ECOLOGICAL AND DEMOGRAPHIC TRENDS AND PATTERNS OF *Metamasius callizona* (CHEVROLAT), AN INVASIVE BROMELIAD-EATING WEEVIL, AND FLORIDA'S NATIVE BROMELIADS

By

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ECOLOGICAL AND DEMOGRAPHIC TRENDS AND PATTERNS OF *Metamasius callizona* (CHEVROLAT), AN INVASIVE BROMELIAD-EATING WEEVIL, AND FLORIDA'S NATIVE BROMELIADS

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In 1989, an immigrant bromeliad-eating weevil from Mexico, *Metamasius callizona* (Chevrolat), was detected in Broward County, Florida. Despite an eradication attempt, its population increased and spread in the surrounding natural areas. This thesis examines seasonal and ecological trends and patterns of *M. callizona* and Florida's native bromeliads. A multi-tiered method was designed to map areas for monitoring *M. callizona* and host bromeliads in five Natural Areas in south Florida. Data were collected monthly from June 2001 to June 2005 and included two data sets: 1) Demographic data on a population of selected living bromeliads; and 2) the collection of fallen dead bromeliads within the monitored areas; the dead bromeliads were examined for cause of death and for *M. callizona* specimens. Data collected from data set 1 were used to examine seasonality and survivability in two species of bromeliads, *Tillandsia fasciculata* Swartz and *T. utriculata* L (chapters 4 and 5). Data from data set 2 were used to examine seasonal fluctuations in the *M. callizona* population (chapter 3). Both data sets were used

to compare habitats and bromeliad communities and to make an assessment on the future of Florida's native bromeliads (chapter 6). Conclusions were the following: *Metamasius callizona* does not exhibit seasonal trends, except, perhaps, on *T. utriculata*. *Tillandsia fasciculata* exhibited mild seasonal fluctuations while *T. utriculata* spiked in early spring. Survival analysis showed *T. fasciculata* to have a higher proportion of its population killed by *M. callizona* than by other deaths; *T. utriculata* had a higher proportion of its population killed by other deaths than by death caused by *M. callizona*. Seasonal differences and differences in the response to attack by *M. callizona* can be explained by the different reproductive strategies of *T. fasciculata* and *T. utriculata*. *Tillandsia fasciculata* reproduces vegetatively and by seed, and therefore has larger, more stable populations; *T. utriculata* reproduces only by seed, and therefore has small, more ephemeral populations. Observations on the bromeliad populations from the five Natural Areas showed *T. fasciculata* to have a higher percentage of survival than *T. utriculata*; that *T. balbisiana* had a low incidence of attack by *M. callizona*; and that the population in Fakahatchee Strand Preserve State Park, where no confirmed *M. callizona* specimens were collected, had an overall high percentage of survival for all species included. The other four Natural Areas had an ongoing infestation of *M. callizona*, and the number of dead, fallen bromeliads collected had a similar percentage killed by *M. callizona*, 71 – 82%. The future of Florida's native bromeliads may vary depending on the species, and will depend on 1) the increased rate of mortality caused by *M. callizona* in relation to the species' ability to outgrow or outrun *M. callizona*; 2) the range and rarity of the species; and 3) the distribution of the bromeliad patches.

CHAPTER 1
INTRODUCTION

In 1989, an immigrant bromeliad-eating weevil from Mexico, *Metamasius callizona* (Chevrolat), was detected in Broward County, Florida. Despite an eradication attempt, its population increased and spread in the surrounding natural areas (Frank and Thomas 1994). Since then, the weevil has spread across south Florida and has been causing great damage to native bromeliad populations (Frank and Cave 2005).

Metamasius callizona's natural range is in Guatemala and southern Mexico (Frank and Cave 2005). *Metamasius callizona* is one of 32 known species of bromeliad-eating weevils in the Neotropics (Frank 1999). The adult ranges in size from 11 to 16 mm in length (Frank and Cave 2005) and has a black body with a transverse stripe across its elytra that is colored orange, red, or yellow; rarely, the stripe is not present (Fig. 1). *Metamasius callizona* is a holometabolous insect and, in the laboratory, reared on pineapple stems, the insect had a mean developmental time of 57.49 days to grow from within 24 hours of the time the egg was laid to adulthood (Salas and Frank 2001). In the laboratory, after mating once, adult females laid eggs for the duration of their lives, with no periodicity, with an average fecundity of 39.6 eggs per female and an average life span of about 0.5 year (Frank et al. 2006).

All life stages of *M. callizona* live on host bromeliads, which the larvae and adults consume (Frank 1996a). The adults are capable of flying and function as the dispersal unit. Adult weevils consume leaf tissue but do not threaten the life of the host bromeliad; the larva, by mining the meristematic tissue, kills the plant (Larson 2000a). An adult

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female cuts a slit in the base of a bromeliad leaf and inserts an egg. When the larva emerges from the egg, it mines the leaf, but after growing too large, the larva exits the leaf and begins to mine the stem of the plant (Frank 1996a). This sort of damage results in a characteristic death; the stem of the plant falls out, and the inside is a cavity filled with chewed plant tissue, sometimes containing weevil specimens or one to several empty pupal chambers.

Florida has one native bromeliad-eating weevil, *Metamasius mosieri* Barber (Frank and Cave 2005). Not much was known about *M. mosieri* until after *M. callizona* entered Florida and began causing damage to the bromeliads, which brought researchers into greater contact with *M. mosieri* (Frank and Cave 2005). *Metamasius mosieri* does not cause significant damage to bromeliad populations, as does *M. callizona*. No specialist predators of *M. mosieri* have been discovered, but it is speculated that the Florida weevil population is limited in part because it is restricted to small-sized plants and because it has particular environmental needs (Frank and Cave 2005). Exposure to sunlight has been shown to be a limiting factor for certain species that live in bromeliads. *Wyeomyia mitchellii* (Theobald), a fly that oviposits in tank bromeliads, has been shown to have a preference for bromeliads in shaded habitats (Frank and O'Meara 1985); and bromeliad communities in general have been shown to be more similar between bromeliads growing under same conditions (sun-exposed or shaded) than between species of bromeliads (Lopez and Rios 2001). However, the mechanism(s) that limits the growth of *M. mosieri* populations is yet unknown. It is possible that a specialist natural enemy exists but has not yet been discovered; or that habitat conditions limit its range (such as sun exposure, humidity levels, and wind exposures).

Chemical control of the weevil is impossible for economic, practical and ecological reasons (Larson 2000b). Because *M. callizona* lives inside the host bromeliad, in the canopy, huge amounts of chemical would have to be applied to potentially affect the weevil. The amount and dispersal of the chemical would be outrageously expensive, and, if it were broadcasted aerially, would harm many non-target species. The only possible method for controlling *M. callizona* is to use classical biological control. Classical biological control is the practice of introducing a natural enemy (usually from the same area that the pest came from) to suppress a pest population.

A biological control project was initiated by J. H. Frank and is still ongoing (Frank and Cave 2005). Despite searches in 6 countries (Mexico, Panama, Honduras, Guatemala, Belize, Paraguay and Peru), only one candidate biological control agent has been found, a new species of tachinid fly, *Lixadmontia franki* Wood and Cave, from the cloud forests of Honduras, attacking a related host species, *Metamasius quadrilineatus* Champion (Cave 1997, Wood and Cave 2006). Tests have shown that the fly will parasitize *M. callizona* and it is now being reared and tested for suitability for release (Frank and Cave 2005). Tests have also shown that *L. franki* will parasitize *M. mosieri*, but that it has a preference for *M. callizona* over *M. mosieri*; probably because *M. callizona* is larger than *M. mosieri* and closer to the size of *M. quadrilineatus*.

Bromeliads (Bromeliaceae) originated in the Neotropics, estimated about 60 million years ago near the end of the Cretaceous period (Benzing 1980; Isley, 1987). Most native bromeliad lands are in South and Central America; only a few species are found in the southeast portion of North America (Benzing 1980; Isley 1987). Three genera (*Tillandsia*, *Catopsis* and *Guzmania*) in the subfamily Tillandsioideae are found in

Florida (Isley 1987). All of Florida's native bromeliads (16 species in total) are epiphytes and grow in hardwood, pine, and swamp forests (Benzing 1987; Larson 2000c). Twelve of the 16 species of bromeliads are susceptible to attack by *M. callizona* (Frank and Cave 2005).

Most bromeliads are frost-intolerant and, therefore, the number and total biomass of bromeliad species drops dramatically from subtropical south Florida to north Florida, where seasonal temperatures are more pronounced and freezes are greater in number and duration (Benzing 1980; Myers and Ewel 1990). Florida's bromeliads require sufficiently humid conditions in order to survive and are more abundantly found over or near water, along rivers or streams or in swamps (Larson 2000c).

The spread of *M. callizona* is dependent on the range of its host plants. Since 1989, *M. callizona* has spread across most of south Florida (Fig. 2; Ferriter 2006) and it is likely that the weevil will continue to spread until it has covered the range of all potential host bromeliads (Frank and Cave 2005). While, since its arrival, *M. callizona* has been causing great damage to wider ranging species of bromeliads, particularly *Tillandsia fasciculata* Swartz and *T. utriculata* L., it has recently been found in the Big Cypress National Preserve (Frank 1996b). The Big Cypress National Preserve and the Everglades in general support the greatest diversity of bromeliads in Florida, including the wider ranging species as well as several rare species (*T. flexuosa* Swartz, *T. paucifolia* Baker, *T. pruinosa* Swartz, *Guzmania monostachia* L., *Catopsis berterioniana* Schultes, *C. floribunda* Brongniart, and *C. nutans* Swartz; Larson 2000c). The arrival of *M. callizona* into this area heralds the potential for the loss of numerous species of bromeliads (Frank and Cave 2005).

Conservation of Florida's bromeliads is not a trivial matter. In a worse case scenario, 12 species of bromeliads native to Florida could be lost, along with the ecosystems of vertebrate and invertebrate animals these plants support (Frank and Cave 2005). All of Florida's native bromeliads associate with other organisms to create small, complex ecosystems. Some species, such as *T. pruinosa* and *T. balbisiana*, have mutualistic associations with ants (Benzing 1980). Many tank bromeliads, such as *T. utriculata*, *T. fasciculata*, and *G. monostachia*, hold water in the axils of their leaves, which support aquatic ecosystems (Frank 1983). Numerous arthropods have been collected from tank bromeliads but many have yet to be identified and very little is known about the dynamics of these associations (Frank et al. 2004).

Bromeliads also support canopy animals such as raccoons, snakes, rodents, and birds (Butler 1974). Bromeliads are a source of water during the dry Florida winters. They are a food source for phytophagous insects (other than *M. callizona*, and which are usually not harmful to the plant in the long run). These phytophagous insects serve as prey for carnivorous animals. Bromeliads offer a place for many animals to build a home, or to provide a base upon which to build a nest (Frank 1983, Butler 1974).

Bromeliads are pivotal to life in the canopy, and as such they are an important part of nutrient cycles (Benzing 1980). Bromeliads are adapted to absorb nutrients through their leaves. They obtain their nutrition from rainwater that has leached through the canopy, from the waste material of the organisms that live in and on them, from insects or other small animals that die in the plant, from detritus that falls from the canopy, and from algae that grow in the tank water (Frank 1983).

