarab and Kozár 1988). Annual losses in the United States due to damage and cost of control reach millions of dollars (Miller and Davidson 2005, Kondo et al. 2008). The citrus industry has reported losses of \$22.8 million in California (Hawthorne 1975) and \$7 million in Florida (Piper 2011). In Georgia, losses of more than \$70 million in the ornamental plant and turf industry have been reported (Oetting et al. 2003).

Among the 1,148 soft scale species currently recognized (Ben-Dov et al. 2015), most are innocuous herbivores and a few even produce valuable products. For example, the wax from *Ericerus pela* (Chavannes) and some *Ceroplastes* spp. is used for candles, polish for furniture, ornaments, traditional medicine, and even as human food in India and China (Qin 1997). The most studied soft scale insect species are considered pests of economic importance in agricultural, horticultural and silvicultural crops (Kosztarab 1996, Ben-Dov and Hodgson 1997). Kosztarab (1997a) estimated that worldwide

management costs and losses from soft scale insect infestations were more than \$1 billion annually (1/5 of that by all Coccoidea). Gill and Kosztarab (1997) listed 50 economically important soft scale pest species, their most common host plants, and countries where they have caused the greatest damage. Thirty of this listed species injured ornamental plants and fruit trees in the United States. Miller and Miller (2003) listed 146 soft scale species from all over the world that were either pests (66 species) or potential threats (80 species) to agriculture in the United States.

Factors influencing the pest status of soft scales. The host plant susceptibility is one of the features affecting the level of scale infestations, mostly determined by genetic and environmental factors (Vranjic 1997). Even within the same host plant species, different genotypes can manifest various degrees of host susceptibility to infestation (Maxwell et al. 1972, McClure 1985, Schvester 1988). This susceptibility also varies in time and space, so outbreaks may vary from year to year and among regions (Vranjic 1997).

Environmental factors have been suggested to change the host physiology to the point of inducing temporary resistance to particular scale species (Agarwala and Sharma 1961, Flanders 1970). Investigations of *Parthenolecanium corni* (Bouché) in apple, plum and ornamental trees in Europe have revealed physiological fluctuations in the host plant beyond any hereditary predisposition after being exposed to infestation, where the scale became almost absent (Voukassovitch 1931, Thiem 1933a, 1938, Welsch 1937, and Priesner 1938). Thiem (1938) termed this self-cleaning phenomenon “pheno-

immunity.” This phenomenon also has been observed in *Eulecanium tiliae* (L.) and *Saissetia oleae* (Olivier) in North America (Quayle and Rust 1911, Quayle 1938, Graham and Prebble 1953, Peterson 1960). The mortality resulting from this phenomenon is almost as complete as that seen in genetic immunity (Flanders 1970). It is, however, only a temporary condition, after which the plant becomes susceptible and outbreaks of the scale population follow soon after (Flanders 1970). Pheno-immunity to coccid infestation occurred under meteorological conditions generally considered favorable for plant growth but under apparently unfavorable edaphic conditions (excessive wetness or dryness, inadequate humus and blocky structure of the soil) (Ebeling 1938). In the case of *P. corni*, the pheno-immunity of the host plants became obvious only after the accidental translocation and establishment of the scale in regions where its natural enemies were absent (Flanders 1970). Further studies concerning pheno-immunity have not been published after Flanders (1970), but the phenomenon has been mentioned as important and probably common in Coccoidea, although often ignored or underestimated in insect-host plant interactions (Miller and Kosztarab 1979, Marotta and Tranfaglia 1997).

Nutrients in the soil and the plant are important to the severity of scale infestation (Kunkel 1997). Small changes in the nutrient concentration of plant sap can have a dramatic effect on the population growth (Larsson 1989). A population of *Toumeyella parvicornis* (Cockerell) increased after urea was added to its pine host trees

(*Pinus banksiana* Lamb.), whereas it decreased after the addition of potassium (Smirnoff and Valero 1975).

Environmental stress is another factor influencing scale insect populations and their hosts (Vranjic 1993). Soft scales are present in all natural and man-made habitats. In urban environments, their populations thrive on trees under physiological stress, such as water or nutrient deficiency (Kosztarab 1988). Correct timing and application of fertilizers and water to host plants should be considered a cultural control strategy to minimize the impact of scale insect damage (Vranjic 1997). Air quality may also have an impact in the level of scale infestations (Kosztarab 1988, Xie et al. 1995). In a study of *Eulecanium giganteum* (Shinji) on its host *Styphnolobium japonicum* (L.) in Taiyuan City, China, the population density of the soft scale was positively correlated with air pollutants (suspended particles, fallout dust, CO, S, NO_x and SO₂), mostly due to automobile traffic (Xie et al. 1995). It was concluded that the density of the scale insect population could be used to monitor air pollution in city streets.

Temperature and humidity are the main abiotic factors limiting the range and abundance of soft scale insects, although many scale insects can tolerate adverse environmental conditions (Kosztarab 1996). Warm temperatures produced by accumulation of heat in particular urban areas seem to benefit scale populations (Meineke et al. 2013). The abundance of *Parthenolecanium quercifex* (Fitch) was higher on willow oaks (*Quercus phellos* L.) at sites with warmer temperature in Raleigh, North Carolina.

An important biological factor affecting scale population abundance is whether the species is completely or partially parthenogenetic (Kunkel 1997). Parthenogenesis allows the population to reproduce rapidly under favorable environmental conditions, especially when the food source is abundant (Kunkel 1997).

Feeding habits and hosts. Some soft scales are polyphagous, but most species are oligophagous or monophagous. For example, *Eriopeltis* and *Luzulaspis* spp. feed on herbaceous plants, *Parthenolecanium* spp. prefer woody plants, *Physokermes* spp. feed exclusively on conifers, and *Toumeyella* spp. feed mainly on gymnosperms from the families Cupressaceae, Pinaceae, and Taxaceae (Kosztarab 1996).

Most scale insects that are considered serious pests are species that have been inadvertently introduced (Miller and Miller 2003). The majority of these invasive scale species are polyphagous (Miller et al. 2005). Polyphagous species are more prone to become major pests when introduced to new areas because their wide host range facilitates their establishment (Mitter and Futuyma 1983, Kosztarab 1996), and the lack of natural enemies to control their populations (Stocks 2013). Polyphagous scale insect species often develop host-induced biotypes (i.e., variability in their shape, color and size, depending on the host plant), which has led to misidentification of pest species such as *P. corni* (Ebeling 1938). Correct identification of the pest species is a crucial factor in any pest management program (Pedigo and Rice 2009).

We have discussed the genetic and environmental factors that influence the levels of scale insect infestations, which also influence their host plant responses. The

different ways in which a host plant reacts to feeding by the scale is also determined by the species involved in the association (Vranjic 1997). Different host plant species may respond differently to infestation by the same scale species. Shoot elongation of sycamore and horse chestnut decreases under infestation by *Pulvinaria regalis* Canard, whereas lime trees increase shoot elongation when infested by scale insects (Speight 1991). The density of scale population and the duration of infestation have been negatively correlated to host plant growth (Washburn et al. 1985, Speight 1991), derived from damage exerted by the insects on their host plants.

Damage. Soft scales are phloem-sucking insects. After settling at a feeding site, they pierce the host plant tissue with a set of modified stylets until reaching the phloem vessels, after which they begin sucking plant sap (Raven 1983). Phloem sap is rich in carbohydrates but poor in soluble nitrogen compounds, so the insects have to ingest large quantities of sap to meet their nutritional requirements (Malumphy 1997). The excess carbohydrate solution, known as honeydew, is eliminated through a complex anal apparatus and mechanism unique to soft scales (Williams and Williams 1980).

Soft scale insects can cause direct damage to the host plants as the stylets penetrate and injure the vascular and photosynthetic tissues (Gill and Kosztarab 1997, Vranjic 1997). Saliva of some species contains enzymes (proteinases and cellulases) capable of breaking down cells, generating damage to both vascular and photosynthetic tissues in the vicinity of the stylets (Carter 1973). The necrosis produced by individual

scale insects is normally localized. In heavy infestations, however, aggregated injury may lead to dieback of twigs and branches (Vranjic 1997).

Another consequence of infestations is a considerable loss of plant nutrients, which retards plant growth and reduces the host plant's ability to respond to environmental stress and to recover from infestation. Furthermore, infested host plants are weakened and more susceptible to attack by other insects and pathogens (Hanson and Miller 1984).

Honeydew excreted by soft scales can cause indirect damage. Honeydew is a liquid composed of water, sugar, amino acids and minerals – a composition that makes honeydew an ideal substrate for sooty molds (saprophytic fungi that form a black film on the leaf surface). As sooty mold spreads on the leaf surface, it reduces the photosynthetic rate and interferes with the gas exchange through leaf stomata, resulting in decreased plant vigor (Kosztarab and Kozár 1988, Bach 1991, Mibey, 1997, Stauffer and Rose 1997). The black sooty mold also traps heat from the sunlight, potentially scorching the leaves (Gill 1997). The presence of sooty mold [as a result of infestation by *Saissetia oleae* (Olivier)] makes olive fruits unsuitable for processing when the fruits become stained and dirty (Gill and Kosztarab 1997). The presence of honeydew and sooty mold also reduce the aesthetic value of the plants (Williams and Kosztarab 1972).

Life Cycle and Biology

It is difficult to generalize about the life cycle and biology of soft scales because their biologies vary greatly, even among species of the same genus (Kosztarab 1996). The life cycle of females consists of the egg stage, two or three nymphal instars, and the adult stage. Males have a derived form of incomplete metamorphosis consisting of two feeding nymphal instars followed by the non-feeding “prepupal” (third-instar), “pupal” (fourth-instar) and adult stage (Marotta 1997).

First instars, or “crawlers,” disperse by crawling away from the brood chamber or ovisac. They typically settle near their mothers (Mendel et al. 1984) but can disperse passively by wind or phoresis (Greathead 1997). Studies have documented that crawlers of different soft scale species can be transported by air for 55 meters to more than 4 kilometers from the source (Quayle 1916, Hoelscher 1967, Reed et al. 1970, Washburn and Washburn 1984, Yardeni 1987). Washburn and Frankie (1981) demonstrated that although crawlers of *Pulvinariella mesembryanthemi* (Vallot) could adhere to clothing and animal hairs or feathers, the poor survival on animals suggests that dispersal by wind could be a more effective way for soft scale crawlers to disperse than phoresis.

After finding a suitable feeding site, a crawler settles and pierces plant tissue with its stylet to feed from phloem. In general, first instars lack a waxy cover or “test” and, consequently, are more susceptible to extreme environmental stresses and insecticides (Kosztarab 1996, Marotta 1997). Females are morphologically distinguishable from males in the subsequent instars (Williams 1997).

A female second instar grows until it molts into either an adult in some species [e.g., *E. pela* (Qin 1997)] or in most cases a third instar [e.g., *Ceroplastes* spp. (Hamon and Williams 1984, Park et al. 1992)]. In most univoltine species, such as those in the genera *Eulecanium*, *Parthenolecanium*, *Shpaerolecanium*, and *Physokermes*, the overwintering stage is the second instar (Kosztarab 1996). Second instars of *Parthenolecanium prunosum* (Coquille) move from the leaves to the branches before leaf senescence to overwinter (Michelbacher and Ortega 1958). This overwintering migration appears to coincide with changes in host plant phenology (Marotta and Tranfaglia 1997). Some other species, including multivoltine species such as *Ceroplastes floridensis* Comstock, overwinter as young adults on host branches. The overwintering stage may even vary within the same species; for example, *Ceroplastes sinensis* Del Guercio can overwinter as either a third instar or an adult (Stathas et al. 2003a). Female third instars are similar in external appearance to adults and live only two to four days. As a result, the third instar is not always identified in life cycle studies (Marotta 1997).

Second instar males (for those species where males are present) are often gregarious and may cluster on twigs or branches (Marotta 1997). Males secrete translucent platelike tests or “puparia” (Kozstarab 1996), waxy covers that attach themselves to the plant surface. The puparia have been used for species identification (Kawecki 1954, Richards 1958, Miller and Williams 1990). Puparia are maintained in subsequent stages and protect the developing males from natural enemies and harsh

environmental conditions (Miller and Williams 1997). The third “prepupal” and fourth “pupal” instars are characterized by the presence of wing buds, visibly laterally on the thorax. Once fully developed, the adult male emerges from under the puparium and flies searching for a mate. Adult males have only rudimentary mouthparts and are unable to feed. Males live only a few hours or rarely a few days, during which their only purpose is to locate and mate with females (Kozstarab 1996, Marotta 1997). Mating behavior of soft scales males has not been studied, but males of armored scales are able to reproduce and begin searching for females immediately after eclosion (Bennett and Brown 1958, Van Duyn and Murphey 1971, Hanks and Denno 1993), orienting to pheromones emitted by females (Heath et al. 1979, Einhorn et al. 1983). Despite having wings, males of armored scales are weak fliers and mate only with local populations of females (Rice and Moreno 1970, Moreno et al. 1972).

Adults of soft scales are sexually dimorphic. Males have two pairs of wings, but the hind pair is either absent or reduced to halteres (or “hamuloalteres”) attached to the front wing with one or more setae (Giliomee 1997). They have a defined head, thorax and abdomen. In contrast, females are wingless and neotenic (i.e., resemble the appearance of immature stages), with head, thorax and abdomen partially fused, forming what looks like an unsegmented body. As it feeds, an adult female undergoes a series of changes prior to oviposition, such as an increase in size and volume, change of color, dorsoventral swelling, and formation of either a cavity under the venter, known as the “brood chamber” in the Ceroplastinae, and Coccinae tribe Coccini, Paralecaniini and

Saissetiini, Eulecaniinae and Myzolecaniinae, or a white, waxy ovisac beneath or behind the body as in the Filippiinae, Eriopletinae, and the Coccinae tribe Pulvinariini (Marotta 1997).

Soft scales reproduce sexually or, more commonly, parthenogenetically (Saakyan-Baranova et al. 1971, Kosztarab 1996). Species in some genera such as *Parthenolecanium* and *Pulvinaria* sometimes differ in their modes of reproduction (Saakyan-Baranova et al. 1971, Kosztarab 1996). Some species, such as *P. corni* and *Pulvinaria vitis* (L.), can reproduce both sexually and parthenogenetically (Schmutterer 1952, Canard 1958a, Phillips 1963, Pellizzari 1997).

Fecundity varies substantially among species and among individuals of the same population. *Eucalymnatus tessellatus* (Signoret) produces fewer than 24 eggs per female (Vesey-Fitzgerald 1940), whereas *Ceroplastes destructor* Newstead produces as many as 6,355 eggs per female (Wakgari and Giliomee 2000). The variation in individual fecundity ranged from 70 to 1,000 eggs in *Coccus hesperidum* L. (Tereznikowa 1981), 100 to 5,000 eggs in *P. corni* (Kawecki 1958), and 566 to 5,533 offspring in *S. oleae* (Beingolea 1969). Volume (calculated as the product of length, width, and height of the test) was positively correlated with fecundity in *P. corni* (Birjandi 1981).

Intraspecific variation in biological and morphological characters is widespread among soft scales (Danzig 1997). Morphological variations include different shapes, sizes and coloration of the adult female; biological variations include different modes of reproduction, sex ratio, and seasonal development. Host plant, climatic conditions, and

altitude have been reported as the factors responsible for extreme variation of sex ratios and/or parthenogenesis, and have been studied in *C. hesperidum* (Thomsen 1929, Nur 1979, 1980), *E. pela* (Danzig 1980, 1986, 1997), *P. corni* (Thiem 1933a,b Canard 1958a, Saakyan-Baranova et al. 1971), *P. vitis* (Newstead 1903, Schmutterer 1952, Danzig 1980, 1986, Malumphy 1992), and *Saissetia coffeae* (Walker) (Thomsen 1929, Nur 1979, 1980).

Information on the voltinism in soft scales is sporadic in the literature (e.g., Gill 1988, Kosztarab 1996, Ben-Dov and Hodgson 1997, Krischik and Davidson 2003). Table 1.1 summarizes the information available on the voltinism of soft scale species reported from around the world; it is organized according to current taxonomy (Hodgson 1994, Ben-Dov et al. 2015) and included host associations and location(s) provided in the studies cited.

I was able to find information of 70 species of soft scales, 76% of which are univoltine or bivoltine under outdoor environmental conditions in crop production and urban landscape systems (Table 1.1). Some species have as many as five generations (e.g., *C. hesperidum* in southern California) (Gill 1988). We found no correlation between voltinism and soft scale insect taxonomic position. Multivoltine species are found in all soft scale insect subfamilies and tribes.

Marotta and Tranfaglia (1997) discussed the main causes for variations in voltinism in soft scale species, with temperature and humidity among the most important. A cosmopolitan soft scale species might show variation in voltinism in

different geographic and climatic zones. For example, *Ceroplastes rubens* (Maskell) has one generation in Japan and China (Itioka and Inoue 1991, Xia et al. 2005) and two generations in Australia (Loch and Zalucki 1997). Voltinism also varies among climatic zones within the same country, with the warmer climatic zones having more generations. *Ceroplastes destructor* has one generation in central and southern New South Wales and two generations in northern New South Wales, Australia (Qin and Gullan 1994). In inland regions of Greece with hot and dry summers and cold winters, *S. oleae* has only one generation (Argyriou 1963). In regions with high summer humidity and mild winters, such as coastal areas and well-irrigated and fertilized groves in the Iberian Peninsula and Israel, this species has a second generation (Peleg 1965, De Freitas 1972).

Voltinism in polyphagous soft scale species can differ among their host plants. *Parthenolecanium orientale* Borchsenius has one generation on peach but two on grapes and locust trees in the Shandong and Henan Province in China (AQSIQ 2007). *Ceroplastes floridensis* has one generation on *Rhododendron* spp. from Florida to Maryland (Kehr 1972), two on holly (*Ilex* spp.) in Georgia (Hodges et al. 2001), and three on citrus and holly in Florida (Johnson and Lyon 1991). Host plant characteristics, including phenology, physiology and both genetic and induced resistance to infestation, were important factors underlying the variations in voltinism on different host plant species (Marotta and Tranfaglia 1997). *Saissetia oleae* has one generation when feeding on citrus and two generations on olive in Italy (Nuzzaci 1969b, Longo and Russo 1986).

In soft scales with more specialized feeding habits, voltinism might vary among varieties (cultivars) of the same host species. *Coccus hesperidum* has one or two generations per year on the 'Valencia Late' variety of orange [*Citrus sinensis* (L.) Osbeck], whereas it often produces three annual generations on 'Hamlin' (Panis 1977a).

Plant physiology and the availability of nutrients from the host are important factors for soft scale development, to the point where substantial metabolic changes in the scale insect can be induced. For example, enzyme activity was positively correlated with development of *S. oleae* on different hosts (Ishaaya and Swirski 1976). Under optimal conditions, amylase, invertase and trehalase are important enzymes in food digestion and energy supply of the scale. The activity of trehalase in scale insects feeding on potato sprouts was about 3.5 to 4-fold that of those reared on oleander and citrus plants. Invertase and amylase activity was about 40% and 60% greater, respectively, when the scale insect fed on potato sprouts, compared to enzyme activity on oleander and citrus plants. Consequently, the developmental duration of *S. oleae* reared on potato sprouts was shorter (2.5 to 3 months) than when reared on oleander (4 to 5 months) and citrus (more than 6 months).

Table 1.1 summarizes the data about the number of generations for each soft scale species under outdoor conditions in crop production and urban landscape systems. Yet, some species are able to develop multiple generations per year under optimal, and (often) controlled conditions, in a laboratory or a greenhouse (data not included in the table). For example, although *C. hesperidum* can produce one to six

generations per year outdoors, seven generations per year are possible in greenhouses (Saakyan-Baranova 1964). A more extreme case is seen in *Parasaissetia nigra* (Nietner), which usually has one generation with a partial second generation outdoors, but can produce as many as six generations in greenhouses (Ben-Dov 1978).

Integrated Pest Management

Armored and soft scales have been ranked as the most prevalent and difficult arthropod pests to control by ornamental plant producers and landscape managers in the southern United States (Fulcher et al. 2012). Between the 1940s and the early 1970s, the control of scale insects relied heavily on the use of insecticides (Ben-Dov 1997, Pedigo and Rice 2009). Between the late 1950s and 1960s, with the increasing concerns about the adverse impacts of pesticides on non-target organisms and the environment, as well as the development of pesticide resistance, there began a switch to integrated pest management (IPM) practices (CAST 2003, Miller and Davidson 2005). Stern et al. (1959) referred to “integrated control” as an approach based on the selective use of chemical tactics to conserve natural enemies in the ecosystem and minimize disruption of the biological control they exert. The authors also introduced the concepts of “economic injury level” (where a pest population produces damage, exceeding the cost of control) and “economic threshold” (pest population level where control measures are taken to prevent the pest population from reaching the economic injury level), which provide the basis for decision making in any IPM program (CAST 2003, Pedigo and Rice 2009). As its name suggests, “integrated pest management”

implies the use of multiple approaches (e.g., cultural, chemical, and biological) in a compatible way, by which pest populations are kept at levels where economic damage is avoided, while maintaining the quality of the environment (CAST 2003, Pedigo and Rice 2009).

Knowledge of the seasonal biology and life history of any scale insect pest is fundamental to the implementation of an IPM program by allowing appropriate timing of pest management activities (Pedigo and Rice 2009). Also important is an understanding of the dynamics of the insect pest population. Life tables provide an integrated and comprehensive description of development times, survival rates of each growth stage, fecundity, and life expectancy of the populations studied. Life tables often are used as means of projecting the growth and predicting the size of such populations (Chi 1990, Carey 1993, Medeiros et al. 2000, Southwood and Henderson 2000, Soroushmehr et al. 2008). Ecological life tables are reliable tools for studying insect population dynamics, accounting for the survival and reproductive rates of the populations. Life tables are based on recording of sequential measurements, which show population changes throughout the life stages of the insect in its natural environment (Harcourt 1967, Schowalter 2011). Despite the importance of life tables, one is available only for a single species of soft scale, *Saissetia coffeae* (Walker) (Abd-Rabou et al. 2009).

Understanding pest life history is the starting point for pest managers. It is equally important to have specific information and tools that help predict the timing of

crawler emergence in order to achieve the most efficacious control (Mussey and Potter 1997, Hodges and Braman 2004, Fulcher et al. 2012). Even with significant progress over the past 50 years, there is still a need to optimize monitoring and management tactics against scale insects (Fulcher et al. 2012).

Monitoring. Monitoring of soft scale infestations relies on visual detection of their populations. Sampling plans vary among crop systems but typically involve collecting a set number of leaves or branches and determining the density (e.g., citrus in Martínez-Ferrer et al. 2015, olive in Tena et al. 2007, and tea in Naeimamini et al. 2014). Because many soft scale species are cryptic, the scouts should be trained and experienced in detecting signs and symptoms of the infestations. Damage and other organisms associated with the soft scale insects may be used to determine the area of focus. The presence of honeydew and black sooty mold, although do not necessarily indicate infestation by soft scales, provides clues on areas or trees where sampling effort should concentrate. Similarly, the presence of a large number of honeydew-collecting-ants may also indicate the presence of phloem-feeding insects. These plants should be inspected for the presence of soft scale insects and other pests.

Phenology is the study of the correlation of weather parameters (temperature and humidity) and the seasonal occurrence of biological events on plants and insects (Huberman 1941, Tauber et al. 1986, Herms 2004). It has been used to build prediction calendars for centuries (Huberman 1941). The development of degree-day models and the use of plant phenological indicators are among the phenological tools that provide

the means to make effective pest management decisions and minimize the impact of chemical control applications on the environment (Barton et al. 2008).

Predictive degree-day models. Degree-days (DD), also known as heat or thermal units, represent the amount of heat accumulated in a time period (e.g., 24 h) within a certain range of temperature necessary for development, and are used to predict biological events in cold-blooded animals and plants based on the relationship of biochemical reactions regulated by temperature (Roltsch et al. 1998, Murray 2008, Pedigo and Rice 2009). The completion of each developmental stage or phenological event within the life cycle of an insect requires a specific amount of heat and this quantity can be calculated (expressed in degree-days). Studies of biological development over time (phenology) of insects correlated with accumulated DD provide information to build “insect predictive models”. The models predict the occurrence of specific phenological event(s) or life stage(s) of interest (e.g., crawler emergence), allowing proper insecticide treatment timing (Mussey and Potter 1997, Schwartz 2003, Trudgill et al. 2005).

The calculation of degree-days is based on daily fluctuations of temperature and its values. A degree-day estimation method relies upon the assumption that a daily temperature profile can be represented by geometric shapes and described by appropriate equations (Roltsch et al. 1998). The most commonly used equation is the the standard method (also called simple, rectangle, or maximum-minimum method), where the base temperature (e.g., lower developmental threshold) of the insect is

subtracted from the average daily temperature (Schwartz 2003, Pedigo and Rice 2008). Another commonly used method (and its equation) is the sinewave curve, in which a single, symmetrical curve is fitted to min/max daily temperatures (Arnold 1960, Baskerville and Emin 1969, Allen 1976).

Hermes (2004) summarized the steps to build a predictive DD model: 1) identify and monitor a phenological event of a plant and/or pest; 2) determine an appropriate base temperature (using 10°C/50°F as a default, if unknown); 3) select a starting date for DD accumulation (1 January in most cases); 4) record maximum-minimum weather temperatures from location (or nearest weather station); 5) calculate the number of DD accumulated each day using a DD method (equation); 6) record, as the phenological event occurs, the DD accumulation from the starting date; and, 7) use the value obtained to predict the same phenological event in future years.

Plant phenological indicators. Plants that are used for phenological observations are called indicator plants. Because plants respond to DD accumulation in the same way that insects do, plant phenological events can be correlated with growing DD and used as indicators of insect pest activity (Hermes 2004, Barton et al. 2008). Easily observable plant phenophases, such as bud break or leaf flush, can be associated with events in the life cycle of an insect that are not as easily observed, such as egg hatch. Such correlations can then be used to predict when an insect pest will appear in the landscape and when it may be most susceptible to effective management tactics (Ascerno 1991, Barton et al. 2008, Murray 2008). Good indicator plants should be

common to a wide geographical area, hardy, easy to recognize and grow, with short and well-defined bloom periods, and with blooms and fruits that are apparent at a distance (Barton et al. 2008, Pedigo and Rice 2009).

Potential shortcomings when using indicator plants arise because different individuals or cultivars of the same plant species vary in their phenophases, and in years in which plants and insects are not well synchronized, may lead to incorrect control decisions. Periodic verification of plant indicator species under local environmental conditions can help to overcome this issue (Lanthier 2001).

Hodges and Braman (2004) developed a degree-day model and a plant phenological indicator model to predict scale insect crawler emergence. The crawler emergence of *Pulvinaria acericola* (Walsh and Riley) in Athens, Georgia, United States, corresponded to 892 to 1,229 degree-days (DDC), estimated based on a sinewave equation and a base temperature of 10.56°C. The plant phenological event timed to crawler emergence was the initiation of bloom of tulip poplar (*Liriodendron tulipifera* L.) and oakleaf hydrangea (*Hydrangea quercifolia* Bartram). Thus, based on the results of Hodges and Braman (2004), pest managers should begin monitoring for the presence of crawlers when 890 DDC are accumulated, as well as at the start of bloom of either tulip poplar or oakleaf hydrangea.

The development of models to predict crawler emergence and schedule proper management strategies, such as the application of contact insecticides, are important in an integrated pest management program. Relatively few studies have pinpointed the

timing of crawler emergence of soft scale pests despite the importance of this information (Table 1.2). I was able to locate published records of only 49 soft scale insect species where crawler emergence timing and locations were clearly indicated. Few such studies are from the Southern Hemisphere. It is difficult to generalize on the influence of abiotic and biotic factors on the timing of crawler emergence based on such a small dataset. Some patterns, however, are apparent and well known. For example, the crawlers of *P. corni* emerge earlier in the southern states of Georgia and Tennessee (Hodges and Braman 2004, Klingeman et al. 2002) than in northern states (Asquith 1949, Krischick and Davidson 2003, Herms 2004, Hoover et al. 2011). In the United States, crawlers of most univoltine/bivoltine soft scale species emerge in April through June (spring through early summer). Populations in the Southern Hemisphere produce crawlers in October through February (spring through early summer). The specific timing varies among species; for example, in Chile, *C. hesperidum* hatches in one generation between December and January, whereas the first generation of *P. corni* hatches between October and early November (Table 1.2).

Economic threshold. An economic threshold is rarely established for soft scale pests in crop production systems. Economic threshold is not established for ornamental plants where consumer tolerance for the presence of pests and the associated damage is low. Treatments are applied whenever scale insect populations are observed and/or damage becomes noticeable on ornamental plants grown in nurseries or landscapes (Bethke 2010). For other perennial fruits and nut crops, the economic threshold varies

with crop species. The economic thresholds of *C. floridensis* in citrus orchards of Egypt are 24.4, 26.6-28.4 and 25.1-27.0 individuals per twig in June, October and December, respectively (Salem and Zaki 1985, Helmy et al. 1986). The decision to apply treatments will also depend on mortality (due to natural enemies and other causes) in the scale populations. Bentley and Day (2010) suggested that insecticidal treatment against *P. corni* on fruit trees in the Central Valley of California could be omitted if a large (but unspecified) number of scale insects are parasitized in the summer.

Cultural control. The goal of cultural control is to make the environment less favorable for pest development and reproduction. In urban landscapes, cultural and plant management practices resulting in optimal plant growth and health should be promoted (Maxwell et al. 1972, CAST 2003). Healthy and vigorous plants can withstand more pressure from pests, diseases and weeds than can stressed plants (CAST 2003). Cultural practices, such as proper fertilization, pruning, and irrigation, contribute to maintain healthy plants in the urban landscape (CAST 2003). Excessive fertilization should be avoided to prevent an increase in foliar nitrogen and free amino acids, which promotes population growth of sap-sucking insects (Dreistadt 2008). Heavy infestations limited to twigs and branches of small plants can be managed by pruning (Kabashima and Dreistadt 2014). Pruned olive trees harbored 2 times fewer nymphs and half as many adult *S. oleae* as unpruned trees (Ouguas and Chemseddine 2011). In areas with hot summers, pruning also opens the canopy and increases scale insect mortality through greater exposure to heat and natural enemies (Kabashima and Dreistadt 2014).

