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# Occurrence and Phenology of Polistine Wasps (Hymenoptera: Vespidae) in Southern Louisiana

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OCCURRENCE AND PHENOLOGY OF POLISTINE WASPS (HYMENOPTERA: VESPIDAE) IN  
SOUTHERN LOUISIANA

A Thesis

Submitted to the Graduate Faculty of the  
Louisiana State University and  
Agricultural and Mechanical College  
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in

The Department of Entomology

by  
Scott Nacko  
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## ABSTRACT

Phylogenetic studies suggest that historically all paper wasps (Vespidae: Polistinae) in North America have tropical origins. However, paper wasps have adapted to thrive in temperate conditions. Subtropical and temperate climates allow for a study of adaptive traits which can be retained or lost within populations, and ultimately help elucidate the process of social wasp evolution. Additionally, species occurrence patterns can help us to understand partitioning and resource use within populations. We investigated the occurrence and phenology of each Polistine species found at four sites in southern Louisiana around Baton Rouge, and also examined the occurrence and behavior of a closely associated brood parasite, *Chalcoela iphitalis*. Based on nest height analysis we found two statistically different groupings: lower nesting species (*Mischocyttarus mexicanus*, *Polistes dorsalis*, *P. metricus*) and higher nesting species (*P. exclamans*, *P. fuscatus*, *P. bellicosus*). Patterns of occurrence in wasp nest attachment substrate also were found, with 32% of all nests occurring on *Sabal palmetto* or *Sabal minor*. Two periods of nest initiation were observed: spring nests in March-May and late season or fall nests in July-September. Late season nests made up roughly 40% of all nests observed and were represented by all species. Late season nests of *P. dorsalis*, *P. bellicosus*, *P. metricus*, and *M. mexicanus* demonstrated a significantly shorter colony duration than did spring nests, however the highest number of adults recorded at the nest was significantly less only in *P. bellicosus*. Results suggest niche partitioning between species in relation to nest site usage, as well as a possible bivoltine colony cycle in some paper wasp species of southern Louisiana.

## CHAPTER 1. INTRODUCTION & OBJECTIVES

### 1.1 INTRODUCTION

Polistine wasps are key model organisms for understanding species evolution and adaptation. As predatory stinging insects, they have relevance to both the health of natural ecosystems and the well-being of humans. In this study, the occurrence of Polistine species in various suburban settings is examined. This study also investigated the phenology or cyclic nesting biology of these wasps in Baton Rouge Louisiana, an area with a subtropical climate. By providing data on species nest occurrence in suburban habitats we may help to either mitigate unwanted human-wasp interactions or increase the efficacy of these organisms as beneficial insects. Further, findings regarding the phenology of temperate and tropical species in a subtropical climate could have implications for the evolution of eusociality in paper wasps.

### 1.2 OBJECTIVES

1.) Phenology: Compare overall productivity and durational period of spring nests to late season nests. This will include number of nests observed being initiated in spring and summer, number of adult wasps and total number of cells on each nest, and length of time that brood is present.

2.) Nest site occurrence: Determine nest site preferences for Polistine wasps in Baton Rouge. Identification of plant species utilized by wasps as well as species abundance data will be recorded.

3.) Record occurrence and oviposition behavior of a common brood parasite, *Chalcoela iphitalis*.



## CHAPTER 2. LITERATURE REVIEW

### 2.1 VESPIDAE: POLISTINAE

The subfamily Polistinae, commonly known as paper wasps, is an entirely eusocial group (exhibiting cooperative brood care, overlap of generations, and a caste system) belonging to the larger family Vespidae. Worldwide, the Vespidae family is diverse and contains six subfamilies including both eusocial and solitary species (Bugguide.net). The Polistinae diverged from other Vespidae around 140 million years ago (Arévalo et al. 2004), and lack defined morphological differences in castes; they are believed to be primitively eusocial compared with more advanced eusocial Vespinae (Pardi 1996). In North America there are approximately 27 species of Polistinae in three genera: *Polistes*, *Mischocyttarus*, and *Brachygastra* (Henderson & Pickett 2000), however worldwide the subfamily contains at least 27 genera (Wenzel 1998) and 943 species (Arévalo et al. 2004). A major behavioral divide within the subfamily comes from a difference in nesting biology; the swarm founding species in which new nests are initiated by groups of workers then joined by egg layers, and the independent founding species in which new nests are initiated by one or multiple egg layers without workers (Arévalo et al. 2004). *Polistes* and *Mischocyttarus* are both solitary founding species, while *Brachygastra* is a swarm founder.

### 2.2 LIFE HISTORY

The nesting biology of paper wasps in temperate zones is largely that of independent founding (Arévalo et al. 2004), beginning with one or multiple egg laying foundresses which construct a nest made with wood or plant fibers (West-Eberhard 1969). Different terminologies

are applied to females based on their reproductive condition: Foundresses are those which have mated, overwintered, and are beginning nests; the dominant egg layer on a nest is called the queen, workers are those eclosing in spring or early summer who do not reproduce, and gynes are those eclosing late in the season who do not work but have not yet overwintered (Strassmann et al. 1988). Polistine wasps are predatory, capturing a variety of soft bodied arthropods including many species of Lepidoptera as food for their developing larvae (Stamp & Bowers 1988). After having raised the first brood of workers, responsibilities of the queen then become egg laying and engaging in policing or dominance behavior at the nest while workers take on duties such as foraging for prey, nest construction, gathering pulp, and gathering water (Pardi 1948). Colonies will then produce reproductive gynes and males before the declining period, during which reproductives depart from the nest to mate or overwinter and the nest is subsequently abandoned. There has been no reported evidence of perennial colonies to date (Yamane 1996). Nests in temperate and subtropical zones exhibit a high degree of annual synchrony, meaning that most nests at any given time of year will be in similar developmental stages, and each year new nests are built. Nests typically have a duration of 4.5 months in temperate zones (Yamane 1996) to 8 months in subtropical zones (Strassmann et al. 1988).

West-Eberhard (1969) gives a detailed account of differences between the life history of a temperate zone species, *Polistes fuscatus* and a tropical species *Polistes canadensis*.

Allowance of subordinate egg laying individuals to stay on the nest by queens in temperate species may be an adaptation helping to further the nest development when the nesting period length is reduced by seasonality. This same behavior is not observed in tropical *P. canadensis* queens, which aggressively cast out subordinate egg layers. Despite the fact that *P. canadensis*

occurs in a tropical environment with warm temperatures year round, nests do not last for multiple years. Instead, they exhibit asynchronous development, with nests representing all developmental stages occurring at any given time. New nests are most often associated with declining mature nests, evidenced by observations made by West-Eberhard (1969) of queens on new nests having been marked on the declining nest or observed visiting the declining nest. One marked queen at a new nest visited a declining nest ten times in 5.5 hours, engaging in food solicitation and trophallaxis during each visit before returning to her own nest.

### 2.3 BIOGEOGRAPHY

Paper wasps have adapted to a wide range of climates and environments; the genus *Polistes* contains approximately 200 species and is cosmopolitan, occurring in both the New World and the Old World from tropical to cold temperate climates (Yamane 1996). *Mischocyttarus* occurs only in the New World, however this genus contains 245 mainly tropical species with only three species occurring in the temperate climates of North America (Silveira 2008). Recent phylogenetic studies suggest that historically, the genus *Polistes* arose in the tropics of the Old World. Species in North America have clear tropical origins and are monophyletic, having colonized the continent from South America (Santos et al. 2015). This is important in the understanding of behavioral evolution and adaptation, specifically that of monogyny in paper wasps. If the genus first evolved in a tropical setting, monogyny must not be a specific adaptation to temperate zone climates which has long been the predominant theory (Santos et al. 2015). Carpenter (1993) reports that social wasps may have evolved during the historical breakup of Gondwanaland, a supercontinent consisting of modern day South

America, Africa, and Australia. This provides more evidence that social wasps in modern day North America arose from tropical ancestors.

#### 2.4 SATELLITE NEST FORMATION

Satellite nesting is a phenomenon which has been observed in *Polistes exclamans*, *P. canadensis*, *P. instabilis*, and *P. fuscatus* where “queens or workers sometimes leave their original nest and start new nests nearby that must be joined by workers from the original nest if they are to succeed” (Strassmann 1981a). Strassmann examined the production of satellite nests and early males in *Polistes exclamans* in central Texas. These satellite nests were initiated near (0.15-11 m) the parental nest in the months of May through July. After worker emergence on a satellite nest, the queen will remain on the satellite leaving the main nest to be governed by an egg laying worker. Both satellite nest and early male production were theorized to be responses to high nest predation, parasitism, or queen mortality. Strassmann (1981a) also states that satellite nesting is most likely an adaptation to the long arid summers in Texas, which may cause falling leaves leading to exposed and predated nests. Page et al. (1989) studied satellite nests and reproductive plasticity in a population of *Polistes fuscatus* in Wisconsin, and found that satellite nests were governed by spring produced female offspring, never by alpha foundresses or spring queens. Their results also show a possible correlation between satellite nests and polydomous nests, or those consisting of multiple combs.

#### 2.5 USE AS BENEFICIAL INSECTS

Paper wasps are considered opportunistic predators which feed on a variety of prey species. Foragers have the ability to learn from past experiences and return to successful

locations or cues, i.e. odors, visible leaf damage, or landmarks and can thus be considered facilitative specialists which may repeatedly feed on one prey species (Richter 2000). *Polistes* wasps have been shown to be important as control agents for cabbage pests and other agricultural pests (Gould & Jeanne 1984). Significant weight gain and quality of cabbage plants were observed in plots foraged by *Polistes* compared with control plots. Stamp & Bowers (1988) showed that *Polistes* wasps have both direct and indirect effects on buck moth larvae by killing some and causing the surviving larvae to alter their behavior and feed in smaller groups closer to the base of the plant where only lower quality food is available. Lawson (1959) found that *P. exclamans* and *P. fuscatus* were responsible for more than half of the mortality observed in a population of tobacco hornworm caterpillars in North Carolina, and that placement of wooden nest boxes containing nests of these species at field sites often prevented economic loss of tobacco leaves (Rabb & Lawson 1957).

## 2.6 PREDATORS AND PARASITOIDS

There are many predators and parasitoids associated with the Polistinae which attack either the brood, the adults, or the whole nest. Of the whole nest predators, ants (*Crematogaster* spp.), birds, and mammals are the most common, while brood parasites include a wide variety of insects from Ichneumonidae to Crambidae (Strassmann 1981b). Strassmann gives a detailed account on such parasitoids in a population of *P. exclamans* in Texas. The sooty-winged *Chalcoela* is a moth in the family Crambidae which feeds on larvae and pupae in wasp nests; the adult moth lays eggs in wasp nests at night. Another brood parasite, a wasp in the family Eulophidae, infested over 60% of all nests in population with as many as 80 individuals eclosing from a single parasitized pupal cell in the *Polistes* nest. Ichneumonid wasps in the

genus *Pachysomoides* infested one fifth of all nests in the population. Oviposition behavior of *P. fulvus* has been previously observed by S. Nacko (pers. obs.) on an early stage *Polistes fuscatus* nest in Pennsylvania, the female parasitoids invading the nest and ovipositing onto cell walls during periods of absence when the foundress was foraging. Jeanne (1979) describes a moth in the family Teneidae which feeds on meconia as well as living wasp pupae in the nests of Brazilian *Polistes canadensis*. A study in Missouri revealed Pteromalidae, Elasmidae (now Eulophidae), Crambidae, and Ichneumonidae all emerged from nests of *P. exclamans* or *P. metricus* (Whiteman & Landwer 2000). Predators of adult wasps include robber flies in the family Asilidae as well as birds, while parasites include twisted-winged insects (Strassmann 1981b).

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## CHAPTER 3. OCCURRENCE OF POLISTINE WASPS IN SOUTHERN LOUISIANA

### 3.1 INTRODUCTION

There are only three genera of paper wasps in North America, two of which occur in Louisiana (Bugguide.net). *Mischocyttarus* is primarily a tropical wasp, with only three species occurring in the US and Canada; *Mischocyttarus mexicanus cubicula* Richards 1978 occurs in Cuba and the Bahamans, as well as in the US in Texas, Florida, and Georgia, and is the only representative of this genus known to occur east of Texas (Hermann & Chao 1984b). However it was previously unknown from Louisiana; Hermann et al. (1985) searched for it in Louisiana in the summer of 1984 but could not find it. The first available records in the state come from the Louisiana State Arthropod Museum in 1991 (collected in Assumption Parish) and 2003 (St. Tamany Parish), with additional records in 2009 (Orleans Parish) and 2016 (St. Mary Parish) from Bugguide.net. In Lake Placid, Florida, it is known that this species will nest year round and utilizes primarily saw palmetto (*Serenoa repens*) leaves as a substrate and shelter for nest placement. In this location, the mean daily temperature for December was 17° C and mean daily temperature for July was 28° C (Litte 1977). This compares to Baton Rouge weather mean temperature of 11.8° C in December and 28.3° C in July (Anonymous 2017a). In more northern parts of its range, *M. mexicanus* overwinters like other temperate-zone paper wasps (Hermann & Chao 1984a). Hermann & Chao (1984b) described the nesting habits of *M. mexicanus* in a more northern location on Sapelo Island, Georgia, and noted that a three to four month overwintering period was necessary, however the authors did not report where the wasps spent this quiescent period. Contrary to reports of nests being found primarily on saw palmetto

by Litte (1977), nests on Sapelo Island were found only on cabbage palm (*Sabal palmetto*) and on wooden or metal frames of manmade structures, despite the fact that saw palmetto also occurs on Sapelo Island.

*Polistes*, the second paper wasp genus found in Louisiana, includes 8 different species in the state; these are *exclamans*, *dorsalis*, *fuscatus*, *metricus*, *bellicosus*, *annularis*, *carolina*, and *dominula* (Bugguide.net, 2016). *Polistes bahamensis* is also thought to occur in Louisiana (Pers. Communication from Matthias Buck). In environments where many species occur, I am interested in examining nest site usage in urban and suburban habitats in order to better understand the nesting biology of these wasps and provide information for potential mitigation or encouragement of wasp habitat in a particular area.

In this study, I examined height from ground level, nest attachment substrate, abundance, direction, and nest site light intensity for each species, as well as abundance and overwintering behavior in the recently arrived species, *Mischocyttarus mexicanus*. I hypothesize that partitioning of nests sites occurs among the species.

### 3.2 MATERIALS AND METHODS

This study took place from September 2015 through February 2017. Study sites encompassed the area of Baton Rouge including Bluebonnet Swamp (30°22'11.6"N 91°06'16.1"W), Burden Research Station (30°24'30.6"N 91°06'20.6"W), LSU Reproductive Biology Center (30°16'19.5"N 91°05'59.1"W), and LSU main campus (30°24'52.4"N 91°10'37.9"W). These sites represent a variety of habitats found in suburban settings; Bluebonnet Swamp is comprised largely of native swampland and woodland immediately

surrounded by an urban setting. LSU Reproductive Biology Center consists of open grass fields, farmland, and native woodland. Burden Research Station consists of both upland and lowland trees along with ornamentals and suburban areas, and LSU main campus is largely suburban. To locate as many nests for study as possible, areas were systematically searched for nests in the springtime when paper wasp nests were beginning and throughout the summer. Searches were conducted preferably on warm and sunny days, with search increments of 3-4 hours each day. Areas for visual search included sheltered sites such as palm fronds, picnic shelters, eaves of buildings, as well as low shrub vegetation. Wasps were also occasionally observed flying directly into a specific location, leading to the discovery of a nest in that manner. In addition to visual searching, LSU Residential Life's work order system, Maximo®, contained reports of paper wasp nests on or near student housing which were utilized.

Upon discovery, each nest was assigned a number, and its location, species, attachment substrate, height, and direction (when applicable) were recorded. Species identifications were made primarily by S. Nacko using the key to *Polistes* in Buck et al. (2008), with the aid when needed of Dr. Matthias Buck at the Royal Alberta Museum (Edmonton, Canada). Heights were measured with a Bosch 100ft laser measurer (Walnut Ridge, Arkansas), placed flat at ground level below the nest. Light intensity was used as a measure of relative exposure of a nest site, and along with temperature, was recorded weekly at each nest site until the nest became abandoned; these recordings were made with an Onset HOBO® UA-002 Pendant Temperature Light Data Logger (Bourne, MA 02532). Plant identifications were made with the aid of Dr. Robert Mirabello at the LSU School of Plant, Environmental and Soil Sciences. Voucher specimens of each species were deposited in the Louisiana State Arthropod Museum.