Besides these very important ecological roles, bromeliads offer excellent opportunities for ecological experiments, such as studying nutrient cycles (Nadkarni 1992, McNeely 1998). Other studies that would be useful include "island studies" (bromeliads are similar to islands since many of the species they support must find ways to migrate from one bromeliad to another bromeliad, across generations) and ecological succession (bromeliads are much more slow growing than the ecosystems they support, and as the plant grows from seedling to adult to death, the ecosystem changes). The ecosystems supported by bromeliads provide a format for studying trophic levels, as well as numerous species, many yet to be identified, for studying systematics. Bromeliaceae are a large, diverse family whose members are good candidates for studying evolution.

Bromeliads can be used to monitor pollution (Benzing 1991). As a bromeliad absorbs nutrients through its leaves, it will also absorb airborne pollutants. Bromeliads would make better indicators than lichens because bromeliads are vascular plants, similar to most of the natural vegetation in Florida (Benzing 1991). Urbanization and energy demands are going to continue to grow in south Florida; bromeliads could be used to monitor the effect such growth is having on surrounding natural areas. Bromeliads can also be used to monitor climate change (Nadkarni 1992). If temperatures rise, their range should expand; and, conversely, if temperatures drop, their range should contract.

Bromeliads serve as an excellent avenue for educating the general public about conservation efforts, as well as getting the public involved in the process. Bromeliads are an asset to Florida's State Parks (Larson 2000d). Many people visit Florida's parks to photograph or to create paintings of the bromeliads, or just to drive or walk among them and find pleasure in their presence.

In an effort to help conserve Florida's native bromeliads and to assist in the biological control project that was initiated to control *M. callizona*, this thesis looks at seasonal trends and patterns for *M. callizona* and some of the native bromeliads that act as its host. As well, survival analysis was used to determine the effect that *M. callizona* is having on two bromeliad species, *T. fasciculata* and *T. utriculata*. Research was performed in five Natural Areas: Myakka River State Park, Loxahatchee National Wildlife Refuge, Highlands Hammock State Park, Fakahatchee Strand Preserve State Park, and St. Sebastian Buffer Preserve State Park.

Figure 1-1: Adult *Metamasius callizona*. Photo: J. C. Yawn.
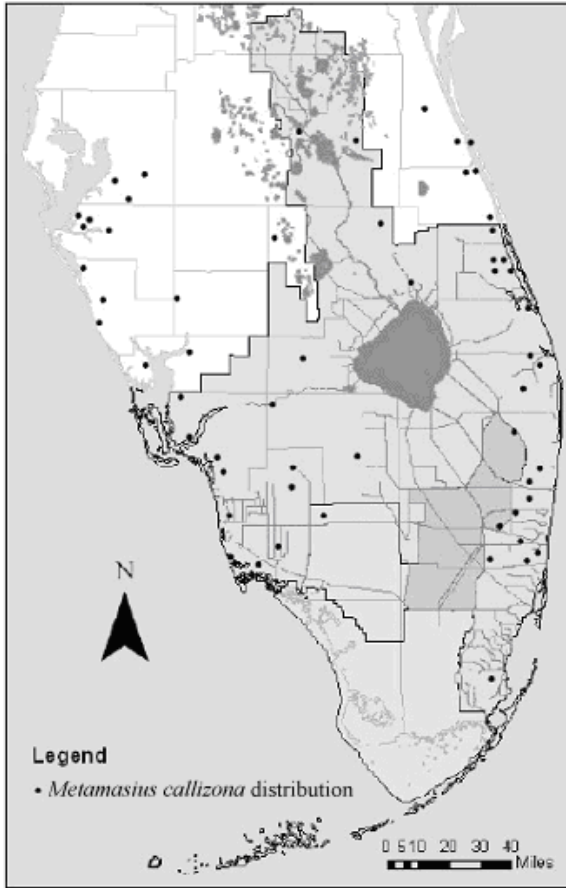
Figure 1-2: Distribution of *Metamasius callizona* in south Florida (Ferriter 2006).

CHAPTER 2
METHOD AND MATERIALS

This method was designed to monitor bromeliad populations in south Florida and

the invasive bromeliad-eating weevil, *Metamasius callizona* (Chevrolat) that arrived in

Florida in 1989 and that has since been attacking Florida's native bromeliads.

Bromeliads were monitored in five Natural Areas in south Florida: Myakka River

State Park (MRSP), Loxahatchee National Wildlife Refuge (LNWR), Highlands

Hammock State Park (HHSP), Fakahatchee Strand Preserve State Park (FSSP), and St.

Sebastian Buffer Preserve State Park (SSSP) beginning in June 2001 and ending in June

2005. Myakka River State Park was chosen as the primary research site because it had a

large bromeliad community which included both *Tillandsia fasciculata* Swartz and *T.*

utriculata L. (two of the large bromeliad species that have a wide range in south Florida

and that have been under heavy attack by *M. callizona*) and because *M. callizona* had

only recently been found in the park (in September 2000, one year before the start of this

research; Frank 1996b). The other four Natural Areas were selected in order to

incorporate localities with different species of bromeliads into the study and based on the

availability of volunteers to collect data.

Data were collected from demarcated Sections that were defined using a multi-

tiered method. Tiers were defined by bromeliad habitat and Bromeliad Host density.

Bromeliad Hosts are the substrates upon which the bromeliads grow; usually a host was a

tree, however some were vines or stumps, and a few of the bromeliads grew terrestrially.

The tiers, by decreasing size, were called Natural Area, Region, Area, Section, and Bromeliad Host (see Table A-1 in Appendix A).

Sections were mapped using a baseline from which to triangulate trees, Bromeliad Hosts, and other landmarks. These numbers were transcribed to grid-mapping paper using a compass and straight-edge. The maps were used to define the boundaries for data collection and to calculate the area monitored.

Materials for mapping a Section included two 91 m surveyor tapes; one 1.5 m stick with a small portion sanded level on the back end, with 2 pegs stuck in to which a compass could be affixed; a compass with holes drilled in it to fit the pegs on the stick; surveyor flags to mark Bromeliad Hosts; stakes to hold down surveyor tapes; and a log book for recording data.

To map a Section, a baseline was laid along some definable path (an actual path or road, or a chosen stretch in a stand of trees). Compass bearings were taken for the baseline. The objects to be mapped (the trees, including the Bromeliad Hosts and other obvious, persistent landmarks) were positioned by triangulating each object, using at least 2 compass bearings from the baseline. Rough estimations show this method of mapping is accurate to within approximately a third of a meter; the further the objects were from the baseline, the greater the loss in accuracy. Information recorded for each object included compass bearing and baseline reading for each line of sighting, the type (hardwood, pine or palm) and size of the tree (or other object); and whether it was a Bromeliad Host.

Two data sets were collected monthly within the demarcated Sections: 1)
Demographic data on a population of selected living bromeliads growing in the canopy;
and 2) Collection of fallen dead bromeliads within the demarcated Sections.

For data set 1, a portion of the Bromeliad Hosts within each Section was randomly
selected and the bromeliads on these Bromeliad Hosts made up the population of
bromeliads being monitored. Each Bromeliad Host was sketched from a particular spot
(indicated on the Section map), and its resident bromeliads were added in the sketch for
relocation purposes. Each bromeliad was assigned a unique number and identified to
species (if possible; *T. utriculata* and *T. fasciculata* are difficult to distinguish when they
are small and medium-size plants). Data collection included class-size (small, medium or
large). Class sizes were based on longest leaf length. Botanists have traditionally used
leaf area and dry weight to measure size of plants. The disadvantage of these
measurements is that they require killing the plant. Length of longest leaf was developed
as a non-lethal method for measuring *T. utriculata* and was related by regression to
water-impounding capacity of leaf axils (Frank and Curtis 1981). Length of longest leaf
was measured together with dry weight and leaf area by Frank et al. (2004). Size
classifications vary according to species; Table C-1 in Appendix C gives the size
classifications used in this study for species included.

Health ratings were assigned monthly for the selected bromeliads. The health
rating was an indicator of the condition of the bromeliad's health and was based on
assessment of certain outwardly physical characteristics, such as the color and fullness of
the leaves and physical injuries that were visible. Health ratings ranged from 3.0
(thriving and well; no injuries, discoloration, or dehydrated leaves) to 1.0 (completely

dead; no green left remaining on the plant). The 3.0 to 1.0 range was divided into four quarters: 3.0 to 2.5 (healthy); 2.4 to 2.0 (moderately stressed); 1.9 to 1.5 (heavily stressed); and 1.4 to 1.0 (seriously stressed; ultimately ending in death). Table D-1 (Appendix D) outlines these four quarters and the characteristics that indicate where a bromeliad would be categorized.

Bromeliads were chosen based on apparency; if a Bromeliad Host was covered with bromeliads, this was noted, but only the most obvious were mapped. When a selected bromeliad died or disappeared, evidence would be sought to determine the cause of death or disappearance. To replace dead or lost bromeliads, Bromeliad Hosts were updated and replaced every 6 months. If all of the bromeliads being monitored on a Bromeliad Host died or disappeared, then the Bromeliad Host was examined thoroughly for any remaining bromeliads, and these were monitored; if there were no more bromeliads available, then a new Bromeliad Host in the Section was randomly selected to take its place.

For data set 2, the Section maps defined the area on the ground to be searched for dead bromeliads that had fallen from the canopy. The bromeliads were examined for cause of death. If weevil specimens or pupal chambers were present, they were collected. An attempt would be made to rear larvae and pupae to adulthood because it is difficult to distinguish *M. callizona* larvae and pupae from that of Florida's native bromeliad-eating weevil, *M. mosieri* Barber.

MRSP, the primary research site, was mapped first; subsequently, five new Areas were added to existing Regions, and 1 new Region was added. The other four Natural Areas were included later than June 2001 and ended before June 2005. Only LNWR had

a new Area added after its initial mapping. MRSP data were collected by me. The other Natural Areas were mapped by me, but monitored by volunteers using my method.

Table B-1, in Appendix B, shows the total hectarage mapped for each Natural Area, the mapping and monitoring schedules, and the bromeliad species that were monitored. The five Natural Areas that were monitored represented different habitats and bromeliad communities. MRSP was monitored monthly for 49 months. Total land area monitored in MRSP covered 2.98 hectares. Seventeen Areas were mapped in hardwood forests, hammocks and mixed hardwood/palm forests. Seven hundred thirty-nine bromeliads were selected for monitoring; the population was composed of approximately 72% *Tillandsia fasciculata* Swartz, 27% *T. utriculata* L., and 1% *T. balbisiana* Schultes.

LNWR was monitored for 28 months until monitoring was interrupted by hurricane activity in August and September 2004. Total land area monitored was 0.05 hectares and included 115 selected bromeliads. Three areas were mapped, one in the interior of a cypress dome and two on the edge of the cypress dome. The bromeliad population was approximately 81% *T. fasciculata* and 19% *T. balbisiana*. At the start of the study, no *T. utriculata* bromeliads were apparent in the cypress dome. Wildlife Biologist Marian Bailey informed me that *T. utriculata* used to be present in the Refuge, but she only knew of one remaining specimen, located near the Administrative Building; it was infested with *M. callizona* and soon died as a result of the infestation.

HHSP was monitored for 33 months. Total land area monitored was 0.45 hectares in hardwood forest; two Areas were mapped, one in an orange grove and one in hardwood forest. Twenty-one bromeliads were selected for monitoring, of which 33% were *T. fasciculata*, 13% were *Tillandsia simulata* Small, and 54% were *T. utriculata*.

Tillandsia simulata is precinctive to Florida (Larson 2000c). Only two *T. simulata* plants were spotted in the monitoring area, making this a small sample. *Tillandsia variabilis* Schlechtendal was present in HHSP but not in the Sections that were monitored.