Pruning is effective in reducing populations of *S. oleae* and citricola scale [*Coccus pseudomagnoliarum* (Kuwana)], and might work with other soft scales (Kabashima and Dreistadt 2014). Milne (1993) demonstrated that the rate of development of immature *Ceroplastes destructor* Newstead in greenhouses was significantly higher on host plants watered to saturation compared to those treated with medium and low water regimens. Although Milne (1993) did not identify the mechanism by which higher irrigation rate increased the rate of development, his findings suggest that excessive irrigation should be avoided. Plants prone to problems, such as those performing poorly or repeatedly damaged by pests, should be replaced by a pest-resistant species or cultivar that is better adapted to local conditions (Kabashima and Dreistadt 2014).

Biological control. Besides the benefits of knowing the biological and phenological information for management of a scale pest, knowledge of its ecological interactions with natural enemies is fundamental (Pedigo and Rice 2009). Biological control refers exclusively to the purposeful use of natural enemies to reduce pest status contrary to “natural control” where agents other than natural enemies (such as food or weather) are involved without purposeful manipulation. The object of biological control is to regulate the density of a pest population to prevent it from reaching the economic injury level (Pedigo and Rice 2009) using natural enemies of insect pests, including parasitoids, predators and pathogens. Several natural enemies, mostly involving parasitoids and predators, have been imported and released for biological control of soft scale insects. The efficacy of entomopathogenic fungi depends on the environment,

unless the conditions are appropriate for them to thrive, they do not become pathogenic, making them undesirable as biological control agents (Evans and Hywel-Jones 1997).

Biological control involves three strategies: 1) “classical” biological control, where exotic species are imported to control introduced pests (Rose and DeBach 1990b); 2) “augmentation”, where the suppression of a pest population by existing natural enemies is increased by mass rearing or other amplification approaches (Rose 1990); and 3) “conservation”, where existing species in an area are kept and protected mostly through identification and mitigating negative influences that suppress natural enemies and enhance their habitat, such as minimizing pesticide applications (Rose and DeBach 1990a, VanDriesche and Bellows 1996). Conservation biocontrol is often used in IPM programs and is usually effective for native pests because it takes advantage of the potential of natural enemies already established to regulate the pest population if given the opportunity (VanDriesche and Bellows 1996). When a non-native pest species has been introduced in to a new environment, it often lacks its complement of natural enemies to keep it from reaching pest status (Stocks 2013), prompting the implementation of the first two strategies of biological control mentioned.

Among the natural enemies of scale insects, the hymenopteran superfamily Chalcidoidea has been the most effective group in the biological control of scale insects (DeBach and Rosen 1991). Species of the Aphelinidae, Encyrtidae and Eulophidae are the most common natural enemies of soft scale insects (Hayat 1997, Prinsloo 1997,

Viggiani 1997). Encyrtids have been used successfully in some classical and augmentative biological control programs against members of *Ceroplastes*, *Coccus* and *Saissetia* (Kapranas and Tena 2015). For example, *Encyrtus* spp. have been used to control *C. hesperidum* in Texas, as well as *Pulvinaria delottoi* Gill, *Pulvinariella mesembryanthemi* (Vallot) and *S. oleae* in California (Bartlett 1978). The encyrtid *Anicetus beneficus* Ishii and Yasumatsu has been used successfully in managing the populations of *Ceroplastes rubens* Maskell in citrus orchards (Yasumatsu 1951, 1953, 1958, 1969, Smith 1986, Takagi 2003). Successful control of *C. rubens* was achieved an average of 2.5 years after release with parasitism reaching 60-80%.

Despite the success stories, biological control programs do not always reduce scale insect pest populations. Earlier attempts of classical biological control of *C. pseudomagnoliarum* in the San Joaquin Valley were unsuccessful (Gressitt et al. 1954, Bartlett 1978, Kennett 1988, Kennett et al. 1995). Observations of *Metaphycus luteolus* (Timberlake) and *Metaphycus helvolus* (Compere) successfully suppressing *C. pseudomagnoliarum* in southern California (Bartlett 1978), but not in the San Joaquin Valley (Bernal et al. 2001), point to the importance of matching natural enemy species with local environmental conditions. In addition, the complex interactions observed among endemic and introduced parasitoid species, as well as the need to employ such a parasitoid complex to achieve sufficient population suppression (Schweizer et al. 2002), are likely typical for other soft scale pests.

Although predators are not frequently released in scale insect biological control programs, they can exert population regulation complementary to those by parasitoids (Hanson and Miller 1984). Reports of coleopterans preying on soft scale insects include members in the families Coccinellidae, Anthribidae, Nitidulidae, Sylvanidae, Scarabaeidae, and Anobiidae (Ponsonby and Copland 1997). Many species in these families feed opportunistically and only a few (especially coccinellids) actually keep scale populations at low levels. Only 20% of coccinellid species prey on aphids, whereas 36% prey on coccids worldwide (Hodek and Honek 2009, Rosado et al. 2014). *Chilocorus* spp. feed on species of soft scales in the genera *Ceroplastes*, *Coccus*, *Cryptes*, *Mesolecanium*, *Metacaronema*, *Milvuscutulus*, *Paralecanium*, *Parthenolecanium*, *Pulvinaria* and *Vitrococcus* (Herting and Simmonds 1972, Gordon 1985, Joshi and Rai 1987). Some species of coccinellids that are commercially available, such as *Harmonia axyridis* (Pallas) or *Coleomegilla maculata* (De Geer) (Smith and Krischik 2000), are generalist feeders, with potential for controlling soft scale infestations (Hodek and Honek 2009). Hubbard and Potter (2005) documented a reduction of 48% in the numbers of crawlers from *Eulecanium cerasorum* (Cockerell) females that had fallen prey to *Hyperaspis* sp. larvae. *Hyperaspis campestris* Herbst was able to reduce the population of *Pulvinaria floccifera* (Westwood) to below the economic injury level within two years of release (Bogdanova 1956). Successful controls of *Toumeyella parvicornis* (Cockerell) by *Hyperaspis conviva* Casey were documented in Manitoba (Bradley 1973), Michigan and Minnesota (Orr and Hall 1931). Augmentative releases of large numbers of

Cryptolaemus montrouzieri (Mulsant) were reportedly successfully in reducing the populations of *Chloropulvinaria floccifera* Westwood (Mzhavanadze 1984) and *Chloropulvinaria aurantii* Cockerell (Prokopenko 1982).

In addition to coccinellids, Anthribidae is considered economically important as coleopteran biological control agents of soft scales (Ponsonby and Copland 1997). Predation levels of *Physokermes inopinatus* Danzig and Kozár and *Physokermes piceae* (Schrank) by *Anthribus nebulosus* (Forster) reached 55% and 59%, respectively (Kosztarab and Kozár 1983), whereas that of *E. pela* by *A. niveovariegatus* Reolofs was 75% (Deng 1985).

Neuropterans in the families Chrysopidae (green lacewings), Hemerobiidae (brown lacewings), Coniopterygidae (dustywings), and Raphidiidae (snakeflies) are predators of soft scale insects (Miller et al. 2004, Ben-Dov et al. 2015, Oswald 2014). Most records of predation involve the Chrysopidae (Miller et al. 2004).

Predators, in other groups such as other hemipterans, thrips, larvae of flies, mites and spiders (Clausen 1978, Kosztarab 1996), are rarely reported as capable of reducing populations of soft scale insects. Species of hemipterans in the family Miridae have been reported to prey on soft scales (Wheeler 2001). Larvae of some cecidomyiid genera (*Cocidomyia*, *Diadiplosis*, *Epidiplosis*, *Lestodiplosis*, and *Megommata*) feed on soft scales (Harris 1997). Soft scales also are associated with mites in the families Phytoseiidae and Cheyletidae, and spiders in the families Agelenidae, Clubionidae and Linyphiidae (Hodges and Braman 2004). Mansour and Whitecomb (1986) found that

populations of *C. floridensis* did not achieve economic damaging level on tree branches where spiders (Miturgidae and Theridiinae) were left undisturbed.

Entomopathogenic fungi have been reported to be more effective than predator and/or parasitoid in some host plant species. *Verticillium lecanii* (Zimmermann) Viegas and *Fusarium* spp. achieved higher mortality than parasitism in *C. destructor* populations, whereas the opposite occurred in *C. sinensis* populations, on citrus in Northland, New Zealand (Lo and Chapman 1998). In tropical regions where humidity is high, *V. lecanii* is the main mortality factor of *C. viridis* (Murphy 1997). The efficacy of entomopathogenic fungi depends on appropriate environmental conditions, which may or may not be available at the time of application (Evans and Hywel-Jones 1997). Although earlier adoption of entomopathogenic fungi was limited by difficulty in formulation and higher cost (Quinlan 1986), recent advances in formulation and mass production have allow greater use in crop production.

Natural enemies are able to suppress soft scale populations below economic threshold in most circumstances. Parasitoids, predators, entomopathogenic fungi, leaf abscission and rainfall resulted in 96% mortality in *C. viridis* populations (Rosado et al. 2014). Conservation of resident natural enemies is considered a more efficient and sustainable strategy than releases of beneficial organisms in gardens and landscapes (Kabashima and Dreistadt 2014). Habitat manipulation and pesticide management are the main strategies used in natural enemy conservation (Rose and DeBach 1990a). Soft scale pests become problematic when the activity of their natural enemies is disrupted

by excessive use of insecticides (Raupp et al. 2001). Insecticides compatible or less harmful to the natural enemies should be used. Applications of non-compatible insecticides should be made when natural enemies are not active. Although rarely documented for soft scales, the complex interactions between natural enemies and vegetational diversity in urban landscapes (Raupp et al. 2010) and crop systems (Andow 1991) likely influence soft scale populations and pest status. Local biotic and environmental conditions can also influence the activity of natural enemies (Hanson and Miller 1984). Ants can interfere with foraging and prevent oviposition by parasitoids through direct attack or incidental disturbance (Bartlett 1961, Bach 1991, Buckley and Gullan 1991, Itioka and Inoue 1996a, 1996b). Exclusion of honeydew-seeking ants has been shown to increase the numbers of predators while reducing scale populations (Vanek and Potter 2010).

Chemical control. Chemical control should always be considered the last resort, and it should be applied only when justified by the economic threshold. If chemical control is to be used, several features must be considered before its application: 1) proper identification of the pest species; 2) pest life cycle: number of generations per year (voltinism), egg hatch, and crawler emergence dates (the last one is essential if a non-systemic insecticide is to be used); and 3) delay of pesticide application if wind or rain is expected, or if the pest's natural enemies are active (Kosztarab 1996, Pedigo and Rice 2009).

In ornamental plant production systems where economic threshold does not exist, growers and landscape care professionals rely heavily on insecticides as preventive and curative tools against soft scale pests. In other perennial crop systems, chemical tools may be employed when other preventive management strategies, such as biological control (Bentley and Day 2010), have failed.

Insecticides registered for the management of soft scale pests can be broadly categorized into contact and systemic insecticides. Systemic insecticides, which include members of organophosphates, neonicotinoids, tetramic acid derivatives and diamides, function as contact insecticides when applied as topical sprays directly onto the scale insect populations and the affected plant tissues. When applied with an indirect method (soil drench, soil injection, basal trunk spray, trunk injection, granule and pellet), systemic insecticides are absorbed by plant tissues and translocated to the canopy. Systemic properties of these insecticides make them the preferred management tool against scale insect pests on large trees, in sensitive areas and in the urban landscapes.

Systemic insecticides have longer residual efficacy than contact insecticides. Some ornamental plant growers and landscape care professionals have used systemic insecticides in preventive management against certain recurring pests, such as soft scales (Chong, personal observations). The residual longevity of systemic insecticides allows sufficient population suppression of certain soft scale species with only one application per year. Typically, the application is made just before crawler emergence to ensure the highest concentration of active ingredients in the plant tissues (Kabashima

and Dreistadt 2014). Although systemic insecticides have the benefits of greater flexibility and residual longevity, their uses in all crop systems should be conducted with care because of their potential impacts on pollinator health (Cowles 2014, Pisa et al. 2014, Johnson and Corn 2015) and their implications in outbreaks of spider mites (Raupp et al. 2004, Szczepaniec et al. 2011, Szczepaniec and Raupp 2012a, Szczepaniec and Raupp 2012b, Szczepaniec et al. 2013).

Contact insecticides registered for the management of soft scale pests in the United States include carbamates, organophosphates, pyrethroids, neonicotinoids, juvenile hormone mimics, fenoxycarb, pyriproxyfen, flonicamid, buprofezin, tolfenpyrad, spirotetramat, diamides, azadirachtin, horticultural oils and insecticidal soaps. Topical applications of contact insecticides should target crawlers to achieve the greatest penetration of active ingredients into scale insect bodies (Kosztarab 1996, Kabashima and Dreistadt 2014). Older nymphs and adults are covered with a layer of wax, which is impenetrable to aqueous insecticide solution. Crawlers and settled first instars lack the protective waxy test; therefore, they are most vulnerable to environmental stresses (such as dessication) and insecticide applications (Marotta 1997, Kabashima and Dreistadt 2014). The application of contact insecticides should cover the entire crawler emergence period. Where concerns for the negative impacts of insecticides on pollinators, natural enemies and other non-target organisms are high, short residual or compatible insecticides (such as horticultural oil and insect growth regulators) should be used (Kosztarab and Kozár 1988, Kabashima and Dreistadt 2014).

Voltinism is an important factor to consider in designing a soft scale management program. When timed and conducted properly, insecticide applications have the potential of reducing the population of univoltine species within one season (Chong, unpublished data). Multiple applications of contact insecticides that target different generations may be required to suppress the population of a multivoltine species (Bethke 2010, Chong, unpublished data).

Research Project

Two species of soft scale insects, *P. corni* and *P. quercifex*, are common pests on oaks (*Quercus* spp.) throughout the southeastern U.S. (Sanders 1909, Williams and Kosztarab 1972, Schultz 1984, 1985, Hodges and Braman 2004). The life history and phenology of these species on willow oak (*Quercus phellos* L.), as well as the composition, seasonal activity and impact of their natural enemies have been studied only in a few states. Predictive phenological models for crawler emergence based on degree-day accumulation and plant indicators have been developed for *P. corni* in Georgia (Hodges and Braman 2004). They also included a list of natural enemies associated with the soft scale. The seasonal activity and ecological roles of the main parasitoid and predators of *P. quercifex* have been studied in Virginia (Schultz 1984, 1990). Despite these two reports, information needed to manage these species of *Parthenolecanium* at a regional level is lacking.

To expand our knowledge and fill existing gaps in the biology and ecology of *Parthenolecanium* spp. in the urban landscape of the Southeast, we developed a

research project to better understand the biology and ecology of *P. corni* and *P. quercifex* in urban landscapes. We documented the life history and phenology of the scale species by studying their life cycle and female fecundity. We developed regional predictive models for crawler emergence and studied the composition, seasonal activity and impact of natural enemies of *Parthenolecanium* spp. in Georgia, South Carolina, North Carolina, and Virginia. This research project was developed under the advisement of Dr. Juang-Horng Chong at the Clemson University Pee Dee Research and Education Center, South Carolina, in collaboration with Dr. S. Kristine Braman (University of Georgia), Dr. Steven Frank (North Carolina State University), and Dr. Peter Schultz (Virginia Polytechnic Institute and State University).

An additional project tested whether *Parthenolecanium* spp.-infested willow oaks can function in the landscape as banker plants for parasitoids that could attack other scales in the landscape. All aspects of this research involve information necessary to develop a regional control program of *Parthenolecanium* spp. and to provide general guidelines towards an integrated management program for soft scales.

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Table 1.1. Voltinism in soft scale species

Subfamily	Tribe	Genus	Species	Host ^a	Location	Generations per year	Reference
Cardiococcinae	Cardiococcini						
Ceroplastinae	Ceroplastini	<i>Ceroplastes</i>	<i>albolineatus</i>	<i>Pittocaulon praecox</i>	Mexico	2	(Narada and Lechuga 1971)
			<i>ceriferus</i>	Various <i>Citrus</i> spp. Burford holly (<i>Ilex cornuta</i> 'Burfordi')	Italy; Maryland, Virginia, USA Japan Georgia, USA	1 1 1-2	(Kosztarab 1996, Mori et al. 2001) (Ohgushi 1969) (Hodges and Braman 2004)
			<i>cirripediformis</i>	Fruit trees <i>Citrus</i> spp. Various Various Guava Passion fruit (<i>Passiflora edulis</i>)	Chile Georgia California, USA Texas, USA Egypt Central coast, Peru	1 1 1 2 2 3	(Bayer CropScience Chile 2014) (Tulashvili 1930) (Ben-Dov 1993, Kosztarab 1997b) (Johnson and Lyon 1991) (Bakr et al. 2010) (Marin-Loayza and Cisneros-Vera 1996)
			<i>destructor</i>	<i>Citrus</i> spp. <i>Citrus</i> spp., guava (<i>Psidium guajava</i>), <i>Syzygium malaccensis</i> Various <i>Citrus</i> spp.	New Zealand South Africa Central and southern New South Wales, Australia Queensland, Northern New South Wales, Australia	1 1 1 2	(Olson et al. 1993, Lo et al. 1996) (Wakgari and Giliomee 2000) (Qin and Gullan 1994) (Smith 1970, Qin and Gullan 1994)
			<i>floridensis</i>	Apple, persimon <i>Rhododendron</i> spp. Holly (<i>Ilex</i> spp.) <i>Citrus</i> spp. <i>Citrus</i> spp., grapefruit, mango <i>Citrus</i> spp., <i>Cinnamomum japonicum</i> <i>Citrus</i> spp. Citrus, guava, banana Various Orange, Passion fruit (<i>Passiflora edulis</i>)	Yunnan, China Florida to Maryland, USA Georgia, USA Greece Israel Fujian, China Queensland, Australia Egypt Florida, USA Peru	1 1 2 2 2(3 partial) 2 2 2-3 3 3	(Yun 1994) (Kehr 1972) (Hodges et al. 2001) (Argyriou and Kourmadas 1980) (Yardeni and Rosen 1995, Pellizzari 1997) (Kaiju 2011) (Smith et al. 1997) (Salem and Hamdy 1985, Helmy et al. 1986, Abd-Elhalim Moharum 2011) (Johnson and Lyon 1991) (Marin-Loayza and Cisneros-Vera 1996)
Ceroplastinae	Ceroplastini	<i>Ceroplastes</i>	<i>japonicus</i>	Poplar, bay laurel, maple, persimmon Various <i>Citrus</i> spp.	China; Italy Croatia Japan	1 1 1	(Pellizzari and Camporese 1994, Davis et al. 2005, Yongxiang 2008) (Masten-Milek et al. 2007) (Ohgushi 1969)
			<i>pseudoceriferus</i>	Persimmon Lychee, mango	China; Korea Southern Taiwan, Republic of China	1 3	(Park et al. 1990, Wang et al. 2006) (Wen and Lee 1986)
			<i>rubens</i>	Various <i>Citrus</i> spp. <i>Citrus</i> spp., <i>Schefflera actinophylla</i>	Shanghai and Kunming, China Japan Australia	1 1 2	(Tao et al. 2003, Xia et al. 2005) (Yasumatsu 1958) (Loch and Zalucki 1997)
			<i>rusci</i>	Fig tree Fig tree (<i>Ficus carica</i>)	Mediterranean coast, France Algeria; Greece; Turkey	1 2	(Benassy and Franco 1974) (Argyriou and Santorini 1980, Ozsemerci and Aksit 2003, Biche et al. 2012)

Subfamily	Tribe	Genus	Species	Host ^a	Location	Generations per year	Reference
Ceroplastinae	Ceroplastini	<i>Ceroplastes</i>	<i>rusci</i>	Quince	Egypt	2	(Ragab 1995)
				<i>Citrus</i> spp., fig tree	Italy; Spain	2	(Inserra 1970, Longo and Russo 1986, De la Cruz Blanco et al. 2010, Pellizzari et al. 2010)
				Soursop (<i>Annona muricata</i>), fig	Southern Vietnam	4	(Vu et al. 2006)
			<i>sinensis</i>	<i>Ilex</i> spp.	Virginia, USA	1	(Williams and Kosztarab 1972, Kosztarab 1996)
				<i>Citrus</i> spp., pear	Greece; Italy	1	(Frediani 1960, Stathas et al. 2003a)
				<i>Citrus</i> spp.	Coastal districts, Australia	1	(Snowball 1970)
				<i>Citrus</i> spp.	New Zealand	1	(Cottier and Wellington 1939)
Cissococcinae	Cissococcini	<i>Vinsonia</i>					
Coccinae	Coccini	<i>Coccus</i>	<i>hesperidum</i>	Citrus	Eastern Sicily, Italy	1	(Longo and Benfatto 1982)
				Citrus	Southern France	1-3	(Panis 1977a)
				Citrus	Western Sicily, Italy	2-3	(Monastero 1962)
				<i>Citrus</i> spp.	South Africa	3	(Annecke 1966)
				Various	New Zealand; southern California, USA	3-5	(Bernal et al. 1998, Charles et al. 2005)
				Various	Israel	6	(Avidov and Harpaz 1969)
Coccinae	Coccini	<i>Coccus</i>	<i>pseudomagnoliarum</i>	<i>Citrus</i> spp.	Greece	1	(Argyriou and Ioanides 1975)
				<i>Citrus</i> spp.	Israel	1	(Ben-Dov 1980)
				<i>Citrus</i> spp.	Southern Italy	1	(Barbagallo 1974)
				<i>Citrus</i> spp.	Turkey	1	(Oncuer and Tuncyurek 1975)
				<i>Citrus</i> spp.	Australia	1	(Smith et al. 1997)
				<i>Citrus</i> spp., hackberry	California, USA	1	(Flanders 1942,)
		<i>viridis</i>	<i>Citrus</i> spp.		Queensland, Australia	3-4	(Smith et al. 1997)
		<i>Eucalymnatus</i>	<i>tessellatus</i>	Palms (Arecaceae), crepe-jasmine, mango	South Florida, USA	1, 2	(Hamon and Williams 1984)
		<i>Kiljia</i>	<i>acuminata</i>	Mango	Egypt	2, 3	(Hassan et al. 2012, Angel and Radwan 2013)
		<i>Mesolecanium</i>	<i>nigrofasciatum</i>	<i>Acer</i> , <i>Platanus</i> , <i>Prunus</i> Blueberry, peach, plum, maple, sycamore, mistletoe	Pennsylvania, Maryland, Eastern USA	1	(Simanton 1916, Kosztarab 1996, Meyer et al. 2001)
	Paralecaniini	<i>Pseudocribrolecanium</i>	<i>andersoni</i>	Citrus	South Africa	3-4	(Brink and Bruwer 1989)
	Pulvinariini	<i>Milviscutulus</i>	<i>mangiferae</i>	Mango	Coastal plain, Israel	3	(Avidov and Zaitzov 1960)
		<i>Neopulvinaria</i>	<i>innumerabilis</i>	Various hardwoods	Colorado, USA	1	(Cranshaw et al. 1994)
				Red oak	Georgia, USA	1	(Hodges and Braman 2004)
				Maple (<i>Acer</i> spp.), honeylocust (<i>Gleditsia triacanthos</i>), linden (<i>Tilia</i> spp.)	Minnesota, USA	1	(Krischik and Davidson 2003)
		<i>Protopulvinaria</i>	<i>pyriformis</i>	Various fruit trees	Chile	2	(Bayer CropScience Chile 2014)
				<i>Citrus</i> spp.	Spain	2	(Llorens 1990)
				Avocado	Israel	2	(Blumberg and Blumberg 1991)
		<i>Pulvinaria</i>	<i>acericola</i>	<i>Hedera helix</i>	Israel	3	(Blumberg and Blumberg 1991)
				Red maple	Georgia, USA	1	(Hodges and Braman 2004)
				Maple, dogwood, holly, andromeda, gum	Virginia, USA	1	(Day 2008)

Subfamily	Tribe	Genus	Species	Host ^a	Location	Generations per year	Reference
Coccinae	Pulvinariini	<i>Pulvinaria</i>	<i>amygdali</i>	Peach, plum, quince	New York, USA	1	(Harman 1927)
			<i>citricola</i>	Various	Japan; Florida, Maryland, Virginia, USA	1	(Williams and Kosztarab 1972, Gill 1988)
			<i>delottoi</i>	Iceplant (Aizoaceae)	Southern Africa; Northern California, USA	1	(Tassan and Hagen 1995, Gill, 1988)
			<i>floccifera</i>	Burford holly, bradford pear	Georgia, USA	1	(Hodges and Braman 2004)
				Camellia, holly, taxus, rhododendron, hydrangea, maple, English ivy	Virginia, USA	1	(Williams and Kosztarab 1972, Day 2008)
				Guava, citrus, fig	Egypt	1	(Abd-Rabou et al. 2012)
				<i>Taxus baccata</i> , , <i>Pittosporum toriba</i> , <i>Ilex aquifolia</i> , <i>Citrus</i> spp., <i>Camellia sinensis</i>	Iran	1	(Hallaji-Sani et al. 2012)
				Citrus	Japan	1	(Takahashi 1955)
				Various	Spain	1	(Soria et al. 1996)
				Citrus	Tokyo, Japan	2	(Takahashi 1955)
				Conifers	Turkey	2	(Ülgentürk et al. 2004)
			<i>hydrangeae</i>	Hydrangea, cherry, others	Australia; Europe; Japan; California, East Coast, USA	1	(Williams and Kosztarab 1972, Gill 1988)
			<i>polygonata</i>	Mango	India	1	(Chatterji and Datta 1974)
				Various	China	2-3	(Peng et al. 1990)
				Citrus	Taiwan	3	(Takahashi 1939)
			<i>psidii</i>	Guava	Egypt	2, 3	(Bakr et al. 2012)
			<i>rhois</i>	poison oak (<i>Rhus diversiloba</i>), peach, plum, apple and currant (<i>Ribes</i>), prune	California, USA	1	(Essig 1958)
			<i>vitis</i>	Peach	Canada	1	(Phillips 1963)
				Poplar, alder, beech, willow, hawthorn	New Zealand	1	(Charles et al. 2005)
				Various	Eastern USA	1	(Essig 1915)
		<i>Pulvinariella</i>	<i>mesembryanthemi</i>	Iceplant (Aizoaceae)	Northern California, USA	2	(Tassan and Hagen 1995)
		<i>Pulvinariella</i>	<i>mesembryanthemi</i>	Iceplant (Aizoaceae)	Southern California, USA	3-4	(Tassan and Hagen 1995)
Coccinae	Saissetiini	<i>Parasaissetia</i>	<i>nigra</i>	<i>Ficus</i> , <i>Hedera</i>	California, Florida, USA	1 (2 partial)	(Smith 1944)
		<i>Parthenolecanium</i>	<i>corni apuliae</i>	Grapevine (<i>Vitis vinifera</i>)	Italy	2	(Nuzzaci 1969a)
			<i>corni corni</i>	<i>Corylus</i>	Greece	1	(Santas 1985)
				Hazelnut	Turkey	1	(Ecevit et al. 1987)
					France	1	(Canard 1958a)
				Various	New Zealand	1	(Charles et al. 2005)
				Plum	Krasnodar, Russia	1	(Borchsenius 1957)
				Various	Virginia, USA	1	(Day 2008)
				Deciduous fruits, nuts (<i>Prunus</i> spp.) and ornamental trees and shrubs (Toyon, <i>Ceanothus</i> spp.)	California, USA	1	(Kawecki 1958, Madsen and Barnes 1959)

Subfamily	Tribe	Genus	Species	Host ^a	Location	Generations per year	Reference
Coccinae	Saissetiini	<i>Parthenolecanium</i>	<i>corni corni</i>	Grape	Chile	2	(Bayer CropScience Chile 2014)
				Black poplar (<i>Populus nigra</i>)	Hungary	2	(Kosztarab 1959)
				Peach	Pennsylvania, USA	2	(Asquith 1949)
				Peach	Krasnodar, Russia	2	(Borchsenius 1957)
				Black locust (<i>Robinia pseudoacacia</i>)	Krasnodar, Russia	3	(Borchsenius 1957)
			<i>fletcheri</i>	Conifers (<i>Biota, Cupressus, Juniperus, Tsuga, Thuja</i>)	Hungary	1	(Kosztarab 1997b)
				Conifers, arborvitae, yew, pachysandra, Eastern red cedar	Virginia, USA	1	(Kosztarab 1997b)
				Arborvitae, yew, juniper, cypress, hemlock	Pennsylvania, Illinois, USA	1	(Stimmel 1978, Hoover 2006)
			<i>orientale</i>	Peach	Henan, Shandong, China	1	(AQSIQ 2007)
				Locust and grape	Henan, Shandong, China	2	(AQSIQ 2007)
			<i>perlatum persicae</i>	Citrus spp.	Argentina	1	(Teran and Guyot 1969)
				Various fruit trees	Chile	1	(Bayer CropScience Chile 2014)
				Various	Israel	1	(Ben-Dov 1993)
				Various ornamental plants	USA	1	(Kosztarab 1996)
				Grapevine (<i>Vitis vinifera</i>)	Australia; Southern Greece	1	(Stathas et al. 2003b, Buchanan 2008)
				Various	New Zealand	1-2	(Charles et al. 2005)
				Various	Former Soviet Union	2	(Borchsenius 1957)
				Various	Central Asia	2	(Ben-Dov 1993)
			<i>pomeranicum</i>	Yew	Europe	1	(Del-Bene 1991)
			<i>pruinatum</i>	Walnut	California, USA	1	(Michelbacher and Swift 1954)
				Grapevine (<i>Vitis vinifera</i>)	Australia	1	(Buchanan 2008)
			<i>quercifex</i>	Oaks (<i>Quercus</i> spp.), hickory, birch, persimmon, American sycamore	Virginia, USA	1	(Williams and Kosztarab 1972)
				Coast live oak, valley oak	California, USA	1	(Swiecki and Bernhardt 2006)
			<i>rufulum</i>	<i>Quercus frainetto</i> , <i>Q. cerris</i> , <i>Q. ithaburensis</i> ssp. <i>macrolepis</i>	Greece	1	(Gounari et al. 2012)
				<i>Quercus robur</i>	Northeastern Italy	1	(Rainatto and Pellizzari 2009)
		<i>Saissetia</i>	<i>coffeae</i>	Various fruit trees	Chile	1	(Bayer CropScience Chile 2014)
				Olive tree	Chile	2	(González and Lambrot 1989)
				N/A	California, USA	1-2	(Hamon and Williams 1984)
				Various	New Zealand	2+	(Charles et al. 2005)
				Various	Florida, USA	2+	(Gill 1988)
				Olive tree	Israel	3, 4	(Rosen et al. 1971)
			<i>oleae</i>	Citrus	Corsica, French Riviera, France; Greece; Israel; Calabria, Sicily, Italy; Portugal; Almazora, Spain; Tunisia; Aegean Sea coast, Turkey	1	(Argyriou 1963, Peleg 1965, Panis 1977b, De Freitas 1972, Jarraya 1974, Tuncyürek and Oncüer 1974, Blumberg et al. 1975, Longo and Russo 1986)
				Olive tree	Greece; Italy; Spain	1	(Bibolini 1958, Argyriou 1963, Briales and Campos 1986; Noguera et al. 2003)
				Various fruit trees	Chile	1	(Bayer CropScience Chile 2014)
				Various	Inland California, USA	1	(Dreistadt 2004)