To analyze trends in wasp nest height data (n=169), Proc Mixed was utilized on the program SAS®, followed by Tukey’s Test ( $\alpha < 0.05$ ) to determine significant differences.

### 3.3 RESULTS

In my preliminary investigation the most frequently encountered on the LSU campus from August through December of 2015 were *P. bellicosus* and *P. fuscatus*, with *P. dorsalis*, *P. metricus* and *P. exclamans* being less abundant and *P. annularis*, *P. carolina*, and *P. dominula* absent altogether. By the end of 2016 a total of 319 nests were located, with the order of species from most to least commonly encountered as follows: *P. bellicosus* (93) > *M. mexicanus* (66) > *P. dorsalis* (61) > *P. fuscatus* (38) > *P. metricus* (24) > undetermined (19) > *P. exclamans* (17) > *P. annularis* (1). No *Polistes carolina*, *dominula*, or *bahamensis* were encountered at study sites. A single nest of *P. annularis* was found at LSU main campus in 2016, otherwise this species is not represented in our study. Species were “undetermined” in instances where single females were only observed once, making identification more ambiguous. As a nest attachment substrate, *Sabal palmetto* was the most frequently used plant species, and was used by the highest number of wasp species (Table 3.1). *P. bellicosus* utilized the greatest number of plant species, constructing nests on 9 different plants. Painted wood was the most frequently used non-plant substrate; however metal was the only substrate which all wasp species utilized (Table 3.2). Results from nest height data analysis show two significantly different groupings ( $F_{(5, 163)} = 10.2, P < .0001$ ) ; on average the higher nesting species (*P. exclamans*, *P. fuscatus*, *P. bellicosus*) with means between 257 – 360 cm, and on average the lower nesting species (*M. mexicanus*, *P. dorsalis*, *P. metricus*) with means between 161 – 176 cm (Figure 3.1).

Table 3.1. Plant species utilized as Polistine nest sites. Numbers in parenthesis indicate the number of nests of that species.

Plant Species	Number of Nests	Wasp Species
<i>Sabal palmetto</i>	75	<i>bellicosus</i> (35), <i>mexicanus</i> (30), <i>metricus</i> (6), <i>dorsalis</i> (4)
<i>Sabal minor</i>	27	<i>mexicanus</i> (16), <i>dorsalis</i> (9), <i>bellicosus</i> (1), <i>metricus</i> (1)
Undetermined	16	<i>bellicosus</i> (11), <i>mexicanus</i> (4), <i>fuscatus</i> (1)
<i>Livistonia chinensis</i>	7	<i>mexicanus</i> (6), <i>exclamans</i> (1)
<i>Juniperus</i> sp.	6	<i>bellicosus</i>
<i>Chaemerops humilis</i>	3	<i>bellicosus</i>
<i>Tachycarpus fortunei</i>	2	<i>mexicanus</i> , <i>metricus</i>
<i>Nandina domestica</i>	2	<i>bellicosus</i>
<i>Ilex vomitoria</i>	1	<i>mexicanus</i>
<i>Serenoa repens</i>	1	<i>exclamans</i>
<i>Azalea</i> sp.	1	<i>bellicosus</i>
<i>Loropetalum</i> sp.	1	<i>bellicosus</i>
<i>Musa</i> sp.	1	<i>metricus</i>
<i>Celtis laevevata</i>	1	undetermined
<i>Cycas revoluta</i>	1	<i>bellicosus</i>

Table 3.2. Other substrates utilized as Polistine nest sites. Numbers in parenthesis indicate the number of nests of that species.

Substrate	Number of Nests	Wasp Species
Painted Wood	53	<i>dorsalis</i> (20), <i>fuscatus</i> (11), <i>bellicosus</i> (9), undet. (6), <i>metricus</i> (3)
Metal	35	<i>fuscatus</i> (8), <i>metricus</i> (7), <i>dorsalis</i> (7), <i>bellicosus</i> (5), <i>exclamans</i> 3), <i>mexicanus</i> (2), undet. (2), <i>annularis</i> (1)
Non-painted Wood	22	<i>fuscatus</i> (9), <i>metricus</i> (5), <i>dorsalis</i> (2), undet. (3), <i>mexicanus</i> (2), <i>bellicosus</i> (1)
Cement	9	<i>exclamans</i> (5), <i>dorsalis</i> (2), <i>fuscatus</i> (1), undet. (1)
Painted Cement	8	<i>bellicosus</i> (4), <i>exclamans</i> (2), <i>metricus</i> (1), <i>fuscatus</i> (1)
Plaster	6	<i>dorsalis</i> (2), <i>exclamans</i> (1), <i>fuscatus</i> (1), undet. (2)
Plastic	4	<i>dorsalis</i> (3), <i>fuscatus</i> (1)
Re-Used Nest	2	<i>dorsalis</i> (2)
Glass	1	<i>mexicanus</i>
Rubber	1	<i>bellicosus</i>
Old Polistes Nest	1	<i>fuscatus</i>

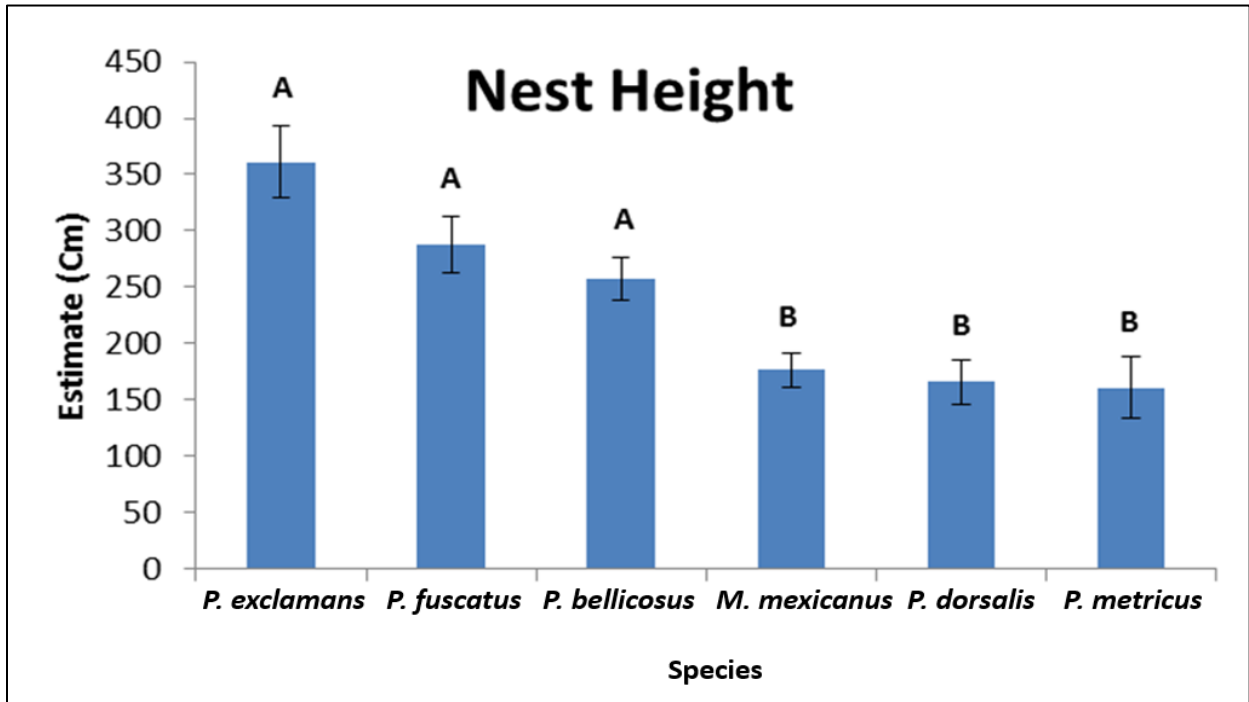


Figure 3.1. Mean heights for Polistine nests in southern Louisiana. Different letters above bars indicate significant differences.

Substrates that each species nested on varied; Of the species in the higher mean group, *P. exclamans* utilized cement (30%) most frequently, *P. fuscatus* utilized unpainted wood most frequently (45%), and *P. bellicosus* utilized palmetto leaves (73%) most frequently (Figure 3.2). Similarly, in the “low” nesting species *M. mexicanus* utilized palmetto leaves most frequently (90%), *P. metricus* utilized palmetto leaves (30%) and metal (30%) equally, and *P. dorsalis* utilized painted wood (33%) most frequently (Figure 3.3). *M. mexicanus* was strongly associated with ornamental plantings of *Sabal palmetto* (n=30) or other palmettos including *Sabal minor* (16), *Livistonia chinensis* (6), and *Tachycarpus fortunei* (1); other substrates utilized for nest attachment included metal (2), unpainted wood (2), glass (1), and one *Ilix vomitoria* branch.

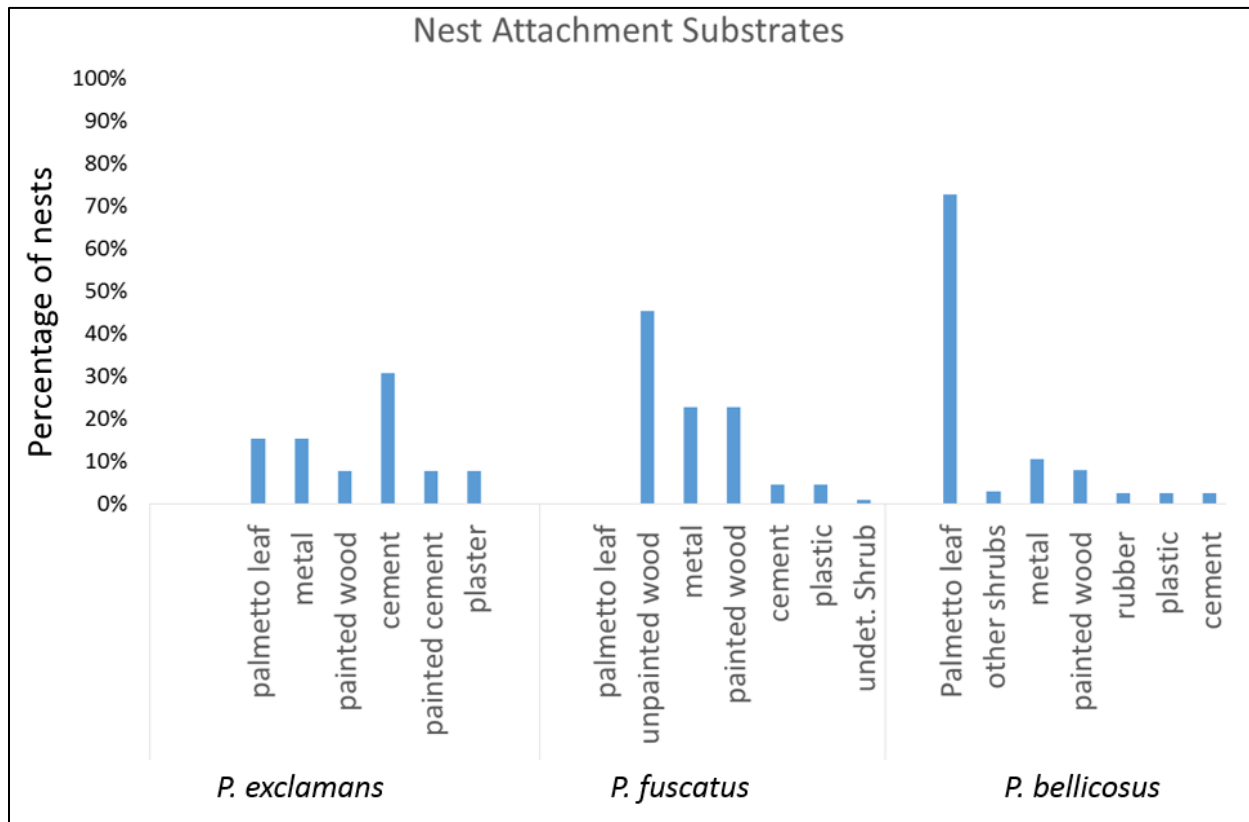


Figure 3.2. Percentage of nests per substrate in higher nesting species



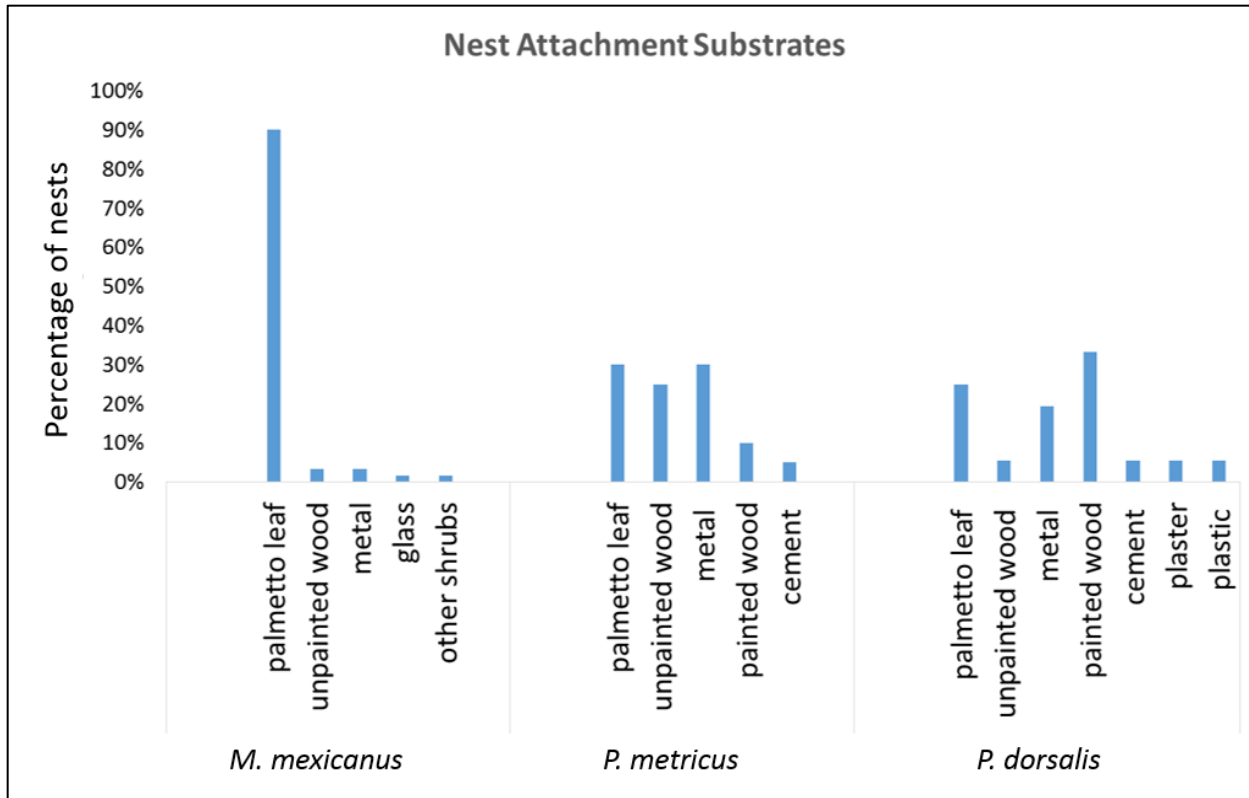


Figure 3.3. Percentage of nests per substrate in lower nesting species.

During the span of this project, three interactions were observed between species at nest sites. During one such encounter between a wandering female of *P. fuscatus* and a small nest of *P. dorsalis*, aggressive posturing was displayed in all individuals (n=5) but no physical contacts occurred (Figure 3.4).



Figure 3.4. Interaction between *Polistes fuscatus* (left) and *Polistes dorsalis* (right).

*M. mexicanus* nests were rarely found on substrates other than palmetto leaves, and at sites where *Sabal palmetto* was not found, the species was less abundant; we found only 1 nest at LSU Reproductive Biology Center, and 10 nests at Bluebonnet Swamp. Compared with 24 nests found on LSU main campus and 31 at Burden Research Station, sites where *S. palmetto* is abundant in the landscaping. One *M. mexicanus* nest built on a leaf of *S. palmetto* was observed from November 2015 through March 2016, with approximately 12 individuals remaining on the nest throughout that time period. Other observations of nests from the summer of 2016 through February of 2017 were similar, with clusters as large as 20 individuals remaining on nests throughout the winter months (Figure 3.5). None of the *Polistes* in this study, all temperate species, were observed overwintering on natal nests.