FSSP was monitored for 24 months. Total land area monitored was 0.04 hectares and included four Areas, three in swamp forest, and one on the side of a service road running through swamp forest. Seventy-seven bromeliads were selected for monitoring; the population was composed of 32% *T. fasciculata*, 10% *T. utriculata*, 12% *T. balbisiana*, 29% *T. pruinosa* Swartz, 3% *T. variabilis*, and 14% *Guzmania monostachia* L. The three Areas in the swamp were small patches each with a dominant species (*T. utriculata*, *T. pruinosa*, and *G. monostachia*); the Area on the service road was a combination of the species listed for FSSP. The percent composition of the species given here is likely not representative of the surrounding land because FSSP has more species than those included in this study (*T. flexuosa* Swartz, *T. paucifolia* Baker, *Catopsis berterioniana* Schultes, *C. floribunda* Brongniart, and *C. nutans* Swartz; Larson 2000c), and because the bromeliads tend to grow in patches such as the three out of four Areas mapped in FSSP.

SSSP covered 0.57 hectares; three Areas were mapped, one each in a cypress dome, a swamp forest, and an oak hammock. One hundred eighteen bromeliads were selected for monitoring and included 78% *T. fasciculata*, 10% *T. balbisiana*, 11% *T. paucifolia*, and 1% *T. simulata*. *Tillandsia paucifolia* were located on the edge of the cypress dome and co-existed with small and medium sized *T. fasciculata* and *T. balbisiana*.

CHAPTER 3
DOES *Metamasius callizona* (CHEVROLAT) EXPERIENCE SEASONAL
POPULATION FLUCTUATIONS?

Introduction

In 1989, an immigrant bromeliad-eating weevil from Mexico, *Metamasius callizona* (Chevrolat), was detected in Broward County, Florida. Despite an eradication attempt, its population increased and spread in the surrounding natural areas (Frank and Thomas 1994). Since then, the weevil has spread across south Florida and has been causing great damage to native bromeliad populations (Frank and Cave 2005).

Previous surveys for *M. callizona* had been undertaken to demarcate the ever-increasing area occupied by it, and to collect specimens for laboratory use (Frank and Thomas 1994, Frank 1996b). Seldom was a site revisited once weevils were found, so the data could not readily reveal seasonal trends in abundance. This chapter, in contrast, is a result of repeated visits to a select number of sites. It evaluates evidence for seasonal trends of *M. callizona* populations in five natural, protected areas.

Method and Materials

Metamasius callizona specimens were collected in Myakka River State Park (MRSP), Loxahatchee National Wildlife Refuge (LNWR), Highlands Hammock State Park (HHSP), Fakahatchee Strand Preserve State Park (FSSP), and St. Sebastian Buffer Preserve State Park (SSSP). MRSP was the primary research site and monitoring there began in June 2001 and ended in June 2005. Monitoring began in the other four Natural Areas after June 2001 and ended before 2005. Table B-1 in Appendix B outlines the

mapping schedule for the five Natural Areas, as well as the hectarage mapped and the bromeliad species included in the study.

Weevil larvae, pupae and adults were collected from dead bromeliads that had fallen from the forest canopy within demarcated Sections. These demarcated Sections were defined using a multi-tiered method (see chapter 2 for details on this method and Table A-1 in Appendix A that defines the Tiers).

Monitoring was conducted monthly. All dead bromeliads susceptible to weevil attack that fell into a selected Section were opened and examined. The number of weevil specimens found in a Section was recorded along with the date, time, life stage of the specimen (adult, pupa or larva; no eggs were collected), and whether the weevil specimen was alive or dead. If possible, larvae and pupae were reared to adulthood for species identification.

The average number of living adults and living or dead pupae and larvae found for each Natural Area was divided by the hectarage monitored for each Natural Area and plotted against time. The weevil population was treated as a Poisson distribution because it was not dense and was not randomly distributed. Upper and lower boundaries (plus and minus 2 standard errors) for each plot were included. The plots were examined for peaks that regularly rose above the upper boundaries of a baseline population size, indicating seasonal fluctuation.

Results and Discussion

None of the plots indicate seasonal fluctuations in the weevil population. *Metamasius callizona* was found in all seasons and no peaks rose significantly higher than any other (exceeding the upper boundaries). Fig. 3-1 shows the average number of *M. callizona* specimens found per hectare plotted against time (months) for Myakka

River State Park (MRSP). Fig. 3-2 shows the average number of weevils found per hectare plotted against time (months) for the other four Natural Areas.

These results indicate that, overall, the weevil population remains constant and is active throughout the year. With an estimated mean generation time of 13 – 17 weeks (Salas and Frank 2001; Frank and Thomas 1994), *M. callizona* could potentially have three to four generations per year. In the laboratory, after mating once, adult females laid eggs for the duration of their lives, with no periodicity, with an average fecundity of 39.6 eggs per female and an average life span of about 0.5 year (Frank et al. 2006). The lack of periodicity supports the conclusion herein that the weevils do not experience seasonal fluctuations. Constant activity, multiple generations per year, single mating with high fecundity, and long life span without regulation have contributed to the fast expansion of *M. callizona* populations, and to the high levels of destruction incurred upon native bromeliad populations by *M. callizona*.

Lack of seasonality is probably due to the subtropical climate that exists in south Florida, and to the fact that the weevil lives inside its host plant, where it is protected from extreme changes in the weather. There are wet and dry seasons in south Florida (Myers and Ewel 1990), however, most of Florida's bromeliads undergo only moderate fluctuations in physiological condition (flowering excepted) with these changing seasons (see chapter 4).

Tillandsia utriculata, one of Florida's bromeliads that are susceptible to weevil attack, has suffered greatly since 1989. Unlike Florida's other native bromeliads, *T. utriculata* does not propagate vegetatively, but dies after producing seeds (Benzing 1980; Isley 1987); and tends to go through growth spurts with the onset of spring (see chapter

4). In MRSP, of the 13 large, weevil-killed *T. utriculata* found containing weevil specimens, 10 fell at the beginning of the rainy season (May, June, and July) and had an average of 6.2 weevil specimens per bromeliad, including living and dead larvae and pupae, and living adults. Three infested plants were found outside the rainy season (February, October and March, one per month) and each contained only one weevil specimen.

The sample of large *T. utriculata* bromeliads in MRSP was small, and therefore does not offer conclusive evidence of weevil seasonality on this particular host plant of this particular class size. However, with the observed growth spurts in the spring and the higher average number of weevils found during the months of May through July, it is possible that in a large patch of infested *T. utriculata* plants the weevil may exhibit seasonality. A study that examines a large *T. utriculata* population (such as a well-established colony with at least a few hundred bromeliads and at the forefront of an infestation) would be necessary to determine the accuracy of this statement. The other Natural Areas studied did not have large *T. utriculata* populations.

A large amount of land must be covered in order to collect a meaningful number of weevil specimens. Pupal chambers in an infested area can be found in much larger numbers than adults, larvae or pupae; however, the pupal chambers are highly persistent and cannot be used to determine seasonality. Weevil specimens were collected from LNWR, HHSP, and SSSP, but in very low numbers (total numbers collected for each site were 4, 5, and 11, respectively). The greatest number of weevil specimens (132) was found in MRSP, where more bromeliads were surveyed over a longer time than at the other Natural Areas (Table B-1). Weevil specimens were collected regularly for the first

two years (from June 2001 to June 2003, a total of 113 weevil specimens was collected)

but declined in the final two years (from July 2003 to June 2005, only 19 were collected).

This may be due to the loss of bromeliads, especially large *T. utriculata*, in the Sections

that were being monitored.

Fluctuations in the weevil population are not seasonally affected (except, perhaps,

in the case of *T. utriculata*). Weevil populations are more likely to vary based on the

number and species of bromeliads that make up a patch, the size and density of the patch,

the ability of the patch to support the weevil population, and whether an infestation is

newly initiated or has been present for some time.
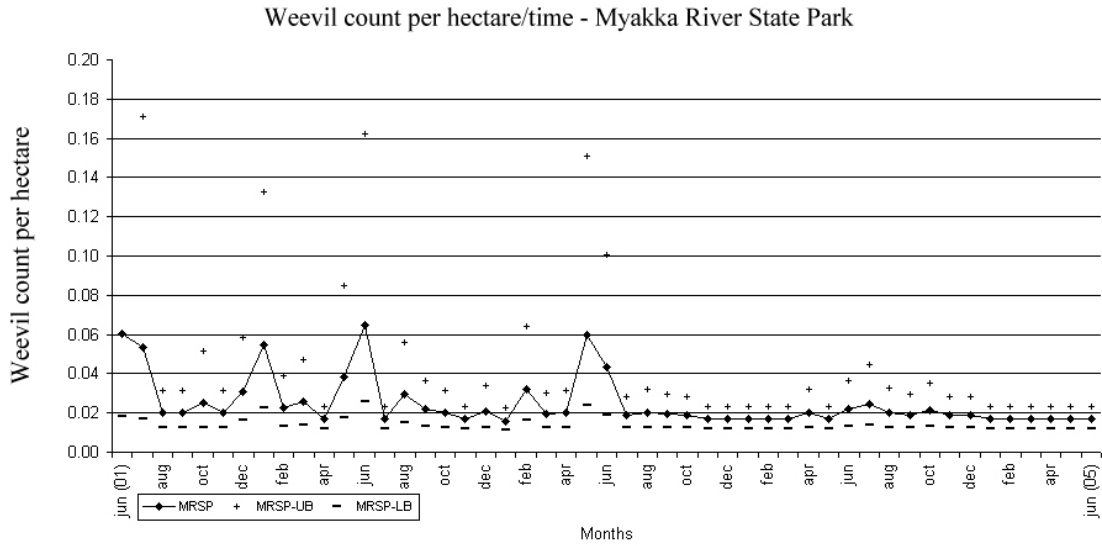
Figure 3-1: Weevil count per hectare/month for Myakka River State Park, Sarasota County, Florida, from June 2001 to June 2005.
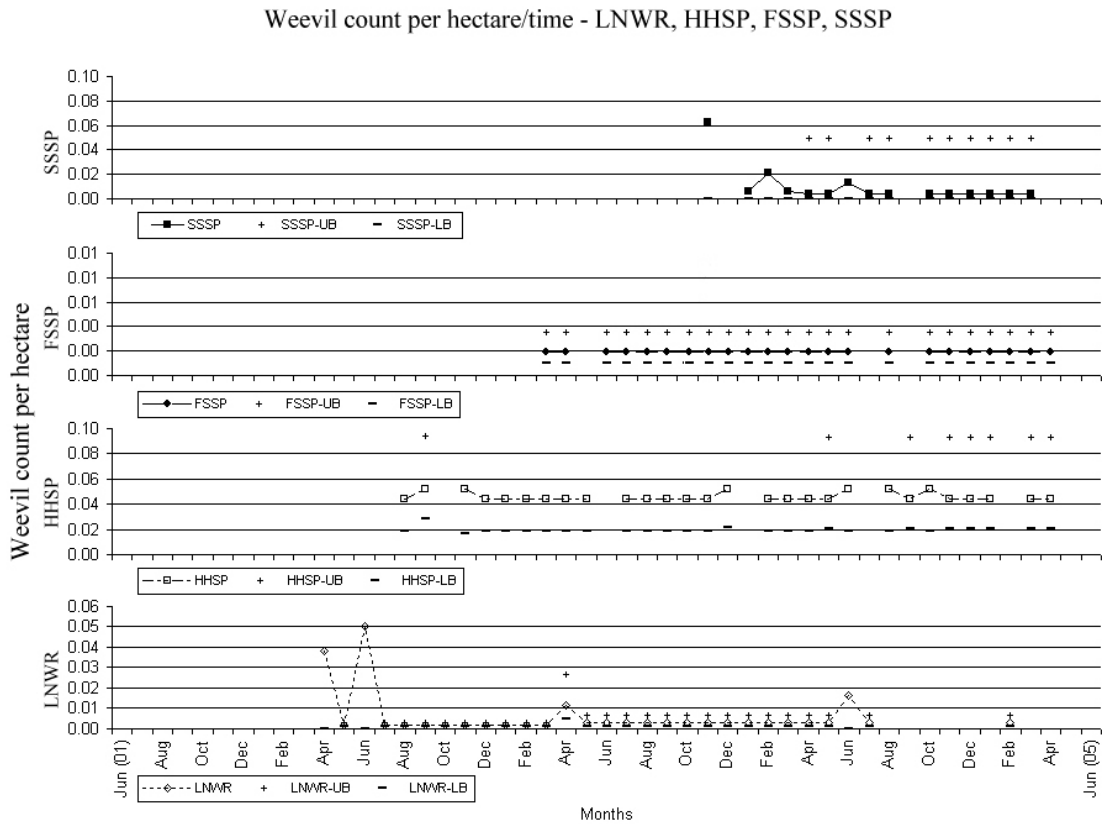
Figure 3-2: Weevil count per hectare/month for Loxahatchee National Wildlife Refuge (LNWR); Highlands Hammock State Park (HHSP); Fakahatchee Strand Preserve State Park (FSSP); and St. Sebastian Buffer Preserve State Park (SSSP).