Subfamily	Tribe	Genus	Species	Host ^a	Location	Generations per year	Reference
Coccinae	Coccinae	<i>Saissetia</i>	<i>oleae</i>	Various	California, USA	2	(Dreistadt 2004)
				Olive tree	Coastal Greece; Israel; Italy; Portugal; Spain	2	(Argyriou 1963, Nuzzaci 1969b, Rosen et al. 1971, Viggiani et al. 1973)
				Citrus	Coastal Greece; Israel; Spain	2	(Argyriou 1963, Blumberg et al. 1975, Llorens-Climent 1984)
				Citrus	Florida, USA; coast of Morocco; Portugal	3	(Panis 1977b)
				Citrus	Subtropical areas, Australia	4	(Waterhouse and Sands 2001)
				<i>Citrus</i> sp.	Peru	5-6	(Beingolea 1969)
Cyphococcinae	Cyphococcini						
Eulecaniinae	Eulecaniini	<i>Didesmococcus</i>	<i>unifasciatus</i>	Stone fruits	Central Asia	1	(Babayan 1973)
			<i>pela</i>	N/A	China	1	(Zhao et al. 1998)
		<i>Ericerus</i>		N/A	Japan	1	(Kuwana 1923)
				N/A	Russia	1	(Danzig 1980)
				Various	Tropical zones	2	(Qin 1997)
		<i>Eulecanium</i>	<i>caryae</i>	Beech, willow, birch, hickory, peach	Quebec, Canada; Virginia, Michigan, USA	1	(Wallner 1969, Williams and Kosztarab 1972, Kosztarab 1996)
			<i>cerasorum</i>	Stone fruit, walnut, pear	California, Maryland, USA	1	(Madsen and Barnes 1959, Kosztarab 1996)
			<i>ciliatum</i>	<i>Acer campestre</i> , <i>A. pseudoplatanus</i> , <i>Crataegus monogyna</i> , <i>C. oxyacantha</i>	Turkey	1	(Ülgentürk and Çanakçıoğlu 2004)
			<i>exressens</i>	Ornamental plants and brodleaved trees	England; California, USA	1	(Gill 1988, Alford 2007)
			<i>kunoense</i>	Various	California, USA	1	(McKenzie 1951, Hussein and Madsen 1962)
		<i>tiliae</i>		<i>Quercus frainetto</i> , <i>Q. cerris</i> , <i>Q. ithaburensis</i> ssp. <i>Macrolepis</i>	Greece	1	(Gounari et al. 2012)
				Various	Bulgaria, Georgia, Russia; California, USA	1	(Hadzibejli 1967, Tzalev 1968, Kosztarab and Kozár 1988)
				Abies, Picea	Georgia	1	(Hadzibejli 1967)
		<i>sericeum</i>		Conifers (<i>Abies</i> , <i>Picea</i>)	Germany	1	(Kosztarab 1997b)
				Greek fir (<i>Abies cephalonica</i>)	Greece	1	(Stathas 2001)
		<i>Nemolecanium</i>	<i>graniformis</i>	Greek fir (<i>Abies cephalonica</i>)	Greece	1	(Stathas 2001)
		<i>Palaeolecanium</i>	<i>bituberculatum</i>	<i>Corylus</i> , <i>Juglans regia</i> , Rosaceae	Europe	1	(Schmutterer 1952)
				Apple	Turkey	1	(Özgökçe et al. 2001)
		<i>Physokermes</i>	<i>hemicyphus</i>	Spruce	Germany	1	(Schmutterer 1956)
				<i>Abies cephalonica</i> , <i>A. borisii regis</i>	Greece	1	(Gounari et al. 2012)
				<i>Picea</i>	Central Europe	1	(Kosztarab and Kozár 1988)
					Pennsylvania, USA	1	(Stimmel 1996)
			<i>inapiatus</i>	Greek fir (<i>Abies cephalonica</i>)	Greece	1	(Stathas and Kozár 2010)

Subfamily	Tribe	Genus	Species	Host ^a	Location	Generations per year	Reference
Eulecaniinae	Eulecaniini	<i>Physokermes</i>	<i>insignicola</i>	Monterey and Bishop pines (<i>Pinus radiata</i> and <i>P. muricata</i>)	California, USA	1	(Gill 1988)
			<i>piceae</i>	<i>Picea</i> spp. <i>Picea</i> spp.	Colorado, USA Serbia	1 1	(Cranshaw et al. 1994) (Graora et al. 2012)
			<i>shanxiensis</i>	N.A.	China	1	(Wu and Yu 2000)
		<i>Rhodococcus</i>	<i>turanicus</i>	Stone fruits	Armenia	1	(Babayan 1986)
		<i>Sphaerolecanium</i>	<i>prunastri</i>	Purpleleaf plum, <i>Pyracantha</i> spp.	Pennsylvania, USA	1	(Hoover et al. 2011)
Eulecaniinae	Eulecaniini	<i>Sphaerolecanium</i>	<i>prunastri</i>	Stone fruits	Greece; Israel; high altitude regions, Italy	1	(Silvestri 1939, Ben-Dov 1968, Argyriou and Paloukis 1976)
				Stone fruits	Southern plains, Italy	2	(Silvestri 1939)
Eriopeltinae	Eriopeltini	<i>Eriopeltis</i>	<i>festucae</i>	Grass	California, USA	2	(Patch 1905)
Filippiinae	Filippiini	<i>Lichtensia</i>	<i>viburni</i>	Olive, <i>Pistacia lentiscus</i> , <i>Hedera helix</i>	Mediterranean basin	2	(Pellizzari 1997)
Myzolecaniinae	Myzolecaniini	<i>Neolecanium</i>	<i>cornuparvum</i>	Magnolia	Virginia, New York, USA	1	(Herrick 1931, Kosztarab 1996)
		<i>Pseudophilippia</i>	<i>quaintancii</i>	<i>Pinus taeda</i> (Loblolly pine)	Eastern USA	2	(Clarke et al. 1989a)
		<i>Toumeyella</i>	<i>liriodendri</i>	Yellow poplar, magnolia, linden, <i>Michelia</i> , <i>Gardenia</i> , <i>Gordonia</i> , <i>Cephalanthus</i> , <i>Tilia</i>	Alabama, California, Illinois, Indiana, Kentucky, Mississippi, Ohio, Pennsylvania, Tennessee, Virginia, West Virginia, USA	1	(Burns and Donley 1970, Gill 1988, Hoover 2006b, Day 2008)
			<i>parvicornis</i>	Jack pine (<i>Pinus banksiana</i>), Scots pine (<i>P. sylvestris</i>), red pine (<i>P. resinosa</i>)	Canada	1	(Rabkin and Le Jeune 1954)
				<i>Pinus contorta</i> , <i>P. sylvestris</i>	Colorado, Nebraska, USA	1	(Cooper and Cranshaw 2004, Clarke 2013)
				<i>Pinus caribaea</i> var. <i>bahamensis</i>	Northeastern USA	1	(Malumphy et al. 2012)
				<i>Pinus</i> spp.	Maryland, North Carolina, Virginia, USA	2	(Miller 1985, Clarke 2013)
				<i>Pinus</i> spp.	Georgia; Southern USA	3-4	(Williams and Kosztarab 1972, Hamon and Williams 1984, Clarke 2013)
			<i>pini</i>	<i>Pinus taeda</i> L. (Loblolly pine)	Georgia, USA	3	(Clarke et al. 1989b)
				<i>Pinus sylvestris</i> , <i>Pinus mugo</i> , <i>Pinus edulis</i> , <i>Pinus nigra</i>	Colorado, USA	1	(Cranshaw et al. 1994, Cooper and Cranshaw 2004)
			<i>pinicola</i>	Pines	California, USA	1	(Kattoulas and Koehler 1965)
			<i>virginiana</i>	<i>Pinus</i> spp.	Virginia, USA	2	(Williams and Kosztarab 1972, Kosztarab 1997b)

Pseudopulvinariinae

^a N/A = Not available

Table 1.2. Periods of crawler emergence in soft scale species

Species	Time of the year	Location	Host ^a	Reference
<i>Ceroplastes albolineatus</i>	Mar. (1 st generation) Sep. (2 nd generation)	Mexico D.F., Mexico	<i>Pittocaulon praecox</i>	(Narada and Lechuga 1971)
<i>Ceroplastes ceriferus</i>	Late Apr. Late May to mid-June June to mid-July June Mid-June Early Sep. to mid-Oct.	Texas, USA Athens, Georgia, USA Pennsylvania, USA Maryland, Tennessee, USA New Jersey, USA Northern Guizhou, China	Various Burford holly (<i>Ilex cornuta</i> 'Burfordii') Various Various N/A Tea	(Johnson and Lyon 1991) (Hodges and Braman 2004) (Hoover et al. 2011) (Smith et al. 1971, Klingemann et al. 2002,) (NJDA 2006) (Lai 1993)
<i>Ceroplastes cirripediformis</i>	Early Feb. (1 st generation) Early June (2 nd generation) Early Oct. (3 rd generation) Late Feb. to Early Mar. Early Apr. Late Apr.	Peru Chile Palmira, Valle del Cauca, Colombia Texas, USA	Passion fruit (<i>Passiflora edulis</i>) Various fruit trees <i>Passiflora edulis flavicarpa</i> Various	(Marín-Loayza and Cisneros-Vera 1996) (Bayer CropScience Chile 2014) (Kondo Rodríguez 2009) (Johnson and Lyon 1991)
<i>Ceroplastes destructor</i>	Early Dec. Nov. Mid-Oct. (1 st generation) Early Apr. (2 nd generation) Mid-Nov.	Kerikeri, New Zealand New South Wales, Australia Queensland, Australia Cape Province, South Africa	Seminole tangelo (<i>Citrus paradisi</i> x <i>C. reticulata</i>) Citrus (<i>Citrus</i> spp.) Citrus <i>Citrus reticulata</i> , <i>Syzygium malaccensis</i>	(Olson et al. 1993) (Snowball 1969) (Smith 1970) (Wakgari and Giliomee 2000)
<i>Ceroplastes floridensis</i>	Early June Early Jan. (1 st generation) Early May (2 nd generation) Early Oct. (3 rd generation) Early Feb. (1 st generation) Mid-Aug. (2 nd generation) May (1 st generation) Aug. (2 nd generation) Apr.-May (1 st generation) July-Aug. (2 nd generation) Oct.-Nov. (3 rd generation) May-June (1 st generation) Nov. (2 nd generation) Late Apr. – May (1 st generation) Late July – Aug. (2 nd generation) Apr. (1 st generation)	Daegu, South Korea Peru Egypt Israel Florida, USA Tifton, Georgia, USA Texas, USA Fujian Province, China	Persimmon Orange, passion fruit (<i>Passiflora edulis</i>) Banana Mango Avocado, citrus, crape myrtle, deodar cedar, elm, holly, Indian hawthorn, loblolly pine, oak <i>Ilex</i> spp. N/A <i>Cinnamomum japonicum</i>	(Han and Lee 1964) (Marín-Loayza and Cisneros-Vera 1996) (Abd-Elhalim Moharum 2011) (Swirski and Greenberg 1972) (Johnson and Lyon 1991) (Hodges et al. 2001) (Drees et al. 2005) (Kaiju 2011)

Species	Time of the year	Location	Host ^a	Reference
	Aug. (2 nd generation)			
<i>Ceroplastes japonicus</i>	Mid-May Early June June	Croatia Korea Italy	Various N/A Bay laurel and maple	(Masten-Milek et al. 2007) (Davis et al. 2005) (Pellizzari and Camporese 1994)
<i>Ceroplastes pseudoceriferus</i>	Mid-June Late Jun. (1 st generation) Late Sep. (2 nd generation) Late Mar. (3 rd generation)	Korea Southern Taiwan, Republic of China	Persimmon Lychee, mango	(Park et al. 1990) (Wen and Lee 1986)
<i>Ceroplastes rubens</i>	June, July Mid-Sep. (1 st generation) Feb. (2 nd generation)	Japan Queensland, Australia	Citrus, persimmon Various	(Itioka and Inoue 1991) (QDAFF 2014)
<i>Ceroplastes rusci</i>	Early May (1 st generation) Aug. (2 nd generation) Late May to early June (1 st generation) Late Aug. to early Sep. (2 nd generation)	Italy Extremadura, Spain	Fig tree Fig tree	(Inserra 1970) (De la Cruz Blanco et al. 2010)
<i>Ceroplastes sinensis</i>	Feb. Late June Early July Nov.	Northland, New Zealand Virginia, USA Central Greece New South Wales, Australia	Citrus <i>Ilex</i> spp. <i>Citrus sinensis</i> Citrus	(Lo et al. 1996) (Kosztarab 1996) (Stathas et al. 2003a) (Snowball 1970)
<i>Coccus hesperidum</i>	Dec. and Jan.	Chile	Various fruit trees	(Bayer CropScience Chile 2014)
<i>Coccus pseudomagnoliarum</i>	Apr. June June June June	Davis, California, USA Greece Italy Spain California, USA	Chinese hackberry (<i>Celtis sinensis</i>) Citrus Citrus Citrus Citrus	(Dreidstadt 2004) (Argyriou and Ioannides 1975) (Barbagallo 1974) (Tena and Garcia-Mari 2008) (Bernal et al. 2001)
<i>Coccus viridis</i>	Sep.	South Florida	Various	(Fredrick 1943)
<i>Didesmococcus unifasciatus</i>	Early June	Central Asia	Stone fruits	(Babayan 1973)
<i>Eulecanium caryae</i>	Mid-May to mid-June Late June	Ohio, USA Michigan, USA	N/A Beech, willow, birch	(Shetlar 2002) (Wallner 1969)
<i>Eulecanium cerasorum</i>	May	Tennessee, USA	Apple, buckeye, dogwood, elm, locust, maple, pear	(Klingeman et al. 2002)

Species	Time of the year	Location	Host ^a	Reference
	Late May	Kentucky, USA	Sweetgum (<i>Liquidambar styraciflua</i>), hackberry (<i>Celtis occidentalis</i>), sugar maple (<i>Acer saccharum</i>), Norway maple (<i>Acer platanoides</i>), honeylocust	(Mussey and Potter 1997, Hubbard and Potter 2005)
	Late May to early June	California, USA	Pear	(Madsen and Barnes 1959)
	June to early July	Pennsylvania, USA	Crabapple, dogwood, elm, maple, honeylocust, Japanese zelkova, pear, sweetgum, <i>Wisteria</i> spp.	(Hoover et al. 2011)
		New Jersey and Midwestern USA	Various	(Krischik and Davidson 2003, Herms 2004)
	June	New Jersey, USA	Various	(NJDA 2006)
<i>Eulecanium kunoense</i>	Early to mid-May (females) March (males)	Walnut Creek, California, USA	Various	(Madsen 1962)
<i>Eulecanium tiliae</i>	Late May to Mid-June	Armenia, Eurasia	Apple, pear, plum; broadleaved trees and shrubs	(Babayan 1976)
<i>Lichtensia viburni</i>	Early to mid-June (1 st generation) Mid-Aug. (2 nd generation)	Mediterranean basin	Olive, <i>Pistacia lentiscus</i> , <i>Hedera helix</i>	(Pellizzari 1997)
<i>Mesolecanium nigrofasciatum</i>	Mid-May to mid-June Late May to early June June June	Ohio, USA North Carolina, USA Pennsylvania, USA New Jersey, USA	Various Blueberry Peach, sycamore N/A	(Shetlar 2002) (Meyer et al. 2001) (Simanton 1916, Hoover et al. 2011) (NJDA 2006)
<i>Neolecanium cornuparvum</i>	May, Aug. July, Sep. Late July to early Aug. Late Aug. Late Aug and Sep. Early Sep.	New Jersey, USA New York, USA Ohio, USA Pennsylvania, USA Michigan, USA Virginia, USA	N/A <i>Magnolia</i> spp. <i>Magnolia</i> spp. <i>Magnolia</i> spp. <i>Magnolia</i> spp. <i>Magnolia</i> spp.	(NJDA 2006) (Herrick 1931) (Herms 2004) (Hoover et al. 2011) (Wallner 1969) (Kosztarab 1996)
<i>Neopulvinaria innumerabilis</i>	May	Tennessee, USA	Alder, ash, beech, boxwood, dogwood, elm, lilac, linden, locust, maple, oak	(Klingemann et al. 2002)
	Mid to Late May	Athens, Georgia, USA	Red oak	(Hodges and Braman 2004)
	Early June	Virginia, USA	Various	(Day 2008)
	Mid-June	Colorado, New Jersey, USA	Various hardwoods	(Cranshaw et al. 1994, NJDA 2006)
	Mid-June to mid-July	Pennsylvania, USA	Maple, pear	(Hoover et al. 2011)
	Mid-June to early July	Midwestern USA	Maple, honeylocust, linden (<i>Tilia</i> spp.)	(Krischik and Davidson 2003)

Species	Time of the year	Location	Host ^a	Reference
<i>Parasaissetia nigra</i>	Dec. and Jan. May (partial 2 nd)	California, USA	Various	(Smith 1944)
<i>Parthenolecaium corni</i>	May Late May to mid-June (1 st generation) Early autumn (2 nd generation) Late May to early July Early June June and July	Tennessee, USA Athens, Georgia, USA California, USA Virginia, USA Midwestern USA	Fruit trees and ornamental plants Pin oak (<i>Quercus palustris</i>), red maple (<i>Acer rubrum</i>), willow oak (<i>Q. phellos</i>) Broom (Fabaceae, Genisteae) Various Various	(Klingeman et al. 2002) (Hodges and Braman 2004) (Birjandi 1981) (Day 2008) (Krischick and Davidson 2003, Herms 2004)
	Mid-June Mid-June to mid-July (1 st generation) Mid-Aug. (2 nd generation) Mid-July Oct. to early Nov. (1 st generation) Jan. (2 nd generation)	New Jersey, USA Pennsylvania, USA California, USA Chile	N/A Various Pear, Elm Grapes	(NJDA 2006) (Asquith 1949, Hoover et al. 2011) (Essig 1915, Madsen and Barnes 1959) (Bayer CropScience Chile 2014)
<i>Parthenolecanium fletcheri</i>	Early June June	Virginia, USA Pennsylvania, USA	Arborvitae, yew, pachysandra, Eastern red cedar Arborvitae (<i>Thuja</i> spp.), yew	(Day 2008) (Hoover, 2006)
<i>Parthenolecanium fletcheri</i>	Mid to Late June Late June July, mid-Aug.	Midwestern USA Central Europe New Jersey, USA	Various <i>Cupressus</i> , <i>Juniperus</i> <i>Platyclusus</i> , <i>Thuja</i> , <i>Tsuga</i> N/A	(Krischick and Davidson 2003, Herms 2004) (Malumphy et al. 2011) (NJDA 2006)
<i>Parthenolecanium orientale</i>	Mid-May	China	Grapevine (<i>Vitis vinifera</i>)	(Li 2004)
<i>Parthenolecanium persicae</i>	Early May Mid-May to mid-June Late July Mid-Nov.	Southern Greece Ohio, USA Henrico County, Virginia, USA Chile	Grapevine Various Barberry Fruit trees	(Stathas et al. 2003b) (Shetlar 2002) (Kosztarab 1996) (Bayer CropScience Chile 2014)
<i>Parthenolecanium prunosum</i>	Late May to June	California, USA	Walnut	(Michelbacher 1955)
<i>Parthenolecanium quercifex</i>	Late May	Virginia, USA	Oaks, hickory, birch	(Schultz 1984)
<i>Parthenolecanium rufulum</i>	Late May	Northeastern Italy	English oak (<i>Quercus robur</i>)	(Rainato and Pellizzari 2009)
<i>Physokermes hemicryphus</i>	Late July	Greece	<i>Abies cephalonica</i> , <i>A. borisii regis</i>	(Gounari et al. 2012)
<i>Physokermes piceae</i>	Mid-June	Wooster, Ohio, USA	N/A	(Herms 2004)

Species	Time of the year	Location	Host ^a	Reference
	Late June	Colorado, USA	Spruce	(Cranshaw et al. 1994)
<i>Protopulvinaria pyriformis</i>	Apr. (males) May (females)	Florida, USA	Avocado	(Moznette 1922)
<i>Pulvinaria acericola</i>	Late May to early June	Virginia, USA	Maple, dogwood, holly, andromeda, gum	(Day 2008)
	June to early July June 8 to 14	Pennsylvania, USA Lexington, Kentucky, USA	Azalea Red maple	(Hoover et al. 2011) (Mussey and Potter 1997)
<i>Pulvinaria amygdali</i>	Mid-June	New York State, USA	Peach, plum, quince	(Harman 1927)
<i>Pulvinaria floccifera</i>	Late May and June Early June	Pennsylvania, USA Virginia, USA	Holly, ivy, <i>Taxus</i> spp. Camellia, holly, <i>Taxus</i> spp., rhododendron, hydrangea, maple,	(Hoover et al. 2011) (Day 2008)
	Mid-June Mid to Late June June	New Jersey Athens, Georgia, USA Tennessee, USA	English ivy N/A Burford holly, Bradford pear <i>Callicarpa</i> spp., <i>Camellia</i> spp., holly, hydrangea, maple, yew	(NJDA 2006) (Hodges and Braman 2004) (Klingeman et al. 2002)
	Late June to early July Mid-July to Late June	Connecticut, Rhode Island, USA Guilan and Mazandaran provinces, Iran	Various Citrus, <i>Taxus baccata</i> , <i>Pittosporum</i> <i>toriba</i> , <i>Ilex aquifolia</i> , <i>Camellia sinensis</i>	(Westcott 1973) (Hallaji-Sani et al. 2012)
<i>Pulvinaria hydrangeae</i>	July	Europe; Australia; New Zealand; USA	Various	(Alford 2007)
<i>Pulvinaria polygonata</i>	March	India	Mango, citrus	(Chatterji and Datta 1974)
<i>Pulvinaria psidii</i>	Early Apr. (1 st generation) Mid-June to early July (2 nd generation) Early to mid-Sep. (3 rd generation)	Egypt	Guava	(Bakr et al. 2012)
<i>Pulvinaria rhois</i>	Mid-Apr.	California, USA	Prune, apple, peach, plum	(Essig 1915)
<i>Pulvinaria vitis</i>	Late May Early to mid-June July-Aug.	Germany; former Soviet Union Ontario, Canada Pacific Northwest USA	Various Peach Grape	(Schmutterer 1952, Borchsenius 1957) (Phillips 1963) (Hollingsworth 2014)
<i>Pulvinariella mesembrianthemii</i>	Early May Late May	Oakland, California, USA El Cerrito, California, USA	Ice plant (<i>Carpobrotus</i> sp.)	(Washburn and Frankie 1981)
<i>Rhodococcus turanicus</i>	Mid-May	Armenia	Stone fruits	(Babayan 1986)

Species	Time of the year	Location	Host ^a	Reference
<i>Saissetia oleae</i>	Apr.-May (1 st generation)	California, USA	Citrus, olive (<i>Olea europaea</i>)	(Gill 1988)
	May (1 st generation)	California, USA; Mediterranean Basin	Citrus, olive	(Bibolini 1958)
	Sep.-Nov. (partial 2 nd generation)	Eastern Spain	Citrus, olive	(Bibolini 1958, Argyriou 1963, Peleg 1965, Nuzzaci 1969b, De Freitas 1972)
	June to July (for 1 generation)	Eastern Spain	Citrus, olive	(Briales and Campos 1986, Noguera et al. 2003, Tena et al. 2007)
	Mar. to Oct. (for 2 generations)	Eastern Spain	Citrus, olive	(Panis 1977b, Llorens Climent 1984, Noguera et al. 2003)
	Oct.-Nov.	Argentina, Chile, Peru, southern Australia	Various fruit trees	(Simmonds 1951, García 1969, González and Lamborot 1989)
<i>Sphaerolecanium prunastri</i>	Mid-May to mid-June June	Ohio, USA Pennsylvania, USA	Various Purpleleaf plum, <i>Pyracantha</i> spp.	(Shetlar 2002) (Hoover et al. 2011)
<i>Toumeyella liriodendri</i>	Aug.	New Jersey, Pennsylvania, Tennessee, USA	Tulip tree, magnolia, linden	(Klingeman et al. 2002, NJDA 2006, Hoover et al. 2011)
	Sep. Late Aug. to Sep.	Virginia, USA Midwestern USA	Tulip tree, magnolia Tulip tree, magnolia, basswood, buttonbush, hickory, linden, redbud, walnut	(Day 2008) (Krischik and Davidson 2003)
<i>Toumeyella parvicornis</i>	June to early July (in 1 generation)	Colorado and Nebraska, USA	<i>Pinus</i> spp.	(Clarke 2013)
	May to late July (in 2 generations)	Maryland, Virginia, North Carolina, USA	<i>Pinus</i> spp.	(Clarke 2013)
<i>Toumeyella parvicornis</i>	Apr. (first of 4 generations)	Georgia, USA	<i>Pinus</i> spp.	(Clarke 2013)
	Mid-June	New Jersey	N/A	(NJDA 2006)
	Mid-June to mid-July	Pennsylvania, USA	<i>Pinus</i> spp.	(Hoover et al. 2011)
	Late June to early July	Midwestern USA	<i>Pinus</i> spp.	(Krischik and Davidson 2003)
<i>Toumeyella pini</i>	Late May to early June	Colorado, USA	<i>Pinus sylvestris</i> , <i>Pinus mugo</i> , <i>Pinus edulis</i> , <i>Pinus nigra</i>	(Cranshaw et al. 1994)
	Mid-June to mid-July June 20	Pennsylvania, USA Wooster, Ohio, USA	<i>Pinus</i> spp. N/A	(Hoover et al. 2011) (Herms 2004)
<i>Toumeyella pinicola</i>	Feb.	Southern California, USA	<i>Pinus</i> spp.	(Dreistadt 2004)
	Mid-Apr. to mid-May.	San Mateo Co., California, USA	<i>Pinus</i> spp.	(Kattoulas and Koehler 1965)
	Late Apr.	San Francisco Bay area, California, USA	<i>Pinus</i> spp.	(Dreistadt 2004)
	Aug. (males)	San Mateo Co., California, USA	<i>Pinus</i> spp.	(Kattoulas and Koehler 1965, Gill 1988)

^a N/A = Not available

CHAPTER TWO

LIFE HISTORY AND PHENOLOGY OF *PARTHENOLECANIUM* SPP. IN THE URBAN
LANDSCAPES OF THE SOUTHEASTERN U.S.

Introduction

Soft scales of the cosmopolitan genus *Parthenolecanium* (Hemiptera: Coccoidea: Coccidae) feed on trees and shrubs (Kozár and Ben-Dov 1997). Of the six species reported as pests in the U.S. (Ben-Dov et al. 2015), three are commonly found in the east region: the European fruit lecanium, *Parthenolecanium corni* (Bouché); the Fletcher scale, *P. fletcheri* (Cockerell); and the oak lecanium, *P. quercifex* (Fitch).

Parthenolecanium fletcheri is a non-indigenous pest from the Palearctic region; it is commonly found in the landscape of the eastern U.S., where it feeds on conifers, mainly cypress (*Thuja* spp) and yew (*Taxus* spp.) (Ben-Dov et al. 2015). *Parthenolecanium corni* is a polyphagous species (host plants include many economically important crops) and the most studied species of the genus (Kawecki 1958, Bailey 1964, Bijardi 1981, Gill 1988, Kosztarab 1996, Ben-Dov et al. 2015). This pest is present mainly in the Palearctic and Nearctic regions, although sporadic detections have been reported elsewhere (Ben-Dov et al. 2015). In the U.S., *P. corni* is considered a serious pest of ornamental plants and fruit trees (Hamon and Williams 1984, Miller et al. 2005). *Parthenolecanium quercifex* is native to North America and feeds mainly on oaks and other members of the Fagaceae (Ben-Dov et al. 2015).

In urban landscapes of the southern U.S., *P. corni* and *P. quercifex* are pests of ornamental woody plants such as hickory, maple, persimmon, sycamore, and wax myrtle but most commonly are found on oaks (Sanders 1909, Williams and Kosztarab 1972, Schultz 1984, 1985, Hodges and Braman 2004). The phenologies of *P. corni* and *P. quercifex* in the Southeast are not well known. Hodges and Braman (2004) developed a phenological model based on degree-day accumulation and identified plant indicator species to predict crawler emergence of *P. corni* on pin oak (*Quercus palustris* Münchh). Neither a comprehensive study of the phenology, nor a regional report for either scale species was included, both necessary steps in designing a management program for these pests.