Figure 3.5. Overwintering cluster of *Mischocyttarus mexicanus* on natal nest.  
15 Dec 2016

In our study, 30% of *P. fuscatus* nests were located inside sheltered locations such as a crawlspace or attic in which the light intensity was between 1 and 40 lumens/ft<sup>2</sup> at the time of recording (n=11). Only 12% (n=3) of *P. metricus* nests were observed in this type of setting and light intensity, and 9.8% (n=6) *P. dorsalis*. No nests of *P. bellicosus*, *P. exclamans*, or *M. mexicanus* were found in enclosed spaces. Out of 319 total nests we observed, 98 were located in a compass direction (i.e. on a building face or side of a plant). Of these, 67% were facing easterly, either northeast (n=35) or southeast (n=31) (Figure 3.6).

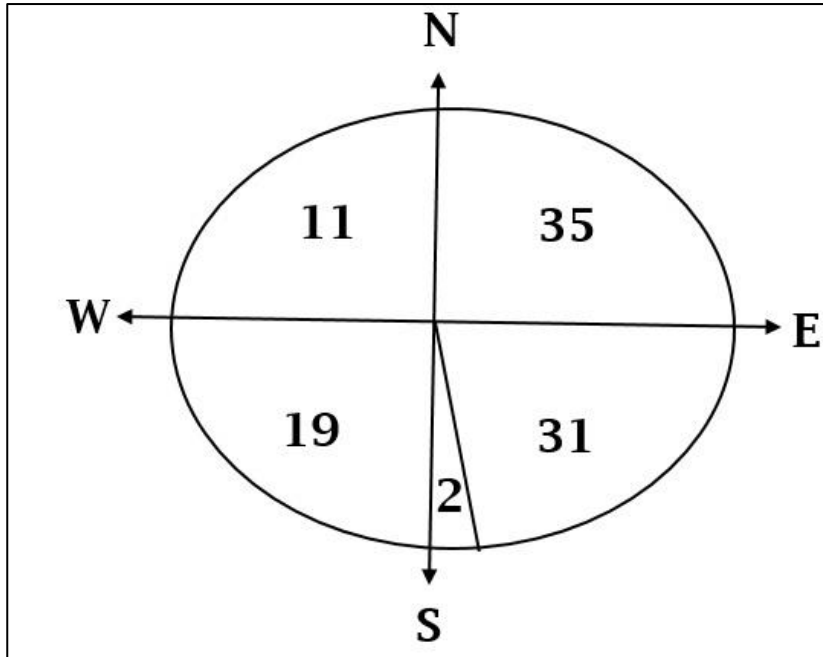


Figure 3.6. Orientation of nests located in a compass direction. Numbers represent the number of nests located in that direction.

### 3.4 DISCUSSION

#### 3.4.1 Nest site partitioning and species abundance

Nest site selection has been shown to be an important aspect of nest survival, with nests hidden from view having greater survival than those that are exposed (Reed & Vinson 1979). Nest site availability is thought to regulate the population size of *Polistes* in a given area (Reed & Vinson 1979), making interspecies competition for nest sites an important factor when the nesting cycle is just beginning. In an environment where many paper wasp species occur, interspecies preferences for height, light intensity, and attachment substrate may help to reduce competition for nest sites. Our results suggest that niche partitioning may occur between these species. Statistical analysis of nest height measurements for each species in our population reveals a group of higher nesting species and a group of lower nesting species.

Additionally, use of nest attachment substrates varied between species within each group, evidenced in two of the higher nesting species *P. bellicosus* and *P. fuscatus*, where the latter was not found on the most frequent substrate of the former. Perhaps the strongest evidence for niche partitioning in our study occurred in the case of *P. bellicosus* and *M. mexicanus*, two species occurring frequently on the same substrate (palmetto leaves). Santos & Presely (2010) state that species which share environmental resources must achieve a partitioning of these resources in order to maintain sustainable populations, often evidenced by the evolutionary pathways of species. Despite utilization of the same nesting substrate, a difference in heights can be observed with *P. bellicosus* having an average height of 257 cm and *M. mexicanus* of 176 cm. *M. mexicanus cubicola* shares its entire United States distribution with all of the *Polistes* species discussed in this study. *P. bellicosus* is primarily a coastal species occurring from Texas, eastward throughout the gulf coast states and into Long Island NY (Buck et al. 2008). In terms of nest site usage, fulfilling niches at different heights would indeed aid in the coexistence of these two primarily coastal species, and would explain the lack of *P. bellicosus* and *M. mexicanus* nests in proximity to one another during this study.

Light intensity is suspected to be a factor in the selection of nest sites by *Polistes* wasps (Reed & Vinson 1979). *P. fuscatus* nested more readily than *P. metricus* or *P. dorsalis* inside of cavities or enclosed spaces with low light intensities, while *P. bellicosus*, *P. exclamans*, and *M. mexicanus* always nested in the open or partially concealed sites. Similar findings from a study in Texas where low light intensities were favored by *P. carolina*, moderate light intensities by *P. metricus*, and high intensities by *P. exclamans* (Reed & Vinson 1979) support the hypothesis that light intensity is a determining factor for nest site selection in some Polistine species. Being

primarily a northern temperate species, *P. fuscatus* is well adapted to the seasons throughout much of eastern North America (West-Eberhard 1969). In this region leafy vegetation is most often temporary and deciduous, with leaves on most plants only lasting the summer. Nests in sheltered sites such as cavities may have a selective advantage over those attached to vegetation which would provide poor protection from predators and weather conditions during late summer or fall. In subtropical and warm temperate areas, vegetation with perennial leaves (such as the palmettos) is more common, and this niche appears to be already occupied by *P. bellicosus*, *M. mexicanus* and *P. dorsalis*. Similar to results from Reed & Vinson (1979), *P. metricus* nests did not demonstrate any striking patterns of nest site substrate or light intensity, and were found in a variety of sites including both palmetto leaves and sites with low light intensity. Therefore *P. metricus* may be considered an opportunistic species with regards to selection of nest site substrate and light intensity. Factors in nest site selection may have developed evolutionarily both as a response to environmental conditions and interspecies competition.

*P. bellicosus*, *P. dorsalis*, and *M. mexicanus* were the most abundant species in our study. Although *P. annularis* was commonly observed in West Feliciana and Rapides Parishes (pers. obsv.), it was poorly represented during our study, perhaps indicating a lack of sufficient habitats at suburban study sites. It has been reported that this species forages mainly in wooded areas, whereas *P. fuscatus* and *P. exclamans* forage mostly in vegetation of open fields (Rabb 1960). This may explain the absence of *P. annularis* at study sites in Baton Rouge and St. Gabriel LA.

### 3.4.2 *Mischocyttarus mexicanus cubicola* abundance in Baton Rouge

The native range of *Sabal palmetto* includes Cuba, the Bahamas, most of Florida, and the coastline of Georgia and the Carolinas (Deelen & Timothy 1991). This distribution strongly coincides with that of *M. mexicanus* (Hermann & Chao 1984b). *S. palmetto* is not native to the state of Louisiana, though there are small naturalized populations near Lake Charles and New Orleans (Landry & Reese 1996). However most specimens elsewhere in the state are the direct result of landscape architecture. In our study, *S. palmetto* was the most frequently used nesting substrate (n=30, 45%) for *M. mexicanus*. In addition to this, *M. mexicanus* nests were in the low height category, and nests were not found on trees where lower leaves had been previously removed by landscapers. *Sabal palmetto* is widely used in ornamental and landscape plantings (Immel 2001), and is a common plant on LSU main campus. A similar species, *Sabal minor*, is native to Louisiana and is often found in sandy pine forest (Landry & Reese 1996). This plant is less common on LSU campus but could be found in abundance at LSU Reproductive Biology Center and Burden Research Station. Despite its relative abundance we saw only half as many nests of *M. mexicanus* on *S. minor* than on *S. palmetto*. Another native palmetto, *Serenoa repens*, was present in abundance at one of our study sites but contrary to findings from Litte (1977), no nests were observed on it. Our results are consistent with those of Hermann & Chao (1984), where nests on Sapelo Island, GA were found only on *S. palmetto*. The advantage of a strong association with one particular plant species as a nesting substrate is still unclear, however it has been proposed that *S. palmetto* leaves provide more effective protection from bird predation and wind (Hermann & Gonzalez 1985). It is clear that *M. mexicanus* occurs frequently in Baton Rouge, perhaps due to extensive usage of *S. palmetto* as a landscape plant.

The relative abundance of *M. mexicanus* during this study indicates that the species is well established in Baton Rouge and has gone unreported for some time. We provide the first record of this species from East Baton Rouge and Iberville Parishes, bringing the total to six parishes from which the species has been recorded in Louisiana. Range expansion by this tropical species into subtropical and temperate areas is intriguing. Alteration of nesting biology in order to survive in varying climates may allow this species to further expand its natural range in the United States. Our data coupled with the close overlap of species distribution patterns of both *S. palmetto* and *M. mexicanus* suggest that presence of *S. palmetto* may be important both for nesting and overwintering sites (in more temperate zones) for *M. mexicanus*, and species range expansion may be facilitated in areas where *S. palmetto* is present.

#### 3.4.3 Recommendations for encouragement/discouragement in suburban settings

Based on our findings, paper wasps in southern Louisiana and presumably in other such areas demonstrate niche partitioning with regards to nest sites, leading to patterns of wasp nest occurrence in suburban habitats. We can use these patterns of occurrence to encourage wasps in areas where we desire them as beneficial predators, or discourage them in areas of potential conflict. It is already known that placement of wooden nest boxes containing nests of *P. fuscatus* and *P. exclamans* at field sites can prevent economic loss of leaves in tobacco (Rabb & Lawson 1957) and cabbage (Gould & Jeanne 1984) fields. In these cases the wasp colonies were brought in to an existing field, however it may be more feasible to create pre-existing nest sites at field locations in order to eliminate the need of transporting colonies. Incorporating aspects such as height, substrate, and light intensity into considerations when creating suitable nest sites, some possible modifications to field sites can include plantings of *Sabal palmetto* and



*Sabal minor*, placement of screened nest boxes, and construction of metal roof or wooden eaves in order to encourage a diversity of species to start colonies.

Our data also demonstrate that nests located in a compass direction were most often facing easterly. Smith (2004) found no directionality of nests in a population of *Mischocyttarus collarellus* from Brazil, however insufficient data may have hindered trends during that study. An easterly direction would provide exposure to sunlight during morning hours, whereas a westerly direction would expose nests to afternoon sunlight (Smith 2004). Jeanne & Morgan (1992) have demonstrated that thermal properties are an important factor in nest site selection by temperate *Polistes*, with foundresses choosing warmer nest sites in the springtime to facilitate nest development. An easterly orientation could provide sufficient warm temperatures for wasps during morning hours, while shielding them from sunlight during periods of high temperatures during summers in southern Louisiana. The highest temperature recorded during this study was 37.3° C in the shade on 30 August and 22 September 2016, with the record high for Baton Rouge being 40.5° in August of 2000 (Anonymous 2017). The critical thermal maximum for *P. dominula* is 47.1° C, however wasps attempt thoracic thermoregulation at 37° (Kovac et al. 2016).

Open eave shelters or nest box entrances should be oriented easterly in order to maximize thermal properties and further encourage wasp nest initiation and survival at desired locations. In the opposite sense, patterns of occurrence can be utilized in management of unwanted wasp populations in suburban areas where wasps may come into contact with humans. In our study 32% of all wasp nests were built on *Sabal palmetto* or *Sabal minor*, which

were utilized by four different Polistine species at varying heights. Bearing this in mind during landscaping architecture, placement of ornamental palmettos farther from human traveled paths or in areas not frequented by the public could help reduce human-paper wasp conflicts. Removal of lower leaves on *S. palmetto* trees may discourage lower nesting species and keep higher nesting species at a safer height where conflicts are less likely to arise.

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## CHAPTER 4. PHENOLOGY OF POLISTINE WASPS IN SOUTHERN LOUISIANA

### 4.1 INTRODUCTION

Phenology can be defined as the study of cyclic phenomena, the relationship between species activity patterns and climatic conditions (Anonymous 2017a), or adaptations which allow proper timing of the biological activities of a species with relation to annual environmental cycles (Tauber et al. 1986). Many species in temperate zones exhibit phenological patterns of nesting activity, and paper wasps are no exception. The stages of colony development in *Polistes* are uniform throughout temperate and tropical zones, and include the pre-emergence phase, post-emergence phase, reproductive phase, and intermediate phase (West-Eberhard 1969). What differs then between the two climatic zones is temperate nesting synchrony among nests at a particular time of year. Nests of Polistinae in temperate zones are best known to be annual, meaning that each spring a new nest is built (West-Eberhard 1969). The typical biology of paper wasps in North America predicts the foundation of nests and production of workers to occur when day length is increasing in the Spring (April or May), and the production of reproductive individuals coupled with colony decline/abandonment during day length decreasing periods (August – October) (West-Eberhard 1969). Most, if not all, insects possess the ability to perceive environmental cues, often photoperiod or temperature, which signal a changing of the seasons consequently leading to a physiological or behavioral changes in the insect. Photoperiod, temperature, and food availability are important cues which mediate specific events in the lifetime of temperate zone *Polistes* (Tauber et al. 1986). It has been shown that foundress egg production in *P. chinensis* is

largely that of unfertilized haploid eggs under short day conditions, but returns to fertilized diploid eggs under long day conditions. Thus photoperiodic information must be accumulated by the egg laying foundress, much as it is by diapause induced gynes (Tauber et al. 1986).

According to the Köppen climate classification system, Baton Rouge Louisiana has a climate classified as “humid subtropical”, with an average temperature of 19.3° C and rainfall of 1526 mm each year (Anonymous 2017b). Nests in subtropical zones generally demonstrate longer nesting periods (6 to 8 months) than nests at high altitudes but still display annual synchrony (Yamane 1996). In tropical species the annual synchrony of the nesting cycle is lost; nests undergo the same developmental stages and last about the same length of time as elsewhere, however there is no correlation between developmental stage and time of year (West-Eberhard 1986). Yamane (1996) posed the question of why *Polistes* nests in tropical zones still possess a determinate colony cycle if temperature is not a factor, and concluded the answer may come from other ecological factors (predation and parasitism) or phylogenetic constraints (absence of swarm founding, meconium extraction, and nest envelope) within the subfamily.

*Mischocyttarus* is a genus containing 245 mainly tropical species with only three species occurring in the temperate climates of North America (Silveira 2008). In Lake Placid, Florida, it is known that *M. mexicanus* will nest year round and does not display annual synchrony. However in more northern parts of its range, *M. mexicanus* overwinters like other temperate-zone paper wasps (Hermann & Chao 1984). Hermann & Chao (1984) described the nesting habits of *M. mexicanus* in a more northern location on Sapelo Island, Georgia, and noted that a three or

four-month hibernation period was necessary. The nesting biology of this species in Louisiana has not been noted, probably due to its relatively recent arrival in the state.

Here I investigated cyclic nesting patterns (or phenology) of Polistine species found in Baton Rouge and St. Gabriel Louisiana, areas with a humid subtropical climate, including temperate species of *Polistes* and a tropical/subtropical species of *Mischocyttarus*. I hypothesized that due to the lengthy warm season, the nesting cycle in this area becomes asynchronous during the summer months.

#### 4.2 MATERIALS AND METHODS

This study took place from September 2015 through February 2017. Study sites encompassed the area of Baton Rouge including Bluebonnet Swamp, Burden Research Station, LSU main campus, and LSU Reproductive Biology Center (St. Gabriel). To locate as many nests for study as possible, areas were systematically searched for nests in the springtime when paper wasp nests were beginning and throughout the summer. Because air temperature is a major factor affecting wasp activity (Elisei et al. 2008), searches were conducted preferably on warm and sunny days, with search increments of 3-4 hours each day. Areas for visual search included sheltered sites such as palm fronds, picnic shelters, eaves of buildings, as well as low shrub vegetation. Wasps were also occasionally observed flying directly into a specific location, leading to the discovery of a nest in that manner. In addition to visual searching, LSU Residential Life's work order system, Maximo®, provided reports of paper wasp nests on or near student housing which were utilized. Upon discovery, each nest was assigned a number, and its location and species were recorded. A nest was considered to be a "spring" nest if

initiation occurred before the summer solstice (June 20), or a “late season” or “fall” nest if initiation occurred after the solstice. Species identifications were made primarily by S. Nacko using the key to *Polistes* in Buck et al. (2008), with the aid when needed of Dr. Matthias Buck at the Royal Alberta Museum (Edmonton, Canada). Voucher specimens were deposited at the Louisiana State Arthropod Museum.