CHAPTER 4
SEASONAL TRENDS AND PATTERNS OF *Tillandsia fasciculata* SWARTZ AND
Tillandsia utriculata L. POPULATIONS IN MYAKKA RIVER STATE PARK

Introduction

Florida has 16 native species of bromeliads, including three genera (*Tillandsia*,
Catopsis and *Guzmania*) in the subfamily Tillandsioideae (Isley 1987). All of Florida's
native bromeliads are epiphytes and grow in various hardwood, pine, and swamp forests
(Benzing 1980). The canopy is a harsh environment, subjected to drought conditions,
low nutrition availability, and catastrophic events. Bromeliads have adapted to these
conditions through vegetative reduction, novel growth habits, and the evolution of
specialized trichome cells that absorb and secure water (Benzing 1980; Isley 1987).

Most bromeliads are frost-intolerant and, therefore, temperatures limit the range of
most bromeliads (Benzing 1980). In Florida, the number and total biomass of bromeliad
species drops dramatically from subtropical south Florida to north Florida, where
seasonal temperatures are more pronounced and freezes are greater in number and
duration (Benzing 1980; Myers and Ewel 1990). Florida's bromeliads require
sufficiently humid conditions in order to survive and are more abundantly found over or
near water, along rivers or streams or in swamps (Larson 2000c).

Rainfall regulates timing for emergence of the inflorescence and the release of seed
(Benzing 1980). Florida's bromeliads produce inflorescences between midwinter and
spring, seed develops over the span of a year and, in the following spring, the seeds
dehisce and are released just before the spring rains begin (Benzing 1980). This timing

ensures that the wind-dispersed seeds are dry at the time of dispersal, and that once the rains follow shortly thereafter, they are attached to a potential host. *Tillandsia paucifolia* Baker provides an example of how important the timing of seed release relates to rainfall. On Sanibel Island off the southwest coast of Florida, the rainy season starts 4-6 weeks after the season begins on the mainland; *T. paucifolia* populations on the island release seed 4-6 weeks later than mainland *T. paucifolia* populations, in time with the rainfall (Benzing 1980).

Twelve of Florida's native bromeliads are susceptible to attack by an invasive bromeliad-eating weevil *Metamasius callizona* (Chevrolat). Field research has shown that *M. callizona* exhibits no seasonal population fluctuations, with the possible exception on the host bromeliad *Tillandsia utriculata* L. (see chapter 3). This chapter examines the bromeliads that are susceptible to attack by *M. callizona* in Myakka River State Park (MRSP) for seasonal patterns and trends in relation to seasonal changes in rainfall and temperature. The two primary species of bromeliads in this study were *Tillandsia fasciculata* Swartz and *T. utriculata*. Both species are large, long-lived plants (Isley 1987) with a wide distribution across the southern peninsula. *Tillandsia balbisiana* Schultes was also present in the study, but was a very small portion of the bromeliad community in MRSP; only two were included in the selection of bromeliads for monitoring.

Methods and Materials

From June 2001 to June 2005, 739 bromeliads were monitored monthly in Myakka River State Park (MRSP). Bromeliads in the study included those species susceptible to attack from *M. callizona*, which were *T. fasciculata*, *T. utriculata*, and *T. balbisiana*, and included class sizes ranging from very small to very large.

Size classifications, based on longest leaf length, for *T. fasciculata* and *T. utriculata* were: Small, ≤ 15 cm; medium, 15 to 60 cm; and large, > 60 cm. Size classifications for *T. balbisiana* were: Small, ≤ 5 cm; medium, 5 to 15 cm; and large, > 15 cm; the two plants included in this study were large. Defining characteristics between *T. fasciculata* and *T. utriculata* are difficult to distinguish when they are small and medium class-size; as they become large, they are very easy to tell apart. Therefore, only large class-size bromeliads were used in this analysis.

The bromeliads selected for monitoring in MRSP were chosen based on a multi-tiered method. (See chapter 2 for details on this method and Table A-1 in Appendix A that defines the Tiers.)

Monitoring was conducted monthly and consisted of assigning a "health rating" to the individual bromeliads in the study. The health rating was an indicator of the condition of the bromeliad's health and was based on assessment of certain outwardly physical characteristics, such as the color and fullness of the leaves and physical injuries that were visible. Health ratings ranged from 3.0 (thriving and well; no injuries, discoloration, or dehydrated leaves) to 1.0 (completely dead; no green left remaining on the plant). The 3.0 to 1.0 range was divided into four quarters: 3.0 to 2.5 (healthy); 2.4 to 2.0 (moderately stressed); 1.9 to 1.5 (heavily stressed); and 1.4 to 1.0 (seriously stressed; ultimately ending in death). Table D-1 in Appendix D outlines these four quarters and the characteristics that indicate where a bromeliad would be categorized.

A health rating was assigned to each bromeliad, along with an explanation for the health rating (e.g., core falling out of the center of the plant, heavy discoloration, etc.) in

order to determine cause of stress or injury. If a bromeliad died or disappeared, evidence was sought to determine the cause of death or disappearance.

Decomposition analysis, using Minitab® Release 14.20 (Minitab, Inc. 2006), was performed on the following data sets: All monitored bromeliads (*Tillandsia fasciculata*, *T. utriculata* and *T. balbisiana*, all sizes; n = 739); large class-size (longest leaf length > 60 cm; n = 109) of *T. fasciculata*; large class-size (longest leaf length > 60 cm; n = 41) of *T. utriculata*; the average monthly rainfall; and average monthly lowest temperature (rainfall and temperature data were collected in the Bradenton/Sarasota area by the National Weather Service; National Weather Service 2005). Data for each set (the three bromeliad sets; rainfall data and lowest temperature data) were decomposed into trend and seasonal components using a multiplicative model to get median raw seasonal values for the twelve months of each year. Raw seasonal values were used to calculate seasonal indices for adjusting the data (setting the median of the raw seasonal values to equal 1) and to plot boxplots for comparing the medians and variance for each month. Trend lines for each data set were calculated using least squares regression.

Cross correlations were made for the three bromeliad data sets ('all bromeliads'; large class-size *T. fasciculata*; and large class-size *T. utriculata*) with the average monthly rainfall and with the average lowest temperature. The number of lags was set at +/-17 using the calculation (sqrt (n)) +10; n=length of the time series (49 months). Alpha level (5%) was calculated with the formula

$\alpha = 2/\text{sqrt}(n-[k])$

where n = length of the time series and [k] = the absolute value for each lag time. The cross correlation coefficient (CCF) was determined for each lag time. The CCF with the

greatest significant difference was tabulated with its corresponding lag time and alpha value.

Results and Discussion

'All bromeliads', large *T. fasciculata*, and large *T. utriculata* all had increasing trends over the four year study (see Fig. 4-1a,4- 2a, and 4-3a). All bromeliads and large *T. fasciculata* had moderately rising trends with an increase of about 0.1 in the health rating. Large *T. utriculata* had a more pronounced rise in trend, increasing its average health rating by 0.3 points. Rainfall had a slightly rising trend with the average increasing by 5 cm. Average lowest temperature had a slightly decreasing trend with an average decrease of 2°C.

Seasonal rainfall does not have a smooth decline and rise; rather, average rainfall is significantly greater (and exhibits higher variability) in June, July, August and September compared to the months from October to May (Fig. 4-4b). In October, average rainfall drops suddenly, with little variation in this month. Most of the winter and early spring months show little variability, except for December and, to a lesser extent, November. 'All bromeliads' and large *T. fasciculata* show improvements in physiological condition with increased rainfall in June.

Seasonal average lowest temperature begins decreasing in October, reaches a low point in January, and then begins to rise. Overall, there is little variation; variation is greatest in December and January. The seasonal plot for lowest average temperature is very similar to the seasonal plot for the health ratings of 'all bromeliads' (Fig. 1b) and large *T. fasciculata* (Fig. 2b). Health ratings for large *T. utriculata*, which have similar health ratings from June to February, increases significantly in March, April and May

(Fig. 4-3b), when the average lowest temperatures are rising; however, it does not follow the increase in temperature closely.

Highest cross correlation factors (CCFs) for 'all bromeliads', large *T. fasciculata* and large *T. utriculata* at their respective lag times are higher than their associated *P*-values (Table 4-1); therefore, the null hypothesis that the cross correlation for the lag time is equal to zero is rejected (i.e. there is correlation). 'All bromeliads', *T. fasciculata* and *T. utriculata* all have higher CCFs for temperature than for rain. All bromeliads and *T. fasciculata* have much more significantly higher CCFs than *T. utriculata*, whose CCFs are only slightly larger than the associated *P*-values.

Lag times for 'all bromeliads' and *T. fasciculata* are -1, except for 'all bromeliads' versus average rain, which is zero. These numbers are consistent with the graphs, where often the response of the bromeliads lags a month behind, or responds in time with, the changes in temperature and rainfall. In Fig. 2a ('all bromeliads') and 2b (*T. fasciculata*), the median health ratings remain similar from September to October while the temperature falls. As temperature continues to decline (November and December), 'all bromeliads' starts to decline as well, while *T. fasciculata* continues to maintain similar health ratings and does not begin to decline until January into February and March, when temperatures start to rise. The health ratings for 'all bromeliads', as well, decline from January to March. The rest of the year, health ratings for 'all bromeliads' and *T. fasciculata* health ratings follow the temperature as it rises.

In Fig. 4-1b and 4-2b, 'all bromeliads' and *T. fasciculata* maintain similar health ratings from September to November when the average rainfall suddenly drops. 'All bromeliads' follows rainfall pattern more closely throughout the rest of year. This is

probably because 'all bromeliads' includes small and medium-sized bromeliads as well as large bromeliads. Small and medium bromeliads respond more readily to changes in environmental extremes due to their smaller mass and their inability to hold as much water or nutritional debris (Benzing 1980).