Careful timing of control measures is critical in managing landscape pests (Ascerno 1991, Raupp et al. 1992, Mussey and Potter 1997). Application of chemical control targeting a specific insect pest life stage is an example of how plant and pest phenology could affect management decisions. The first instar or “crawler” of soft scale insects lacks the protection of a waxy cover or deposit (Hodges and Braman 2004), and, therefore, is vulnerable to the application of contact insecticides. Many plant and pest managers, however, may not know when and how to identify or determine the timing of crawler emergence (Raupp 1985). The lack of knowledge of the biology and life cycle of *P. corni* and *P. quercifex* hinders the development of a well-timed and effective management program in urban landscapes.

Insect activity can be predicted through the use of phenology models, based on degree-day (DD) accumulations or plant phenological indicators (Mussey and Potter 1997, Roltsch et al. 1999, Trudgill et al. 2005). Phenological models are key for timing control actions against pests, at least at a regional level (Orton and Green 1989, Herms 2004).

Previous research has developed degree-day and plant phenological models to predict activities of insect pests of woody ornamental plants in the landscape, including scale insects (Raupp et al. 1992, Mussey and Potter 1997, Herms 2004). Hodges and Braman (2004) developed a degree-day model and identified plant phenological indicator species to predict the crawler emergence of five species of scale insects (including *P. corni*) in urban landscapes in Athens, Georgia. Crawler emergence of *P. corni* was observed between 1064 to 1622 DDC (degree-days Celsius) at the standard base temperature of 10.6°C and 1184 to 1296 DDC at the experimental base temperature of 12.8°C. The emergence also coincided with full bloom of oak leaf hydrangea. Degree-day accumulation was conducted with sine-wave method in this study; Hodges and Braman (2004) did not compare the accuracy of multiple degree-day approximation methods. The work was also conducted in the state of Georgia; similar information from other states in the region is still unavailable.

Predictive models for crawler emergence based on plant phenology or degree-day accumulations depend on the timing and duration of the life cycle of the target pest (Mussey and Potter 1997). Life tables are informative about the dynamics of an insect

pest population, providing time frames that allow management practices to achieve the maximum effect in reducing survival rates of target pests (Watt 1964, Morris 1963, Harcourt 1969). Life tables have been developed for sternorrhynchan pests, such as aphids (Gao et al. 2011, Madahi and Sahragard 2012), whiteflies (Asiimwe et al. 2006), mealybugs (Chong et al. 2008, Francis et al. 2012) and soft scales (Abd-Rabou et al. 2009). Birjandi (1981) estimated the abundance and fecundity of *P. corni* in Berkshire, England but did not calculate life table parameters, such as the intrinsic rate of increase. Information about individual life stages and a life table analysis of *Parthenolecanium* spp. in the U.S. urban landscape are still missing, despite the economic and ecological importance.

The goal of our research is to provide plant and pest managers with biological information and phenological predictive models for managing *Parthenolecanium* spp. in the urban landscape. We have identified the following objectives: 1) to better understand the life history of *Parthenolecanium* spp. on willow oaks in South Carolina; 2) to determine the correlation between fecundity and size of adult females; 3) to develop a life table for *Parthenolecanium* spp.; and 4) to develop degree-day and plant phenological models to predict crawler emergence of *Parthenolecanium* spp. in the southeastern U.S.

Materials and Methods

Life history of *Parthenolecanium* spp. We collected scale insects by convenient sampling of populations from six willow oaks (*Quercus phellos* L.) at the Pee Dee

Research and Education Center in Florence, South Carolina. The trees were planted in narrow islands of turfgrass surrounded by the pavement of a parking lot. They were about 7—9 m tall, 10—30 cm in diameter at breast height, and 5-6 m in canopy width. The trees were found to be infested with a mixed population of *P. corni* (20%) and *P. quercifex* (80%). It is difficult to distinguish between the adult females of *P. corni* and *P. quercifex*; identification of the two species can be achieved only by examining crawlers under stereo-microscopes at high magnification (Hodges and Williams 2003). The biology and morphology of *P. corni* and *P. quercifex* on willow oak are similar; therefore, the two species were treated in this study as a group, *Parthenolecanium* spp. The scale population was not treated with insecticides during the study.

One twig (10 to 15 cm) was collected weekly from each of the four cardinal directions of each tree in March to November and biweekly in December to February from 2009 to 2013. Five leaves were selected emulating true random sampling (to the best extent) and detached from the twigs; the average number of first- and second-instar scales found feeding on each leaf was counted under a stereomicroscope. The life stages found on the twigs (overwintering second and third instars, and adult) were examined under a stereomicroscope and the numbers of each life stage were recorded. The amount and arrange of scales on a leaf or twig varies from one to the other; therefore, each leaf or twig was considered a unique, independent observational unit. The average density (number of individuals per leaf or cm of twig) of each developmental stage was plotted against time to identify seasonal changes in density.

Fecundity was determined by collecting and dissecting 18 gravid females (one female per twig, three twigs from each of six trees) near the end of the reproductive period in early to mid-May 2012—2014. The developmental biology and physiology of each scale on each twig is unique; therefore, each scale was considered an independent observational unit. Each female (with its eggs) was weighted on a digital balance. Eggs were counted under stereomicroscope on a 5x5 cm paper subdivided into 2x2 mm squares. Measurements of the physical characteristics of the scale tests (height = greatest distance from venter to dorsum, perpendicular to venter; length = greatest distance from distal margin of anterior end of head to distal margin of posterior end of abdomen, parallel to mid-dorsal line; and width = widest distance between the two sides, perpendicular to mid-dorsal line) were taken with the software ProgRes CapturePro v2.8.8 (I-Solution™, Image and Microscope Technology Inc., Vancouver, BC, Canada). Relationships between the number of eggs and the physical characteristics of the test, and the weight of the egg mass per female were analyzed through linear regression (PROG REG; SAS Institute 2011). Parasitized scales were excluded from the assessment.

A life table of *Parthenolecanium* spp. on willow oak in South Carolina was developed. The data for this study were obtained from the same six willow oaks and scale populations used in the life history study. The scale population sampled on each tree was considered as a cohort. The life table was based on 1) the number of

individuals surviving in the population at each sampling date in one generation, and 2) the age-related fecundity of adult females from the fecundity study.

The survival rate (l_x) is the probability that a first instar nymph will reach a specific sampling week (x); the age-related fecundity (m_x) is the average of eggs produced by each adult female at week x (Birch 1948). The survival rate was estimated based on the average total numbers of live individuals at each life stage in each week between April 2012 and June 2013 (one generation), expressed as a fraction of an initial population of crawlers (first instars) (Southwood and Henderson 2000). After plotting the graph, based on the number of eggs produced by a female during the entire ovipositing season, the fecundity per week was calculated by relating the corresponding area under the graph to the total number of eggs produced (i.e., the peak of the graph).

The following life table parameters were estimated for each cohort from each tree: gross reproductive rate, $GRR = \sum m_x$; net reproductive rate, $R_o = \sum (l_x m_x)$; mean generation time, $T_G = \sum (x l_x m_x) / \sum (l_x m_x)$; intrinsic rate of increase, $r_m = (\ln R_o) / T_G$; and finite rate of increase $\lambda = \exp (r_m)$.

Degree-day predictive model for scale phenology. Willow oak trees infested with *Parthenolecanium* spp. in Griffin, Georgia (2 trees at 33° 14' 60" N, 84° 17' 37" W, 273.11 meters above sea level); in Florence, South Carolina (6 trees at 34° 17' 17" N, 79° 44' 16" W, 36.42 meters above sea level); in Raleigh, North Carolina (5 trees at 35° 46' 26" N, 78° 40' 39" W, 105.58 meters above sea level); and Virginia Beach, Virginia (1 tree at 36° 52' 21" N, 76° 10' 14" W, 6.95 meters above sea level; and 1 tree at 36° 53' 50" N,

76° 10' 50" W, 6.75 meters above sea level) were monitored weekly from March to June in 2011 to 2013. Most locations belong to zone 8a in the USDA Plant Hardiness Zone Map (USDA-ARS 2012), except for Raleigh, North Carolina which belongs to zone 7b. The dates of first crawler emergence were recorded at each site. A mixed population of *P. corni*-*P. quercifex* on willow oak was found in all four states studied [Georgia (50-50%), South Carolina (20-80%), North Carolina (60-40%), and Virginia (30-70%)].

Degree-day accumulation was estimated for each site in degree-days Celsius (DDC), from January 1 to the date of first crawler emergence each year using online climatic information from weather stations nearest the locations of the infested trees in each state [AB4KN Fayetteville, Georgia (15 km from the Griffin test site); AS045 KD4VH Quinby, South Carolina (8 km from the Florence test site); CW2094 Raleigh, North Carolina (10 km from the Raleigh test site); CW7042 Norfolk, Virginia (6 and 7 km from the Virginia Beach test sites)]. The online degree-day models from the Integrated Plant Protection Center at Oregon State University (OSU 2014) were used to calculate the degree-day accumulations.

Three-year (2011–2013) degree-day models were developed in this study using three common estimation methods (simple-average, single-sine and single-triangle) and three base temperatures [7.2°C (45°F), 10°C (50°F), and 12.8°C (55°F)]. These base temperatures have been used to predict egg hatch of scale insects in urban landscapes (Mussey and Potter 1997), whereas the base temperature for *P. corni* development has been experimentally established at 12.8°C in Athens, Georgia (Hodges and Braman

2004). The predicted crawler emergence dates and degree-day Celsius accumulations of the 3-yr models were compared against actual dates and their corresponding DD accumulation in 2014 to validate the model. The models where predicted dates and cumulative DDC had the smallest differences with the actual dates of crawler emergence were chosen as best models for each state.

A regional model to predict crawler emergence was built after comparison of all combinations of each of the three base temperatures with the three methods in all states. The base temperature and method resulting in the lowest differences in DD accumulation and dates across all states was chosen as the regional model. Afterwards, a DDC accumulation for the regional model was calculated as an average of the DDC of the model for each of the three states. The regional model DDC was then tested against the DDC actual dates of crawler emergence in each state for validation.

Plant phenological indicators. Plant species widely available at each test site and with distinctive phenophases were identified as indicator plants of crawler emergence at Griffin, Georgia; Raleigh, North Carolina; Florence, South Carolina; and Virginia Beach, Virginia. Plant phenophases corresponding to three phenological stages (flower buds visible, first flower open or petals visible, 50% flowers open, and all flowers fully bloomed) in the flowering sequence on the BBCH (Biologische Bundesanstalt, Bundessortenamt and Chemical industry) scale system (Finn et al. 2007) were recorded for candidate plant species that researchers in each state had chosen based on their observations. The corresponding phenological stage for each plant indicator species

identified was matched with first crawler emergence in 2010 to 2012 in all four states, and additionally in 2013—2014 in South Carolina and Virginia. To validate previous observations at the Clemson University Pee Dee Research and Education Center (PDREC) in South Carolina, we also monitored additional indicator plants at four other sites within the city of Florence in 2014.

Results and Discussion

Phenology and life history. *Parthenolecanium* spp. are univoltine in South Carolina; Hodges and Braman's (2004) reported one complete and a second partial generation of *P. corni* in Georgia. Eggs hatched between mid-April to early June (Fig. 2.1). After eclosion, crawlers dispersed to and fed on nearby leaves. First instars of *P. quercifex* (Williams and Kosztarab 1972) and *P. corni* (Kosztarab 1996) are known to settle on the underside of leaves. Hubbard and Potter (2005) reported finding crawlers of the calico scale, *Eulecanium cerasorum* (Cockerell), settling mostly on the underside of leaves. The numbers of first instars settled on the underside of leaves varied between host plant species: about 85% on hackberry and Norway maple leaves, 93% on sweetgum leaves, and 99% on honeylocust leaves (Hubbard and Potter 2005). We observed and collected first instars on both sides of willow oak leaves, but we did not assess the differences between the two sides in the numbers of settled first instars. Results of further studies exploring differences in crawler settlement on leaf surfaces of different hosts might provide insights into the best ways to apply and target contact insecticides against *Parthenolecanium* spp.

First instars are oval, elongate, dorso-ventrally flattened, pale brown to yellow, and 0.3 to 0.5 mm in length. Some first instars became almost transparent after settling on their feeding site until the next molt. The timing of peak densities (calendar-based) for each instar varied from year to year. The highest densities of first instars were reached on 29 May 2009, 24 May 2010, 16 May 2011, 7 May 2012, and 27 May 2013, with 155, 130, 108, 55, and 71 individuals per leaf, at 887, 726, 616, 690, and 636 DDC (10°C base temperature, simple average) respectively (Fig. 2.1.). When all individuals from a generation emerge, about half of the population is lost before reaching the second instar. Mortality of first instars is discussed later.

First instars molted into second instars from mid-September to late October (Fig. 2.1). The highest densities of second instars were reached on 19 October 2009, 25 October 2010, 17 October 2011, 10 September 2012, and 4 November 2013, with 20, 5, 18, 16, and 26 individuals per leaf, at 3,187; 3,160; 3,047; 2,658, and 2,767 DDC respectively (Fig. 2.1). Just before leaf senescence in November, they migrated to the twigs to overwinter (Fig. 2.2), which agrees with Marotta and Tranfaglia's (1997) conclusion that the second instar is the overwintering stage of Nearctic coccids. In each generation, the highest densities of second instars on twigs were reached on 23 February 2009, 15 March 2010, 13 December 2010, 13 February 2012, and 2 January 2013, with 22, 11, 4, 3, and 4 individuals per centimeter of twig, at 86, 56; 3,297; 59, and 1 DDC respectively (Fig. 2.2).

Second instars resemble first instars, except for their increased size (0.6 to 0.9 mm in length). Additionally, the median apical seta of each anal plate of the first instar is elongated (at least half of the body length), but not in the second instar (Williams and Hodges 1997). The anal plates and the anal cleft are at the posterior end of the body in the first instar, whereas the anal plates seem to have “migrated” anteriorly to about 4/5 of the body in the second instar, almost double the length of the anal cleft.

As leaf buds of host trees began to break in mid-March to early April, the surviving second instars (about half of the original population) molted into the third instars (Fig. 2.2). The third instar lasted about 4 d, after which they eclosed into adults. The short duration of third instar and its close resemblance to the adult (differentiated by an increase in size, and the appearance of genital aperture and modified integumentary secretory system) (Marotta 1997) made third instars difficult to detect.

During adulthood, the females increased greatly in size and produced copious amounts of honeydew. The density of adult females ranged from 1 to 10 individuals per centimeter of twig and stayed alive on the twigs for about 4 to 5 wk. Females began to produce eggs in their brood chambers 5 to 7 d after adult eclosion. The eggs hatched within 20 to 25 d. In Virginia, the female of *P. quercifex* begins oviposition in early May and eggs hatch in late May (Williams and Kosztarab 1972). The maturation period of eggs of *Parthenolecanium* spp. seemed similar to that of *S. oleae* and *Ceroplastes rusci* (L.), where hatching occurred within 2 to 3 wk, and 3 to 4 wk after deposition, respectively (Alford 2012).

Parthenolecanium spp. are mainly parthenogenetic (Saakyan-Baranova et al. 1971, Nur 1980, Kosztarab 1996, Rainato and Pellizzari 2009). In our study, no males of *Parthenolecanium* spp. on willow oak were found. Males of *P. quercifex*, however, have been found on willow oak trees in North Carolina, in the same area of our study, but not the same willow oak trees sampled for our research (E. Meineke, personal communication). Although males of *Parthenolecanium* spp. are considered rare (Gill 1988, Kosztarab 1996), males of *P. corni* can be predominant in the population (Thiem 1933, Canard 1958, Saakyan-Baranova et al. 1971). We also found that mixed female populations of *P. corni*-*P. quercifex* on willow oak are common in Georgia, North Carolina, South Carolina and Virginia. The ratios of *P. corni* were higher than *P. quercifex* only in North Carolina (60:40), in contrast to those in the other three states. The exceptional tendency of *P. corni* to produce males and its higher ratio to *P. quercifex* in the North Carolina female population suggests a likely presence of *P. corni* males in North Carolina.

Fecundity. Females deposited 177 to 2,398 eggs over 3 wk in this study. The fecundity of *Parthenolecanium* spp. in South Carolina falls within the range of previously reported fecundity of *P. corni*, which varies from 100 to 5,000 eggs (Fenton 1917, Kaweki 1958, Bailey 1964, Santas 1985, Babaian 1986).

We confirmed that the fecundity of *Parthenolecanium* spp. was proportional to female body size (Marotta 1997). All body size parameters evaluated in this study yielded a significant correlation with the number of eggs deposited in the linear

regression (Fig. 2.3). Based on our results, all parameters were able to predict fecundity, but the weight of the adult female (and its eggs) was more accurate than the three parameters used for scale size, with length as the strongest predictor among them (observations with least dispersion from the predicted line). Birjandi (1981) also demonstrated a positive correlation between the volume of *P. corni* and its fecundity [fecundity = $236.66 + 35.23(\text{volume})$]. Our results suggest that, instead of using volume, measuring weight or length and using the linear regression equations developed in this study may be an adequate and simpler method for estimating fecundity of *Parthenolecanium* spp. in a pest management program or an ecological/biological study. This method would save researchers time and effort in measuring all body size parameters or counting all eggs produced by multiple females.

Survivorship. Accumulated mortality of the first instars approached 50% of the population in one generation, which was higher than the mortality of other life stages (32.7% of second instars and 1.6% of third instars) (Fig. 2.4). High rates of mortality during the first instar are common in soft scales (Podoler et al. 1979, Birjandi 1981, Washburn and Washburn 1984, Santas 1985, Rainato and Pellizzari 2009). Lack of success in finding an appropriate feeding site is considered one of the main mortality factors of first instars (Podoler et al. 1979, Washburn and Washburn 1984). Arthropod predation can be another important cause for high mortality of the first instars of *P. corni* (Birjandi 1981). The lack of or a minimum amount of a protective waxy cover also

makes first instars vulnerable to abiotic elements such as high temperature, low humidity, heavy rain and wind (Marotta 1997).

Life table parameters. The gross reproductive rate (GRR) was estimated at 695.98 ± 79.34 ♀/♀; net reproductive rate (R_o) of 126.36 ± 19.03 ♀/♀; a mean generation time (T_G) of 52.61 ± 0.05 weeks; an intrinsic rate of increase (r_m) of 0.04 ♀/♀/week; and a finite rate of increase (λ) of 1.04 times per week. According to Bellows et al. (1992), values of R_o over 1 or r_m over 0 would indicate a population that is increasing, whereas values of R_o below 1 or r_m below 0 would indicate a decreasing population. Our R_o values indicate a population with high rates of increase. Our r_m value indicates a population that increases, but at a relatively slow pace. According to Birch (1948), a relatively low intrinsic rate of increase (r_m) might be partially attributed to higher rates of reproduction late in the adulthood of female scales (Figure 2.5).

Abd-Rabou et al. (2009) conducted the only other locatable life table analysis for a soft scale (*S. coffeae*), and a comparison could not be made because the biology of *Parthenolecanium* spp. differs from that of *S. coffeae*. Although the values of an intrinsic rate of increase of 0.04 and finite rate of increase of 1.04 of *S. coffeae* at 18°C were apparently the same as *Parthenolecanium* spp., the values for *S. coffeae* were obtained per day, whereas those of *Parthenolecanium* were obtained per week.

Analysis of life tables of *S. coffeae* (Abd-Rabou et al. 2009) showed that temperature and generation time were related in *S. coffeae*. As temperature increased, generation time decreased. It would be interesting to evaluate whether temperature

plays a similar role in the life history of *Parthenolecanium* spp., by comparing life table parameters at different temperatures. If temperature plays a different role in generation time for each *Parthenolecanium* species, it might constitute a physiological method for distinguishing *P. corni* from *P. quercifex*. *Parthenolecanium corni* has one to three generations (Borchsenius 1957), whereas *P. quercifex* is exclusively univoltine (Williams and Kosztarab 1972, Swiecki and Bernhardt 2006). In our study, both species are univoltine.

Degree-day predictive models. The calendar dates for first crawler emergence in 2011 to 2014 ranged from 12 April to 7 May in Georgia, 17 April to 11 May in South Carolina, and 27 April to 18 May in Virginia. We excluded North Carolina from the analysis because we had information only for crawler emergence of *Parthenolecanium* spp. in two years (11 May 2011 and 30 April 2012), not enough to build a 3-yr predicting model for the state.

First crawler emergence in Georgia ranged from 23 May to 15 June between 1997 and 2000 (Hodges and Braman 2004), more than a month later than our results. Schultz (1984) also reported the hatching of crawlers in Virginia Beach more than a month later than our dates. However, we consider drawing conclusions about apparent earlier crawler emergence times based on our observations premature because we have gathered information on crawler hatching only for three years. Studies in future years should explore whether this difference in hatching time might be actually differing, and if so, the factors underlying such change.

We monitored first crawler emergence weekly, but first crawler emergence of entire populations (in different trees) actually occurs over several days, rather than on the single day we made the observation. Thus, for the crawler emergence date we used the middle date of the week encompassing the day of crawler emergence observed (Table 2.1). Accordingly, we also provided the corresponding DD accumulations for the crawler emergence date (Table 2.2).

We developed degree-day models for Georgia, South Carolina and Virginia through combinations of three estimation methods and three base temperatures (Table 2.2). The models were tested for accuracy of prediction with actual dates of crawler emergence in 2014 (Table 2.2). All estimation methods and temperatures tested were relatively accurate predictors (most fell within five days before and three days after the day of crawler emergence), but particular combinations seemed to be more accurate in each state: simple average with 12.8°C for Georgia, simple average with 7.2°C in South Carolina, and simple average with 12.8°C and single sine with 7.2°C in Virginia.

A standard base temperature of 10°C (50°F) is used when the lower developmental threshold is not known for the species studied (Herms 2004). In our case, a base temperature of 12.8°C (55°F), applied to any one of the three DD-predicting methods tested, proved sufficient for a regional model. The average regional DDC accumulation was 229 with simple average, 293 with single sine, and 265 with single triangle method. After the regional-models were compared with the actual days of crawler emergence in 2014, DDCs fell 6 days before or 2 days after actual emergence in

all three states. This validated all three regional models as good predictors. Because of its simplicity and for practical purposes, simple average (229 DDC) is preferred as a regional model within an IPM program.

The base temperatures used in the present study included standard temperatures for predicting crawler emergence for scale pests (Mussey and Potter 1997) and an experiment-derived base temperature of 12.8°C (55°F) reported by Hodges and Braman (2004) for *P. corni* in Georgia. Estimations using experiment-derived base temperatures have yielded less variation than those obtained from standard temperatures (Hodges and Braman 2004). Because we used mixed populations of two species of *Parthenolecanium* and tested the models along different latitudes, we considered it appropriate to compare the predictive models with common standard base temperatures other than the experiment-derived temperature. We confirmed, at a regional level, that the experiment-derived base temperature of 12.8°C worked better than the other temperatures tested. Particular models, however, were found to work better within each state.

Our range of DD accumulation (218-329) for first crawler emergence of *Parthenolecanium* spp. in Griffin, Georgia, using a single-sine method with a base temperature of 12.8°C, differed from the DD accumulation range of 1,184 to 1,296 DDC reported previously for *P. corni* in Athens, Georgia (Hodges and Braman 2004). The differences in ranges of DDC obtained by us and those by Hodges and Braman (2004) could be partially attributed to the use of different programs to calculate the DDC.

Hodges and Braman (2004) used the DEGDAY utility program (Higley et al. 1986), whereas we used the online degree-day models from the Integrated Plant Protection Center at Oregon State University (OSU 2014). Griffin is located 115 km southwest of Athens, an earlier crawler emergence might be expected in Griffin, where DD should accumulate at a faster rate.

Temperature data used to calculate degree-days are the major source of error in degree-day models (Herms 2004). Although the use of weather data from standardized sources over several years tends to cancel the errors when estimating insect development, the error derived from temperature data was considered a concern in our study. If the weather station is far from the actual site, the temperature will likely be different. The distance and the difference in DD between the weather station and the test site were not the same across the states, so this represents an issue in developing a regional model.

Other variables that can influence the accuracy of degree-day estimation methods include time of the year, geographic and physical location, and biology of the organism under study (Roltsch et al. 1999). Roltsch et al. (1999) found the single-triangle method yielded less error during the winter and early spring months in California when compared to single-sine. Our results suggest that both methods with 7.2°C as base temperature work as predictors in northern sites (such as Virginia). At southern locations, however, the three DD models tested for estimation yielded fewer DD and day differences.

Plant phenological indicators. Little is known about plant species as indicators of crawler emergence of *Parthenolecanium* spp. in the southeastern region, except for the study by Hodges and Braman (2004). They reported oak leaf hydrangea (*Hydrangea quercifolia* Bartram) as an indicator species for predicting first crawler emergence of *P. corni* in Athens, Georgia. The plant was in full bloom in 1997, 1999, and 2000 at the time of first crawler emergence, and had completed blooming one week before crawler emergence in 1998. In our study in Griffin, Georgia, indicator plant species identified locally as predictors differed from the one identified in Athens.

When crawlers of *Parthenolacanium* spp. emerged in 2010 and 2011, dandelion (*Taxacum* spp.) and knock-out rose (*Rosa* 'Radrazz') were at full bloom in Georgia, and honeysuckle (*Lonicera* spp.) was at full bloom in Virginia. At the same time, southern magnolia (*Magnolia grandiflora* L.) was at first bloom in North Carolina.

At the time crawlers emerged in 2012, Chinese privet (*Ligustrum sinense* Lour.), dandelion, and knock-out rose were in full bloom in Georgia. Southern magnolia was beginning to bloom in South Carolina and North Carolina. Flower buds of confederate jasmine [*Trachelospermum jasminoides* (Lindley) Lemaire], peonies (*Paeonia* spp.), and yellow daylily (*Hemerocallis* 'Happy Returns') were developing in Virginia.

When crawlers emerged in South Carolina in 2013, southern magnolia was in first bloom, and honeysuckle was in 50% bloom. During 2013 and 2014 in Virginia, yellow daylily was in full bloom, and first petals were visible on the confederate jasmine.

In 2014, first bloom of southern magnolia was validated as an accurate plant indicator for crawler emergence of *Parthenolecanium* spp. in all sites surveyed in South Carolina (Table 2.3). Even though crawlers began to emerge two days earlier at sites in the city of Florence than at the PDREC site, the southern magnolia phenophase (first bloom) still was synchronized with scale phenology. The difference in time of scale emergence between sites might be partly attributed to the scales' local response to urban warming (Meineke et al. 2013).

The identification of vulnerable points in the life cycle of a pest is a basic principle of any pest management program (Pedigo and Rice 2009). The most vulnerable stage of soft scales is first instar. We determined that all first instars of *Parthenolecanium* spp. emerged by early June in South Carolina (Figure 2.2). This might seem a suitable time to apply contact insecticides to achieve optimal control, except that the parasitoids associated with the scales are also active, and remain so until mid-September (Chapter 3). An approach commonly used in integrated management programs is to conserve natural enemies (Pedigo and Rice 2009). Thus, mid-September may be a better time to spray contact insecticides to reduce scale populations without adversely affecting their natural enemies. If systemic insecticides are used, they should be applied by late May, before all crawlers hatch.

The regional range in DDC accumulation we provided (403–481 with simple average) can be used as a guideline to predict crawler emergence of *Parthenolecanium* spp. from Georgia to Virginia. An easy way to check when this range of DDC has

accumulated is to consult the “online phenology and degree-day models” (<http://uspest.org/cgi-bin/ddmodel.us>), specifying “12.8” (Celsius) as the lower threshold, choosing “simple average” as the predicting method, and the start date of “January 1” of the year when the prediction is sought. Additionally, plant indicator species that can be used to start scouting for crawler emergence include Chinese privet, dandelion, or knock-out rose in full bloom in Georgia; honeysuckle at 50% bloom in South Carolina and Virginia; and, confederate jasmine, peonies, or yellow daylily in flower bud in Virginia. First bloom of southern magnolia can be used as a regional indicator because it was the only species commonly observed in all states.

Our life table parameters for *Parthenolecanium* spp. on willow oak, besides indicating a thriving population in South Carolina, can be used as a reference for the population dynamics of the same species covered in other locations (and/or conditions) or to compare other soft scale species of similar biology. Population dynamics also are important a pest’s relationship with its natural enemies because information on parasitoids and predators can be used to anticipate their impact on pest populations.

We have provided a better understanding of the life cycle of *Parthenolecanium* spp. on willow oak, as well as phenological tools to predict the appearance of its most vulnerable stage in the landscape. Although these aspects are basic in managing *Parthenolecanium* spp., the knowledge of its natural enemy populations, especially the composition and impact on scale populations, also is crucial for understanding how to

control these pests. The next chapter covers this component, which typically is regarded as essential in any integrated management program.

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Table 2.1. Date of first crawler emergence in 2011 to 2014 in Georgia (GA), South Carolina (SC), North Carolina (NC), and Virginia (VA).

State	2011	2012	2013	2014
GA	17 April	11 April	1 May	7 May
SC	4 May	18 April	8 May	7 May
NC	4 May	2 May	—	—
VA	11 May	25 April	8 May	14 May

Table 2.2. Degree-day accumulation for date of first crawler emergence (2011 to 2013) of *Parthenolecanium* spp. and their differences from predicted dates (2014) using three estimation methods and three base temperatures in three southeastern states.

State	Estimation Method	Base Temperature (C°)	DD accumulation				DD difference (predicted-actual)	Predicted Day 2014	Day Difference (predicted-actual)
			2011	2012	2013	Predicted 2014			
Georgia	Simple average	7.2	511	663	449	541	-51	May 4	-3
		10.0	323	440	279	347	-31	May 5	-2
		12.8	171	264	158	198	-12	May 6	-1
	Single Sine	7.2	565	712	507	595	-70	May 2	-5
		10.0	387	502	346	412	-46	May 3	-4
		12.8	249	329	218	265	-30	May 4	-3
	Single Triangle	7.2	547	696	489	577	-65	May 3	-4
		10.0	365	483	325	391	-41	May 4	-3
		12.8	225	308	199	244	-23	May 5	-2
South Carolina	Simple Average	7.2	713	521	646	627	-19	May 6	-1
		10.0	487	488	425	467	30	May 9	2
		12.8	308	308	248	288	19	May 9	2
	Single Sine	7.2	781	790	718	763	45	May 10	3
		10.0	562	573	489	541	33	May 2	-5
		12.8	386	391	309	362	22	May 9	2
	Single Triangle	7.2	759	768	696	741	46	May 10	3
		10.0	538	547	467	517	33	May 10	3
		12.8	361	365	289	338	21	May 9	2
Virginia	Simple Average	7.2	577	542	369	496	-89	May 9	-5
		10.0	392	335	231	319	-70	May 9	-5
		12.8	239	189	134	187	-53	May 10	-4

Table 2.2. Continued.