Weekly visits were made to each nest from time of discovery until nest abandonment in order to record number of adults, cells, and caps present during each visit. Behavioral observations, such as dominance interactions or movements between nests, were also recorded while visiting each nest. Use of a small handheld camera (Canon Powershot SX200 IS) aided data collection; macro photography with flash illuminated the contents of brood cells. To avoid being stung in cases of aggressive colonies, standard zoom was utilized to photograph nests and record data in a field notebook. The number of adults present during each observation was an estimate at best, often confined to the number of wasps visible on the face or periphery of the nest and excluding any which may be completely hidden on top of the nest. “Peak adults” for a given nest was defined as the highest number of adults observed on that nest over the full course of observations, as is similar to “peak caps” being the highest number of silken covered cells (or pupal caps) over the course of observations. Cell number was defined as the total number of cells, with or without cap remnants, per nest after abandonment. Failure in our case was defined as nest abandonment, orphanage, knockdown, or human caused fatality. A nest was considered abandoned once it contained no brood and no adult females. Abandoned nests were collected for further measurements in the laboratory. A nest was considered to be “multiple foundress” if more than one female was consistently recorded ( $\geq 2$ )

on the nest during the pre-emergence phase. Because eggs and larvae require adult care to survive (West-Eberhard 1969), we define colony duration as the length of time during which live eggs and/or larvae are present in the nest; pupae were not used in the calculation of duration. Rate of growth was determined by plotting number of cells over the course of the first 13 observations per nest in pre and early post-emergence nests. Temperature and light intensity were recorded weekly at each nest site with an Onset HOBO® UA-002 Pendant Temperature Light Data Logger (Bourne, MA 02532).

To analyze trends in cell, adult, cap, and duration data between spring and fall for each species, Proc Mixed was utilized on the software program SAS®. A Tukey's test ( $\alpha < 0.05$ ) was then utilized to determine where significant differences occurred. Sample sizes were not adequate of survived *P. fuscatus* and *P. exclamans* nests discovered at the time of spring initiation for analysis of colony duration. *P. exclamans* nests were not used in analysis due to lack of sufficient replicates.

#### 4.3 RESULTS

A total of 319 active paper wasp nests had been located by October 2016; the first recorded nest initiation of the year occurred on 3 March (*P. fuscatus*), with the last recorded initiation on 4 October (*P. fuscatus*). Of the total nests, 188 (or 58.9%) were spring nests while 131 (or 41%) were late season. The species most often observed on spring nests were *Mischocyttarus mexicanus* (n=59) and *Polistes bellicosus* (n=43), followed by *P. dorsalis* (n=28), *P. fuscatus* (n=17), *P. metricus* (n=15), and *P. exclamans* (n=13) (Figure 4.1). In comparison *P. bellicosus* (n=50) and *P. dorsalis* (n=33) were the two most often observed on late season nests,



followed by *P. fuscatus* (n=21), *P. metricus* (n=9), *M. mexicanus* (n=7), and *P. exclamans* (n=4) (Figure 4.2). Examining just *Polistes* and excluding *Mischocyttarus*, we find that 50.9% of nests were initiated in the spring and 49% in late season. Spring initiations began during the first week of March and reached a peak in April before declining in May and reaching a low point in June. A similar pattern was observed with initiations beginning again in July and reaching a peak in August before declining in September and reaching a low point in October (Figure 4.3). No nests were initiated during November-February.

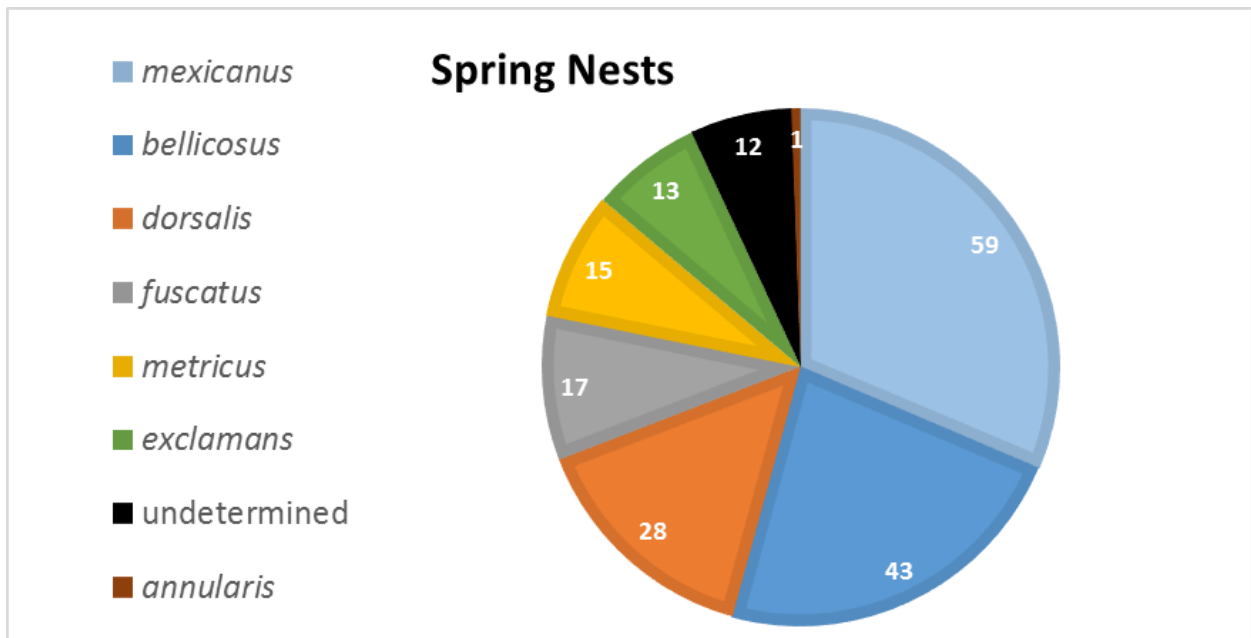


Figure 4.1. Proportion of spring nest initiations per species

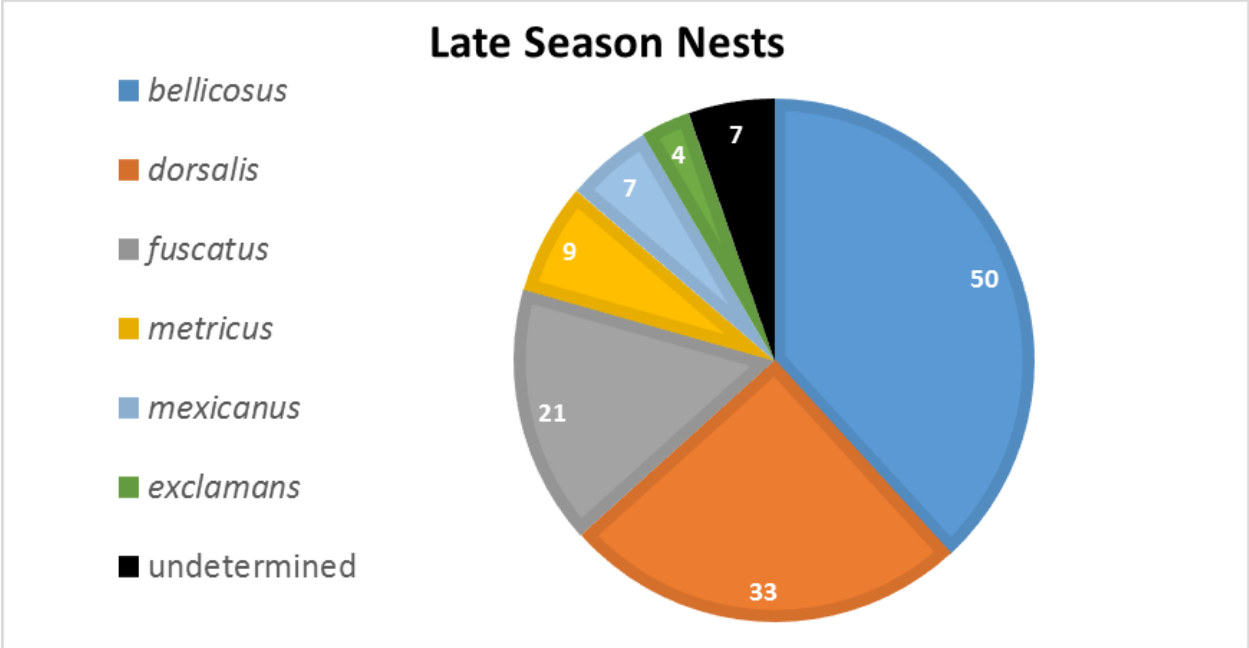


Figure 4.2. Proportion of late season nest initiations per species.

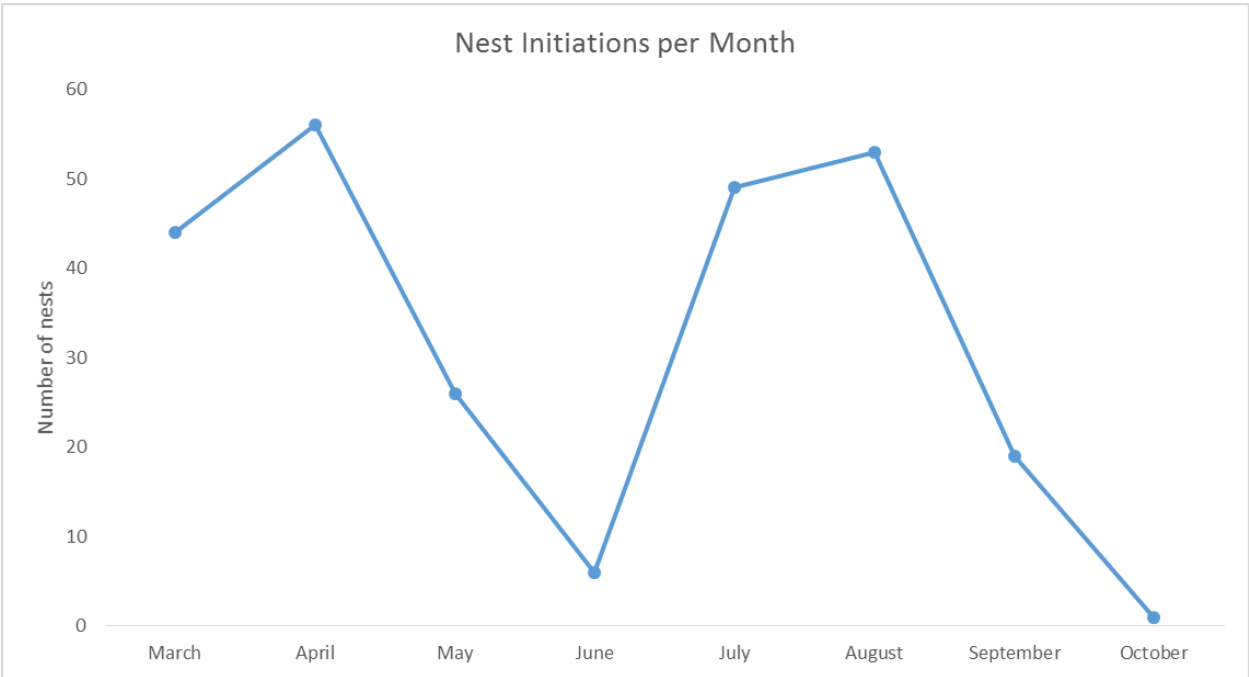


Figure 4.3. Nest initiations per month during 2016.

In a comparison of percentage of nests having a single versus multiple foundresses, two species (*P. metricus* and *P. exclamans*) were exclusively single foundress during the spring while others ranged from 35%-57% single foundress (Figure 4.4). Overall percentage of multiple foundress nests increased in late season nests of every species (Figure 4.5). *P. metricus* and *P. dorsalis* had 100% mortality of single foundress late season nests, whereas *P. bellicosus* had 66%, *P. fuscatus* 40%, and *M. mexicanus* 75% (Figure 4.6). Out of 139 total nests located by the end of June 68 (or 48.9%) had failed.

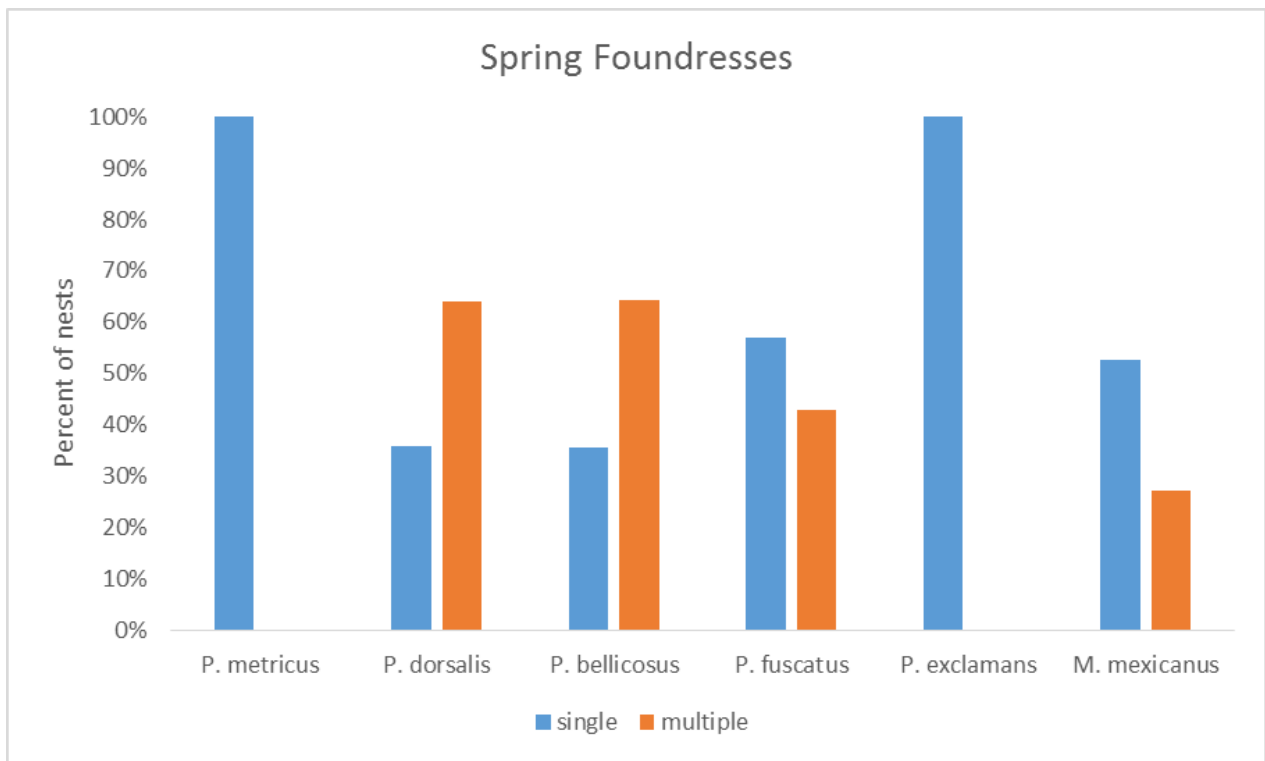


Figure 4.4. Percentage of spring nests having a single vs multiple foundresses

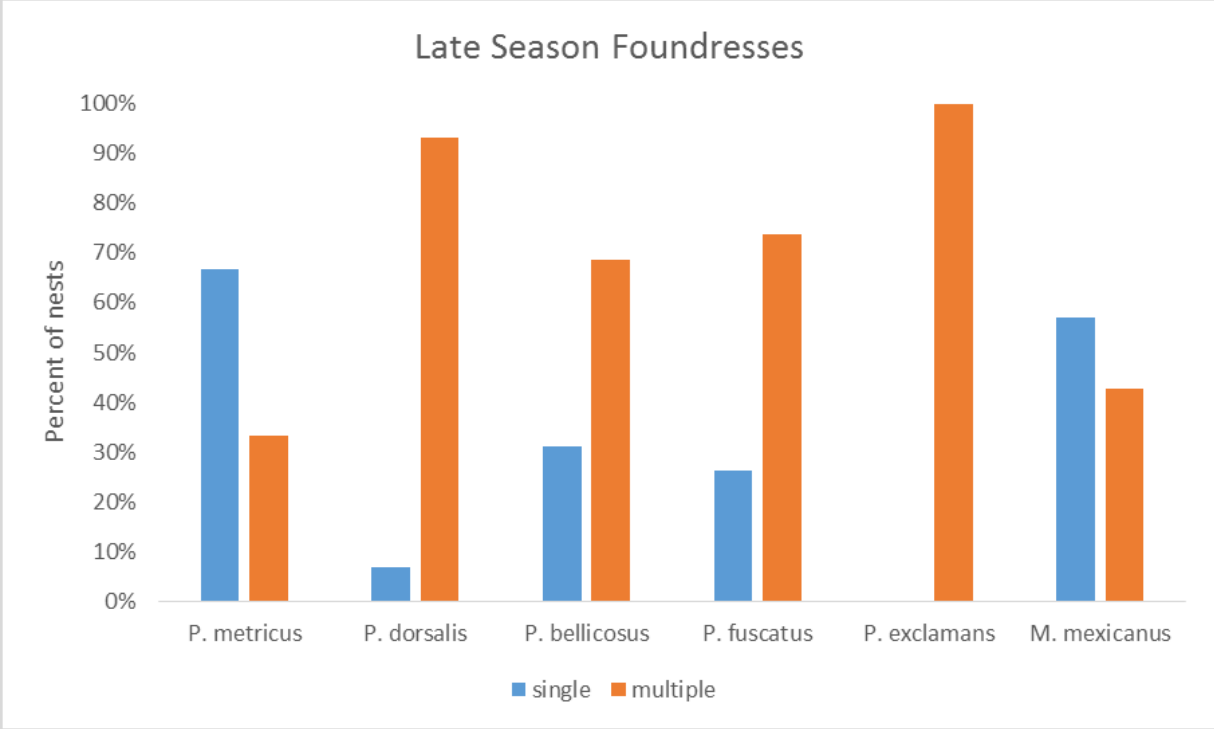


Figure 4.5. Percentage of late season nests having a single vs. multiple foundresses.