Health ratings for the large *T. fasciculata* increase in the spring before an increase in rainfall in April and May. The health ratings for *T. utriculata* have a sharp increase in health ratings in March, April and May, before the increase in rainfall. The ability of the large bromeliads to show improved physiological condition before an increase in rainfall may be a reflection of their lesser dependence on rainfall because they can hold water in their tanks for many months (Benzing 1980) and/or nutrition acquisition since the tank water holds animals and plants, both living and dead, that contribute to the nutrition of the bromeliad (Frank 1983). The large bromeliads may be affected more by the decreased winter temperatures than by lower rainfall, but once temperatures rise, new growth occurs and damaged cells can be repaired.

However, *T. fasciculata*'s health ratings continue to rise into the summer as the temperatures rise. The health ratings for *T. utriculata* spike in the springtime, then fall to a lower level where they remain throughout the year, seemingly not too affected by rainfall or temperature (note the CCFs in Table 4-1 which are not as significantly high as those for 'all bromeliads' or *T. fasciculata*). Also, the lag times for *T. utriculata* are -8 (rainfall) and 3 (temperature), which would indicate a response from *T. utriculata* (an increase in health rating) eight months after the summer rains, or three months before the increase in temperatures, neither of which is sensible.

Both *T. fasciculata* and *T. utriculata* are monocarpic and die after going to seed; however, *T. fasciculata* also propagates vegetatively, and grows in large clumps. *Tillandsia utriculata* reproduces primarily by seed and only very rarely produces offsets (Isley 1987). These two life strategies result in different life histories (Benzing 1980). Because *T. fasciculata* partitions its resources, an individual plant releases less seed which results in fewer new colonies; however, the offsets retain a secure perch and, because an offset grows rapidly on the nutrition of its dying parent, it reaches reproductive age much more quickly (one to two years compared to 10 to 15 years from seedling).

Tillandsia utriculata puts all of its resources into making seed. Of the 41 large *T. utriculata* in this study, 23 produced an inflorescence; 83% of the time, the first sign of inflorescence growth happened in March, April and May, the same months in which the health ratings spiked. (The other 17% happened in January, February, June, and July, with only 1 spike per month.) Increase in temperature (or some other environmental variable, such as day length) may act as an environmental cue to the plant to maximize nutritional uptake for the development of seed, which will occur over the following year (seeds were released in March and April).

Interestingly, of the 13 large *T. utriculata* bromeliads in MRSP that were killed by *M. callizona* and that contained weevil specimens (living adults, living or dead pupae or larvae), the highest weevil specimen to bromeliad ratio found from this dead population occurred in May (four dead bromeliads with 7.5 weevil specimens per bromeliad), June (five dead bromeliads with 6.6 weevil specimens per bromeliad), and July (one dead bromeliad with three weevil specimens). The remaining three dead bromeliads were

found in February, March, and October, respectively, each with a weevil specimen to bromeliad ratio of one. When reared on pineapple tops in the laboratory, *M. callizona* required an average of 57.5 days to develop from egg to adult (Salas and Frank 2001). Allowing for longer developmental time in the field, an egg laid in March, when *T. utriculata*'s health ratings spiked, could reach adulthood within 8 to 16 weeks (May to July), the same months with the highest number of weevil specimens to bromeliad.

Metamasius callizona showed no seasonality (see chapter 3), except in this small population of large, weevil-killed *T. utriculata* bromeliads. It may be that *M. callizona* is exploiting increased nutritional acquisition that the plant would have used for growth and/or seed production. However, the number of dead *T. utriculata* containing weevil specimens was relatively small (n = 13). To determine whether *M. callizona* exhibits seasonality on this class-size of this species would require further studies, preferably on a large, well-established *T. utriculata* colony with at least a few hundred bromeliads and at the forefront of an infestation.

Fluctuations in the health ratings for 'all bromeliads', large *T. fasciculata*, and large *T. utriculata* remained, for the most part, in the upper quarter (3.0 to 2.5) and just dipped into the 2nd quarter (2.4 to 2.0) during the winter months (see Fig. 1b, 2b, and 3b). Bromeliads tend to die quickly, or to not show outward symptoms of internal damage (such as by *M. callizona* larval chewing) until the plant is at the point of falling out of the canopy. The exception to this is when *T. utriculata* dies from going to seed; that is a long process that happens over the span of the year when the seed is developing.

In conclusion, the bromeliad population as a whole (all bromeliads) and the large class-size of *T. fasciculata* bromeliads showed definite seasonal patterns and had

significantly high CCFs with average monthly rainfall and with average lowest

temperatures. For both data sets, temperature had higher CCFs and followed more

closely the seasonal patterns of the bromeliads than did rainfall. *Tillandsia utriculata*

spiked seasonally, in the spring months, and had significantly high CCFs, but not much

higher than the associated alphas; the lag times for *T. utriculata* were nonsensical. The

health of large class-size *T. utriculata* is not affected much by changes in temperature or

rainfall.
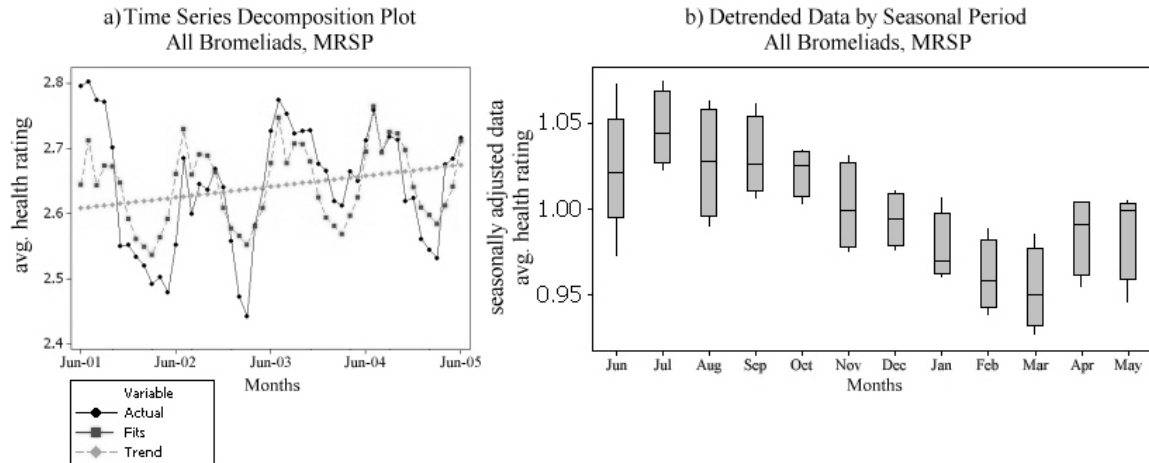
Figure 4-1: Time series decomposition plot and seasonally adjusted data for 'all bromeliads'. a) Time series decomposition plot (n=739). b) Seasonally adjusted data using seasonal indices to plot medians and variation for each month.
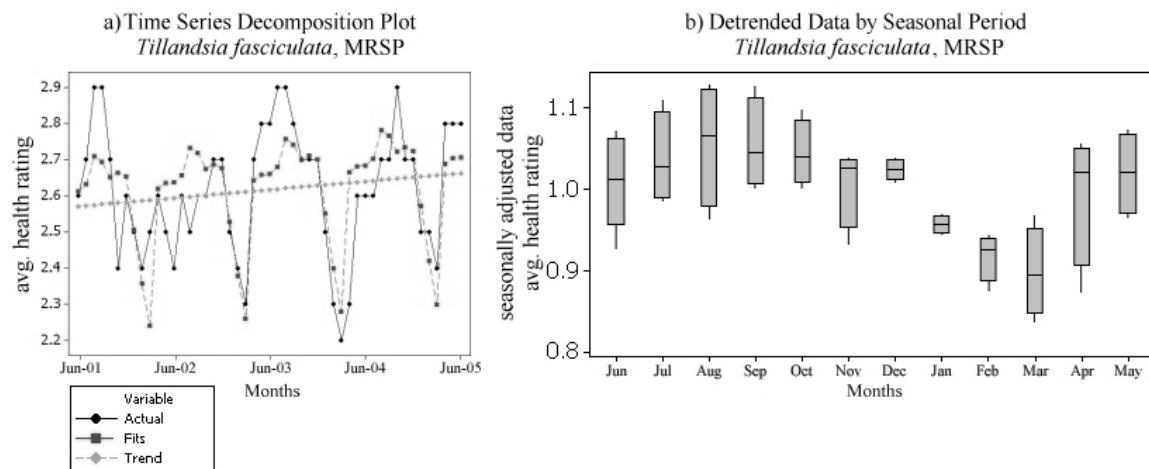
Figure 4-2: Time series decomposition plot and seasonally adjusted data for large class-size *Tillandsia fasciculata*. a) Time series decomposition plot (longest leaf length > 60 cm; n=110). b) Seasonally adjusted data using seasonal indices to plot medians and variation for each month.
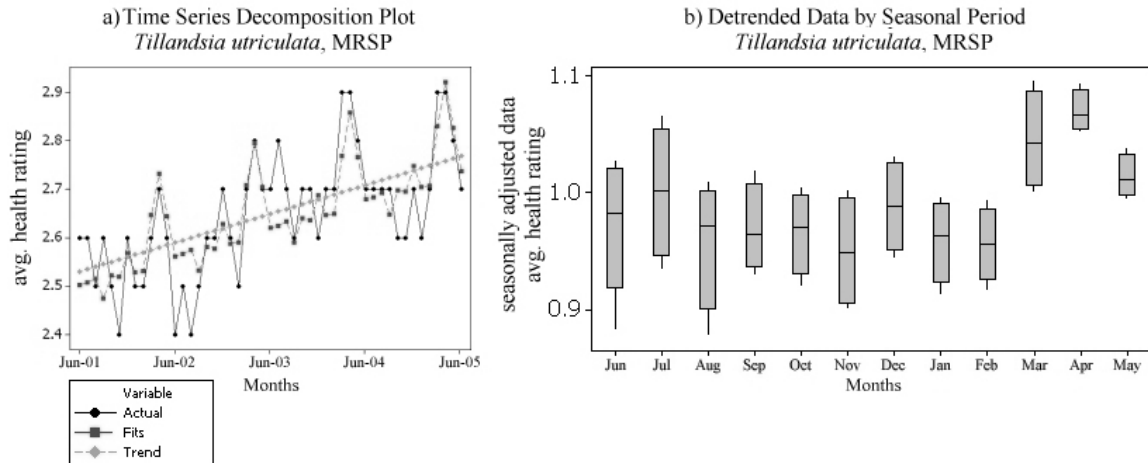
Figure 4-3: Time series decomposition plot and seasonally adjusted data for large class-
size *Tillandsia utriculata*. a) Time series decomposition (longest leaf length >
60 cm; n=41). b) Seasonally adjusted data using seasonal indices to plot
medians and variation for each month.
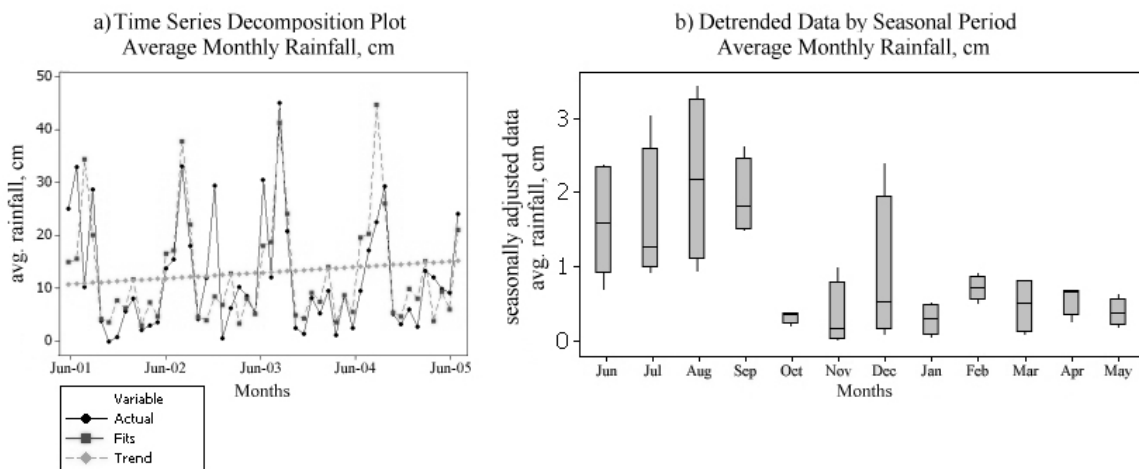
Figure 4-4: Time series decomposition plot and seasonally adjusted data for average
monthly rainfall (cm). a) Time series decomposition plot; data collected by
the National Weather Service in the Bradenton/Sarasota area in south Florida
(National Weather Service, 2005). b) Seasonally adjusted data using seasonal
indices to plot medians and variation for each month.
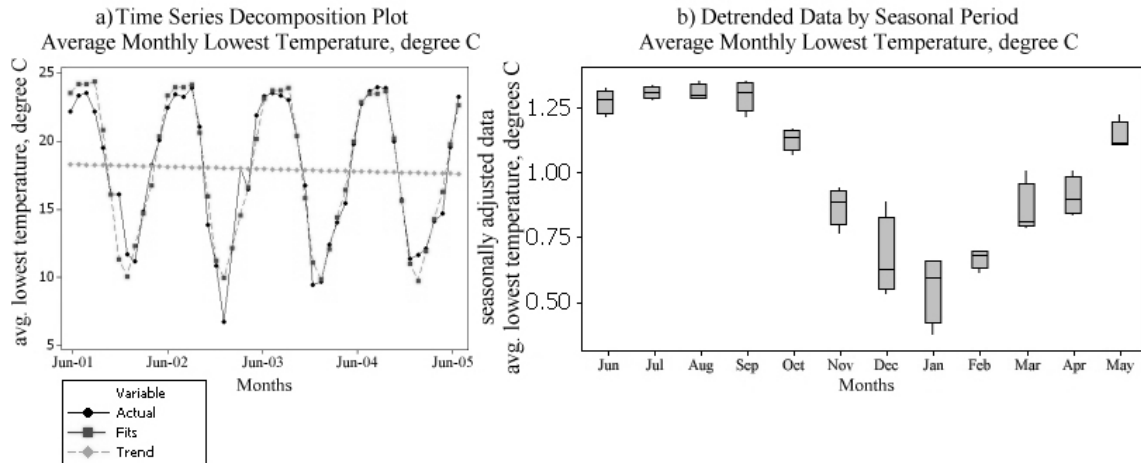
Figure 4-5: Time series decomposition plot and seasonally adjusted data for average
monthly lowest temperature (C). a) Time series decomposition plot; data
collected by the National Weather Service in the Bradenton/Sarasota area in
south Florida (National Weather Service, 2005). b) Seasonally adjusted data
using seasonal indices to plot medians and variation for each month.