State	Estimation Method	Base Temperature (C°)	DD accumulation				DD difference (predicted-actual)	Predicted Day 2014	Day Difference (predicted-actual)
			2011	2012	2013	Predicted 2014			
Virginia	Single Sine	7.2	620	594	435	550	-83	May 10	-4
		10.0	431	398	284	371	-73	May 9	-5
		12.8	288	248	178	238	-57	May 9	-5
	Single Triangle	7.2	606	577	411	531	-86	May 9	-5
		10.0	417	378	264	353	-74	May 9	-5
		12.8	172	229	163	188	-89	May 6	-8

Table 2.3. Dates of first crawler emergence of *Parthenolecanium* spp. on willow oak in 2014 at four sites within the city of Florence and one site outside the city.

Site	Number of trees	First day of crawler emergence	Phenophase
Florence city			
Site 1	4	May 6	First flower open
Site 2	2	May 6	First flower open
Site 3	2	May 6	First flower open
Site 4	2	May 6	First flower open
Pee Dee Research and Education Center	6	May 8	First flower open

Figure 2.1. Average weekly abundance of *Parthenolecanium* spp. life stages on willow oak leaves in South Carolina from 2009 to 2013.

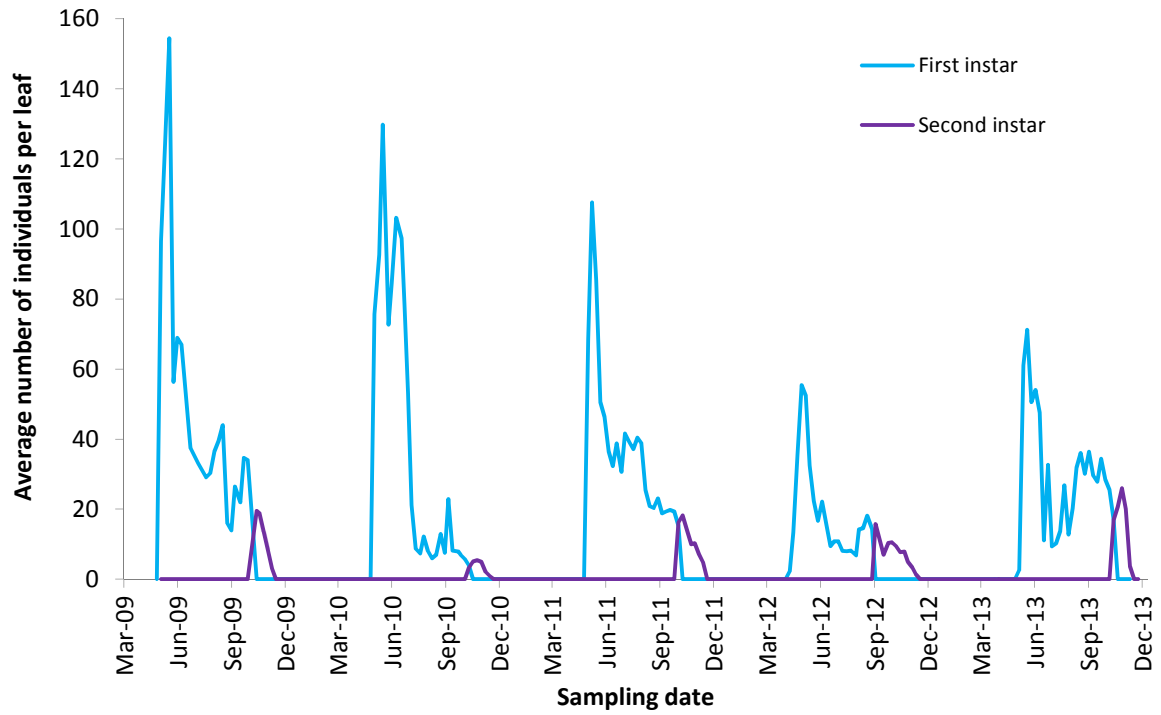


Figure 2.2. Average density of *Parthenolecanium* spp. life stages on willow oak twigs in South Carolina from 2009 to 2013.

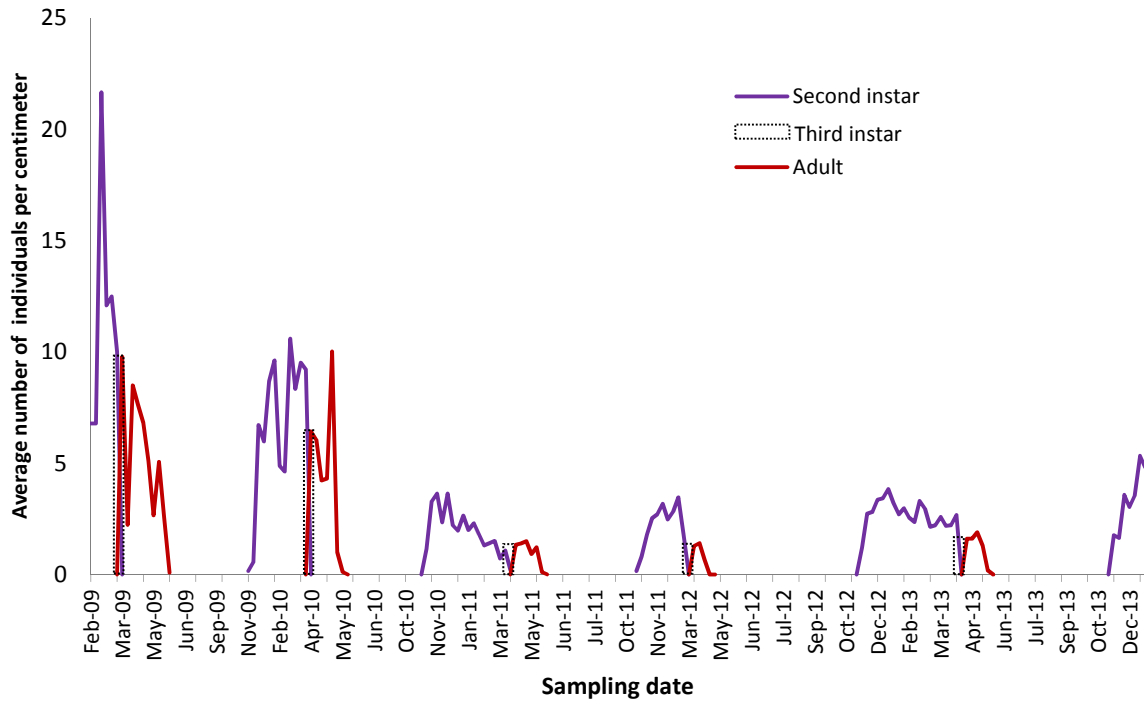


Figure 2.3. Relationship between the fecundity and the weight of the female (with eggs), and length, width and height of the adult female of the lecanium scales.

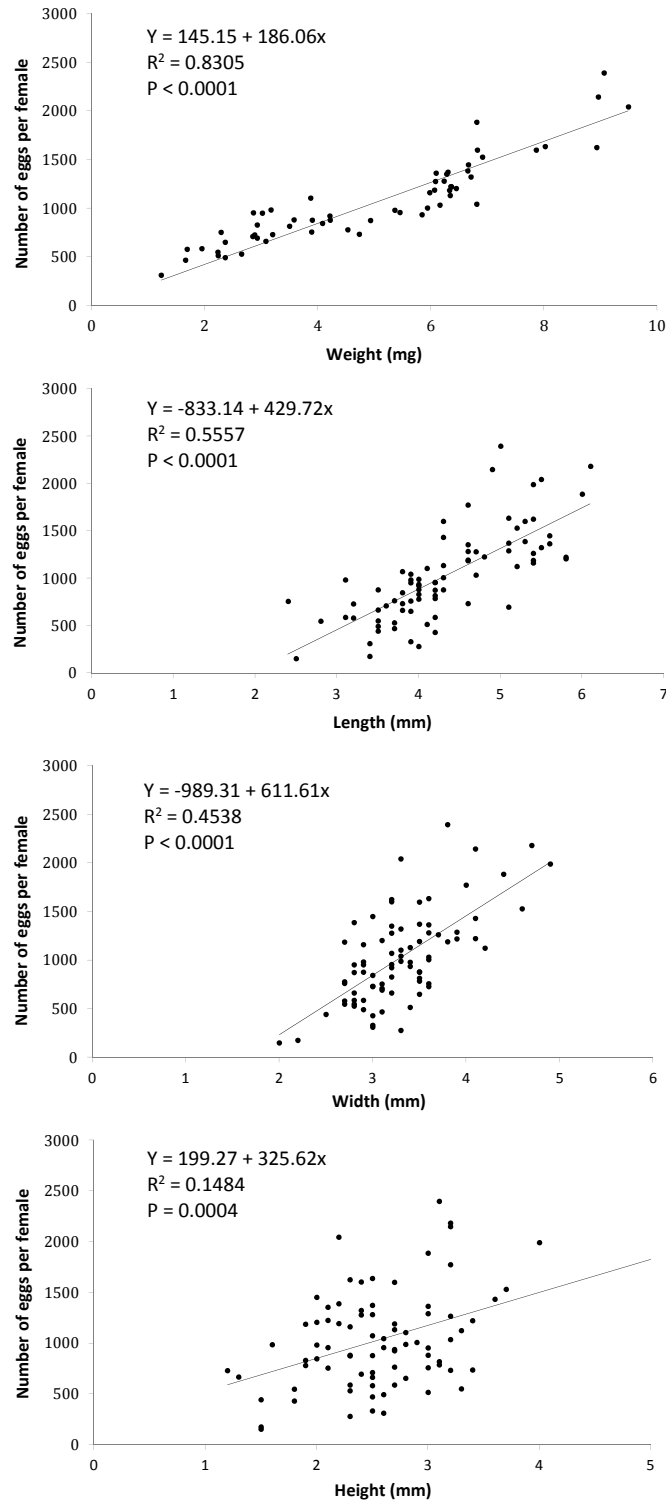


Figure 2.4. Mortality rates in one generation (April 2012- June 2013) of *Parthenolecanium* spp. on willow oak in South Carolina.

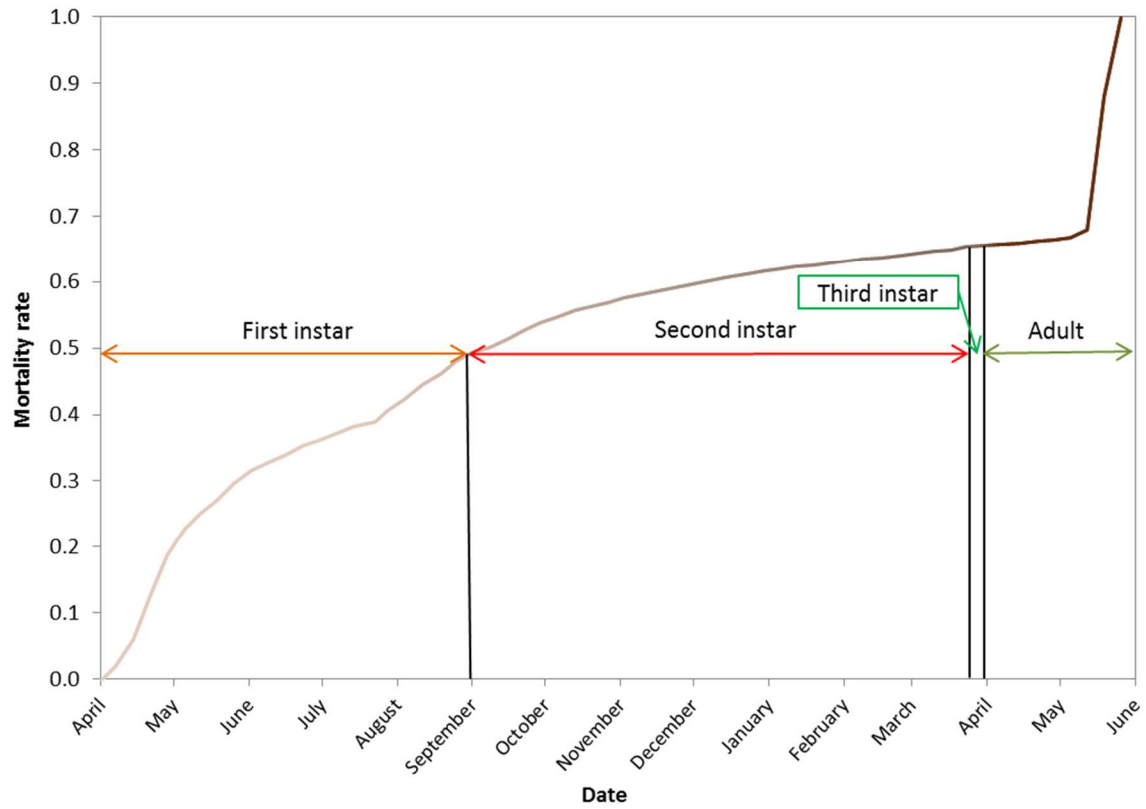
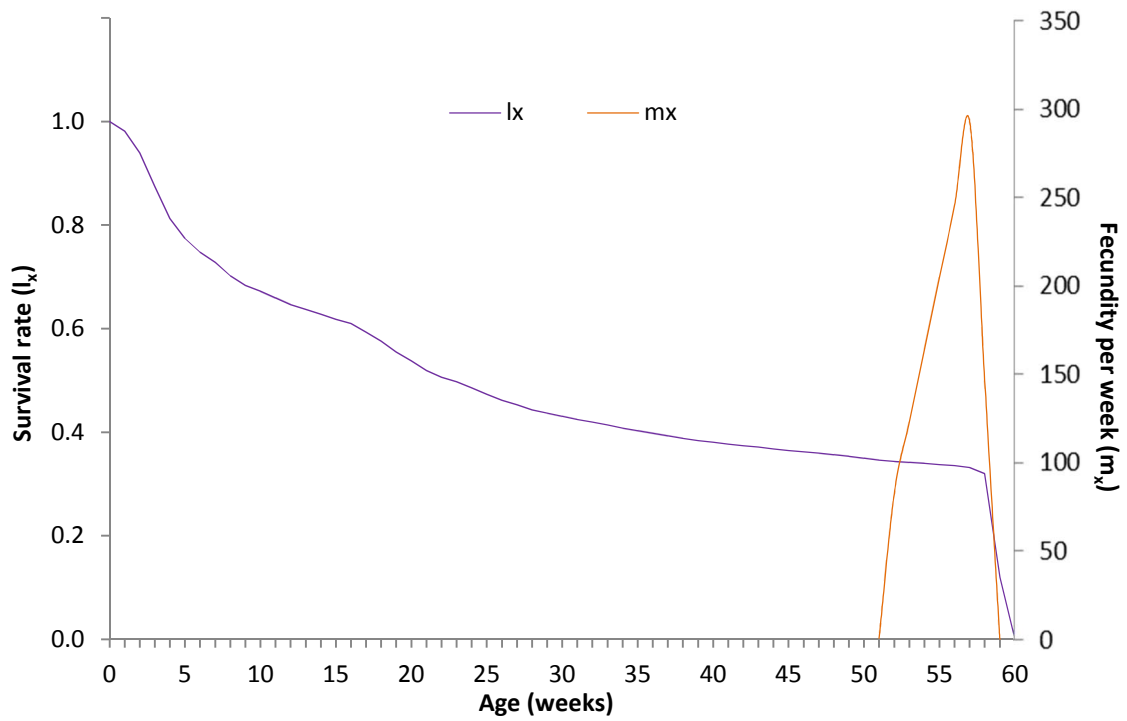


Figure 2.5. The age-specific survival rate (l_x) and fecundity (m_x) of *Parthenolecanium* spp. in South Carolina.



CHAPTER THREE

SPECIES COMPOSITION, SEASONAL ACTIVITY AND IMPACT OF PARASITOIDS AND
PREDATORS OF *PARTHENOLECANIUM* SPP. (HEMIPTERA: COCCIDAE) IN THE
SOUTHEASTERN U.S.

Introduction

Parthenolecanium corni (Bouché) (the European fruit lecanium scale) and *P. quercifex* (Fitch) (the oak lecanium scale) are two of the most commonly encountered soft scale species infesting ornamental and shade trees in urban landscapes (Johnson and Lyon 1991, Gill 1988). In a study of their life histories in the southeastern U.S., we determined that *P. corni* and *P. quercifex* are univoltine, with crawlers beginning to emerge between mid-April and mid-May in Georgia, South Carolina, North Carolina, and Virginia (Chapter 2).

Natural enemies are effective in suppressing populations of *P. quercifex* and *P. corni* (Ebeling 1959, Johnson and Lyon 1991, Schultz 1984, Gill 1988, Kosztarab 1996, Carrillo et al. 2001, Japoshvili et al. 2008). More than 40 species of natural enemies are associated with *P. corni* (Kawecki 1958, Peck 1963, Williams and Kosztarab 1972, Hamon and Williams 1984). Hodges and Braman (2004) found 3 parasitoid species, 1 anthribid species, 3 coccinellid species, 1 green lacewing species, mites, 1 ant species, and 2 spider species associated with *P. corni* populations on pin oak (*Quercus palustris* Münchh.), red maple (*Acer rubrum* L.) and willow oak (*Quercus phellos* L.) in Georgia.

However, the authors did not report the impact of these natural enemies on the scale population. Schultz (1984) reported an assemblage of five species of parasitoids and two coleopteran predators of *P. quercifex* and their seasonal activity in Virginia. Schultz (1984) identified *Encyrtus fuscus* L. and *Blastothrix* sp. (Hymenoptera: Encyrtidae) as internal parasitoids of the adult females, *Coccophagus lycimnia* (Walker) (Hymenoptera: Aphelinidae) as an internal parasitoid of the immatures, and *Pachyneuron altiscutum* Cook (Hymenoptera: Pteromalidae) as a hyperparasitoid. Species in the genus *Eunotus* spp. (Hymenoptera: Pteromalidae), such as *Eunotus lividus* Ashmead, represent examples of a particular ecological role. The adult female parasitoid oviposits in gravid scales and the parasitic larva prey on the eggs within the scales (Kirkpatrick 1962, Graham 1992); therefore, Schultz (1984) reported the ecological role of *E. lividus* as an egg predator, but the species is, in general terms, considered as a parasitoid. Mortality reached 10 to 60% of the scale population due to parasitism by the five chalcidoid species reported by Schultz (1984). *Tricorynus confusus* (Fall) (Coleoptera: Anobiidae) was observed for the first time as a predator of soft scales, and *Hyperaspis signata* (Oliver) (Coleoptera: Coccinellidae) was a known predator of scale insects (Schultz 1984). Schultz (1984) and Hodges and Braman (2004) constitute the only literature on natural enemies of *Parthenolecanium* species in urban landscapes of southeastern states. There are no current reports of the species composition and ecology of communities of natural enemies in these and other states in the southeastern U.S.

An understanding of the life history and phenology of *P. corni* and *P. quercifex* (Chapter 2) is the starting point for designing an integrated management program. These two aspects are used to establish appropriate timing of control measures against the most vulnerable stage of the insect pest (i.e., first instar) (Mussey and Potter 1997, Herms 2004, Hodges and Braman 2004). Another key element in the development of an integrated management program is the knowledge of ecological interactions between the pest and its natural enemies (Pedigo and Rice 2009). Natural enemies help prevent some insect populations from reaching pest status. Natural enemies also reduce potential damage by insects already established as significant pests (CAST 2003, Pedigo and Rice 2009). Biological control is usually (but not always) a safe, environmentally friendly part of integrated management programs (CAST 2003, Pedigo and Rice 2009).

This study aims to expand our understanding of ecological interactions between *Parthenolecanium* spp. and their natural enemies in urban landscapes of Georgia, South Carolina, North Carolina, and Virginia. We identified the following objectives: 1) determine the composition and seasonal activity of parasitoid and predator communities in each state; 2) to compare the diversity of natural enemy communities within and among states; 3) to document parasitoid brood size and scale insect stage at the time of adult parasitoid emergence; 4) to determine the impact of natural enemies on the fecundity of scale insects; and 5) to document the level of parasitism in scale insect populations.

Materials and Methods

Sampling locations, scale insects and host plants. Groups of in-ground, established willow oaks were sampled in Griffin, Georgia (two sites, two trees per site), Florence, South Carolina (six trees at one site), Raleigh, North Carolina (five trees at one site), and Virginia Beach, Virginia (two sites, one tree per site). The trees were about 7–9 m tall, 10–30 cm in diameter at breast height, 5–6 m in canopy width, and were growing in narrow islands (covered with turfgrass and surrounded by pavement) next to roads or in parking lots. All trees were infested by mixed populations of *P. quercifex* and *P. corni*. The ratios of *P. quercifex*-*P. corni*, identified according to the diagnostic characters described by Hodges and Williams (2003), were 50:50 in Georgia, 80:20 in South Carolina, 40:60 in North Carolina, and 70:30 in Virginia. The trees were not treated with insecticides during the study.

Species composition and seasonal activity of parasitoids. The species composition of the parasitoid populations affecting the lecanium scales in all four states was determined by specimen rearing and sampling with yellow sticky cards.

For specimen rearing, twigs (5–10 cm) were collected weekly from the trees. A single twig was collected from each tree in Georgia from January 2012 to May 2013; two twigs per tree in South Carolina from February to June 2009, March to July 2010, March to November 2011, January to September 2012 and March to August 2013; a single twig from each tree in North Carolina from April to July 2012; and four twigs (one per cardinal direction) from a single tree in Virginia from May to August 2010 and March to

August 2011—2013. Scale species other than the lecanium scales were removed before storing the twigs in cotton-capped vials and held in the laboratory at 20—25°C, and 35—45% relative humidity until adult parasitoid emergence. The parasitoids in South Carolina were preserved in 70% ethanol until identification. In the other states, desiccated specimens were recovered from vials for identification.

Yellow sticky cards (7.5 x 12.5 cm) were deployed on trees at 1.5 to 1.8 m from the ground, close to the edge of the canopy, and collected and replaced weekly at each site. A preliminary study was done in South Carolina and Virginia to evaluate differences between the abundances of parasitoids in the four cardinal directions. Analyses of variance (ANOVAs) (PROC GLM; SAS Institute 2011) did not detect significant differences in scale insect abundances among the four cardinal directions in South Carolina ($F = 0.029$; $df = 3, 24$; $P = 0.993$) and Virginia ($F = 0.142$; $df = 3, 4$; $P = 0.930$). Therefore, a single sticky card per tree was used for counting specimens, independently of the cardinal direction from which the trap was collected. Yellow sticky cards were collected from May to August 2010 and February to August 2012 and 2013 in Georgia, February to August 2011—2013 in South Carolina, May to August 2010 and February to August 2011—2012 in North Carolina, and May to August 2010 and February to June 2011—2013 in Virginia.

Each 7.5 x 12.5 cm yellow sticky card was divided into 2.5 cm² squares. Five squares were randomly selected on one side of the card for counting (Urbaniak and Plous 2014). The side was chosen randomly (emulated) to minimize variability. Data

from the 5 squares were extrapolated to estimate the total abundance on one side of each card. Seasonal activity was determined for parasitoid species representing at least 5% of the total parasitoid population. Abundances were plotted against sampling dates for each representative species (or genus).

Species composition and seasonal activity of predators. Predators associated with the lecanium scales were collected weekly in March–August 2011–2013 by sampling the willow oaks at Florence, South Carolina dislodged with the “beat-sheet method”. Branches were struck against the sheet and predators were collected and preserved in 70% ethanol. Samples were identified and the abundances recorded. Additional assessment of predator composition and abundance was done by inspecting sticky cards collected from Georgia (February–August 2012–2013), South Carolina (March–September 2012–2013), North Carolina (April–July 2010–2012), and Virginia (April–July 2010–2012) under stereomicroscope. Predators in Georgia were also reared from twigs collected originally to assess parasitoid emergence. The numbers of predators collected at each sampling date were used to determine their seasonal activity.

Identification of parasitoids and predators. Parasitoids were identified to genus based on keys by Gibson et al. (1997), Prinsloo (1997), Hayat (1997), and Viggiani (1997). *Coccophagus lycimnia* was identified (under the synonym *Coccophagus lecanii* [Fitch]) in the keys by Compere (1931). The remaining species within each genera found, were tentatively identified with characters typically used for this purpose [e.g., patterns of

setae on wings and other structures of the body; color of scutellum, head, legs, etc.; shape and color of antennal parts (e.g., scape) or structures on it (e.g., sensillae); size of body or structures]. Collections of representative individuals from each unconfirmed parasitoid species reared from twigs were sent for identification to specialists at two locations in the U.S. Unfortunately, the results of the identification to species were not available yet before this dissertation was published.

Predators were identified to species based on keys and descriptions by Tauber (1974) for lacewing (Chrysopidae) larvae, Brooks (1994) for adult lacewings, Rees et al. (1994) for coccinellid larvae, and Gordon (1985) for adult coccinellids. *Tricorynus confusus* (Coleoptera: Anobiidae) was identified based on the description and keys by White (1971, 1982). *Anthribus nebulosus* Forster (Coleoptera: Anthribidae) was identified using the keys to genus by Valentine (1998) and diagnostic characters provided in Hoebeke and Wheeler (1991). Identification of adult beetles was confirmed by comparing reference specimens collected in this study to those in the Florida State Collection of Arthropods (FSCA), Gainesville, Florida. Voucher specimens were deposited at the Clemson University Arthropod Collection.

Analyses of parasitoid and predator species diversity and community similarity indices. Diversity of the parasitoid and predator communities in each state was compared using three of the most commonly employed species diversity indices: species richness (R), effective number of species [or exponential of Shannon entropy, $\exp(H')$], and Gini-Simpson ($1-\lambda$). Species richness index is a raw count of abundance for each

species present in the community, whereas the other two indices take into account richness and evenness (relative abundance) among species in the community (Magurran 1988). Differences among states and years for each diversity index were analyzed using three-way ANOVAs (trees nested within states) at $\alpha = 0.05$ and compared with least square mean differences (for states) and Tukey's studentized range (for years) (PROC GLM; SAS Institute 2011). Similarity of natural enemy communities among the states was estimated through the non-parametric, abundance-based Chao-Jaccard community similarity index. All species diversity indices and Chao-Jaccard community similarity index were estimated with EstimateS (ver. 9.1, Colwell 2013) using 200 bootstrap runs, randomization without replacement, and an upper abundance limit of 5 individuals for rare species.

Parasitoid brood and scale insect stage at the time of adult parasitoid emergence. To identify species of parasitoids emerging from the second-instar and adult lecanium scales, parasitized scales were collected in South Carolina in 2013 (10 individuals each of nymphs and adults daily on 16 and 23 April, and 20 adults daily on 30 April, 6, 15 and 21 May). Scale insects were presumed parasitized and chosen based on their appearance (parasitized second instars turn dark brown to black, with a clear ring around its base; parasitized adult scales are darker and the shape of the test is irregular and/or enlarged, compared to unparasitized tests). Only one selected scale was left on each twig, which was kept in capped vials under laboratory conditions (as described above) until adult parasitoid emergence. The number of mummies yielding each

parasitoid species was recorded. Additionally, percentages of each parasitoid species classified as solitary, single-species gregarious or mixed-species gregarious broods were calculated. The percentage of females within each brood was also determined. All percentages were calculated from the total number per species of actual parasitoids emerged, not from the mummies yielding them.

An additional experiment was conducted to detect potential differences in the size of scale insects as a result of parasitism. Ten isolated mummies of the solitary *Encyrtus* sp. and ten isolated mummies of the gregarious *Blastothrix* sp. from the next experiment were chosen. Each mummy was considered an individual observational unit. Their sizes were measured as the volume of the test (length x width x height). Measurements to calculate the volume of the tests (height – the greatest distance from the venter to the dorsum, perpendicular to the venter, length – the greatest distance from the distal margin of the anterior end of head to the distal margin of the posterior end of the abdomen, parallel to the mid-dorsal line, and width – the widest distance between two sides, perpendicular to the mid-dorsal line) were taken with the software ProgRes CapturePro v2.8.8 (I-Solution™, Image and Microscope Technology Inc., Vancouver, BC, Canada). An initial ANOVA was conducted to compare means of test sizes of parasitized and unparasitized scales, at $\alpha = 0.05$ (PROC GLM; SAS Institute 2011), followed by T-tests for individual parasitoid species (PROC TTEST; SAS Institute 2011).

Impact of parasitism on scale insect fecundity. Gravid, parasitized adult scales were collected by emulating (to the best extent) random sampling of one hundred

scales from a single tree on 10 May 2014 (just before egg hatch) in South Carolina. The scales were isolated individually (while still attached to the twig) in a capped vial and kept in the laboratory (under conditions described above) until crawler emergence was complete. Each isolated scale was considered a unique, independent observational unit. The number of crawlers emerged from each parasitized scale was counted and the adult parasitoids emerged were collected and identified. Differences among means of numbers of crawlers emerged from scales were tested by ANOVA, followed by linear contrasts comparing number of crawlers produced by unparasitized scales and those from parasitized scales, at $\alpha = 0.05$ (PROC GLM; SAS Institute 2011). Further analysis of differences among the number of crawlers emerged from scales parasitized by individual parasitoid species and unparasitized scales were statistically analyzed by t-tests (TTEST; SAS Institute 2011).