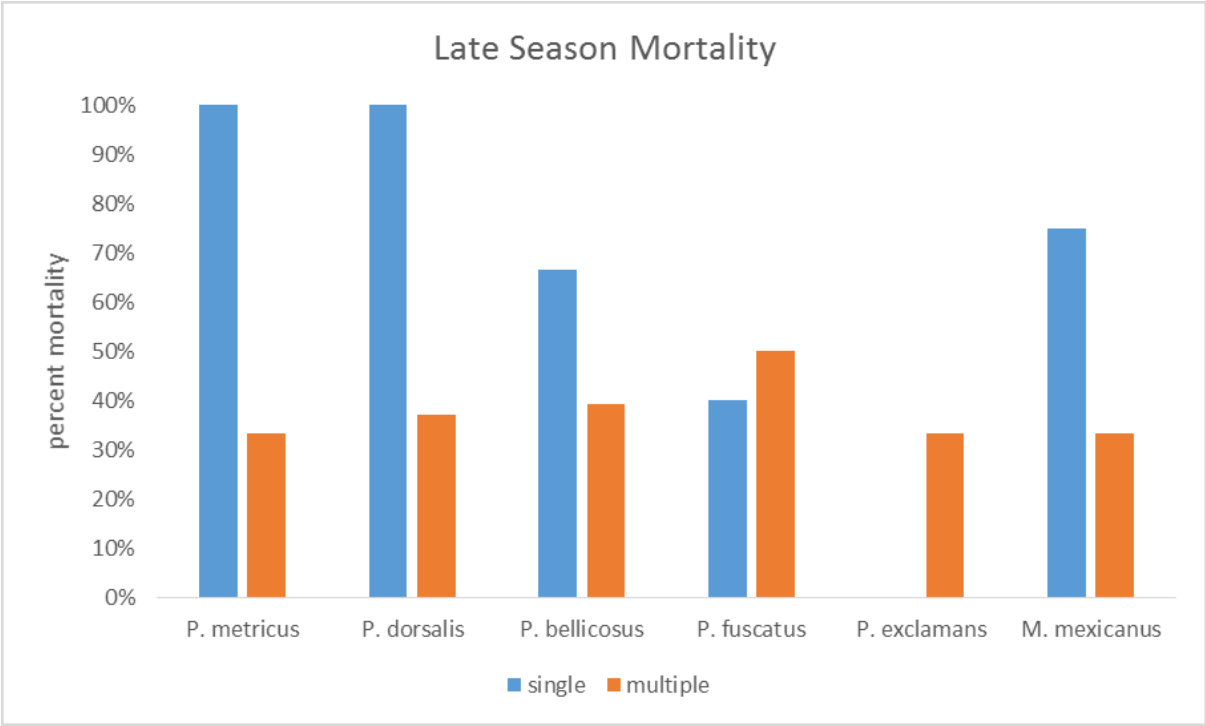


Figure 4.6. Percentage of late season nests having either a single or multiple foundresses which did not survive to produce at least one brood.

Sample sizes used in cell, adult, and cap data varied depending on species or season (Table 4.1). In late season nests, all species tested (*P. dorsalis*, *P. bellicosus*, *P. metricus*, and *M. mexicanus*) demonstrated a significantly shorter length of colony duration (defined as length of time eggs or larvae are present in the nest) than in spring nests. No significant difference in colony duration was observed among species in late season, however spring nests of *M. mexicanus* had a significantly longer colony duration than did *P. bellicosus* or *P. dorsalis* (Figure 4.7). Of a sample size of 34 total late season nests for which duration data were obtained, 23 nests had a duration less than 105d (d=days), and 14 of these reared multiple broods while 9 did not. Colony duration of late season nests from all species combined produced an overall mean of 87.6d for late season nests. Of the species tested for cells, adults, and caps (*P. dorsalis*, *P. bellicosus*, *P. fuscatus*, *P. metricus*, *M. mexicanus*) only *P. bellicosus* had significantly fewer adults at peak population in late season nests compared to spring nests. The only significant difference in adult number between species was in *P. dorsalis* and *P. metricus*, with *P. metricus* having significantly fewer adults at peak in spring nests (Figure 4.8). For mean cell number, *P. bellicosus*, *P. dorsalis*, and *P. fuscatus* had significantly fewer cells in late season than in spring nests, while *M. mexicanus* and *P. metricus* were fewer but not significantly so. *M. mexicanus* and *P. metricus* spring nests had significantly fewer cells than *P. bellicosus*, *P. dorsalis* and *P. fuscatus* (Figure 4.9). For mean number of caps at peak, *P. bellicosus*, *P. dorsalis*, and *P. fuscatus* exhibited significantly fewer caps in late season nests than in spring nests (Figure 4.10). No wasp species showed significant differences in rate of growth between spring and late season nest (Figure 4.11).

Table 4.1. Sample sizes of nests used in calculation of cell, adult, and cap averages for each species.

Species	Season	Sample size
<i>P. bellicosus</i>	Spring	13
<i>P. bellicosus</i>	Fall	17
<i>P. dorsalis</i>	Spring	11
<i>P. dorsalis</i>	Fall	14
<i>P. fuscatus</i>	Spring	10
<i>P. fuscatus</i>	Fall	9
<i>P. metricus</i>	spring	6
<i>P. metricus</i>	fall	2
<i>M. mexicanus</i>	spring	20
<i>M. mexicanus</i>	fall	3

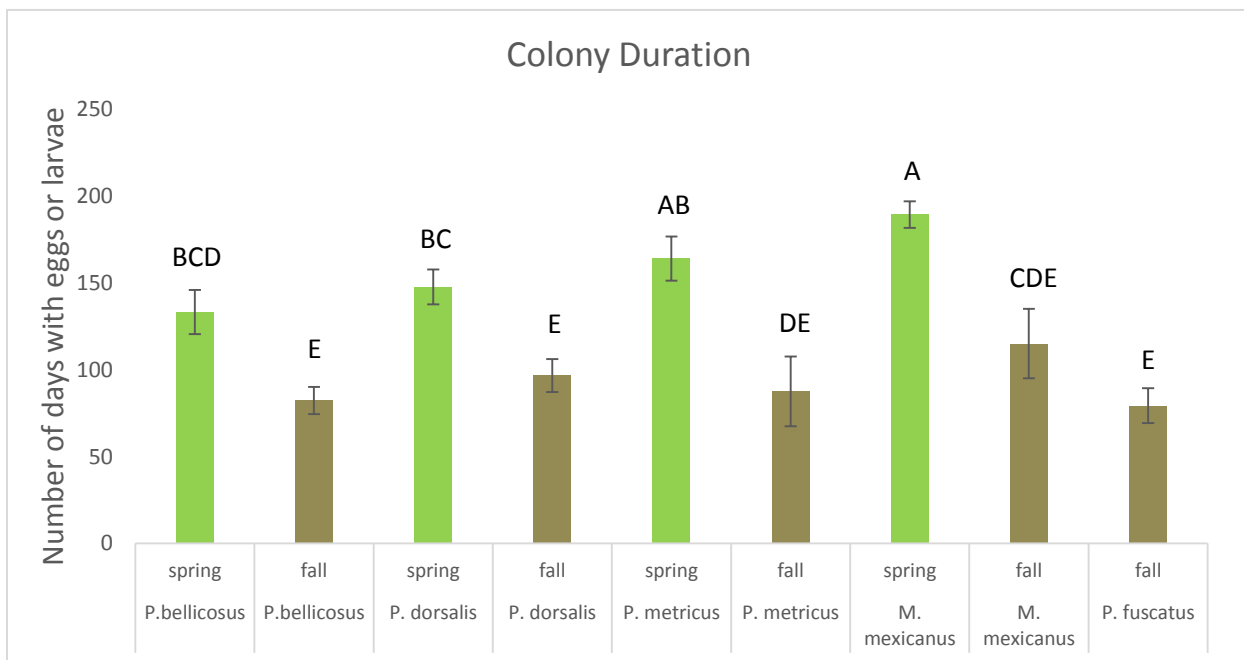


Figure 4.7. Average duration of brood rearing per species in spring and fall nests. Different letters indicate significant differences.

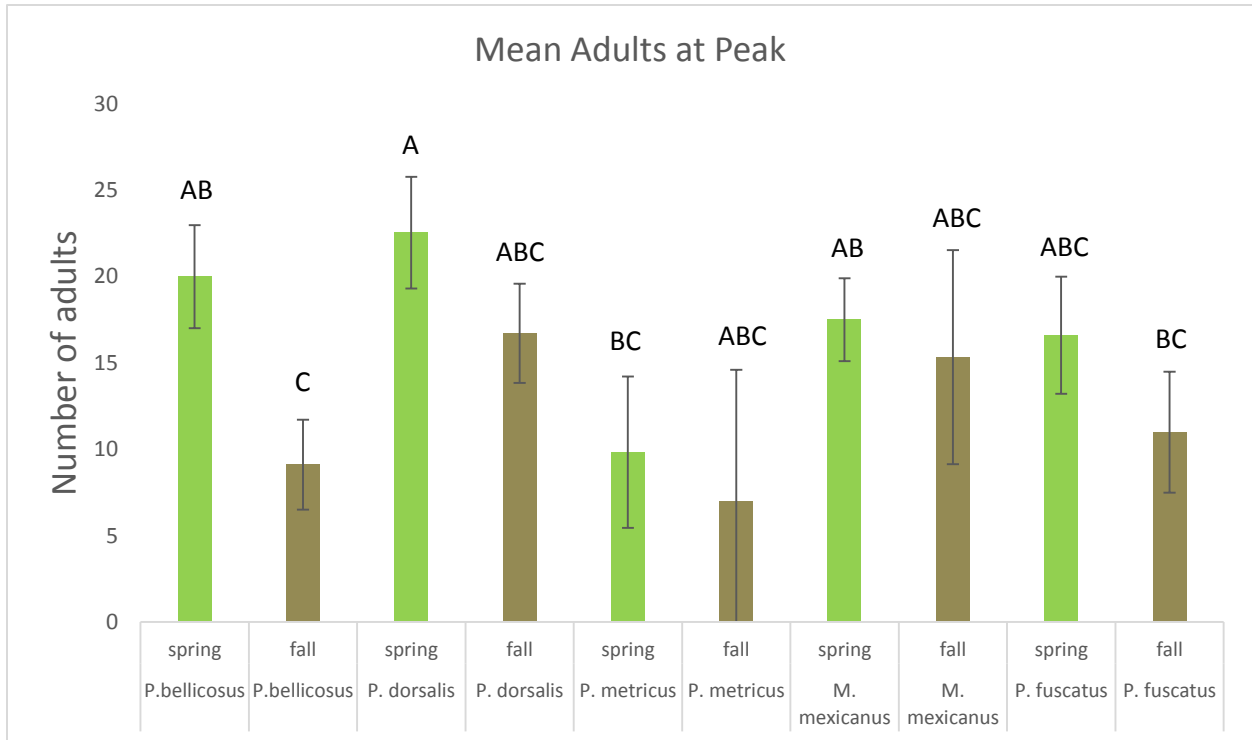


Figure 4.8. Average number of adults at peak per species in spring and late season nests. Different letters indicate significant differences.

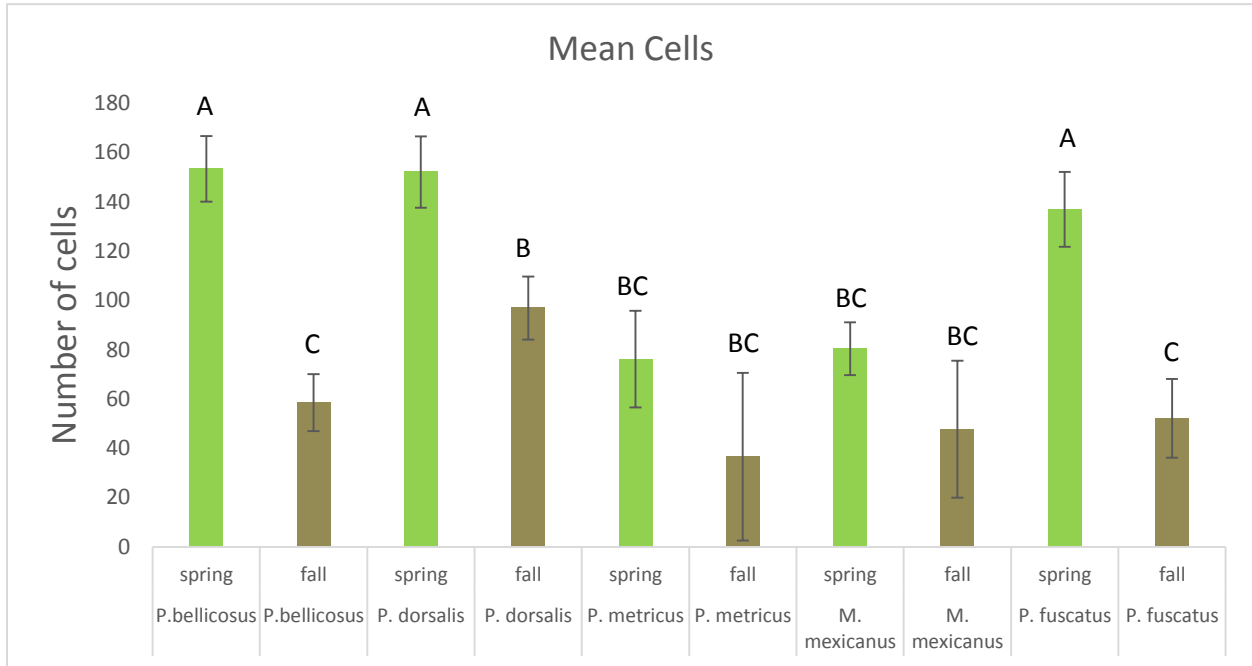


Figure 4.9. Average number of cells attained per species in spring and fall nests. Different letters indicate significant differences.