Table 4-1: Cross correlations for comparing the three bromeliad data sets (all monitored
bromeliads; large class-size *T. fasciculata*; and large class-size *T. utriculata*)
with the average monthly rainfall and the average lowest temperature.
Itemized in the table are the lag time; the cross correlation coefficient (CCF);
and the alpha value (5%).

Data Set	Average Rain (cm)			Average Lowest Temperature (C)		
	Lag time	CCF	Alpha (5%)	Lag time	CCF	Alpha (5%)
All Bromeliads	0	0.487	0.286	-1	0.645	0.289
Large *T. fasciculata*	-1	0.418	0.289	-1	0.614	0.289
Large *T. utriculata*	-8	0.374	0.312	3	0.332	0.295

CHAPTER 5
SURVIVAL OF *Tillandsia fasciculata* SWARTZ AND *Tillandsia utriculata* L. IN MYAKKA RIVER STATE PARK

Introduction

Florida has 16 native species of bromeliads, all of which are epiphytic; 12 of them are susceptible to attack by *Metamasius callizona* (Chevrolat), an invasive bromeliad-eating weevil that escaped into Florida's natural lands in 1989 (Frank and Thomas 1994). Choice of host bromeliad is limited for *M. callizona* by physiological restraints; the host plant must have enough biomass to support larval growth to pupation (Frank and Thomas 1994). *Tillandsia usneoides* L., *T. setacea* Swartz, *T. bartramii* Elliot, and *T. recurvata* L. are not susceptible to attack by *M. callizona* because they do not have enough biomass to support larval growth. The other 12 native bromeliads are large enough to support larval growth, but only after they have reached a certain size. Laboratory research has shown that, for *Tillandsia utriculata* L., the minimal size susceptible to weevil attack is a plant with longest leaf length of 17.1 +/- 0.6 cm (Sidoti and Frank 2002). The larger the bromeliad, the more weevil larvae the plant can support (Frank and Thomas 1994).

Bromeliads have slow growth rates and can take 10-15 years to reach maturity and produce seed (Benzing 1980; Isley 1987). Seeds are dispersed by wind, which may carry them to a potential bromeliad host. Germination rates are very low for bromeliad seeds (Benzing 1981). Mortality rates are very high for seedlings and small plants and decrease dramatically as the plant becomes larger (Benzing 1980, Isley 1980). Large class-sized plants are representative of the reproductive class, and each plant puts out thousands of

seeds (Isley 1987); a decline in the reproductive class could have a serious effect on the success of the following generation (Frank and Thomas 1994).

All of Florida's native bromeliads propagate by seed and by producing vegetative offsets, except for *T. utriculata*, which dies after going to seed (Isley 1987). The two reproductive strategies result in different life histories and mortality rates. Species that propagate by both seed and vegetative offsets tend to be more stable and to live longer (Benzing 1980). Because these species split their resources between making seed and supporting the growth of vegetative offsets, they tend to put out less seed per plant; however, because offsets reach maturity much quicker than a plant starting from seed (one to two years versus 10 to 15 years), these species tend to have more regular seed output (Benzing 1980). When *T. utriculata* goes to seed, the plant dies and leaves no offsets (Isley 1987). This results in a shorter life span, less consistent seed output for a specific location, and a more ephemeral existence (Benzing 1980).

The different class sizes of the bromeliads and the different life strategies of the bromeliad species in south Florida could result in different responses to the attack by *M. callizona.* This chapter examines the effect that *M. callizona* is having on class sizes of bromeliads and on two species of bromeliads (*Tillandsia fasciculata* Swartz and *T. utriculata*) in Myakka River State Park (MRSP) in Sarasota, County, Florida

Method and Materials

From June 2001 to June 2005, 739 bromeliads were monitored monthly in Myakka River State Park (MRSP). Bromeliad species included in the study were *T. fasciculata*, *T. utriculata*, and *T. balbisiana* Schultes (this was a rare species; only six were found, and two included in the study). The bromeliads were classified according to size determined by longest leaf length (see Table C-1 in Appendix C for size classifications

based on longest leaf for *T. fasciculata* and *T. utriculata*). Large class-size bromeliads were identified to species.

The bromeliads selected for monitoring in MRSP were chosen based on a multi-tiered method. (See chapter 2 for details on this method and Table A-1 in Appendix A that defines the Tiers).

Monitoring was conducted monthly and consisted of relocating the selected bromeliads and observing whether each plant was alive, dead or missing. Evidence was examined to determine the cause of deaths and disappearances.

Parametric survival analysis was used to determine differences in the effect that *M. callizona* had on the small, medium and large bromeliad class-sizes; and for the large class-size *T. fasciculata* and large class-size *T. utriculata* bromeliads. Data were treated as a Weibull distribution and survival curves were plotted with a 95% confidence interval. Survival curves were plotted and compared using Log-Rank and Wilcoxon tests for small, medium, and large class-size bromeliads. Failure for these survival curves was defined as either death or disappearance. Data for the small, medium and large class-size bromeliads were then examined using three failure modes: Death by *M. callizona*; death by causes other than *M. callizona*; and disappearance. Median times to failure for each failure mode were plotted for each class-size, including upper and lower boundaries (+ and – 2 standard errors).

Survival curves using two modes of failure (death by weevil; and death by causes other than weevil plus disappearances) were plotted for large class-size *T. fasciculata* and large class-size *T. utriculata*. The two failure modes for *T. fasciculata* and *T. utriculata* were compared using Log-Rank and Wilcoxon tests. Median times to failure for the two

modes of failure were tabulated with upper and lower boundaries (+ and – 2 standard

errors).

Results and Discussion

Bromeliad seedlings and small plants have very high mortality rates, which

decrease dramatically as the plant matures and becomes larger (Benzing 1980, Isley

1987). The survival plots for the three class-sizes of bromeliads in MRSP follow this

trend as well. The three curves begin with a high rate of decline that slows down and

smoothes out near the end (Fig. 5-1). Steepest rate of decline is highest for the small

class-size, followed by the medium class-size, then the large class-size. Log-rank and

Wilcoxon tests have similar Chi square values, both significantly higher than the

associated *P*-value (Table 5-1); therefore, the null hypothesis, that the curves are the

same, was rejected.

These survival curves for the small, medium and large bromeliads (Fig. 5-1) were

plotted with failure defined as a death or a disappearance and show the overall pattern for

mortality experienced by the bromeliads in MRSP. In order to see how deaths and

disappearances vary for the class-sizes, the data for each class-size were analyzed using

multiple failure modes. The three failure modes were used were 'weevil' (death caused

by *M. callizona*); 'other' (verified deaths, caused by anything except death by *M.

callizona*); or 'disappearance' (the plant was missing and could not be relocated). Fig. 5-

2 shows the median time to failure (with upper and lower boundaries) for small, medium

and large class-sizes for the three modes of failure (weevil, other, and disappear).

For small bromeliads, disappearances had a median time to failure of 14.5 months

(-1.3 months, + 1.4; n = 250); other deaths had a median time to failure of 56.6 months (-

12.2 months, + 15.5; n = 53); and weevil deaths had a median time to failure of 124

months (- 56.3 months, + 104; n = 23). Most disappearances were probably caused by flooding, storms, high winds, fallen trees and branches, and herbivory (other than *M. callizona*, such as from lepidopteran larvae or squirrels), and likely resulted in deaths. Other deaths (excluding those caused by *M. callizona*) resulted from the same events that caused disappearances; however, the plant remains were observed to die from rot, burial, desiccation, cold damage, or herbivory.

All of the small bromeliads that were killed by *M. callizona* were at the high end of the small class size (approximately 10 to 15 cm, longest leaf length); and, when a *M. callizona* specimen was found, only one was ever found per plant. This is contrary to laboratory research by Sidoti and Frank (2002) where no bromeliads with a longest leaf length less than 17.1 +/- 0.6 cm supported larval growth; however, small bromeliad deaths in the field were rare (23 out of 327 deaths and disappearances) among the small class-size bromeliads, and no more than a single larva or empty pupal chamber was discovered in this class-size.