Species of *Pachyneuron* are hyperparasitoids of other chalcidoids (Viggiani 1997). Therefore, we also evaluated possible effects of hyperparasitism on the fecundity of scale insects using data from the mixed-species broods in which the hyperparasitoid and their primary parasitoids were found. ANOVA followed by linear contrasts (PROC GLM, SAS Institute 2011) were used to compare the numbers of crawlers emerged from scales parasitized by mixed-species broods with *Pachyneuron* sp. to those from scales parasitized by a single primary parasitoid species.

Parasitism rate. In February—June 2010—2013, four 10—15 cm long twigs (one from each cardinal direction) were collected weekly from each of the six willow oak

trees in South Carolina. Each scale on the terminals was inspected under the microscope for signs of parasitism (emergence holes on the tests or dead/live parasitoids inside the scales). The parasitism rate was calculated by dividing the numbers of parasitized scales by the total numbers of scale insects per twigs. Parasitism rates were then plotted against sampling time to detect the periods of highest parasitism rate.

Results

Species composition and seasonal activity of parasitoids. A total of 21 parasitoid species (4 families, 13 genera in the superfamily Chalcidoidea) were reared from the lecanium scales (Table 3.1). Parasitoid communities in Georgia, South Carolina, North Carolina, and Virginia were composed of 16, 6, 18 and 13 species, respectively. Among the species found, four were shared among the four states; one shared by Georgia, South Carolina, and North Carolina, and; one shared by Georgia, North Carolina and Virginia; six shared by Georgia, South Carolina, Virginia; three shared by Georgia and South Carolina; and one shared by South Carolina and Virginia. Three species were unique to South Carolina, whereas one species was unique to Virginia.

Among the 16 parasitoid species, *C. lycimnia*, *Eunotus* sp., *Metaphycus* sp. 3, and *Pachyneuron* sp. were the most abundant (> 5% of the population) in Georgia (Table 3.1). In South Carolina, *Blastothrix* sp. 1 and *C. lycimnia* accounted for more than 50% of the population, whereas *Encyrtus* sp. 1 and *Pachyneuron* sp. individually composed about 5% of the population. In Virginia, *C. lycimnia*, and *Metaphycus* sp. 2 accounted for 90% of the population. The activity period of the majority of parasitoid species reared

from scales ranged from late March to mid-August in Georgia, South Carolina and Virginia. Rearing in North Carolina yielded only six species (10 specimens): *Aprostocetus* sp. 1 (2), *Aprostocetus* sp. 2 (1), *C. lycimnia* (2), *Eunotus* sp. (1), *Pachyneuron* sp. (2), and *Plagiomerus* sp. (2); they were active from late May to mid-July. Most species reared from twigs were also collected with sticky cards, except for *Ablerus* sp. 2 and *Metaphycus* sp. 3, which were found only by rearing (Table 3.1).

A total of 21 chalcidoid parasitoid species (4 families, 14 genera) was collected with yellow sticky cards (Table 3.2) from four states, 2 of which (*Encyrtus* sp. 3 and *Marietta* sp.) were not found by twig collection. *Coccophagus lycimnia* was the most abundant species in South Carolina, North Carolina, and Virginia, and the second most numerous in Georgia. In Georgia, *Metaphycus* sp. 2 was the most abundant. The other species accounting for more than 5% of the population were: *Aprostocetus* sp. 1. in Georgia, North Carolina and Virginia; *Blastothrix* sp. 1 in all four states; *Coccophagus* sp. 1 in Georgia, South Carolina, and North Carolina; *Encyrtus* sp. 1 in North Carolina; *Eunotus* sp. in all four states; *Metaphycus* sp. 2 in Virginia; and *Pachyneuron* sp. in Georgia, South Carolina, and North Carolina.

Coccophagus lycimnia had a similar activity period in all four states with one or two periods of high activity (peaks): the first peak from early to late April and the second from early May to early June (Fig. 3.1). The periods of activity of *Coccophagus* sp. 1 were similar in all states with two periods of greatest abundance, mid-April to early June and late June to early September (Fig. 3.1). *Blastothrix* sp. 1 and *Blastothrix* sp. 2 became

active a month earlier in Georgia and South Carolina than in North Carolina and Virginia (Fig. 3.2). The *Encyrtus* species group had similar activity periods in all four states. *Metaphycus* sp. 2 (and sp. 1 in South Carolina) tends to have a longer period of activity, the end of August in South Carolina and Virginia (Fig. 3.3). *Aprostocetus* sp. 1 had long periods of activity: late August to mid-September in Georgia and North Carolina in 2010, in Virginia in 2011—2012, and South Carolina in 2012—2013 (Fig. 3.3). *Eunotus* sp. (Fig. 3.4) reached its highest abundance in all four states between mid-April to early June. *Pachyneuron* sp. became active earlier in South Carolina and/or Georgia, while reaching periods of high activity in North Carolina and Virginia by mid-May to mid-June (Fig. 3.4).

Species composition and seasonal activity of predators. A total of 12 predator species of lecanium scales was found in the four southeastern states (Table 3.3). Six species of predators (five coccinellids) were found in North Carolina. Sampling by beat-sheet and sticky cards detected nine species of coccinellids and one anobiid in South Carolina. Three coccinellid species and one anthribid species were found in Virginia. The green lacewing *Chrysoperla rufilabris* (Burmeister) was not found in Georgia. *Chilocorus stigma* Say and *Hyperaspis signata* species group were common in all states.

No predators were collected by sticky cards in Georgia. Only two larvae of *C. stigma*, six adults of *H. signata* sp. group, and two adults of *T. confusus* were reared from twigs collected in Georgia. All specimens of the six species in North Carolina were adults. In South Carolina, larvae comprised 17% of *C. stigma*, one specimen of *Cycloneda sanguinea* (L.), 16% of *Harmonia axyridis* (Pallas), and 1% of *H. signata* individuals

collected. All specimens of *Coccinella septempunctata* (L.), *Coleomegilla maculata* De Geer, *Hippodamia convergens* Guérin-Ménéville, *Scymnus* sp. and *T. confusus* were adults. In Virginia, except for one larva of *C. rufilabris*, all other specimens and species were adults.

In South Carolina, beat-sheet sampling yielded three species (*C. stigma*, *H. signata* sp. group and *C. rufilabris*), accounting for 85% of the predator population (Table 3.4). *Chilocorus stigma* was active mainly from early May to mid-August. *Chrysoperla rufilabris* larvae were most active from early May to late October. *Hyperaspis signata* group was most active from early May to late June (Fig. 3.5).

Analyses of parasitoid and predator species diversity and community similarity indices. The analysis of species diversity for parasitoids yielded statistical differences among states in species richness and effective number of species, but not in Gini-Simpson index (Table 3.4). No difference was detected among trees per state, or years. The parasitoid community in Georgia was different from all other states, particularly from North Carolina (Table 3.5). Composition of parasitoid communities in North Carolina, South Carolina and Virginia was similar. Parasitoid communities differed from year to year, especially in 2010 (values of Chao-Jaccard index below 0.35 when comparing Georgia with North Carolina and Virginia), compared to 2011, 2012 and 2013 (values above 0.50, except for Georgia and North Carolina in 2012).

The only statistically significant difference in predator diversity was among years (Table 3.6). Tukey's comparison was significant between 2011 and 2012 [mean

difference of $0.85 > 0.67$ minimum significant difference (MSD)]. Predator communities among the four states were dissimilar (Chao-Jaccard values below 0.5), except between North Carolina and Virginia in 2012 (Table 3.7).

Parasitoid brood and scale insect stage at the time of emergence. *Coccophagus lycimnia* was the only parasitoid species emerging from second instars and it was exclusively solitary at this time (Table 3.8). *Coccophagus lycimnia* that emerged from adult scales were either solitary or in mixed-species broods. About 50% of *C. lycimnia* in mixed-species broods were associated with *Blastothrix* sp. 1, 33.3% with *Eunotus* sp., and 16.7% with *Pachyneuron* sp. *Blastothrix* sp. 1 was mostly gregarious, with brood size ranging from three to 15 individuals per brood. *Encyrtus* sp. 1 was found mixed with *Eunotus* sp. only once. Males and females of *Eunotus* sp. were found in solitary broods, or in mixed-species broods where they were associated with *Blastothrix* sp. 2 (16.7% of the time), *C. lycimnia* (33.3%), *Encyrtus* sp. 1 (16.7%), and *Pachyneuron* sp. (33.3%). *Microterys* sp. was found in a mixed-species brood with *Pachyneuron* sp. only once. One to six individuals of *Pachyneuron* sp. were found to emerge from a single scale. In mixed-species broods it was found with *C. lycimnia* 25% of the time, 50% with *Eunotus* sp, and 25% with *Microterys* sp. All solitary broods of *Blastothrix* sp. 1 were females, but males were more common in gregarious and mixed-species broods. The sole individual in mixed-species broods of *Blastothrix* sp. 2 and *Encyrtus* sp. 1 was a female. In the case of solitary *Encyrtus* sp. 1, males were more common.

Statistical analyses of scale test size by ANOVA yielded significant differences between unparasitized and parasitized scales ($F = 25.38$; $df = 2, 27$; $P < 0.001$), and t-tests confirmed that adult scales parasitized by the solitary species *Encyrtus* sp. were smaller than those not parasitized ($t = -10.72$; $df = 19$; $P < 0.001$), whereas those parasitized by the gregarious *Blastothrix* sp. were larger compared to unparasitized scales ($t = 4.68$; $df = 19$; $P < 0.001$) (Fig. 3.6).

In *Eunotus* sp., an even proportion of males and females was observed in solitary broods. Males tended to dominate in single-species gregarious broods and females in mixed-species gregarious broods. Six females and one male of *Metaphycus* sp. 2 emerged from a single adult scale. The only *Microterys* sp. specimen (from a mixed-species brood) was a male. Males predominated in all broods of *Pachyneuron* sp.

Impact of parasitism on scale insect fecundity. An initial ANOVA yielded significant differences ($F = 18.13$; $df = 7, 48$; $P < 0.001$), corroborated with analysis by linear contrasts of parasitized scales to unparasitized scales ($P < 0.001$) (Fig. 3.7). Additional analysis by t-tests of number of crawlers produced by individual parasitoid species compared to those produced by unparasitized scales yielded further differences: *Blastothrix* sp. 1 and *Encyrtus* sp. 1 ($t = -8.67$; $df = 19$; $P < 0.001$), *C. lycimnia* ($t = -4.59$; $df = 19$; $P < 0.001$), *Eunotus* sp. ($t = -2.14$; $df = 16$; $P = 0.023$), and *Pachyneuron* sp. ($t = -3.05$; $df = 18$; $P = 0.005$) (Fig. 3.7). These results indicate that all individual parasitoid species significantly reduced scale insect fecundity.

ANOVA of numbers of crawlers produced by *Pachyneuron* sp. and *Eunotus* sp. mixed species brood and the individual species *Pachyneuron* sp. and *Eunotus* did not yield significant differences ($F = 1.58$; $df = 2, 21$; $P = 0.259$). A similar case was seen with *Pachyneuron* sp. and *C. lycimnia* mixed species brood ($F = 0.27$; $df = 2, 20$; $P = 0.772$). As expected, linear contrasts among the numbers of crawlers produced in mixed-species broods containing *Pachyneuron* sp. and those produced in scales parasitized by individual primary species yielded no significant differences: *Pachyneuron* sp. and *Eunotus* sp. ($P = 0.3109$); *Pachyneuron* sp. and *C. lycimnia* ($P = 0.5992$) (Figure 3.7).

Parasitism rate. Parasitoids attacked between 27 to 92% of the scale population in South Carolina from 2010 to 2013 (Fig. 3.8). Parasitism of nymphs reached the highest level by mid- to late April, while parasitism of adults reached their highest values by mid-April in 2010, early May in 2012, and late May in 2011 and 2013.

Discussion

Blastothrix, *Ceraptocerus*, *Encyrtus*, *Metaphycus*, and *Microterys* (Encyrtidae) previously were reported as associates of *Parthenolecanium* spp. (Prinsloo 1997, Noyes 2015). *Ablerus* and *Coccophagus* (Aphelinidae), *Aprostocetus* (Eulophidae), and *Eunotus* and *Pachyneuron* (Pteromalidae) were reported from *P. corni* (Hayat 1997, Viggiani 1997, Hodges and Braman 2004, Noyes 2015). *Blastothrix claripennis* Compere, *B. longipennis* Howard and *Metaphycus* sp. were associated with *P. corni* in Georgia (Hodges and Braman 2004), and *Blastothrix* sp., *C. lycimnia*, *E. fuscus*, *E. lividus*, and *P. altiscutum* were associated with *P. quercifex* in Virginia (Schultz 1984). Noyes (2015) did

not record *Pachyneuron* sp. in the southeastern U.S. nor associate it with *P. quercifex*, but we corroborated previous reports by Schultz (1984, 1985, 1990) of the association of the pteromalid with *P. quercifex* and *P. corni* in Virginia, as well as Georgia, South Carolina and North Carolina.

Although associations with soft scales have been known for *Leptomastix* and *Plagiomerus* spp. (Noyes 2015), the species in those genera found in our research have not previously been reported as associates of *Parthenolecanium* spp. Thus, the present work constitutes the first report of the association of *Leptomastix* sp. and *Plagiomerus* sp. with *Parthenolecanium* spp. as their primary hosts.

Leptomastix sp. was reared from *Parthenolecanium* spp. scales in South Carolina and found on sticky cards in South Carolina and North Carolina. Species of *Leptomastix* are mainly parasitoids of mealybugs (Anga and Noyes 1999, Noyes 2015), but soft scales have been recorded as primary hosts. *Leptomastix nigrocoxalis* Compere has been reported from *Parasaissetia nigra* (Nietner) (CIBC 1970), but the host might have been misidentified (Noyes 2015); *Leptomastix flava* Mercet is known from *Eulecanium rugulosum* (Archangelskaya) (Yazdani and Rajabi 1993). In our research, we consider *Parthenolecanium* spp. to be primary hosts of *Leptomastix* sp.

Species of the genus *Plagiomerus* are known primarily as associates of armored scales (Hemiptera: Coccoidea: Diaspididae) (Noyes 1990, 2015). Nonetheless, *P. cyaneus* (Ashmead) is associated with soft scales (Dozier 1927, Thompson 1955, De Santis 1979, Hayat 1986, Trjapitzin et al. 2004). *Plagiomerus* sp. was reared from adult females of *P.*

corni and *P. quercifex* on twigs in Georgia and South Carolina and was also found on sticky cards collected in all four states surveyed. Therefore, we also consider *Parthenolecanium* spp. to be primary hosts of *Plagiomerus* sp.

Ginsiana sp. and *Saera* sp. collected from twigs in South Carolina were excluded from Table 3.1. *Ginsiana* sp. a parasitoid of psyllids, whereas the host of *Saera* sp. is unknown (Noyes 2015). Three specimens of *Ginsiana* sp. were collected between late March and early April 2010, and one specimen in mid-April 2011. Three specimens of *Saera* sp. were collected between late March and early April 2011. *Coccophagoides* sp. collected from twigs was also excluded from Table 3.1 because it is known to be associated with armored scales and olive scale [*Parlatoria oleae* (Colvée)] (Viggiani 1990, Noyes 2015). Fourteen specimens of *Coccophagoides* sp. were collected from twigs in Georgia between early January to late November 2012, and seven specimens in South Carolina between mid-March to early August 2010—2013. Specimens of *Ginsiana*, *Saera* and *Coccophagoides* were not considered to be associated with *Parthenolecanium* as a primary host in this study. The adult soft scales on the twigs were left untouched until parasitoid emergence; however, after detachment of the soft scale mummies for examination, there were some occasions in which armored scales were found beneath the mummies (Chong, personal observation).

One eulophid initially was identified as a species of *Tetrastichus* (Gibson et al. 1997). *Tetrastichus minutus* (Howard) is a hyperparasitoid of *Parthenolecanium* spp.

(Kawecki 1958, Peck 1963). This species currently is placed in the genus *Aprostocetus* (Noyes 2015); thus, we opted to identify it as “*Aprostocetus* sp. 2”.

We found *Blastothrix* sp. to be mostly gregarious and *Encyrtus* spp. to be mostly solitary (Table 3.8). *Blastothrix* spp. are gregarious parasitoids (Sugonyaev 1965, 1983, Schultz 1984). Gregarious parasitoids influence their hosts differently from solitary parasitoids (Slansky 1986). Parasitism induces substantial changes in the feeding physiology and behavior of insects (Slansky and Scriber 1985). Solitary parasitoids frequently inhibit host behavior, decreasing food consumption, and thus host growth (Slansky 1986). The host of a solitary parasitoid species has fewer nutritional demand than one parasitized by a gregarious parasitoid (Slansky and Scriber 1985), due in part to the relation of density of parasitoids per host (Cloutier and Mackauer 1979, Führer 1981). In gregarious species, when nutrients are insufficient for complete parasitoid development, continuous feeding by the host is allowed by the parasitoids (Slansky 1986). Adult females of gregarious parasitoids normally lay more eggs on larger hosts and more wasps emerge as host size increases (Le Masurier 1987). Accordingly, we found that females of *Parthenolecanium* spp. parasitized by the solitary *Encyrtus* sp. were smaller than those not parasitized, whereas those parasitized by the gregarious species *Blastothrix* sp. were larger compared to unparasitized scales (Fig. 3.6).

In our study in South Carolina, *Blastothrix* sp. and *Encyrtus* sp. 1 prevented the female scale insects from producing eggs (Fig. 3.7), which could have been a result of early emergence influenced by temperature. Blahutiak (1973) mentioned that for

endoparasitoid species feeding on adult female scales, temperature plays an important role in determining the impact of parasitism on fecundity. Temperature regulates the time of the emergence of parasitoids and the number of eggs laid by adult female scales before their premature death. Based on our observations of seasonal activity, *Blastothrix* sp. appears to emerge earlier in South Carolina than in Virginia (Table 3.1, Fig. 3.2). Our observations corroborate those made by Schultz (1984) in Virginia where *Blastothrix* sp. reduced only the fecundity of the scales. The earlier emergence of *Blastothrix* sp. in South Carolina as a result of higher temperatures than those in Virginia could have killed adult female scales before they began to produce eggs.

Pachyneuron associated with soft scales are mainly hyperparasitoids of other chalcidoids (Viggiani 1997). We found mixed broods of *Pachyneuron* sp. and *Eunotus* sp. in South Carolina. Schultz (1984) suggested that *P. altiscutum* might be a hyperparasitoid of *E. lividus* in Virginia, and reported *Eunotus* as an egg predator of *P. quercifex*. Therefore, we would have expected increased crawler production in the mixed brood compared to that of *Eunotus* sp. because *Pachyneuron* sp. is a hyperparasitoid of *Eunotus* sp. Our result, however, was contrary to our expectation (Fig. 3.7). *Pachyneuron* sp. had a higher impact than *Eunotus* sp., and a similar impact to the mix brood in egg production of *Parthenolecanium* spp. Based on our data, we can make assumptions only about the impact of *Pachyneuron* sp. on egg production, but not its ecological role.

Coccophagus lycimnia attacks the immature stages of *P. corni* (Santas 1985, Moglan 2000). Our results support previous suggestions that *C. lycimnia* parasitizes the immature stages of *P. quercifex* (Schultz 1984). In our study, *C. lycimnia* was one of the species emerging in early spring and the only species recovered from second instars. Females predominated in the broods of *C. lycimnia* that emerged from nymphs, but not in the broods that emerged from adults. Females from fertilized eggs develop only in immature stages of their hosts (Bartlett 1978). Males are either primary ectoparasitoids or secondary ecto- or endoparasitoids of other primary parasitoids, including females of their own species (Walter 1983 a,b, Viggiani 1984). Producing females first, which could be fertilized and parasitized by males, might be a behavioral mechanism to maintain the breeding population.

Previous studies in Virginia (Schultz 1984, 1990) reported peaks of activity for *Blastothrix* sp. from late May to early June, for *C. lycimnia* from mid- to late May, *E. fuscus* from mid-May to early June, and two peaks for *E. lividus* in mid-April to early May and Late May to early June. We found similar activity periods in Virginia in most of the corresponding species or genera previously reported (Schultz 1984, 1990). However, *Eunotus* sp. had only one peak from mid-May to early June 2012, but the peaks of activity in 2011 and 2013 were similar to those reported for *E. lividus* by Schultz (1984, 1990). *Pachyneuron* sp. in our study in Virginia reached three peaks of activity, from mid-April to early May, late May to early June, and late June to mid-July, whereas Schultz (1984) reported a single peak in mid-June for *P. altiscutum*. In terms of seasonal

activity, the parasitoids species found in our study in Virginia could be similar to those reported by Schultz (1984), except for *Pachyneuron* sp.

Our findings corroborate previous reports of *Hyperaspis* spp. associated with *P. corni* (El-Ali 1972). *Hyperaspis signata signata*, a southeastern species (Gordon 1985), is associated with *P. quercifex* on willow oak (Schultz 1984). The *H. signata* species group is one of the most abundant predators in all four states surveyed. Species of this complex are predators of immatures and adults of numerous soft scale species (Herting and Simmons 1972, Williams and Kosztarab 1972, Simpson and Lambdin 1983). Eggs of *Hyperaspis* spp. are usually deposited near their prey, on the bark or growth rings of twigs, but not inside the scales (El-Ali 1972). However, in Hubbard and Potter's (2005) study in Kentucky, *Hyperaspis* spp. emerged only from under adult females. *Hyperaspis* spp. were also found to reduce fecundity of *Eulecanium cerasorum* (Cockerell) by 48%. We collected two larvae of the *H. signata* sp. group by beat sheet method, and observed a larva feeding in the brood chamber of an adult female on a twig in South Carolina. *Hyperaspis* spp. have been used for biological control. *Hyperaspis campestris* Herbst, a predator of scale insects on grapes, citrus, and other subtropical crops, was released in tea plantations in the former USSR against *Pulvinaria floccifera* (Westwood) (Bogdanova 1956). Scale populations were reduced below the economic injury level two years after release of the coccinellid (Bogdanova 1956). The eastern North American *H. conviva* Casey can control *Toumeyella parvicornis* (Cockerell) on jack pine, *Pinus banksiana* Lamb., in Manitoba, unless the scale is attended by the ant *Formica obscuripes* Forel

(Bradley 1973). Infestations of *T. parvicornis* on Scots pine, *Pinus sylvestris* L., in Michigan were also suppressed by *H. signata* after being introduced from Minnesota in 1930 (Orr and Hall 1931).

Hodges and Braman (2004) collected *Chrysoperla carnea* (Stephens) from *P. corni* populations in Georgia. Oswald (2014) suggested that *C. carnea* is exclusively Palearctic; therefore, all previous reports in the New World are considered erroneous. *Chrysoperla rufilabris* is widespread in the eastern U.S. (Oswald 2014), and we had confirmed its presence in South Carolina, North Carolina and Virginia. Although we did not collect specimens from Georgia, *C. rufilabris* likely is present.

Schultz (1984) reported *T. confusus* as a predator of *P. quercifex* in Virginia. According to his observations, the larvae feed on the eggs of the scale but their numbers are too small to affect the scale populations. Although we did not find the species in Virginia, *T. confusus* was recovered in South Carolina by beat sheet (6 specimens), and reared from scales on twigs in Georgia (2 specimens), for the first time confirming this predator's association with the lecanium scales in Georgia and South Carolina.

The remaining seven species of coccinellids collected in this study [*C. septempunctata*, *C. maculata*, *C. sanguinea*, *H. convergens*, *H. axyridis*, *Olla v. nigrum* (Mulsant), and *Scymnus* sp.] are generalist predators (Gordon 1985). *Coccinella septempunctata* feeds on *P. corni* (Arnaoudov et al. 2006). *Harmonia axyridis* and some *Scymnus* spp. have been reported to feed on soft scales (Herting and Simmonds 1972, Gordon 1985). *Coccinella septempunctata* and *H. convergens* prey on early instars of the

soft scales *Toumeyella pini* (King) and *T. parvicornis* (Cockerell) on *Pinus* spp. in Colorado (Cooper and Cranshaw 2004). *Cycloneda sanguinea* is a predator of *Coccus viridis* on *Citrus* spp. in Florida (Muma et al. 1961). Coccinellids also feed on honeydew, nectar, pollen, sap, and green leaves (Clausen 1940, Hodek 1967). Although the previously mentioned species of coccinellids might prey on *Parthenolecanium* spp., we did not observe actual feeding. Therefore, they are considered only associates of *P. corni* and *P. quercifex*.

Anthribus nebulosus preys on various species of scale insects, including *P. corni* (Matesova 1966, Herting and Simmonds 1972, Kosztarab and Kozar 1983). This species was introduced in 1978 from Hungary to control scales in Blacksburg, Virginia, and in 1981 was introduced in Virginia Beach (Kosztarab and Kozár 1983). Populations of *A. nebulosus* in Connecticut, Massachusetts and New York might have been accidentally introduced and established long before its intentional introduction in Virginia (Hoebeke and Wheeler 1991). Valentine (1998) mentioned that the species did not become established at Virginia Beach, but we found that *A. nebulosus* has become one of the three most abundant predators of *Parthenolecanium* spp. in Virginia Beach. *Anthribus nebulosus* was reported to be associated with *P. corni* in Georgia (Hodges and Braman 2004), but the two sites at Virginia Beach were the only sites in our study where the predator was found.

Schultz (1984) found considerable variation in the abundance of natural enemies trapped with yellow sticky cards among four trees in Norfolk, Virginia, despite selecting

adjacent trees of similar species and age. In our analysis of parasitoid diversity we did not find significant differences among trees in four different states. Nevertheless, only the means and standard errors on abundances were reported for each species without using statistical analysis (Schultz 1984).

The parasitoid species identified in the four states of study are small (0.4 to 2.5 mm), and are able to fly short distances; thus, the population diversity will most likely remain without major changes from year to year within local ranges. On the other hand, the predators species identified in the four states, such as coccinellids, have bigger and stouter bodies than the parasitoids, which allow them to survive long journeys (Brown et al. 2011). Coccinellids are active fliers whose flight is considered the most important reason for their distribution (Van der Werf et al. 2000). Coccinellids move readily among habitats in the landscape (Evans 1991, Evans and Richards 1997), and effects such as habitat fragmentation are likely to strongly influence their dispersal (Brown et al. 2011). During long-distance dispersal flights at high altitudes on thermal currents, coccinellids are passively transported by wind (Hodek et al. 1993). Deliberate and inadvertent anthropogenic dispersal has been important in the long-distance spread of coccinellids (Evans et al. 2011). A mix of active flight, passive wind dispersal, and anthropogenic spread makes these predators prone to long-distance dispersal (Brown et al. 2011), which might explain most differences seen in coccinellid communities among states.

Our results suggest that the mortality by parasitism in South Carolina (27 to 92%) is higher than that of Virginia, where the mortality ranged from 10 to 60% (Schultz

1984), although this difference might result from differences in methodology for evaluating parasitism. We checked all scales on the twigs for evidence of parasitism, including emergence holes and dead bodies of the actual parasitoids, whereas Schultz (1984) counted only scales with emergence holes. Blahutiak (1972) suggested that the minimum level of parasitism required for effective control of *P. corni* under field conditions was 80%, which was rarely obtained in the field. Of the four years covered in our study (2010–2013), the level of parasitism of adult females reached 79% and 84% in 2011 and 2012, respectively. In our case, such percentages of parasitism might not be considered a rare event.

Conservation is the most widely used biological control strategy (Pedigo and Rice 2009). Protecting and maintaining existing populations of parasitoids and predators requires knowledge about all aspects of the natural enemy community, including diversity, abundance, phenology and impact on pest populations. With this knowledge, pest management practices can be adjusted to avoid harm to the natural enemy community. Among these practices, the most important conservation approach involves the use of insecticides to minimize the impact on natural enemies. Different ways of implementing this strategy include reducing the number of applications or dosage levels, avoiding spraying at particular times, and using different insecticides (either less toxic or non-toxic to natural enemies) (Rose and De Bach 1990, Pedigo and Rice 2009). Schultz (1990) emphasized the importance of finding alternatives when suppression programs coincide with parasitoid activity to minimize the adverse impact on these

beneficial insects. A suggested alternative was to use horticultural oils against scale insects. According to Schultz (1990), optimal suppression was achieved when the application preceded the start of new tree growth. To protect the natural enemies of *Parthenolecanium* spp. in the urban landscape of the Southeast, contact insecticides should not be used when natural enemy activity is evident (Schultz 1984). Thus, this type of insecticide should be applied in early September, when most of the parasitoid activity has ceased and before first instars start molting to second instars.

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Table 3.1. Population composition and activity period of hymenopteran parasitoid species reared from *Parthenolecanium* spp. collected from willow oaks in Georgia, South Carolina and Virginia.