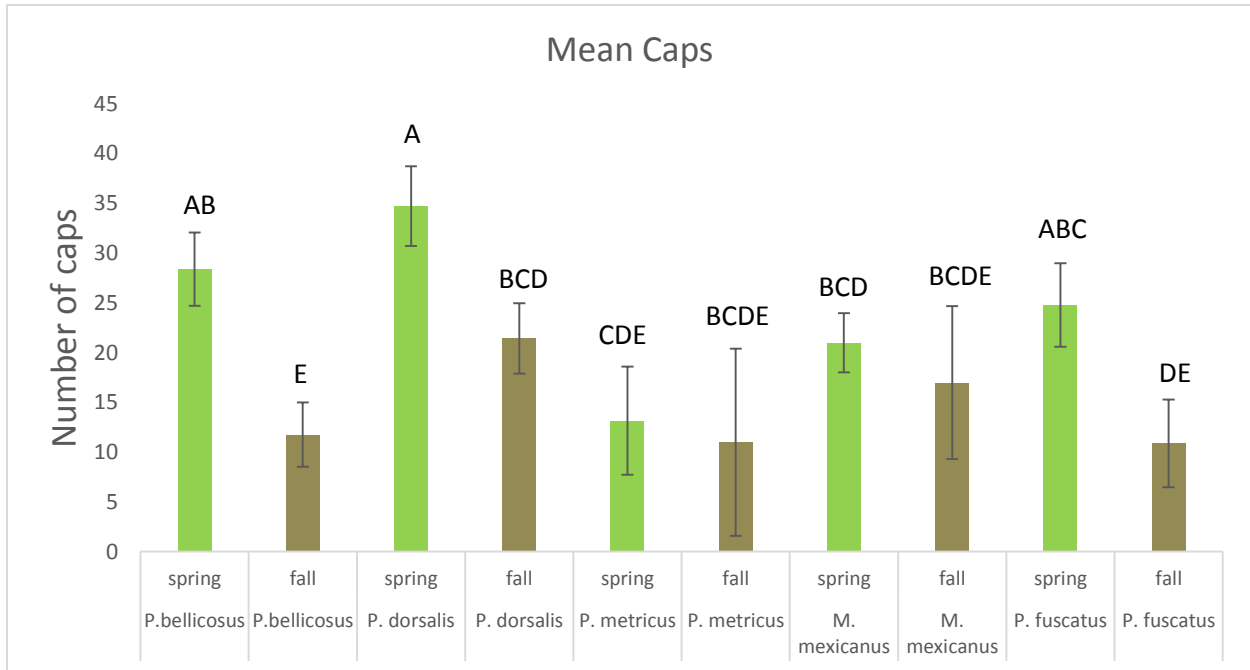


Figure 4.10. Average number of caps attained at peak per species in spring and fall nests. Different letters indicate significant differences.

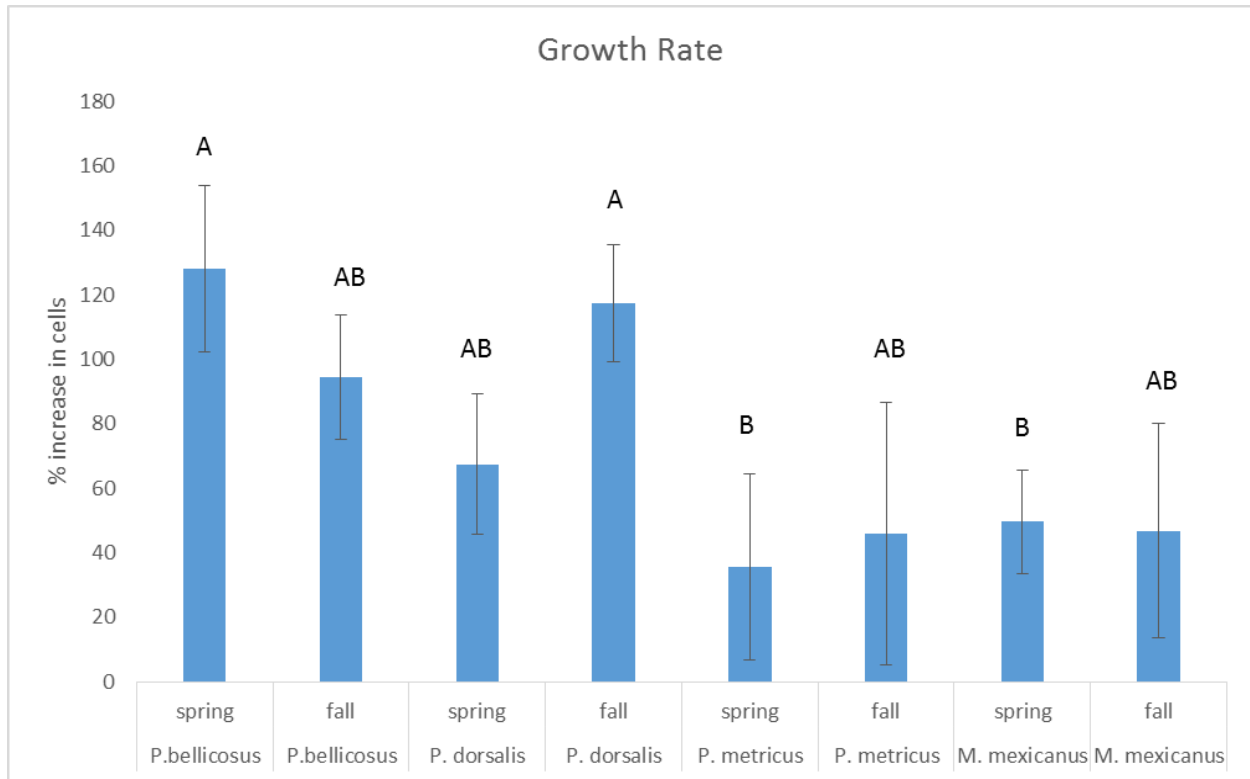


Figure 4.11. Average rate of growth as defined by percent increase in cells over the course of 13 observations per species in spring and late season nests. Different letters indicate significant differences.



Three species (*P. bellicosus*, *P. dorsalis*, *P. fuscatus*) had significantly fewer caps in late season: Only *P. bellicosus* had both fewer caps and fewer adults. The difference in peak adult number between spring and late season nests of *P. dorsalis* and *P. fuscatus* then was not significant, suggesting that despite their difference in caps, the highest number of adults eclosing from these nests during one time period was relatively equal to that of spring nests. Thus late season nests have an abbreviated or shortened nesting cycle with on average fewer cells and caps than spring nests.

Overall, *M. mexicanus* had the longest colony duration in both spring and late season nests, with a mean of 189d and a longest duration of 263d during the spring, and mean of 113d and longest duration of 130d during late season. *P. bellicosus* had the shortest colony duration of both spring and late season nests, with a mean of 133d and the longest duration of 148d during spring and mean of 82d and longest duration of 120d during late season. Overall, the longest duration for any late season nest was 130d (*M. mexicanus*), while the shortest was 47d (*P. bellicosus*) (Table 4.2). The highest adult number for both spring and late season nests was seen in *P. dorsalis*, with a mean of 23 and highest recorded number of 61 in spring nests, and mean of 17 and highest recorded number of 49 in late season. *P. metricus* had the lowest adult number in both spring and late season, with a mean of 9.3 and highest recorded number of 22 in spring nests, and a mean of 7 and highest recorded number of 11 in late season (Table 4.3). *P. bellicosus* had the highest mean cell number (n=153) in spring nests, and *P. dorsalis* had the highest in late season (n=96). *P. metricus* had the lowest cell number in both spring and late season nests, with a mean of 76 and highest value of 167 in spring nests and a mean of 37 and highest value of 57 in late season. The highest cell number attained for fall nests overall was

253 (*P. dorsalis*), while the lowest was 16 (*P. metricus* and *P. fuscatus*) (Table 4.4). The highest number of caps recorded in both spring and late season was seen in *P. dorsalis*, with a mean of 35 and highest number recorded of 103 in spring nests, and a mean of 21 and highest number recorded of 49 in late season (Table 4.5).

Table 4.2. Sample size, maximum and minimum values, mean, and P-value from calculation of colony duration in each species.

Species	Season	Sample Size	Days (L)	Days (U)	Mean	P-Value
<i>P. bellicosus</i>	Spring	5	115	148	133.2	0.0013
<i>P. bellicosus</i>	Fall	13	47	120	82.38	
<i>P. dorsalis</i>	Spring	8	98	209	147.6	0.0005
<i>P. dorsalis</i>	Fall	9	62	126	96.6	
<i>P. metricus</i>	spring	5	127	205	163.8	0.0022
<i>P. metricus</i>	fall	2	79	96	87.5	
<i>M. mexicanus</i>	spring	14	118	263	189.2	0.0011
<i>M. mexicanus</i>	fall	2	100	130	115	
<i>P. fuscatus</i>	fall	8	57	102	79.2	

Table 4.3. Maximum and minimum, mean, and P-value in adult peak for each species.

Species	Season	Adult # (L)	Adult # (U)	Mean	P-value
<i>P. bellicosus</i>	Spring	13	37	20	0.0072
<i>P. bellicosus</i>	Fall	5	21	9.1	
<i>P. dorsalis</i>	Spring	4	61	22.54	0.1814
<i>P. dorsalis</i>	Fall	4	49	16.71	
<i>P. fuscatus</i>	Spring	7	45	16.6	0.2587
<i>P. fuscatus</i>	Fall	4	22	11	
<i>P. metricus</i>	spring	3	22	9.83	0.7475
<i>P. metricus</i>	fall	3	11	7	
<i>M. mexicanus</i>	spring	4	49	17.5	0.746
<i>M. mexicanus</i>	fall	12	18	15.3	

Table 4.4. Maximum and minimum, mean, and P-value in cell number for each species.

Species	Season	Cell # (L)	Cell # (U)	Mean	P-value
<i>P. bellicosus</i>	Spring	103	239	153.3	0.0001
<i>P. bellicosus</i>	Fall	20	171	58.4	
<i>P. dorsalis</i>	Spring	54	238	152	0.0055
<i>P. dorsalis</i>	Fall	34	253	96.85	
<i>P. fuscatus</i>	Spring	46	291	136.9	0.0002
<i>P. fuscatus</i>	Fall	16	106	52.11	
<i>P. metricus</i>	spring	27	167	76.1	0.3157
<i>P. metricus</i>	fall	16	57	36.5	
<i>M. mexicanus</i>	spring	25	135	80.4	0.2751
<i>M. mexicanus</i>	fall	45	50	47.6	

Table 4.5. Maximum and minimum, mean, and P-value in peak cap number for each species.

Species	Season	Cap # (L)	Cap # (U)	Mean	P-value
<i>P. bellicosus</i>	Spring	15	52	28.38	0.001
<i>P. bellicosus</i>	Fall	3	33	11.76	
<i>P. dorsalis</i>	Spring	6	103	34.72	0.0149
<i>P. dorsalis</i>	Fall	8	49	21.42	
<i>P. fuscatus</i>	Spring	6	51	24.8	0.0252
<i>P. fuscatus</i>	Fall	3	37	10.88	
<i>P. metricus</i>	spring	4	19	13.16	0.8424
<i>P. metricus</i>	fall	4	18	11	
<i>M. mexicanus</i>	spring	6	41	21	0.6286
<i>M. mexicanus</i>	fall	17	17	17	

In our study we noted female transfer between nests in 7 separate late season nests; 4 in *P. dorsalis* and 3 in *P. bellicosus*. A multi-foundress *P. bellicosus* nest initiated in March (nest #79) under a palmetto leaf ceased brood production in late July and by 16 August the nest contained only 5 females, 3 males and no brood. On that same day a *P. bellicosus* nest was initiated by three females on a leaf directly below the leaf on which #79 was attached. One female was seen flying from #79 onto the new nest. In another instance a foundress from nest #311, a multi-foundress *P. dorsalis* nest initiated in late August, was seen flying to a mature spring *P. dorsalis* nest just 114 cm away and actively soliciting food for ~60 seconds before returning to her own nest. However in this case the mature spring colony was still actively rearing brood.

#### 4.4 DISCUSSION

##### 4.4.1 Differences between seasons

The post emergence phase and production of workers is largely influenced by climate and may be as little as a few weeks due to reduction in worker number (Yamane 1996). The shortest amount of time required for a complete colony cycle (consisting of the pre and post emergence phase, reproductive phase, and declining phase) was recorded in *P. chinensis* in Hokkaido, Japan, lasting approximately 3.5 months (~105d), however these colonies never lose the worker caste (Yamane 1996). The rearing of only one single brood would reflect the loss of the post emergence phase and subsequently the potential loss of the worker caste in the colony cycle (Yamane 1996). During our study, colony duration was significantly shorter in late season nests compared to spring nests, and number of cells and caps were significantly fewer in three of five species. This initially leads us to believe that there is not sufficient time for two full

colony cycles in Baton Rouge as stated by Strassmann (1981) with regards to *Polistes exclamans* in Texas. However, our results demonstrate despite the fact that late season nests persist for shorter amounts of time and attain fewer cells overall, peak adult number does not significantly differ between spring and fall nests in most species.

A combined mean of 88d was calculated for late season nests overall. Although this mean falls just under the duration for *P. chinensis* in Hokkaido, most nests in our study were found after their day of initiation during the early pre-emergence phase. Therefore our durations are an estimate and may be shorter than what actually occurred. Overall 67% of late season nests persisted for fewer than 105d and over half of these reared multiple broods. We can conclude that there is in fact sufficient time for two colony cycles in Baton Rouge (Lat. 30.4583° N), with the second cycle either lacking or having a shortened post-emergence phase, most similar to that of *P. chinensis* in Hokkaido (Lat. 43.2203° N). Such a shortened nesting cycle may be advantageous to females choosing to initiate late season nests, allowing them to directly reproduce as opposed to relying entirely on kin selection to further their genes. It is also possible that mixed reproductive strategies as described by Gadagkar (1996) in *Ropalidia marginata* may be employed by these females, in which they are able to help rear one entire brood before becoming reproductively active foundresses.

#### 4.4.2 Initiation and synchrony

Relatively equal percentages of spring and late season nests of *Polistes* were observed during this study. Nests observed during the summer months could be in any developmental stage, however a pattern was seen when examining the number of initiations recorded each

month. The two trends in spring and late season initiation demonstrate that Polistine nesting cycle in Baton Rouge follows a bivoltine pattern and peaks in both April and August. These data differ from the observations of a tropical species, *P. canadensis*, made by West-Eberhard (1969) in which initiations were sporadic and no synchrony was observed. However our study did share similar observations in the behavior of foundresses on late season pre-emergence nests of *P. bellicosus* and *P. dorsalis*. West-Eberhard (1969) noted that new nests of *P. canadensis* are often associated with declining mature nests, evidenced by observations of queens on new nests that were previously on declining nests. She observed one marked queen at a new nest visiting a declining nest ten times in 5.5 hours, engaging in food solicitation or trophallaxis behavior during each visit before returning to her own nest. These observations are also similar to those made by Strassmann (1981) on satellite nests of *P. exclamans* in which satellite nests are initiated within proximity of “main nests” by either the queen or workers, and transfer of workers between the satellite and main nest can occur until eclosion of the first brood on the satellite.

#### 4.4.3 Late season vs satellite nests

Because we did not mark individual wasps in our study, determination of origin of foundresses on late season nests was not possible. All nests initiated after the solstice were considered in one category “late season”. Late season nesting is not an entirely new aspect of the biology of temperate zone paper wasps. So called satellite nests, which are sometimes initiated after the solstice have been described previously by Strassmann (1981) in *P. exclamans* in Texas and by Page et al. (1989) in *P. fuscatus* in Wisconsin. Strassmann (1981) discovered that 16-39% of nests built satellites, and satellites in *P. exclamans* were typically initiated by

queens in May through June and by workers in May through early July; early initiation of satellites is favored in order to reduce the impact of possible bird predation. Our late season nest initiations peaked in August, slightly later than reported by Strassmann (1981), and we saw 49% of all *Polistes* nests in 2016 were initiated after the solstice. Strassmann (1981) also noted that nests initiated by workers which were not subsequently joined by other workers were always unsuccessful. Our study supports her findings in that *P. metricus* and *P. dorsalis* had 100% mortality of single foundress late season nests. However *M. mexicanus* had only 75%, *P. bellicosus* 66%, and *fuscatus* 40% mortality of single foundress nests. Percentage of nests attended by multiple females during the pre-emergence phase increased in late season of every species.

Page et al. (1989) reported that 10 out of a population of 107 *P. fuscatus* nests produced a satellite nest in Wisconsin. These satellites were initiated in early July and, contrary to the findings of Strassmann (1981), were only initiated by females who had eclosed in the spring, never by spring foundresses themselves. Satellite *P. fuscatus* nests produced only one brood and were thought to be the consequence of polydomous (consisting of two or more separated combs) colonies having pre-conditioned workers to work on multiple nests. In our study only one such polydomous colony was observed; this colony consisted of two late season *P. dorsalis* nests initiated ~10cm apart in August. Therefore our results also do not fully align with those made by Page et al. (1986). This could be due to the differing environments and species which were studied. Our late season nests consisted largely of *P. bellicosus* and *P. dorsalis* in a warm temperate or subtropical climate while Strassmann (1981) studied *P. exclamans* in a drier

habitat and Page et al. (1989) studied *P. fuscatus* in a cool temperate climate. Responses and behavior of wasps probably differs depending on species and environmental conditions.