For medium-size bromeliads, disappearances had a median time to failure of 37.3 months (- 4.7 months, + 5.4; n = 70); other deaths had a median time to failure of 87.2 months (- 36 months, + 60.8; n = 24); and weevil deaths had a median time to failure of 29 months (- 5 months, + 5.9; n = 31). Causes of disappearances and other deaths were the result of catastrophic events; other deaths were caused by rot or burial, and, for *T. utriculata*, going to seed. The median time to failure for disappearances for medium-size plants is similar to that for the small class-size. The median time to failure for weevil deaths for medium class-size plants is similar to that for the large class-size. The wide size range of the medium class-size bromeliads (15 to 60 cm) moves through a range of

morphological characteristics, starting at the low end with characteristics similar to the small class size, up to the high end of the range where there is greater similarity to the large class-size. As medium class-size plants increased in size and mass, they disappeared less frequently, became less susceptible to catastrophic events and climatic changes; weevil-killed plants were more often found with more than one weevil specimen or empty pupal chamber.

For large bromeliads, disappearances had a median time to failure of 113 months (-55.6 months, + 110; n = 23); other deaths had a median time to failure of 87.5 months (-33.6 months, + 54.5; n = 30); and weevil deaths had a median time to failure of 40.2 months (-7.6 months, + 9.3; n = 51). Disappearances were mostly the result of catastrophes, probably caused by storms or flood conditions; three disappearances were caused by unlawful collection by humans (all three specimens were located near occupied camp grounds, and evidence of knife marks on the bark indicated where the bromeliads had been cut away). Other deaths were caused by catastrophes resulting in rot or burial, and, for *T. utriculata*, going to seed. Weevil deaths had a significantly earlier median time to failure than other deaths or disappearances. Individual large bromeliads were capable of supporting several weevils.

Large bromeliads were identified to species (*T. fasciculata* or *T. utriculata*) and two failure modes (deaths and disappearances combined, and weevil deaths) and their affect on large class-size *T. fasciculata* and *T. utriculata* populations were examined. Disappearances were assumed to be other deaths, based on the assumptions that most of the disappearances would result in death; and that these deaths were not caused *by M. callizona*. These assumptions create a bias towards over-estimating the number of other

deaths (other deaths plus disappearances) and under-estimating the number of weevil

deaths (assumption that disappearances all result in other deaths); however, there would

be a greater bias in under-estimating the number of other deaths to weevil deaths if

disappearances were ignored, because it is a safe assumption that most disappearances

resulted in death, not caused by *M. callizona*; and death and disappearance, at the time of

its occurrence, effectively removed a potential or active reproductive member of the

population.

Survival curves for the two failure modes for large class-size *T. fasciculata* have

high rates of decline in survivability at the beginning, and then smooth out (Fig. 5-3).

The survival curve for weevil deaths has a much higher rate of decline in survivability

than other deaths and disappearances. Large class-size *T. fasciculata* bromeliads have

significantly different survival curves for the two failure modes. Log-Rank and Wilcoxon

tests have similar chi-square values that are much higher than their associated *P*-values

(Table 5-2); therefore, the null hypothesis, that the curves are the same, was rejected.

The significantly higher rate of decline in the survivability for weevil deaths indicates

that mortality caused by *M. callizona* has a higher probability of happening than death by

other causes at any given time. As well, the median time to failure (Table 5-3) for weevil

deaths (41 months, ranging from 33 to 51 months) is significantly earlier than that for

other deaths and disappearances (83 months, ranging from 50 to 133 months).

Survival curves for the two failure modes for large *T. utriculata* have a high rate of

decline in survivability at the beginning, and then smooth out (Fig. 5-4). The survival

curve for other deaths and disappearances has a much higher rate of decline in

survivability than for weevil deaths. Large *T. utriculata* have significantly different

survival curves for the two failure modes. Log-Rank and Wilcoxon tests have similar

Chi-square values that are much higher than their associated *P*-values (Table 5-4);

therefore, the null hypothesis, that the curves are the same, was rejected. The

significantly higher rate of decline in the survivability for other deaths indicates that

mortality caused by other deaths has a higher probability of happening than death by *M.*

callizona at any given time. As well, the median time to failure (Table 5-5) for other

deaths and disappearances (14.17 months, ranging from 10 to 21 months) is significantly

earlier than that for weevil deaths (33.79 months, ranging from 15 to 58 months).

The impact of weevil deaths on the population of large *T. fasciculata* is greater than

the impact of other modes of death; for *T. utriculata*, other deaths and disappearances

have a greater impact than weevil deaths. Both weevil deaths and other modes of death

for large *T. utriculata* have turn over rates that are higher than those for *T. fasciculata*, as

indicated by *T. utriculata*'s steeper survival curves and earlier median times to failure for

both failure modes.

The population of large *T. fasciculata* in MRSP was composed of 32% large

clumps and 68% individual large plants; large clumps and individual plants lost 40 and

38%, respectively, of their population to weevil deaths. Once infestation was apparent,

individual plants were killed relatively quickly, within a season, much like large *T.*

utriculata plants. Once a weevil infestation became apparent on a large *T. fasciculata*

clump, progress of the infestation could take one to three years before killing the clump.

Clumps continued to seed and make offsets while infested by *M. callizona*, but the rate of

tissue consumption by *M. callizona* exceeded the rate of an infested bromeliad's ability to

regenerate itself.

Weevil infestations occurred locally. When one bromeliad on a bromeliad host tree supporting several large *T. fasciculata* bromeliads became infested, the other plants on the tree would soon become infested, until all or most of the large class-size bromeliads were destroyed. Five Sections on the edge of the *T. fasciculata* population lost all of the large class-size *T. fasciculata* bromeliads and could not be replaced. Large class-size *T. fasciculata* bromeliads in the interior suffered localized losses on trees and, as mentioned above, the infested trees tended to be located near each other. In the interior, there were both infested and un-infested Sections; most Sections contained one to several large class-size *T. fasciculata* plants, including clumps.

Weevil infestations in a large class-size *T. utriculata* progressed quickly, within months. During the first 24 months of the study, 41 large *T. utriculata* had been included in the study. Nine of these were killed by *M. callizona*, 10 went to seed and died, and 8 were washed away in floodwater or rising river water. At the end of 24 months, 13 individuals remained. Over the next two years, eight went to seed and died and 2 were washed away in rising river water. At the end of the study, only four large plants remained. The overall selected population had depleted drastically from the start to the end of the study, and within the study Sections, there were very few large *T. utriculata* noticeable. Unlike large *T. fasciculata*, the loss of large *T. utriculata* was obvious.

In conclusion, *M. callizona* has a much greater preference for medium and large class-size bromeliads. The two life strategies of *T. fasciculata* and *T. utriculata* result in two responses to the attack by *M. callizona*; in essence, *T. fasciculata*, with its large stable populations will have to "outgrow" *M. callizona*, and *T. utriculata*, with its more ephemeral life strategy, will have to "outrun" *M. callizona*.
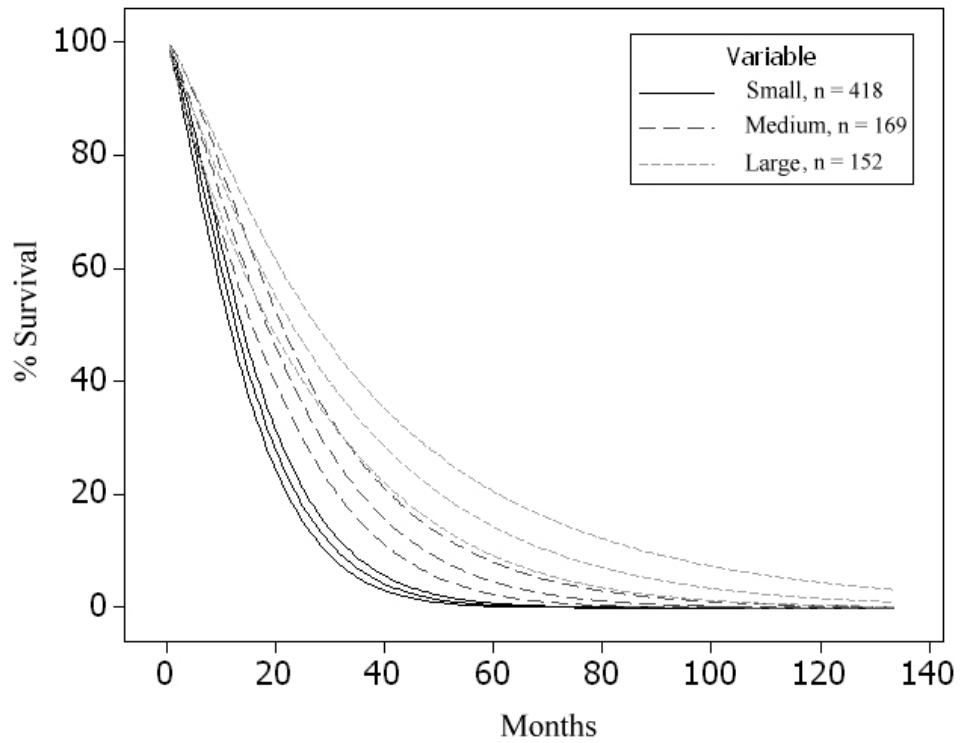
Figure 5-1: Survival plots for small, medium and large class-size bromeliads.

Table 5-1: Test statistics for null hypothesis that all three survival curves are the same for small, medium and large class-size bromeliads.

Method	Chi Square	DF	P-value
Log-Rank	25.6270	2	0.000
Wilcoxon	27.7092	2	0.000
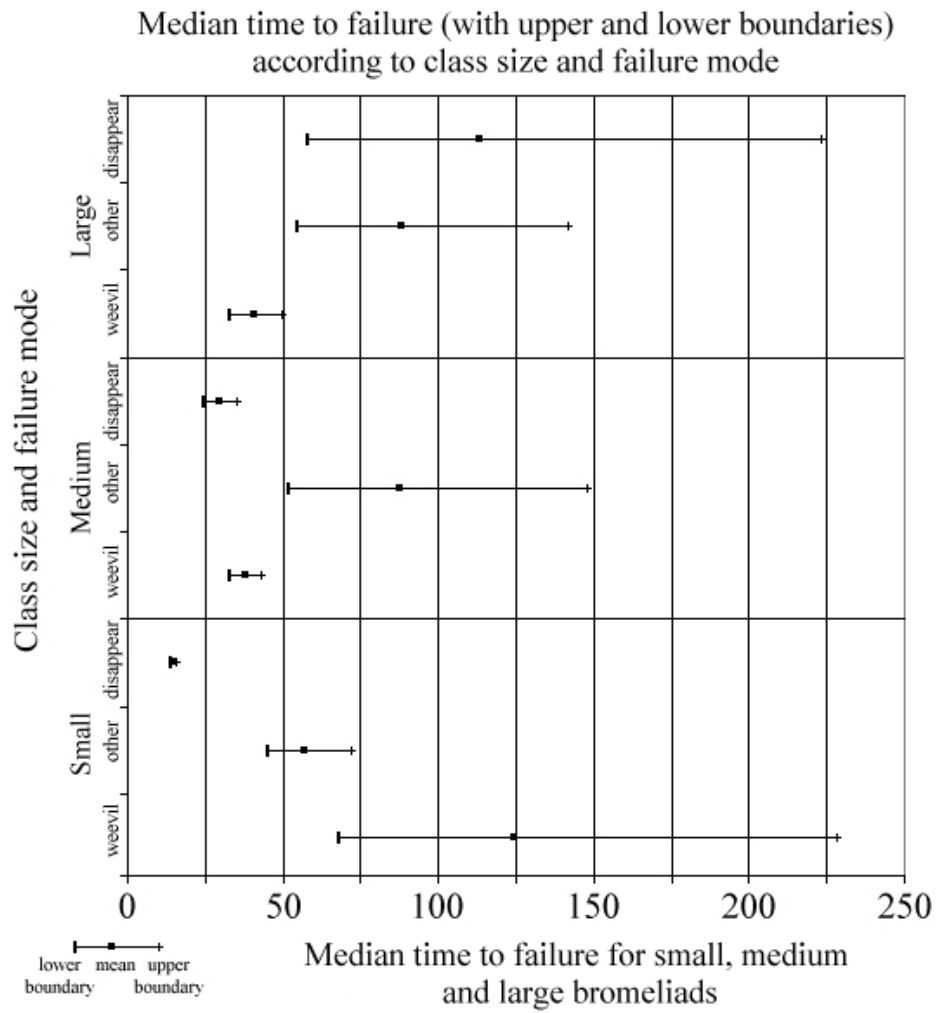
Figure 5-2: Median time to failure with upper and lower boundaries, according to size and mode of failure.