Family	Species	Georgia (2012-2013)(N=406)		South Carolina (2010-2013)(N=2310)		Virginia (2010-2012)(N=235)	
		% Population ^a	Activity period ^a	% Population ^a	Activity period ^a	% Population ^{a,b}	Activity period ^a
Aphelinidae	<i>Ablerus</i> sp. 1	1.1 ± 0.4	early May to mid-September	< 0.1	mid-March to early August	N/P	N/P
Aphelinidae	<i>Ablerus</i> sp. 2	2.0 ± 0.4	early February to late June	N/P	N/P	N/P	N/P
Aphelinidae	<i>Coccophagus lycimnia</i>	21.7 ± 10.3	mid-January to late May	50.0 ± 1.9	early January to late August	69.4	late March to mid-August
Aphelinidae	<i>Coccophagus</i> sp. 1	1.5	mid-March to early May	2.5 ± 0.3	late March to late April, September	0.4	early May
Aphelinidae	<i>Coccophagus</i> sp. 2	N/P	N/P	1.0 ± 0.2	Late April	N/P	N/P
Encyrtidae	<i>Blastothrix</i> sp. 1	4.5	late March to mid-May	20.1 ± 3.1	mid-March to late May	2.6	mid-May
Encyrtidae	<i>Blastothrix</i> sp. 2	1.8	mid-April to early May	0.8 ± 0.3	late March to late April	N/P	N/P
Encyrtidae	<i>Cerapterocerus</i> sp.	N/P	N/P	N/P	N/P	0.4	August
Encyrtidae	<i>Encyrtus</i> sp. 1	1.5	mid-March to mid-May	4.8 ± 0.4	early April to mid-May	0.4	late April
Encyrtidae	<i>Encyrtus</i> sp. 2	N/P	N/P	0.1	early April to early May	0.4	mid-May
Encyrtidae	<i>Leptomastix</i> sp.	N/P	N/P	< 0.1	Late July	N/P	N/P
Encyrtidae	<i>Metaphycus</i> sp. 1	3.5	late February to late April	0.9 ± 0.1	late March to mid-April	0.9	late March to late May
Encyrtidae	<i>Metaphycus</i> sp. 2	0.5	mid-April	1.1 ± 0.3	early May to early June	19.1	late March to mid-May
Encyrtidae	<i>Metaphycus</i> sp.3	10.7	late March to mid-May	< 0.1	Early April	0.4	late May
Encyrtidae	<i>Microterys</i> sp. 1	N/P	N/P	0.7 ± 0.2	mid-March to mid-May	N/P	N/P
Encyrtidae	<i>Microterys</i> sp. 2	0.5	Late June	< 0.1	Late April	N/P	N/P
Encyrtidae	<i>Plagiomerus</i> sp.	0.8 ± 0.2	late January to mid-July	0.4 ± 0.2	early April to late July, September	N/P	N/P
Eulophidae	<i>Aprostocetus</i> sp. 1	3.0	late February to late May	2.0 ± 0.8	mid-April to early September	3.0	mid-May to mid-August
Eulophidae	<i>Aprostocetus</i> sp. 2	0.5	early May	N/P	N/P	0.4	late June
Pteromalidae	<i>Eunotus</i> sp.	8.9 ± 3.5	early January to mid-June	1.1 ± 0.4	mid-January to mid-May	0.9	late April to mid-May
Pteromalidae	<i>Pachyneuron</i> sp.	15.0 ± 5.9	late November to mid-June	6.0 ± 1.4	early February, mid-April to early June	1.7	mid-May to mid-August

^aN/P = not present.

^bAll samples collected from a single tree.

Table 3.2. Composition of parasitoid populations trapped on sticky cards deployed on willow oaks infested with *Parthenolecanium* spp. in Georgia, South Carolina, North Carolina and Virginia.

Family	Species	Georgia (N=528) % Population ^a	South Carolina (N=7323) % Population ^a	North Carolina (N=1615) % Population ^a	Virginia (N=1489) % Population ^a
Aphelinidae	<i>Ablerus</i> sp. 1	0.4 ± 0.1	0.9 ± 0.1	0.9 ± 0.1	0.4
Aphelinidae	<i>Marietta</i> sp.	N/P	0.3 ± 0.1	N/P	N/P
Aphelinidae	<i>Coccophagus lycimnia</i>	12.5 ± 4.1	28.8 ± 3.4	20.3 ± 3.1	40.2 ± 8.2
Aphelinidae	<i>Coccophagus</i> sp. 1	6.3 ± 3.5	6.2 ± 3.8	8.1 ± 0.3	1.9 ± 0.5
Aphelinidae	<i>Coccophagus</i> sp. 2	0.9 ± 0.5	N/P	N/P	< 0.1
Encyrtidae	<i>Blastothrix</i> sp. 1	10.4 ± 6.1	10.7 ± 2.9	6.1 ± 3.4	6.2 ± 0.2
Encyrtidae	<i>Blastothrix</i> sp. 2	N/P	0.2 ± 0.1	N/P	2.0 ± 0.1
Encyrtidae	<i>Cerapterocerus</i> sp.	N/P	N/P	N/P	0.3
Encyrtidae	<i>Encyrtus</i> sp. 1	2.1 ± 0.4	4.0 ± 0.6	6.1 ± 3.7	4.1 ± 0.5
Encyrtidae	<i>Encyrtus</i> sp. 2	0.4	1.0 ± 0.2	N/P	< 0.1
Encyrtidae	<i>Encyrtus</i> sp. 3	0.2	0.1 ± 0.1	N/P	1.1 ± 0.6
Encyrtidae	<i>Leptomastix</i> sp.	N/P	< 0.1	0.4 ± 0.1	N/P
Encyrtidae	<i>Metaphycus</i> sp. 1	N/P	0.5 ± 0.1	N/P	N/P
Encyrtidae	<i>Metaphycus</i> sp. 2	14.6 ± 4.8	2.5 ± 0.1	3.1 ± 0.2	5.9 ± 0.7
Encyrtidae	<i>Microterys</i> sp. 1	N/P	< 0.1	N/P	N/P
Encyrtidae	<i>Microterys</i> sp. 2	0.2	0.1	0.7 ± 0.3	N/P
Encyrtidae	<i>Plagiomerus</i> sp.	2.9 ± 0.6	4.2 ± 0.9	2.4 ± 0.1	1.3
Eulophidae	<i>Aprostocetus</i> sp. 1	6.3 ± 4.7	3.1 ± 0.6	13.2 ± 2.4	5.0 ± 1.2
Eulophidae	<i>Aprostocetus</i> sp. 2	N/P	N/P	0.6 ± 0.1	N/P
Pteromalidae	<i>Eunotus</i> sp.	7.3 ± 4.3	23.3 ± 8.5	9.2 ± 3.9	15.1 ± 1.5
Pteromalidae	<i>Pachyneuron</i> sp.	6.3 ± 1.6	12.6 ± 3.2	6.1 ± 3.7	2.0 ± 0.3

^aN/P = not present.

Table 3.3. Composition and activity period of predators associated with *Parthenolecnaium* spp. in the four southeastern US states. The specimens were collected through rearing of the specimens, sticky cards and beat-sheet method.

Family	Species	Georgia		South Carolina				North Carolina		Virginia	
		Rearing (N=10)		Beat Sheet (N=1036)		Sticky Card (N=98)		Sticky Card (N=90)		Sticky Card (N=46)	
		% ^a	Activity Period ^a	% ^a	Activity Period ^a	% ^a	Activity Period ^a	% ^a	Activity Period ^a	% ^a	Activity period ^a
Anobiidae	<i>Tricorynus confusus</i>	20.0	mid-June	0.3	July	N/P	N/P	N/P	N/P	N/P	N/P
Anthribidae	<i>Anthrribus nebulosus</i>	N/P	N/P	N/P	N/P	N/P	N/P	N/P	N/P	18.0 ± 1.0	mid-April to late June
Chrysopidae	<i>Chrysoperla rufilabris</i>	N/P	N/P	31.0 ± 0.5	early May to mid-July, early September to early November	2.2	late June, mid-July	35.0 ± 1.8	mid-April to late July	46.0 ± 4.0	late March to late July
Coccinellidae	<i>Chilocorus stigma</i>	20.0	late March	33.0 ± 6.5	late March to early November	17.4 ± 0.3	late April to mid-August	4.0 ± 4.2	early May, October	2.2	mid-April
Coccinellidae	<i>Cycloneda sanguinea</i>	N/P	N/P	0.1	mid-April	N/P	N/P	N/P	N/P	N/P	N/P
Coccinellidae	<i>Coccinella septempunctata</i>	N/P	N/P	0.2	mid-April, early July	N/P	N/P	N/P	N/P	N/P	N/P
Coccinellidae	<i>Coleomegilla maculata</i>	N/P	N/P	0.2	early November	2.2	late October, early November	N/P	N/P	2.2	early June
Coccinellidae	<i>Harmonia axyridis</i>	N/P	N/P	2.0 ± 0.2	early April to mid-July, September	N/P	N/P	3.0 ± 0.2	late June, mid-August	N/P	N/P
Coccinellidae	<i>Hippodamia convergens</i>	N/P	N/P	1.8 ± 0.1	late April to early July	N/P	N/P	1.0	mid-May	N/P	N/P
Coccinellidae	<i>Hyperaspis signata</i> sp. group	60.0	late March to mid-May	21.5 ± 0.6	early April to mid-July	68.5 ± 1.4	mid-May to mid-July	45.0 ± 2.8	early April to early June, October	25.0 ± 1.0	mid-April to late June
Coccinellidae	<i>Olla v-nigrum</i>	N/P	N/P	0.1	early May	N/P	N/P			N/P	N/P
Coccinellidae	<i>Scymnus</i> sp.	N/P	N/P	1.3	mid-April to early October	7.4 ± 0.3	late May to mid-July			N/P	N/P

^aN/P = not present.

Table 3.4. Three diversity indices [species richness (R), effective number of species ($\exp H'$), and Gini-Simpson ($1-\lambda$)] of parasitoid species of *Parthenolecanium* spp. collected on sticky cards in four southeastern U.S. states between 2010 and 2013. GA = Georgia, NC = North Carolina, SC = South Carolina, VA = Virginia.

	R	$\exp H'$	$1-\lambda$
GA	6.50 ± 0.78 d	4.76 ± 0.58 b	0.75 ± 0.03 a
NC	9.27 ± 0.49 c	6.68 ± 0.39 a	0.80 ± 0.01 a
SC	13.48 ± 0.57 a	6.36 ± 0.21 a	0.57 ± 0.22 a
VA	10.86 ± 0.67 b	4.83 ± 0.30 b	0.68 ± 0.03 a
GA			
2010	4.75 ± 1.03	3.59 ± 0.56	0.74 ± 0.07
2011	—	—	—
2012	8.00 ± 1.22	6.18 ± 0.96	0.78 ± 0.44
2013	7.00 ± 1.00	4.27 ± 0.92	0.78 ± 0.04
NC			
2010	11.20 ± 0.37	7.43 ± 0.72	0.81 ± 0.03
2011	9.60 ± 0.24	7.52 ± 0.27	0.84 ± 0.01
2012	7.00 ± 0.31	5.10 ± 0.23	0.76 ± 0.01
2013	—	—	—
SC			
2010	—	—	—
2011	11.87 ± 0.51	6.29 ± 0.51	0.22 ± 0.59
2012	16.71 ± 0.18	6.38 ± 0.11	0.78 ± 0.01
2013	11.83 ± 0.54	6.44 ± 0.31	0.79 ± 0.02
VA			
2010	11.50 ± 0.50	4.04 ± 0.34	0.58 ± 0.05
2011	11.00 ± 2.00	4.95 ± 0.75	0.71 ± 0.03
2012	11.50 ± 0.50	5.01 ± 0.23	0.70 ± 0.01
2013	8.00	5.81	0.78
State			
F	32.94	8.92	0.33
df	3, 9	3, 9	3, 9
P	< 0.0001	0.0012	0.8039
Tree (State)			
F	4.71	0.54	0.99
df	3, 9	3, 9	3, 9
P	0.8347	0.8965	0.4852
Year			
F	0.30	0.19	0.77
df	3, 9	3, 9	3, 9
P	0.8270	0.9015	0.5200

Means and SE in the same column followed by the same letter are not significantly different ($P > 0.05$, LS-means).

Table 3.5. Chao-Jaccard index of community similarity of chalcidoid parasitoid species of *Parthenolecanium* spp. collected on sticky cards in four southeastern U.S. states between 2010 and 2013. GA = Georgia, NC = North Carolina, SC = South Carolina, VA = Virginia.

		NC	SC	VA
2010	GA	0.31 ± 0.08	—	0.33 ± 0.20
	NC		—	0.77 ± 0.13
	SC			—
2011	NC		0.90 ± 0.04	0.94 ± 0.01
	SC			0.95 ± 0.02
2012	GA	0.46 ± 0.14	0.63 ± 0.14	0.80 ± 0.03
	NC		0.82 ± 0.03	0.86 ± 0.04
	SC			0.96 ± 0.01
2013	GA	—	0.71 ± 0.08	0.57
	NC		—	—
	SC			0.94

Table 3.6. Three diversity indices [species richness (R), effective number of species ($\exp H'$), and Gini-Simpson ($1-\lambda$)] of predator species of *Parthenolecanium* spp. collected on sticky cards in three southeastern U.S. states between 2010 and 2012. Means are provided with their standard errors. NC = North Carolina, SC = South Carolina, VA = Virginia.

	R	$\exp H'$	$1-\lambda$
NC			
2010	2.00 ± 0.32	1.92 ± 0.33	0.40 ± 0.12
2011	1.80 ± 0.20	1.60 ± 0.17	0.30 ± 0.84
2012	2.80 ± 0.37	2.50 ± 0.31	0.54 ± 0.06
SC			
2010	—	—	—
2011	1.33 ± 0.21	1.32 ± 0.20	0.15 ± 0.09
2012	2.57 ± 0.53	2.07 ± 0.26	0.54 ± 0.08
VA			
2010	2.00	1.90	0.40
2011	2.00 ± 1.00	1.80 ± 0.80	0.30 ± 0.30
2012	3.50 ± 1.50	2.70 ± 0.70	0.55 ± 0.05
State			
F	1.12	1.18	0.08
df	2, 5	2, 5	2, 5
P	0.3605	0.3422	0.9265
Tree (State)			
F	6.72	7.46	3.69
df	2, 5	2, 5	2, 5
P	0.0003	0.0001	0.0079
Year			
F	8.85	8.46	21.42
df	2, 5	2, 5	2, 5
P	< 0.0228	< 0.0249	0.0035

Table 3.7. Chao-Jaccard index of community similarity of predator species of *Parthenolecanium* spp. collected on sticky cards in three southeastern U.S. states between 2011 and 2012. NC = North Carolina, SC = South Carolina, VA = Virginia

		SC	VA
2011	NC	0.43	0.19
	SC		0.20
2012	NC	0.49	0.81
	SC		0.34

Table 3.8. The number and sex ratio of parasitoid species emerging from two life stages of *Parthenolecanium* spp. isolated from willow oaks in South Carolina in 2013.

Species	Scale Life Stage	Number of mummies yielding			% Population			% ♀		
		Solitary	Gregarious		Solitary ^a	Gregarious		Solitary ^a	Gregarious	
			Single sp.	Mixed spp.		Single sp. ^a	Mixed spp. ^a		Single sp. ^a	Mixed spp. ^a
<i>Coccophagus lycimnia</i>	Nymph	14.0	0.0	0.0	100.0	0.0	0.0	93.0 ± 6.9	0.0	0.0
<i>Coccophagus lycimnia</i>	Adult	3.0	0.0	6.0	40.0	0.0	60.0	33.3 ± 27.2	0.0	18.7 ± 8.9
<i>Blastothrix</i> sp. 1	Adult	3.0	11.0	3.0	3.0	80.6	16.4	100.0	39.5 ± 5.5	31.5 ± 12.9
<i>Blastothrix</i> sp. 2	Adult	1.0	0.0	1.0	50.0	0.0	50.0	0.0	0.0	100.0
<i>Encyrtus</i> sp. 1	Adult	9.0	0.0	1.0	90.0	0.0	10.0	30.0 ± 14.5	0.0	100.0
<i>Eunotus</i> sp.	Adult	9.0	4.0	5.0	39.1	39.1	21.8	50.0 ± 50.0	25.0 ± 21.7	55.5 ± 4.5
<i>Metaphycus</i> sp. 2	Adult	0.0	1.0	0.0	0.0	100.0	0.0	0.0	85.7	0.0
<i>Microterys</i> sp.	Adult	0.0	0.0	1.0	0.0	0.0	100.0	0.0	0.0	0.0
<i>Pachyneuron</i> sp.	Adult	2.0	2.0	4.0	9.5	38.1	52.4	16.6	0.0	53.6 ± 14.4

^aPercentage calculated based on total number of individuals from each parasitoid species.

Figure 3.1. Abundance of *Coccophagus lycimnia* (left) and *Coccophagus* sp. 1 (right) collected on sticky cards in four states.

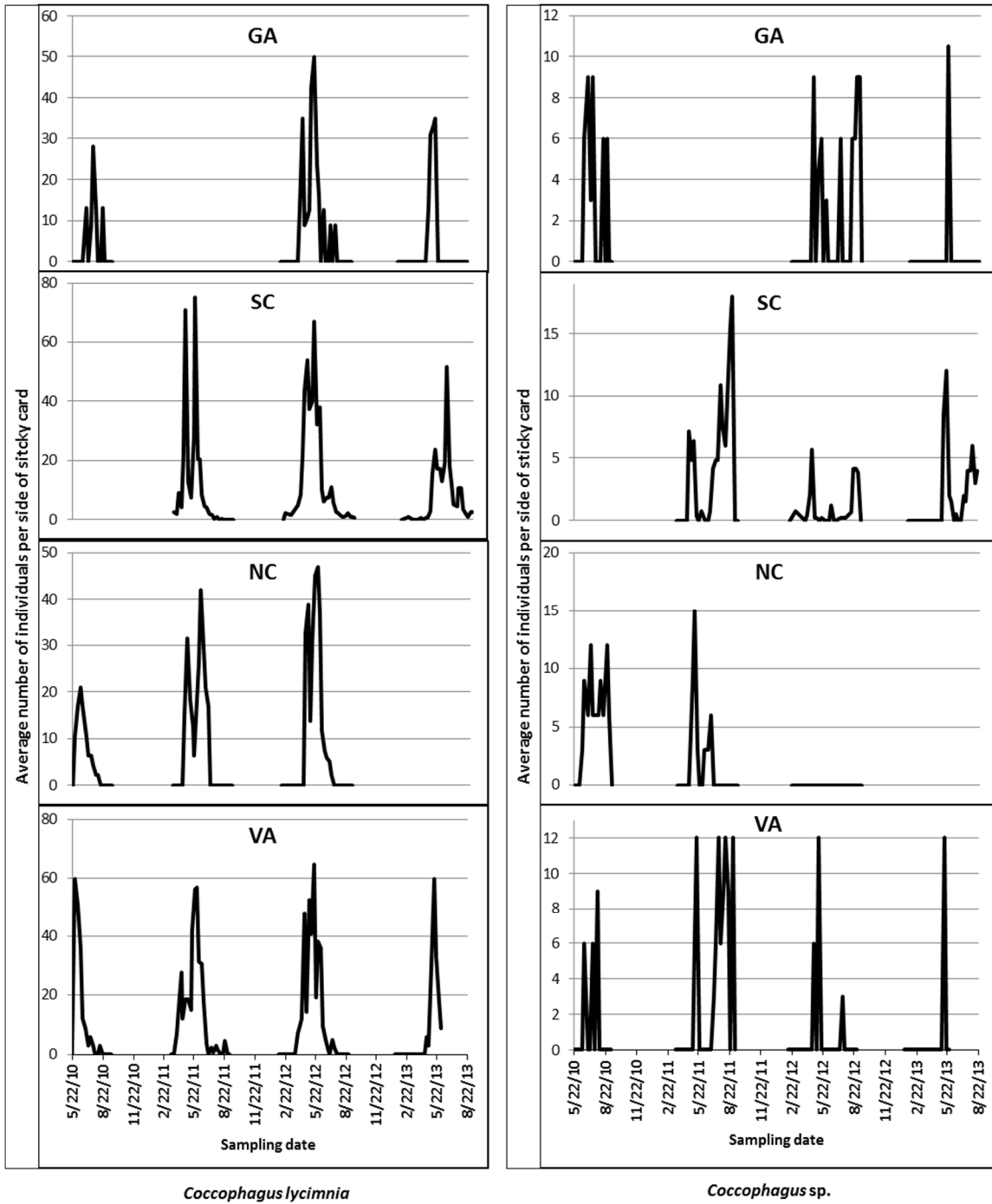


Figure 3.2. Abundance of *Blastothrix* spp. (left) and *Encyrtus* spp. (right) collected on sticky cards in four states.

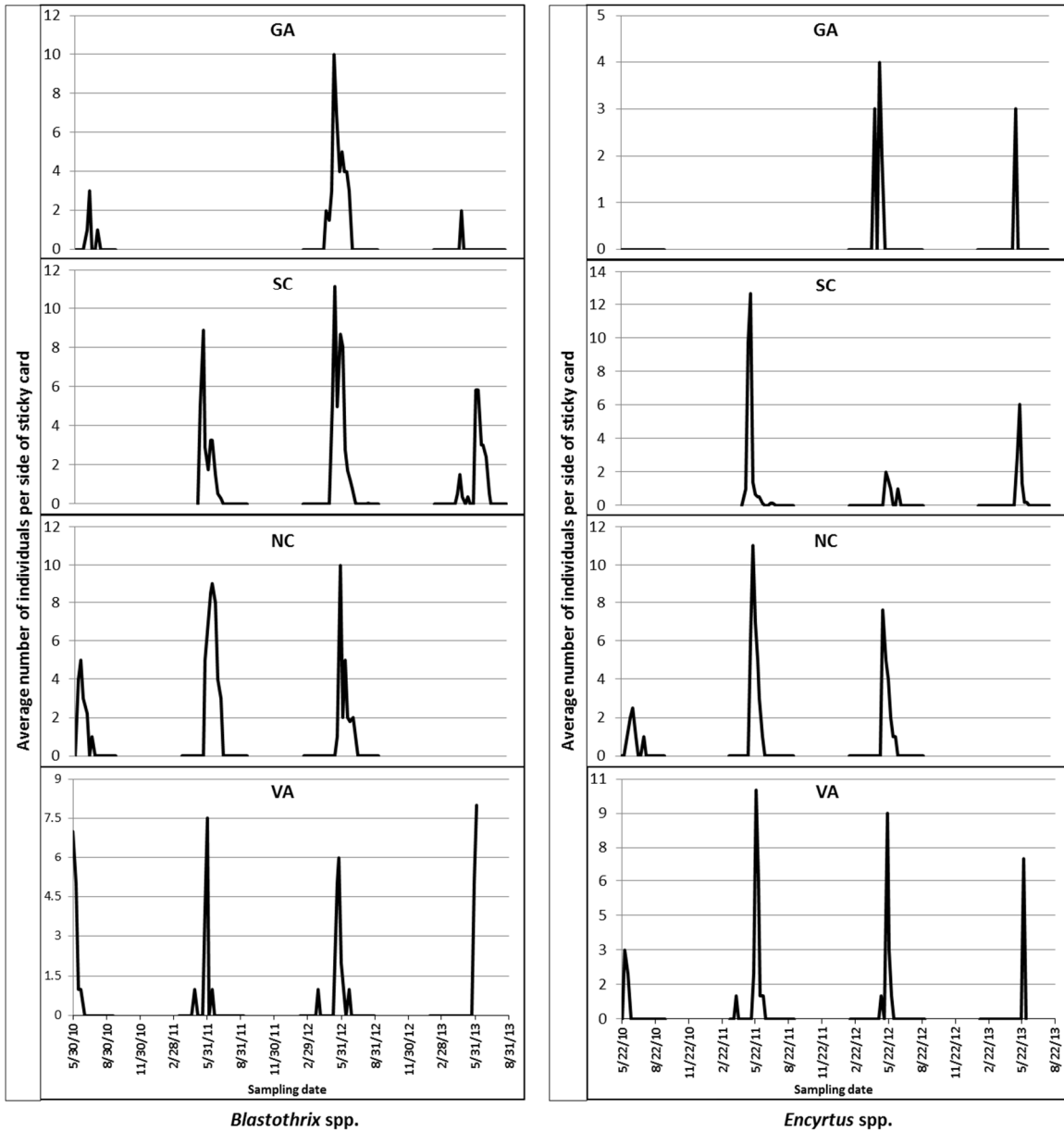


Figure 3.3. Abundance of *Metaphycus* spp. (left) and *Aprostocetus* sp. 1 (right) collected on sticky cards in four states.

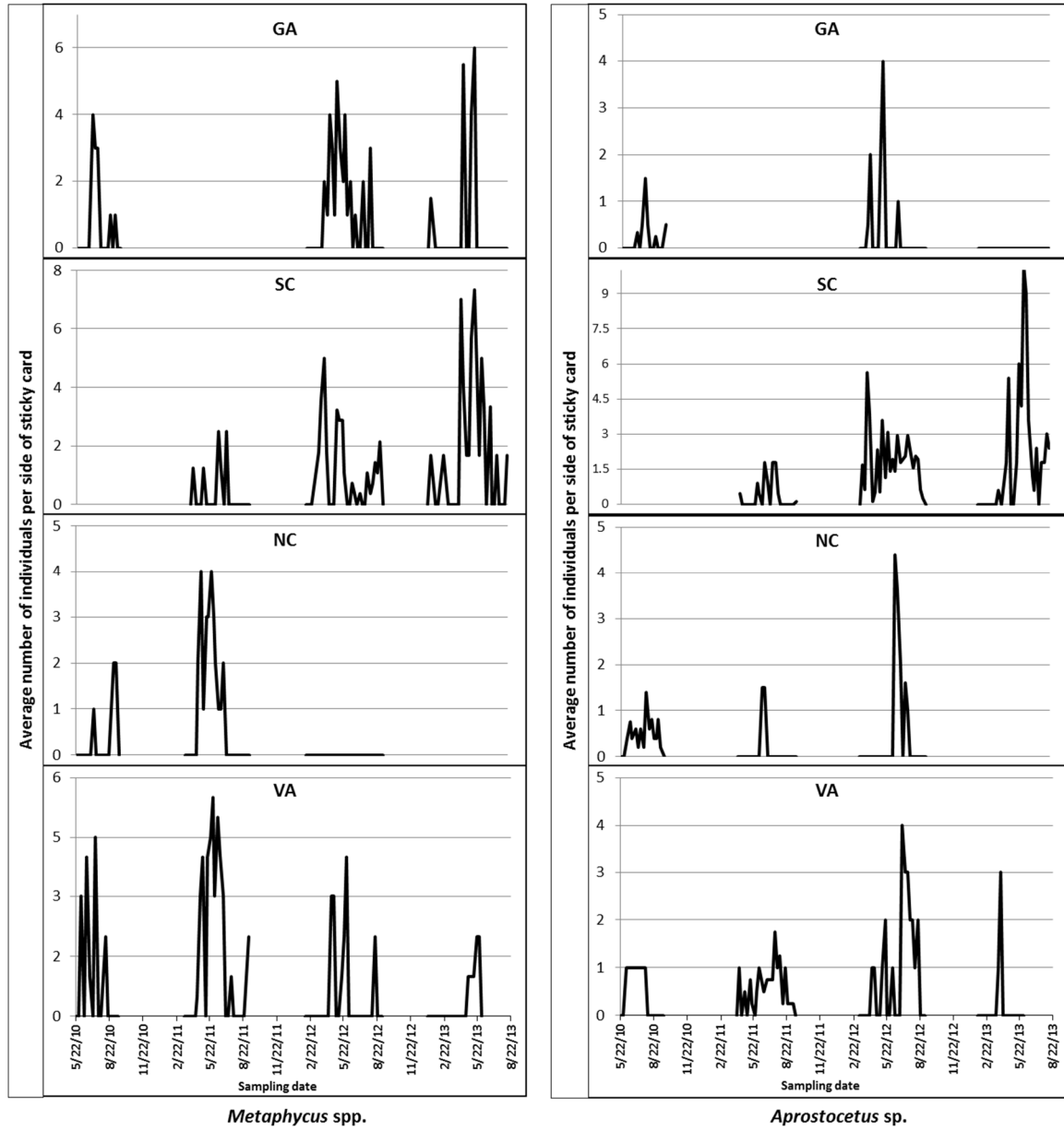


Figure 3.4. Abundance of *Eunotus* sp. (left) and *Pachyneuron* spp. (right) collected on sticky cards in four states.

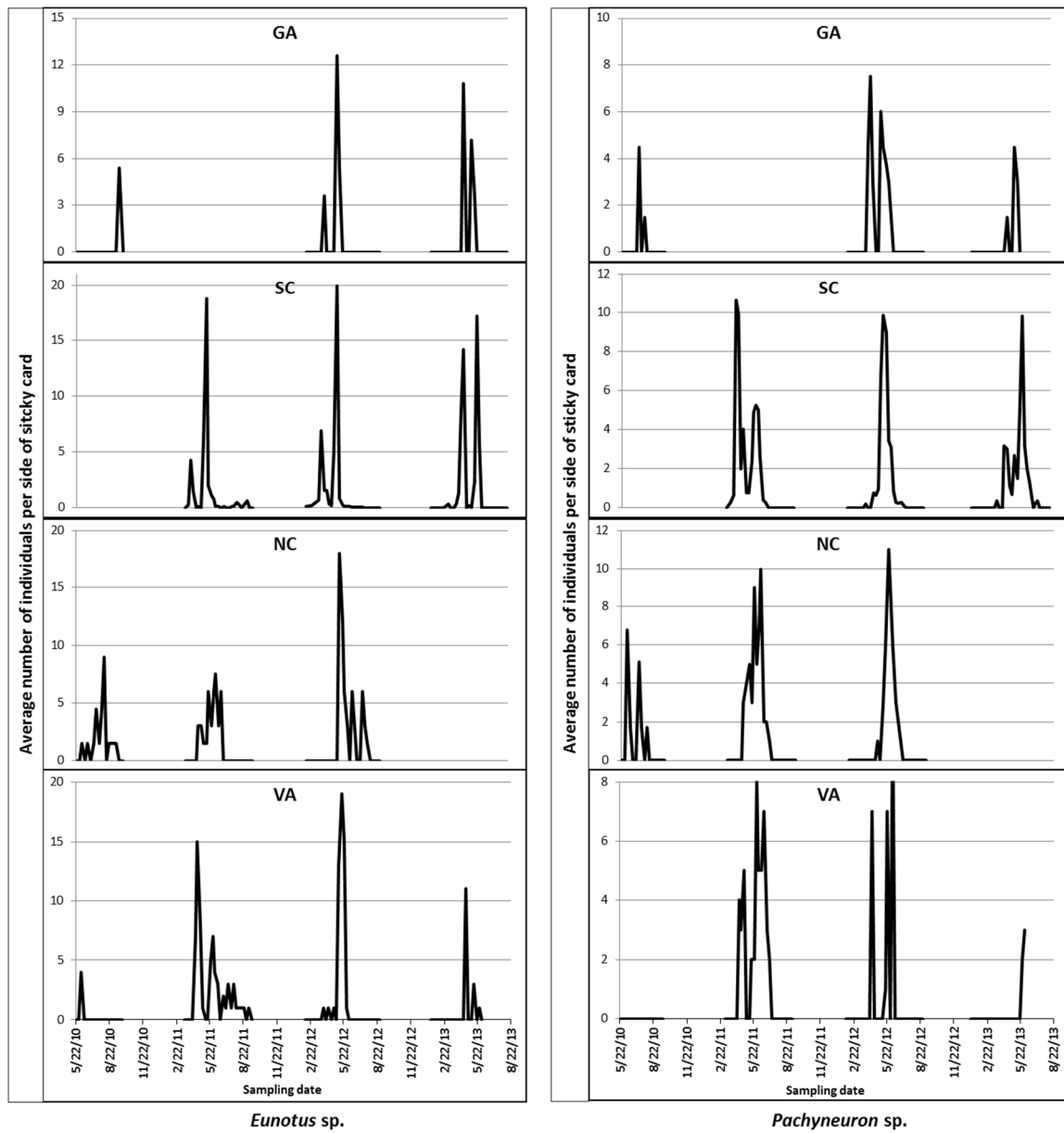


Figure 3.5. Seasonal activity of *Chrysoperla rufilabris* (larvae), *Chilocorus stigma* (larvae and adults), and *Hyperaspis signata* sp. group (larvae and adults) collected by beat sheet in South Carolina.