#### 4.4.4 Theories explaining late season nesting

Having grouped all nests initiated after the summer solstice into one category, the distinction between satellite nests and late season nests which are not satellites perhaps becomes less important. Clearly there is a bivoltine trend in nest initiation observed during the summer of 2016 in Baton Rouge. The failure of nests early in the season is one possible theory explaining the re-nesting of paper wasps in July and August. Strassmann (1981) theorized that satellite nests in *P. exclamans* were adaptive to a high predation rate and long summer, and were built regardless of if the main nest had failed. Strassmann (1981) also reported that 51.6% of all nests in a population of *P. exclamans* lost their queen before July, and similarly the knockdown of nests by birds is a major cause of nest mortality. Page et al. (1986) found 34% of all nests in a suburban population of *P. fuscatus* failed to produce at least one brood. In our study 48.9% of nests failed before July. Wasps surviving from failed nests must then either join an existing nest or initiate a new nest. However 41% of our nests which had failed before July were *M. mexicanus* nests, a species which made up only a small proportion (5%) of late season nests. This discrepancy does not lend itself to the theory of failure as the leading cause of late season nests. We instead propose ancestral evolutionary causation.

Satellite nests of *P. fuscatus* were theorized to have been built as a result of alternative reproductive behavior observed in polydomous colonies (Page et al. 1986). The queen was not able to maintain complete reproductive dominance in these cases when combs were spread



out, allowing for the reproductive behavior of spring produced females who mated and initiated their own nests which were tended by workers that had been pre-conditioned to tend multiple combs. Although no polydomous spring nests were observed in our study, alternative reproductive behavior is a reasonable explanation behind the late season nesting period observed in Baton Rouge. It is well known that females of some social wasp species, such as *Ropalidia marginata*, a Polistine wasp studied in India, have almost equal availability of options for reproduction; these are to leave their natal nest and initiate their own nest either alone or in a group, stay at the natal nest as a worker, or stay at the natal nest and succeed the existing queen (Gadagkar 1996). The tendency of *Polistes* wasps to build late season nests (satellite or not) may indeed be the result of a multitude of reproductive options, such as remaining at the natal nest or founding alone or in a group, which are open to females eclosing early in the season due to the lengthy warm period in Baton Rouge.

It has recently been suggested that *Polistes* arose from solitary bivoltine ancestors, with the separate worker and gyne pathways having evolved from the bivoltine life history of the ancestors (Hunt & Amdam 2008). In this theory, eusociality is thought to have arisen from larval-adult interactions in which adults came to rely on nutritious secretions from larvae, and thus remained at their natal nest to receive this benefit. Differentiation between worker and gyne is then expected to be absent or residual in species which evolved in non-seasonal environments (Hunt & Amdam 2008). We believe such residual phenotypic pathways may be the case at least in *P. bellicosus* and *P. dorsalis* in Baton Rouge, leading to the bivoltine nesting pattern observed during our study.

Photoperiod is known to be an important cue for some Polistine wasps in both the egg laying patterns of foundresses and the induction of diapause in gynes (Tauber et al. 1986). This may provide an explanation to the question of which cues wasps are receiving in Baton Rouge that they are not receiving in more northern localities where nests are typically not initiated after the summer solstice. During the summer solstice in Philadelphia PA, a locality where S. Nacko has previously studied *Polistes* lacking a bivoltine trend in nest initiations, 15 hours of daylight are received. In New Orleans LA on the solstice, 14:04 hours of daylight are received, creating a difference of 56 minutes of daylight between the localities (Anonymous 2017c). Additionally, rate of photoperiodic decline is also different. From July 1<sup>st</sup>-31<sup>st</sup> New Orleans lost 28 minutes of daylight compared with Philadelphia which lost 41 minutes, a difference of 13 minutes. This difference increased to 22 minutes in August. Photoperiodic cues received by wasps in Baton Rouge during July and August may lead to a second period of nest initiation and ultimately reflect traits of ancestral tropical origins of the genus within North America (Santos et al. 2015).

#### 4.4.5 *Mischocyttarus mexicanus cubicola* Phenology in Baton Rouge

*M. mexicanus* is known to nest year round in Cuba, the Bahamas, Puerto Rico, and in south FL (Hermann & Chao 1984a), but has a 4 month period of diapause in more northern localities such as Georgia (Hermann & Chao 1984b). We hypothesized that due to its known plasticity in nesting biology and the relatively long warm season in Baton Rouge, equal amounts of nests would be initiated in the spring and late season. However our results show quite the opposite; *M. mexicanus* was the most frequently observed wasp during the spring, and nest initiations comprised 31% of all spring initiations observed. However this species was among

the least observed on late season nests, comprising only 5% of late season initiations. Of the seven late season *M. mexicanus* nests observed, one was associated with the destruction of a spring nest by a falling tree limb and was most likely a rebuild by those individuals. Our data also show a significant difference between the duration of spring *M. mexicanus* nests and spring *P. bellicosus* and *P. dorsalis* nests. These two *Polistes* species comprised 38% and 25% respectively of late season initiations, and were the most frequently observed on late season nests. It appears then that two different nesting strategies have arisen in this area, with *P. bellicosus* and *P. dorsalis* having a shorter duration in spring nests but an increased proportion of late season nests, while *M. mexicanus* has an increased duration of spring nests with very few late season nests.

With *M. mexicanus* being a primarily tropical and relatively recently arrived species in Baton Rouge, it is not yet known how this species overcomes varying environmental conditions. Our population of spring *M. mexicanus* nests had a mean duration of 189.2 days, the longest in our study; this compares to a similar species, *M. consimilis*, found in the subtropics of Brazil which has a mean duration of 234.9 days (Torres et al. 2011). In Baton Rouge the colony cycle of *M. mexicanus* is approx. 45d shorter than that of *M. consimilis* in Brazil, but wasps appear to be limited by a shorter warm season in Baton Rouge. Another study by Litte (1977) indicated that given known durations of early nest stages and the sizes of mature nests, colony duration was estimated to be 8 months in south Florida but was not directly measured. The fact that *M. mexicanus* nests may normally persist for 8 months would explain the longer mean duration of spring nests observed in this species, but does not explain why the aforementioned reproductive options (initiate a new nest alone or in a group) available to *Polistes* females

eclosing early in the season do not also seem available to *Mischocyttarus* females. It is possible that divergence from the common ancestor has selected against this traits in *Mischocyttarus*. The process of re-queening on a nest would favor females which remain at their natal nest to later become the queen on an already successful nest as opposed to leaving to initiate a new nest. Jeanne (1972) reports cases of queen supersedure in *M. drewensi*, where the dominant egg layer was overthrown by one of her daughters leading to a prolonged colony cycle. Such may also be the case in *M. mexicanus* in Baton Rouge.

One *M. mexicanus* nest during our study was initiated in March 2016 and contained brood into February 2017, giving it a duration of approx. 300 days. On 2 February the nest still contained 2 mid instar larvae and nine eggs. All other *Mischocyttarus* nests at this time had either been abandoned or contained sleeping clusters of diapausing individuals. It was noted that at Bluebonnet Swamp, the site containing this exceptionally long lasting nest, hummingbird feeders had been placed around the vicinity and many were defended by two or three actively feeding *M. mexicanus* females. The behavior of these females away from feeders is unknown. No females were seen flying between the active nest and a feeder. It is suspected that queen turnover occurred on this nest during some point, since queen death is usually the limiting factor preventing nests from persisting for such long periods of time (West-Eberhard 1969). By 16 February the nest had been abandoned, and on 20 February a newly initiated nest was discovered nearby.

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## CHAPTER 5. *CHALCOELA IPHITALIS* (LEPIDOPTERA: CRAMBIDAE) OCCURRENCE, OVIPOSITION BEHAVIOR, AND HOST INTERACTIONS WITH POLISTINE WASPS IN SOUTHERN LOUISIANA

### 5.1 INTRODUCTION

The sooty-winged Chalcoela moth, *Chalcoela iphitalis* (Walker), is a brood parasite in the family Crambidae (Anonymous 2017) which attacks Polistine wasps, including at least ten species of *Polistes* and one species of *Mischocyttarus* in the US and Central America (Madden et al. 2010). Moth larvae are ectoparasites, feeding on pupae or pre-pupae of the wasps before spinning silken cocoons containing layers of air pockets within nest cells. Webbing is not chewed through by the wasps and is often ignored, and new eggs or early instar wasp larvae can sometimes be observed on top of moth silk (Madden et al. 2010). *C. iphitalis* overwinter inside the wasp nest and is typically bivoltine, with an adult emergence in the spring as well as late summer. Infestations can be frequent, with up to 73% of nests parasitized in a population of a particular species (Strassmann 1981).

Parasitism by *C. iphitalis* of a population of *Polistes exclamans* in Texas has been studied by Strassmann (1981) over the course of three years. Average number of mature cells infested per nest ranged from 19-34% and sometimes varied significantly between years. Infestations usually peaked around July or August, with patterns demonstrating that *C. iphitalis* may avoid ovipositing in previously infested nests. Each *C. iphitalis* larva killed one wasp pupa, but holes between cells could be observed indicating that some moth larvae may be feeding on multiple pupae. The ability of *C. iphitalis* to destroy a large percentage of wasp pupae in a small period of time may have a large impact on worker replacement at the nest. Strassmann & Thomas (1980) conducted a principle component analysis on a population of *P. exclamans* and found

that nest decline was associated with *C. iphitalis* infestation. Similarly a study by Starr (1976) concluded that heavy infestation of *C. iphitalis* can be a primary cause of colony failure, and moth diapause inside of old nests may be a factor in the rarity of nest re-use by paper wasps.

Paper wasp nests may be attached to a variety of substrates including natural vegetation as well as manmade structures. In one study approximately 60% of *Polistes* nests located on manmade structures in Illinois were parasitized by *C. iphitalis*, whereas only 20% of nests built on trees or shrubs were parasitized, suggesting that nests in vegetation may be more difficult for moths to locate (Reed and Vinson 1979). In most environments more than one paper wasp species will occur in close proximity, and evidence from a ten year study indicated that *C. iphitalis* does not show host preference between two *Polistes* species studied, *P. fuscatus* and *P. dominula* (Miller et al. 2013). Few references could be found regarding the oviposition behavior of this moth, however Strassmann (1981) reports that “females lay eggs in wasp nests at night”. Strassmann (1981) described the reaction of adult wasps when encountering a moth as the “parasite dance”, during which wasps will react violently by biting or stinging the area where the moth had been and subsequently alarming other wasps through vibrations on the nest. Wasps will sometimes leave the nest and walk over the substrate, continuing the alarm behavior for up to 10 hours after initial detection of the moth (Strassmann 1981). This behavior is not necessarily a unique reaction to *C. iphitalis* and can be observed when an unfamiliar wasp or other arthropod is detected at the nest (pers obsv.). It is also reported that adult wasps will attempt to abort or destroy infested pupae, removing them from the nest, sometimes chewing holes in pupal caps (Strassmann 1981). Similar behavior was noted by Jeanne (1979) in *P. canadensis*, which was thought to display cell wall chewing and



multiple comb building in response to predation by a Teneid moth. Here we examine the behavior of both host and parasite in the laboratory as well as the occurrence in a field population of Polistine wasps in southern Louisiana.

## 5.2 MATERIALS AND METHODS

Study sites for field populations encompassed areas in Baton Rouge and St. Gabriel including Bluebonnet swamp, Burden Research Station, LSU Reproductive Biology Center and LSU main campus. Areas were systematically searched for Polistine nests throughout the spring and summer. Because air temperature is a major factor affecting wasp activity (Elisei et al. 2008), searches were carried out preferably on warm and sunny days when wasps were active, with search increments of 3-4 hours each day for approximately 15 days. Areas for visual search included sheltered sites such as palm fronds, picnic shelters, eaves of buildings, as well as low shrub vegetation. Wasps were also observed flying directly into a location which led to the discovery of a nest in that manner. Upon discovery, each nest was identified to species and visited weekly throughout the duration of the season. Presence of *C. iphitalis* infestation as well as percentage of cells infested were recorded. Because *C. iphitalis* webbing was observed in cells which had never contained pupae (those lacking cap remnants), we used total cell number to calculate our percentage of cells infested for each species. Due to the fact that *C. iphitalis* feeds only on pupal or pre-pupal wasp stages (Strassmann 1981), we excluded nests for calculation which failed before the pupal stage or never contained pupae. Our results support this basis of exclusion in that infestation of a pre-pupal nest was never observed.

In July of 2016, two infested wasp (*P. fuscatus* and *P. bellicosus*) nests which had been abandoned were collected in the field. These nests were brought back to the laboratory and placed together in the bottom of a 12.7 X 10.16 cm cylindrical plastic container whereupon *C. iphitalis* adults (n=29) eclosed soon after. Two active *Polistes dorsalis* nests without evidence of previous *C. iphitalis* infestation were collected from the field and housed in identical separate plastic containers; one nest (A) consisted of two adult females and the other nest (B) consisted of four adult females. All brood stages (eggs, larvae, and pupae) were present in both nests. Both infested wasp nests and active *P. dorsalis* nests were collected at Burden Research Station in Baton Rouge LA. With lids removed, placing the cage housing the moths underneath a cage housing an active *P. dorsalis* nest allowed moths to fly freely to the nest for 30 minute intervals during daytime (temperature= 23.1° C and luminosity= 59) and night time (temperature= 21.9° C and luminosity= 0) trials. Two daytime and two night time observations (27<sup>th</sup> and 28<sup>th</sup> of July) were conducted on each wasp nest, wherein behavior of each species and interactions between wasp and moth were recorded. Because red light is not visible to most insects but provides a minimum amount of light for observation by humans (Turpin 2012), a red light was utilized for observations during night time trials. After each night time observation terminated, cages were separated and seven adult moths were left in each wasp cage to allow further oviposition for 10 additional hours before being removed the next morning; this resulted in 21 total hours during which moths were permitted to oviposit in each wasp cage. Removal of moths from wasp cages was facilitated by physical stimulation from a paintbrush which encouraged downward flight into the moth cage. A 2-way ANOVA procedure (Proc Mixed) was utilized in SAS® to analyze relationships between egg positioning in both nests. Both wasp nests were maintained in the

laboratory and given access to honey, water, and wax worms daily. Moth larval silk was noted in cells if present. Fourteen days after trails ended, two late instar wasp larvae were removed from each nest for examination of moth infestation.

## 5.3 RESULTS

### 5.3.1 Occurrence in field populations

We found 34 nests with evidence of parasitism out of 179 total nests which reached the pupal stage (an infestation rate of 18.9%). The species with the highest infestation was *Polistes bellicosus* (n=46) with 19 or 41% of nests reaching the pupal stage becoming infested. *P. fuscatus* (n=28) had 6 or 21% infested, *P. dorsalis* (n=41) had 6 or 14.6%, *P. metricus* (n=14) had 2 or 14.2%, and *P. exclamans* (n=13) had 1 or 7.6% (Figure 5.1). *Mischocyttarus mexicanus* (n=37) had no observed cases of infestation. *P. metricus* (n=2) had on average 79.4% cells infested, *P. bellicosus* (n=19) had 44%, *P. fuscatus* (n=6) had 33.4%, *P. dorsalis* (n=6) had 22.7%, and *P. exclamans* (n=1) had 19.7%. Overall the percentage of cells infested for all species combined ranged from 100% to 2.7%, with an average of 40% per nest. Substrates which infested nests were built on included *Sabal palmetto* leaf (n=17), wood (n=8), painted wood (n=5), metal (n=2), plastic (n=1), and cement (n=1). No nests built on twigs or branches (n=13) were infested by *C. iphitalis*.

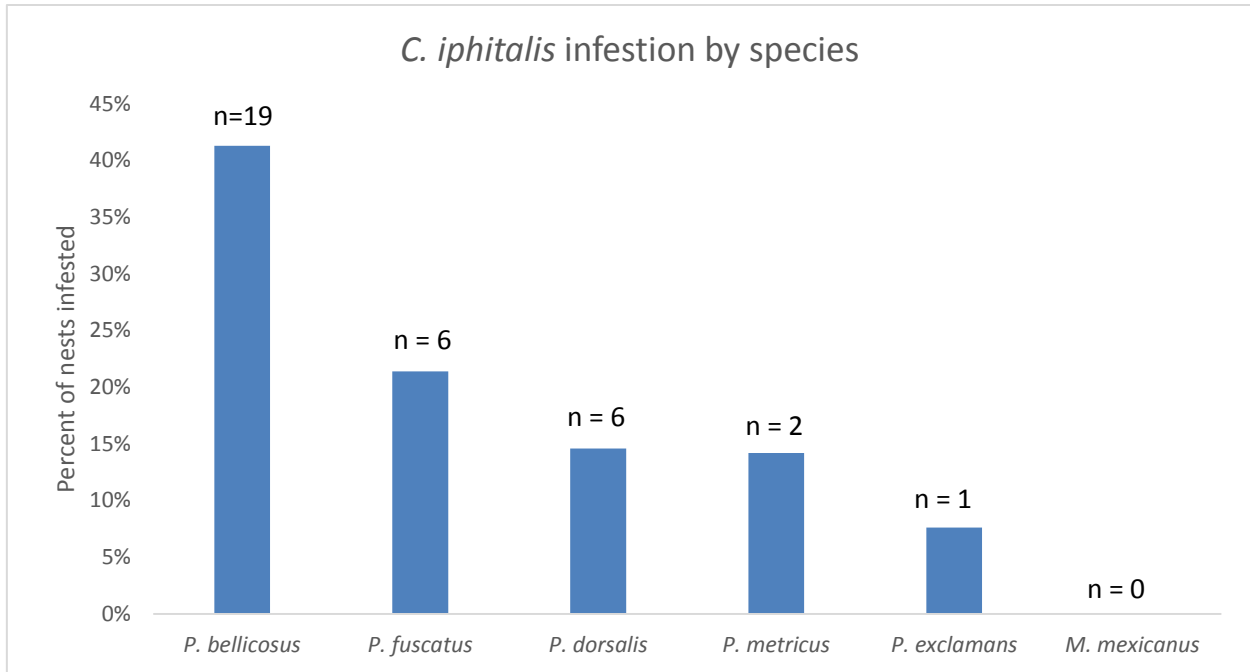


Figure 5.1. Percentage of nests infested with *C. iphitalis*.

### 5.3.2 *Polistes dorsalis* behavior

Moths quickly came into contact with adult wasps at the nest (n=9) only during night time trials, whereupon some wasps would display jerking movements and wing fanning described by Strassmann (1981) as the “parasite dance”. The degree to which parasite dance behavior was displayed varied greatly among individual wasps; some females left the nest in pursuit of the moth or continued this behavioral pattern for the remainder of the 30 minute observational period (n=3), while other individuals spent very little or no time (n=5) performing the same behaviors after contact with moths. One wasp left the nest in pursuit of contacting moths three times, spending ≈ 40 seconds before returning onto the nest each time; No other wasps left their nest during trials. In the first nest (A) containing two adults, one female exhibited a much higher degree of alarm than did the other. The less alarmed female raised her

wings often during contact with the more alarmed female, but spent most of her time walking slowly around the nest. She was also observed grooming and cell checking during this time. The more alarmed female walked jerkily around the nest, fanned her wings, and was not observed grooming or cell checking during the trials. Abdominal wagging on the face of the nest was observed once by the more alarmed female during the alarm behavior. In the second nest (B) 1 out of 4 females displayed the alarm behavior as previously described, however the behavior was displayed only for fifteen minutes after initial contact with the moth before the wasp returned to resting behavior. Two of the remaining three females were recently eclosed (<24hrs) and reacted to the alarmed female by moving away from her and toward the top of the nest. The fourth female raised her wings and made antennal contact with the alarmed female but did not exhibit the same degree of alarm.

### 5.3.3 *Chalcoela iphitalis* behavior

No wasp-moth interactions or moth flights were observed during daytime trials. Moths remained motionless on the walls and floor of their cage with antennae tucked back. During night time trials, moths typically landed within eight centimeters of the wasp nest with antennae fully extended and oscillating (Figure 5.2). In total 14 moth-wasp or moth-nest contacts were observed. Moths and wasps made antennal contact during nine of these incidences, six of which resulted in moth oviposition within seconds of the encounter. When moths made antennal contact with an adult wasp, avoidance behavior was displayed as the moth tucked antennae back and ran rapidly in the opposite direction. In six of the nine incidences after antennal contact was made with an adult wasp or the nest itself, oviposition occurred on the walls, ceiling and floor of the cage, but never on the nest itself. Eggs were laid

singly or in groups of 7 or less. Ovipositing females could be seen moving the tip of their abdomen from side to side as they walked along the surface of the cage. In two instances moths hovered near the nest and made contact with the nest itself or an adult wasp before landing nearby and beginning oviposition. Moths rarely (n=1) were observed landing or walking on a nest surface, and were not observed ovipositing directly onto a nest. After completion of trials, one wasp cage (A) contained 167 *C. iphitalis* eggs while the other cage (B) contained 16 eggs. The majority of eggs were located on the walls and ceiling of the cage, with few or no eggs on the floor (Figure 5.3). Fourteen days after trials ended, all wasp pupae on each nest had eclosed, leaving only late instar larvae for us to examine. No evidence of silk was present by this time. Upon removal of a late instar larva from nest A, two *C. iphitalis* larvae (each ~4 mm in length) were found in the bottom of that cell, and the wasp larva showed signs of predation due to feeding including a sclerotized, discolored, and deformed posterior end (Figure 5.4). Removal of a late instar larva from nest B revealed two larger (~7 mm) *C. iphitalis* larvae which disappeared into an adjacent cell through a hole in the cell wall. Adjacent wasp larvae showed no visible sign of predation. No moth silk was observed in the nests until four weeks after trials started, indicating a 4 week developmental time for moths in the laboratory at a temperature of 22°C.



Figure 5.2. *Chalcoela iphitalis* approaches a *Polistes dorsalis* nest with antennae extended.

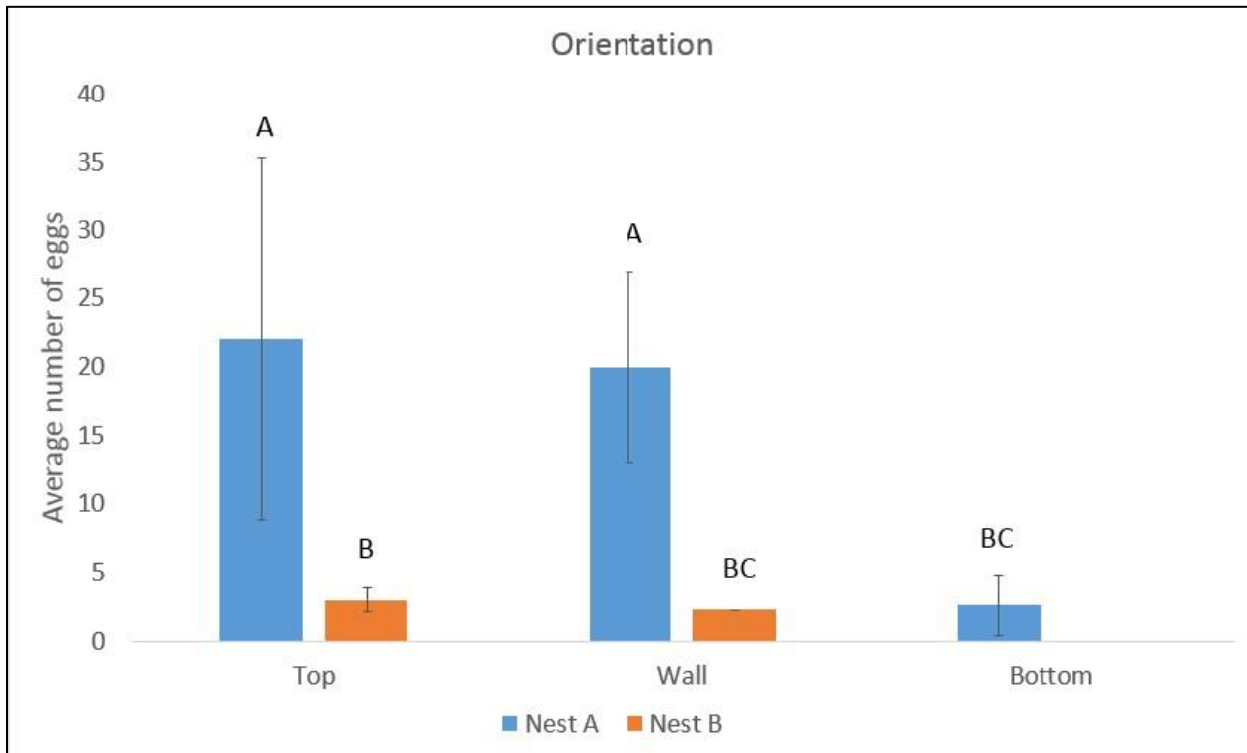


Figure 5.3. Number of *C. iphitalis* eggs found on various cage surfaces after 21 hrs. Letters represent significant differences.



Figure 5.4. A live late instar *P. dorsalis* larva (right) showing damage from feeding by *C. iphitalis* larva (left).

#### 5.4 DISCUSSION

Although *Chalcoela iphitalis* attacks many different host species (Madden et al. 2010), our data suggest a preference of the moth for *Polistes* species as compared with *Mischocyttarus*. The only available host record for *C. iphitalis* from the genus *Mischocyttarus* is in *M. basimacula*, a species occurring in Central America (Madden et al. 2010). During our field study of a population of Polistine wasps in Baton Rouge and closely surrounding areas, *Polistes bellicosus* was the most commonly encountered species and had the highest *C. iphitalis* infestation rate, while *Mischocyttarus mexicanus* was second most commonly encountered species and had no confirmed infestations. The lack of infested *M. mexicanus* nests may be



attributed to either existing defenses in *M. mexicanus* against the moth or insufficient host quality.

Differential parasitism rates by *C. pegasalis*, a closely related species with similar life history to that of *C. iphitalis*, was noted among *Polistes* species in Jamaica (Starr & Nelson 2015). We found that not all species of *Polistes* in our study were attacked equally as often, and percentage of infested cells also differed between species; however the most frequently attacked species did not have the highest percentage of infested cells. This discrepancy may be explained by the variation in average number of cells built by each species, which was previously found by S. Nacko to be significantly fewer in species such as *P. metricus*. If moths lay similar quantities of eggs at each nest, nests with fewer cells should have a higher percentage of total cells infested, which was indeed the case with *P. metricus*. A tradeoff between parasite vigilance behavior and foraging or brood care by adult female wasps was suggested as a possible explanation to differential parasitism among *Polistes* species (Starr & Nelson 2015), however oviposition of *Chalcoela* moths occurs mainly at night when wasps are not foraging (Strassmann 1981), suggesting other possible factors are at play. In the laboratory we found that adult wasps exhibited a varying degree of alarm behavior after the detection of an adult moth. A wasp exhibiting the highest degree of alarm was simultaneously observed performing abdominal wagging, a behavior observed more often in queens than in workers (Gamboa & Dew 1981). Avoidance of the alarmed individual by callow individuals in another instance was also observed, suggesting that alarm behavior may have been correlated with social rank of the individual.

Laboratory experiments also demonstrated that *Chalcoela iphitalis* will oviposit on substrates surrounding the host nest rather than on the nest itself. This makes the substrate which the nest is built on an important factor in avoiding predation by *C. iphitalis*. A substrate which has a large surface area (such as *S. palmetto* leaves or manmade structures) may be more conducive for moth oviposition while a narrower substrate (such as twigs or small tree branches) may inhibit oviposition by the moth. In this study we saw no infestation of nests built on twigs or branches in the field, perhaps explaining similar observations made by Reed and Vinson (1979). Antennal contact by a female moth with either an adult wasp or the wasp nest itself was a prerequisite for oviposition in the laboratory, but moths avoided walking onto or next to the nest. Antennal contact most likely provides host checking and oviposition stimulation, while avoidance behavior serves a function of remaining at a safe distance from alarmed wasps. Both wasp pupae and last instar larvae were attacked by the ectoparasitic moth larvae, which began feeding at the posterior end or bottom of the cell (n=2). It is presumable that upon hatching, caterpillars located the nest pedicel and traveled into the nest, although this was not directly observed. Future studies focusing on behavioral differences of individual wasps during episodes of parasite invasion may provide a basis for which alarm behavior is exhibited within the colony, and provide further explanation for the differential parasitism by *Chalcoela* moths that can be observed between Polistine species in the field.

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APPENDIX – RELEVANT EXTRA MATERIAL

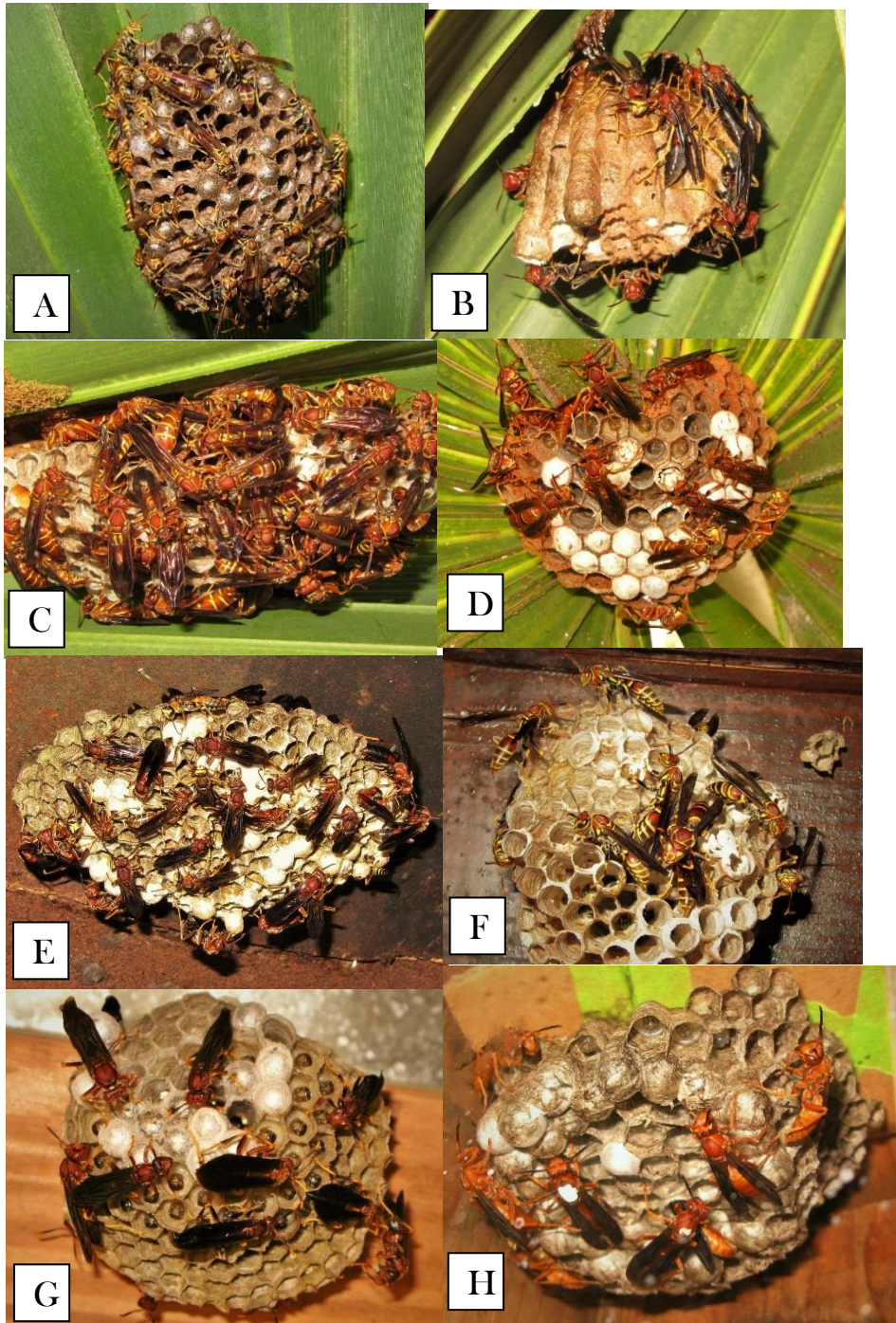


Figure A.1. Polistine species encountered in Louisiana. A – *Mischocyttarus mexicanus*, B – *Polistes metricus*, C- *Polistes dorsalis*, D – *Polistes bellicosus*, E – *Polistes fuscatus*, F – *Polistes exclamans*, G – *Polistes annularis*, H – *Polistes carolina*.



Figure A.2. Wasp nests collected after abandonment in 2016.

## **VITA**

Scott Nacko was raised in Duncannon Pennsylvania and completed two years of undergraduate study in Biology at Bloomsburg University before receiving his bachelor's degree in Entomology from the University of Delaware in 2014. Following his undergraduate studies, Scott worked briefly for the Pennsylvania Department of Agriculture as well as Frontier Scientific before joining the Department of Entomology as a graduate student at LSU. He is a candidate for graduation in May of 2017 and plans to continue research with social wasps after graduation.