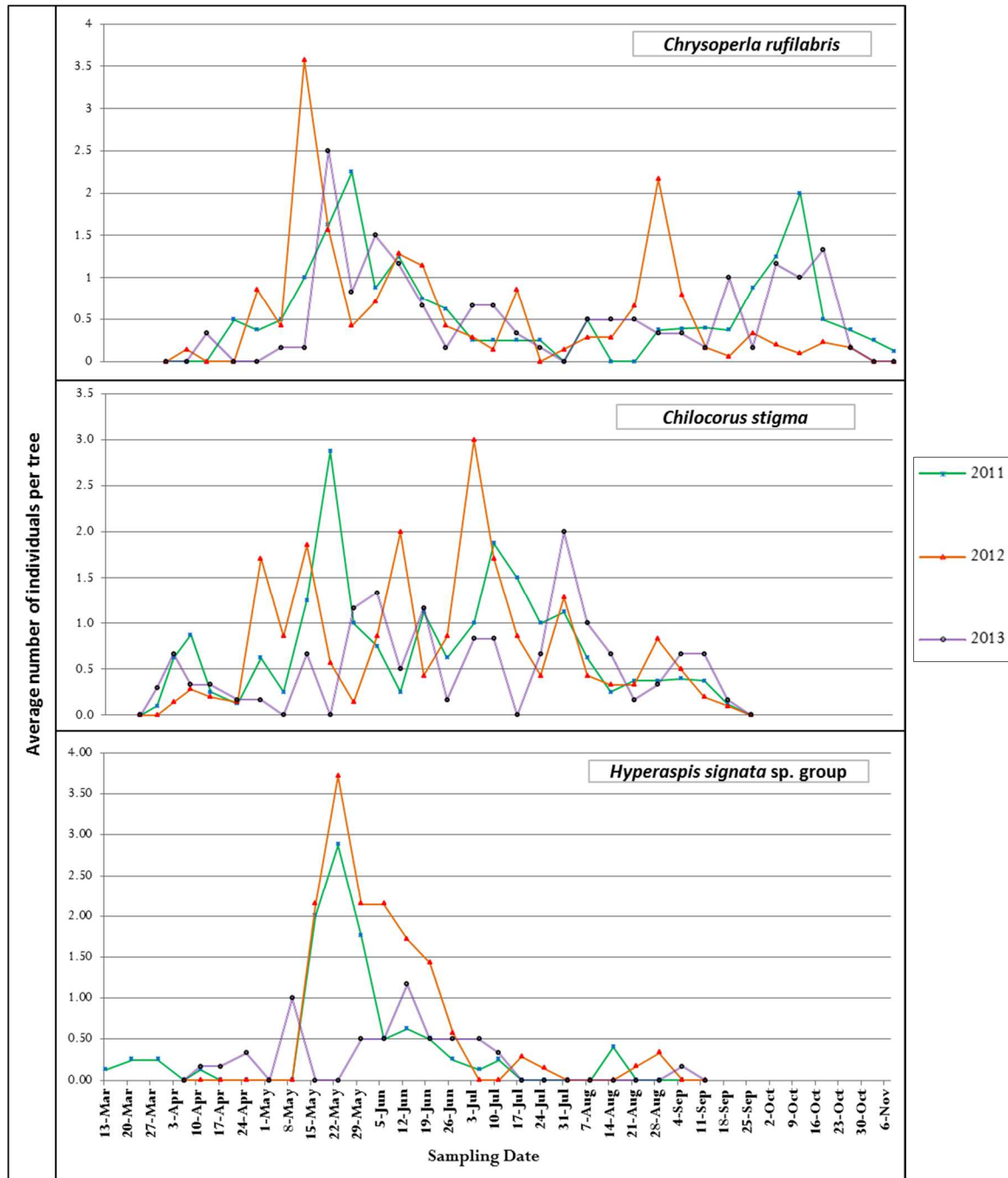
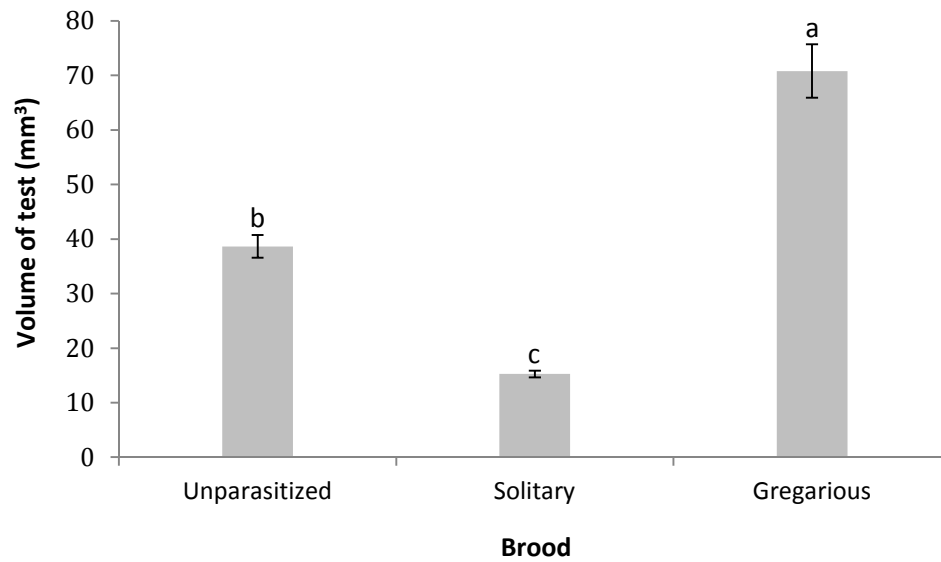
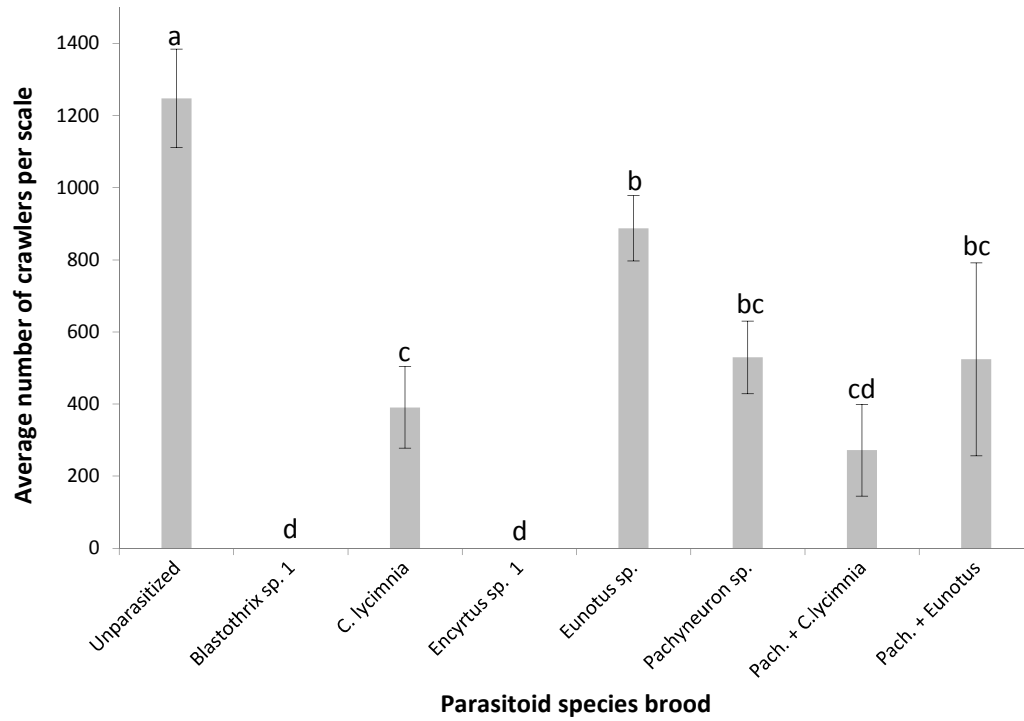


Figure 3.6. Impact of solitary and gregarious parasitoid broods on size (in volume) of the host scale test.



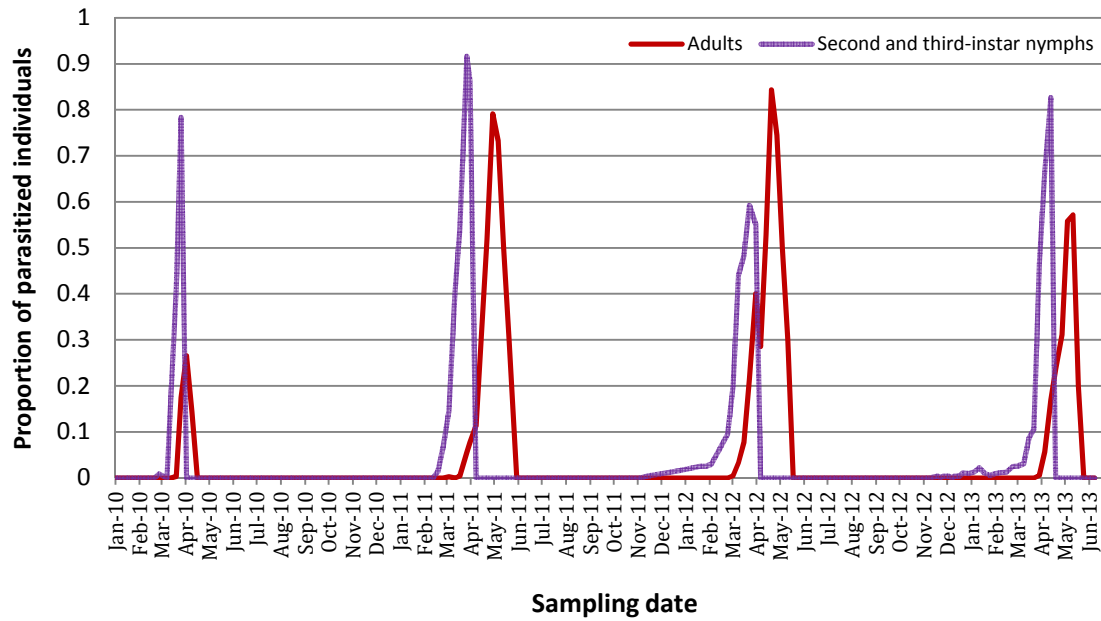
	Unparasitized	Solitary	Gregarious
Mean	38.64	15.25	70.79
Std. Error	± 2.08	± 0.60	± 4.90

Figure 3.7. Impact of parasitoid species on scale fecundity (number of crawlers per female).



	Unparasitized	<i>Blastothrix</i> sp. 1	<i>C. lycimnia</i>	<i>Encyrtus</i> sp. 1	<i>Eunotus</i> sp.	<i>Pachyneuron</i> sp.	<i>Pach.</i> + <i>C.lycimnia</i>	<i>Pach.</i> + <i>Eunotus</i>
Mean	1247.80	0.00	390.80	0.00	887.86	529.50	272.00	524.33
Std. Error	± 136.55	0.00	± 112.91	0.00	± 90.70	± 100.76	± 127.28	± 267.67

Figure 3.8. Proportion of parasitized adults and immature lecanium scales in South Carolina from 2010 to 2013.



CHAPTER FOUR

ASSESSMENT OF *PARTHENOLECANIUM* SPP.-INFESTED WILLOW OAKS AS POTENTIAL BANKER PLANTS OF *COCCOPHAGUS LYCIMNIA* IN THE URBAN LANDSCAPE

Introduction

European fruit lecanium (*Parthenolecanium corni* Bouché) and oak lecanium [*Parthenolecanium quercifex* (Fitch)] are important pests of willow oak trees (*Quercus phellos* L.) in urban landscapes throughout the southeastern U.S. (Schultz 1984, Johnson and Lyon 1991, Hodges and Braman 2004). Although the management of lecanium scales relies mainly on applying insecticides when crawlers are emerging, myriad parasitoids and predators also help suppress scale insect populations. Parasitoids were found to reduce the scale population by 27—92% (Chapter 3).

Coccophagus lycimnia Walker is a heteronomous parasitoid, i.e., females are primary endoparasitoids of scale insects, and males are either primary ectoparasitoids of scale insects or secondary parasitoids of mature females of their own species or other species of chalcidoids, mainly eulophids, aphelinids or encyrtids (Walter 1983). *Coccophagus lycimnia* is a cosmopolitan species that has been reported from 25 U.S. states, including those in the Southeast (Noyes 2015). This generalist parasitoid has a wide host range that includes soft scales [such as citricola scale, *Coccus pseudomagnoliarum* (Kuwana), brown soft scale, *Coccus hesperidum* L., and Mediterranean black scale, *Saissetia oleae* (Olivier)] (Thompson 1953, Peck 1963, Walter

1983, Lampson and Morse 1992, Bernal et al. 2001, Tena et al. 2008), and armored scales [such as chaff scale, *Parlatoria pergandii* Comstock, oystershell scale, *Diaspidiotus ostreaeformis* (Curtis), and San Jose scale, *Comstockaspis perniciosus* (Comstock)] (Peck 1953, Thompson 1953, Tudor 1982). *Coccophagus lycimnia* is a parasitoid of the Florida wax scale, *Ceroplastes floridensis* Comstock, *P. corni* and *P. quercifex* (Peck 1963, Schultz 1984, Japoshvili and Karaca 2002). *Ceroplastes floridensis* is commonly found in the eastern U.S. as a pest of citrus and ornamental landscape plants, such as hollies (*Ilex* spp.), elm (*Ulmus* spp.), *Euonymus* spp., *Photinia* spp., crape myrtle (*Lagerstroemia* spp.), and honey-suckle (*Lonicera* spp.) (Hodges et al. 2001, Robayo Camacho and Chong 2014).

Conservation biological control relies on the maintenance and protection of existing natural enemy populations by minimizing the application of non-compatible pesticides and the management of biotic factors (Rose and DeBach 1990, Landis et al. 2000, Barbosa 2003). Manipulation of biotic factors to enhance or improve the effectiveness of the natural enemies is a basis for natural enemy conservation (Rose and DeBach 1990). Adverse biotic factors include honeydew-seeking ants, which can interfere with natural enemy populations. Another important biotic factor is the host of the natural enemy and the prey, which can be manipulated to promote conditions that allow natural enemy populations to thrive. For example, the use of cultural practices, such as pruning or planting more host plants, can exert a positive effect on natural

enemy populations (Rose and DeBach 1990). The host plants of prey can also act as banker plants for natural enemy populations.

Three related concepts help define “banker plant”: banker plant (in general), banker plant system, and banker plant method (Huang et al. 2011). In a broad sense, banker plants are purposefully grown and infested plants used to help increase populations of predators and parasitoids in an ecosystem, such as the landscape. Banker plant systems are species maintained or added as habitats that sustain breeding populations of natural enemies released on them for control of pests in greenhouses or the field (Osborne et al. 2005, Frank 2010, Huang et al. 2011). Most banker plant systems have been developed in greenhouses (Frank 2010, Huang et al. 2011). A banker plant system consists of three basic elements: the banker plant, the alternative food source, and the beneficial organism(s) (Pratt and Croft 2000, Frank 2010). The banker plant is the plant itself, the food source is the prey or host (or substance) maintained by the banker plant, and the beneficial organism is the natural enemy released, maintained and propagated on the banker plant to be used for biological control. Several methods promote establishment of beneficial populations of natural enemies, one of which is the banker plant method (Huang et al. 2011). It consists of non-target crop plants infested with non-target pests that serve as alternative food sources for beneficial organisms; in this way, populations of natural enemies are sustained and provided a habitat for breeding and increasing their numbers, which in turn disperse to the crop plants harboring the target pests, exerting biological control.

We propose that *Parthenolecanium* spp.-infested willow oak trees can serve as banker plants in the landscape, harboring and building up populations of *C. lycimnia*, which can then move onto other plants in the same landscape and attack other scale insects, such as *C. floridensis*, as reflected in an increase in the parasitism rate of the target scale insect pest.

Materials and Methods

In early June 2013, 24 hybrid hollies (*Ilex* x 'HL10-90' Christmas Jewel® Holly PP14477) were purchased from Parsons Nursery in Georgetown, SC and brought to Pee Dee Research and Education Center, in Florence SC. The bushes were kept under field conditions in a nursery plot and protected from parasitoids by covering them in framed 0.6x0.6x1.2 m white chiffon cages. The bushes were watered daily and no fertilizer was added. The hybrid hollies had only a low number of *C. floridensis*, so the plants had to be infested supplementarily. Branches of *C. floridensis*-infested hollies of an unknown variety were collected from a landscape in Georgetown, brought to the nursery plot, and left in close contact with the hybrid hollies until a scale insect population was established on the leaves (late June).

Once the entire set of 24 hybrid hollies was infested with *C. floridensis*, on June 27, they were divided into two groups. Half (12) of the hollies were transferred to the “banker plant site” located about 1,500 m from the nursery plot, where they were arranged under willow oaks (*Quercus phellos* L.) infested with a mixed population of *Parthenolecanium corni* Bouché and *P. quercifex* (Fitch). Natural enemies, especially

chalcidoid parasitoids are known to reduce infestations of *Parthenolecanium* spp. (Ebeling 1959, Johnson and Lyon 1991, Schultz 1984, Gill 1988, Kosztarab 1996, Carrillo et al. 2001, Japoshvili et al. 2008). More than 20 species of chalcidoid wasps have been identified as parasitoids of *Parthenolecanium* spp. on willow oak, with *C. lycimnia* being the most abundant species (Chapter 3). Half (six) of the hollies in this “banker plant site” group were exposed (uncaged) to allow parasitoid attacks; the remaining hollies were kept caged to prevent parasitoid attacks. If the willow oaks did serve as banker plants for *C. lycimnia*, we expected to detect an increase in the parasitism rate of the *C. floridensis* population by *C. lycimnia* in the exposed cages, compared to those in the unexposed cages.

A second group of 12 *C. floridensis*-infested hybrid hollies was transferred from the nursery plot to the ‘non-banker plant site’ (without any infested oaks) about 3,000 m away from the nursery plot, next to a greenhouse. Half (six) of the hollies were uncaged and half (six) were kept caged. As this site served as the negative control, we expected it not to maintain an active population of parasitoids. Therefore, we anticipated the parasitism rate of *C. floridensis* to be similarly low between the exposed and unexposed populations at the “non-banker plant site”, and the unexposed population in the “banker plant site”. Any parasitism of *C. floridensis* at this site was treated as the background parasitism rate.

The hollies were left at the banker and non-banker plant sites for three weeks (27 June to 17 July). After the exposure period, the uncaged hollies were caged again

and all 24 caged bushes were moved back to the nursery plot. Two 10 to 15 cm infested twigs were randomly collected monthly from each plant for eight months. Parasitism rate of the first twig was calculated by counting the number of scales with emergence holes on the twig and dividing it by the total number of wax scales on the twig.

To verify whether *C. lycimnia* was the parasitoid responsible for the emergence holes counted on the first twig, the identity and abundance of the parasitoids were determined on the second twig. The second twig was put into a vial, plugged with a cotton ball, and kept under laboratory conditions (20-25°C; 35-45% relative humidity). Vials were checked once a week and the numbers of adult parasitoids emerged were recorded. Parasitoids were identified to genus based on the keys by Hayat (1997) and Prinsloo (1997). *Coccophagus lycimnia* was identified using the keys by Compere (1931), where the species is mentioned as the synonym *Coccophagus lecanii* (Fitch). Differences in parasitism rates between treatments (exposed and unexposed hollies) and sites (banker plant, non-banker plant) were evaluated using factorial repeated measures ANOVAs (PROC GLM; SAS Institute 2011). Plants were nested within treatments or sites in each ANOVA. Interactions between dates and treatments, and dates and sites were specified in the models.

Results and Discussion

Differences in parasitism rates were not significant among exposed and unexposed scales at the banker plant site ($F = 1.39$; $df = 1,4$; $P = 0.2659$) (Fig. 4.1) or the non-banker plant site ($F = 0.59$; $df = 1,4$; $P = 0.4611$) (Fig. 4.2). There were also no

significant differences in parasitism rates of treatments between the banker plant site and the non-banker plant site ($F = 4.74$; $df = 1,4$; $P = 0.0544$) (Fig. 4.3). No interaction was found between dates and treatments ($P > 0.05$), or dates and sites ($P > 0.05$). Comparison of means between dates by ANOVA yielded no significant differences ($F = 1.18$; $df = 6,7$; $P = 0.4098$).

The result from the banker plant site did not support our expectation of a higher rate of parasitism in the exposed population. The lack of difference among the exposure treatments is partly because the scale insects were likely already parasitized before being caged. Therefore, we had parasitoids emerging from scales on the unexposed hollies, which was unexpected. Additionally, although *C. lycimnia* is active from early April to late July in the southeastern U.S., by late June its activity has decreased by more than 80%. This lack of parasitoid activity during the time when *C. floridensis* was exposed could have been another reason for low-level parasitism. We do not know when *C. lycimnia* actually attacks scale insects. Another possibility is that the life stage of *C. floridensis* was unsuitable for parasitism at the time of exposure.

A trend ($0.05 < P < 0.1$) for differences in parasitism rates was observed between the two sites, which might point to a possible failure in randomizing the samples within the experiment. We never quantified the levels of infestation of *C. floridensis* in the hollies. Subdividing the levels of infestation by ranges prior to exposure and assigning randomly the treatments and groups to be carried to the experimental sites may have helped implement a completely randomized design for our experiment.

A total of 44 specimens of parasitoids was collected, of which 54.5% were *C. lycimnia* that emerged from scales on twigs. In October, a single specimen of *Metaphycus* sp. emerged from non-exposed *C. floridensis*. The remaining 43.2% corresponded to parasitized scales with holes left after the emergence of unidentified parasitoid species.

The experiment should be repeated under the same design but take into account the following modifications. First, the hollies should be inspected and completely freed of parasitoids and parasitized scales before starting. Second, the scale insects used to infest the host plants should also be free of parasitoids and parasitized scales. Third, to increase the chances of parasitism, the time of exposure of *C. floridensis* under the banker plants should take place in May (during the most active period of *C. lycimnia*), as soon as the scale eggs hatch and crawlers start dispersing. Additionally, *C. lycimnia* reaches its second peak of activity during the second half of May in South Carolina; therefore, the exposure of *C. floridensis* to parasitism should be maintained at least until the first week of June to increase the chances of parasitism by *C. lycimnia*. Fourth, the scale-infested hollies should be properly randomized within the treatment groups and sites.

The intended use of scale-infested willow oaks as banker plants is a new approach where a situation normally perceived as a problem may become beneficial to other crops affected by scale insects. Because willow oaks are ornamental plants often kept in healthy conditions for esthetic purposes or as focal points in the landscape,

maintaining pest infestations purposely most likely will be rejected by tree owners and managers. In addition, scale infestations may adversely influence the survival and esthetics of the trees over the long term. Nevertheless, the potential of scale-infested willow oaks as banker plants and as a resource for conservation biological control programs warrants further evaluation.

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Figure 4.1. Rates of parasitism of exposed (E) and unexposed (U) *Ceroplastes floridensis* at the banker plant site between July 2013 and February 2014.

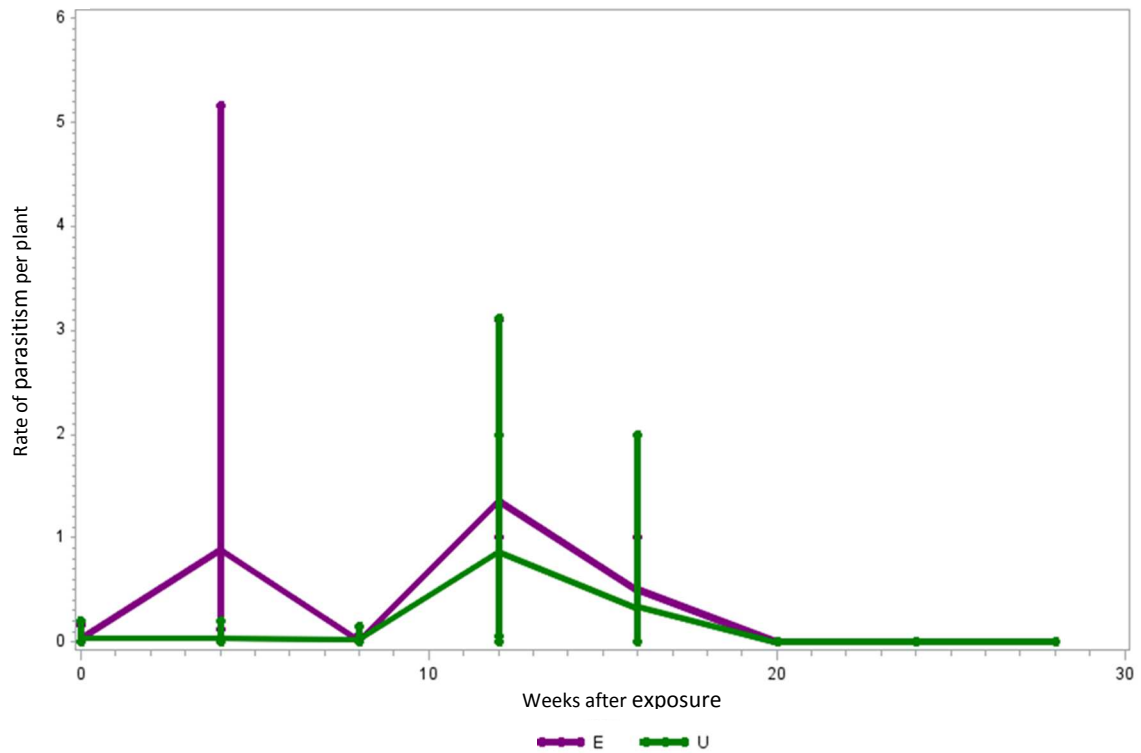


Figure 4.2. Rates of parasitism of exposed (E) and unexposed (U) *Ceroplastes floridensis* at the non-banker plant site between July 2013 and February 2014.

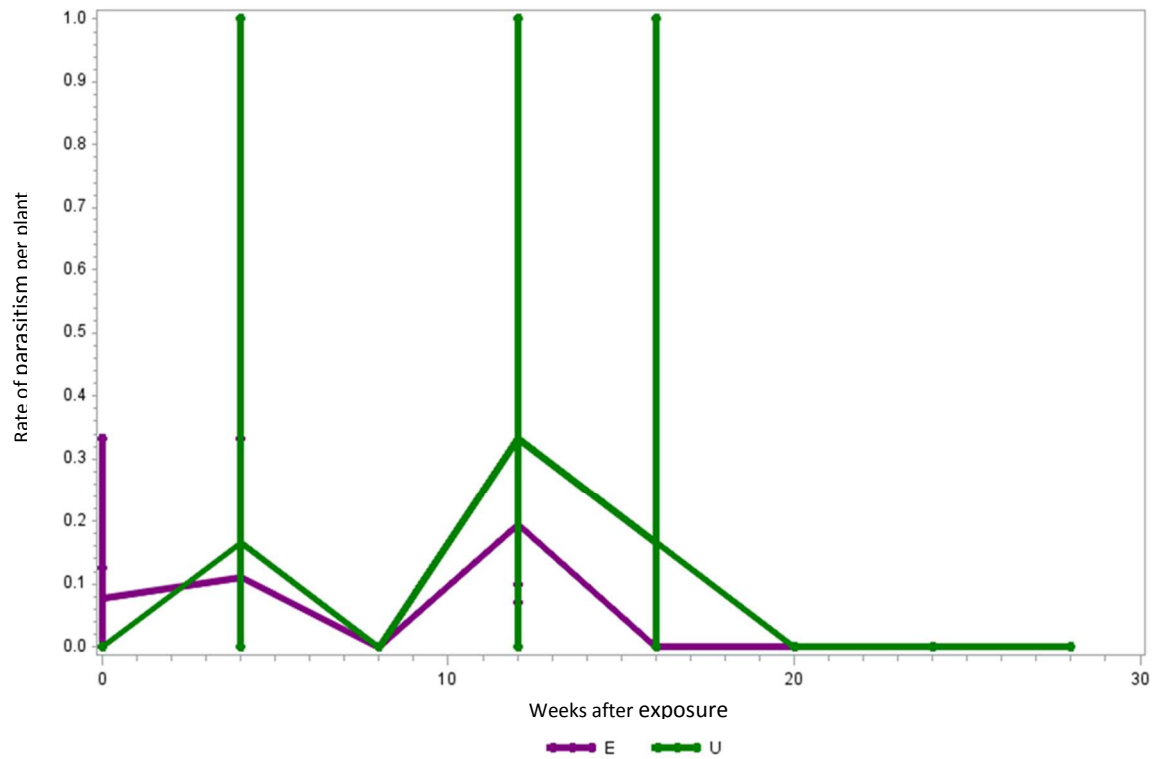


Figure 4.3. Rates of parasitism of combined exposed and unexposed *Ceroplastes floridensis* at the banker plant site (P) and the non-banker plant site (G) between July-February 2014.