Parametic survival plot, failure modes death and disappearance vs. weevil
Large *Tillandsia fasciculata*; MRSP
(Weibull, 95% CI)
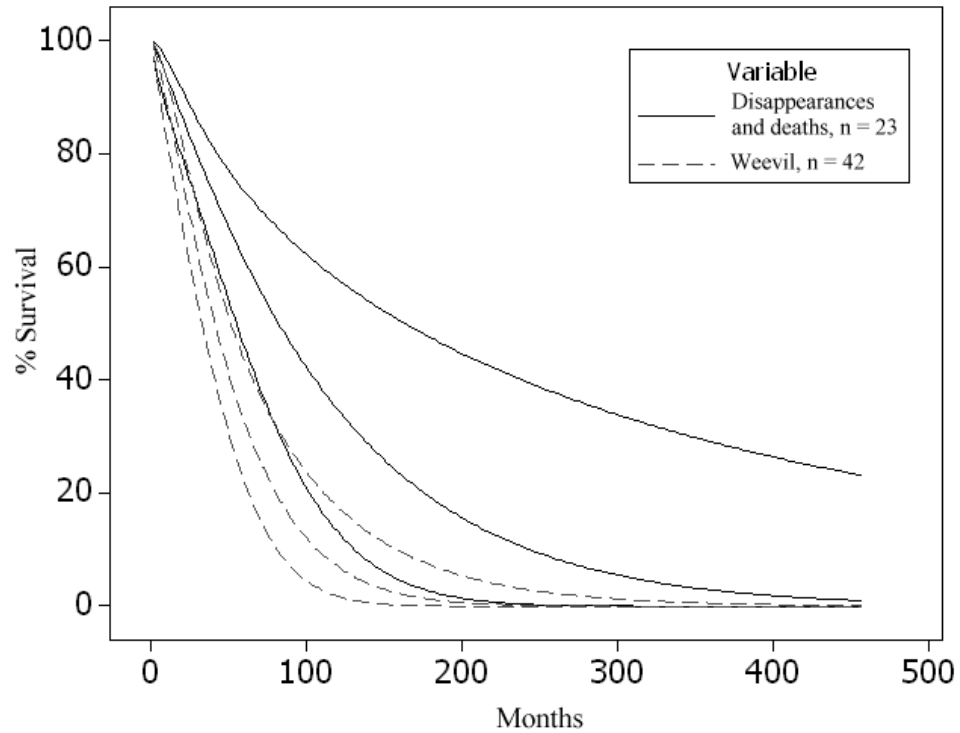
Figure 5-3: Survival curves for two failure modes (death and disappearance, and weevil) for large class-size *Tillandsia fasciculata*.

Table 5-2: Test statistics for null hypothesis that the survival curves are the same for two modes of death (weevil-kill or other-kill) for large class-size *T. fasciculata*.

Method	Chi Square	DF	P-value
Log-Rank	5.63094	1	0.018
Wilcoxon	6.46268	1	0.011

Table 5-3: Median values (months) for failure modes other deaths and disappearances vs. weevil deaths for large class-size *T. fasciculata*.

Other deaths and disappearances			Weevil deaths		
LB	Median	UB	LB	Median	UB
50.15	82.72	133.19	32.48	40.61	50.77

Parametic survival plot, failure modes death and disappearance vs. weevil
Large *Tillandsia utriculata*; MRSP
(Weibull, 95% CI)
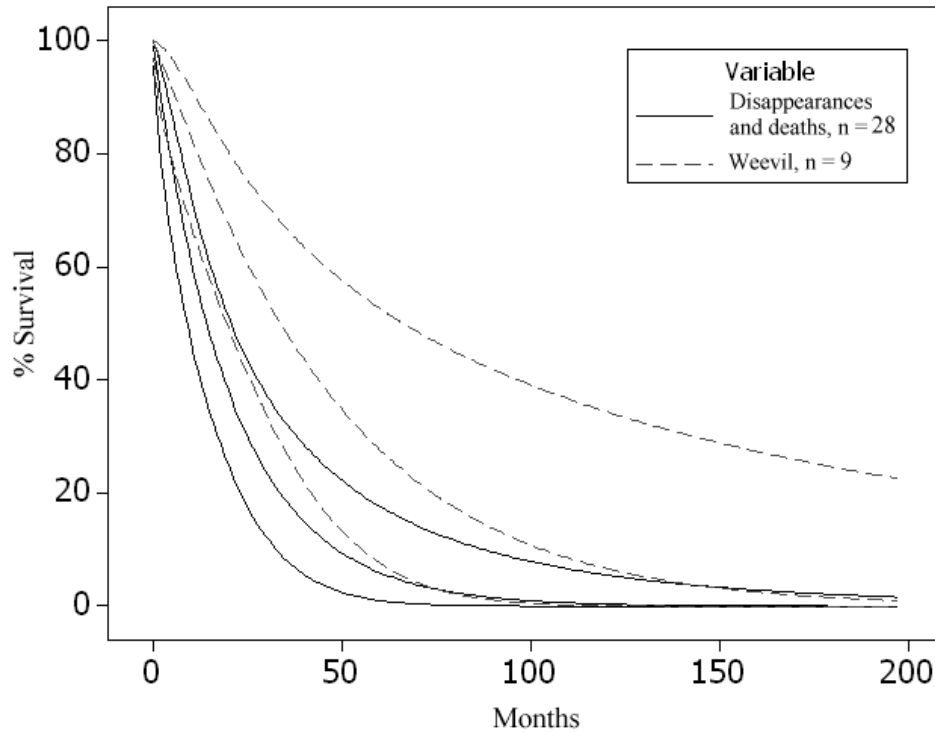
Figure 5-4: Survival curves for two failure modes (death and disappearance, and weevil) for large class-size *Tillandsia utriculata*.

Table 5-4: Test statistics for null hypothesis that the survival curves are the same for two modes of death (weevil-kill or other-kill) for large class-size *T. utriculata*.

Method	Chi Square	DF	*P*-value
Log-Rank	10.0194	1	0.002
Wilcoxon	6.1293	1	0.013

Table 5-5: Median values (months) for failure modes other deaths and disappearances vs. weevil deaths for large class-size *T. utriculata*.

Other deaths and disappearances			Weevil deaths		
LB	Median	UB	LB	Median	UB
9.54	14.17	21.06	14.647	33.79	58.13

CHAPTER 6
Metamasius callizona (CHEVROLAT) AND THE FUTURE OF FLORIDA'S NATIVE
BROMELIADS

Introduction

Since *Metamasius callizona* (Chevrolat) entered Florida and began attacking native

bromeliad populations, many people have been wondering what the future outcome of the

native bromeliad populations will be in the long term. This thesis has attempted to

answer this question to some degree by studying the seasonal trends and patterns

exhibited by *M. callizona* (chapter 3) and some of its host bromeliads (chapter 4), and by

doing survival analysis on different class-sizes of bromeliads and on two species of host

bromeliads with different life strategies, *Tillandsia fasciculata* Swartz and *T. utriculata*

L. (chapter 5).

Because of the large sample sizes required to perform seasonal and survival

analysis, such analyses were performed only on the monitored bromeliad population in

Myakka River State Park, the primary research site. This final chapter will look at the

bromeliad populations in the other four Natural Areas that were monitored, Loxahatchee

National Wildlife Refuge (LNWR), Highlands Hammock State Park (HHSP),

Fakahatchee Strand Preserve State Park (FSSP), and St. Sebastian Buffer Preserve State

Park (SSSP).

Rather than using statistical analysis, this chapter will offer a statistical description

of the bromeliad populations in these five Natural Areas at the end of their respective

monitoring times. By studying these descriptions, a few observations can be made

concerning general trends and patterns that are notable in the different bromeliad

communities and habitats that were represented in this study. This chapter will conclude

by offering some answers to the question of the future outlook for Florida's native

bromeliads.

Methods and Materials

Bromeliads were monitored in five Natural Areas in south Florida: Myakka River

State Park, Loxahatchee National Wildlife Refuge, Highlands Hammock State Park,

Fakahatchee Strand Preserve State Park, and St. Sebastian Buffer Preserve State Park

beginning in June 2001 and ending in June 2005.

The bromeliads selected for monitoring in the five Natural Areas were chosen

based on a multi-tiered method. (See chapter 2 for details on this method and Table A-1

in Appendix A that defines the Tiers). Table B-1 in Appendix B shows the total

hectarage mapped for each Natural Area, the mapping and monitoring schedules, and the

bromeliad species that were monitored.

The selected bromeliad populations were monitored monthly; deaths and

disappearances were recorded along with an assessment on the cause of death or

disappearance. Individual bromeliads were given a unique number and were identified to

species (if possible) and categorized according to size. Size was based on longest leaf

length; Table C-1 in Appendix C gives the leaf length for the species that were included

in this study.

The status of the bromeliad population for each Natural Area was broken down

according to species and categorized as alive, killed by *M. callizona*, killed by cause

other than *M. callizona*, or disappeared. Percentages were plotted as bar graphs for each

Natural Area for *T. fasciculata*, *T. utriculata*, and *Tillandsia balbisiana* Schultes; the results for the remaining species were tabulated.

The fallen, dead bromeliads that were collected monthly from within the Sections were counted for each Natural Area and were categorized as either killed by *M. callizona* or killed by some other cause based on evidence (*M. callizona* specimens found in the plant or other evidence, such as pupal chambers, mined inflorescences, chewed interiors, fallen cores if killed by *M. callizona*; other deaths included rotting material, injuries, going to seed, etc.). These percentages were compared between the Natural Areas.

Results and Discussion

From the data collected in MRSP, survival analysis has shown that the reproductive class of the *T. fasciculata* population suffered greater mortality from *M. callizona* than from other modes of mortality (primarily catastrophic events that resulted in rot or burial after the plant fell from its host, or, the host fell over). The reproductive class of *T. utriculata* suffered a rate of mortality due to *M. callizona* less than that caused by other mortality modes (primarily going to seed and, to a lesser extent, catastrophic events that led to rot or burial; see chapter 3).

Insufficient data were collected in terms of selected bromeliads and/or time monitored to perform survival analysis for bromeliads at the other four Natural Areas (or from the *T. balbisiana* population in MRSP that only included two specimens). Figures 6-1, 6-2 and 6-3 show the percentage of the population that remained alive, that was killed by *M. callizona*, that was killed by a cause other than *M. callizona*, and that disappeared for *T. fasciculata*, *T. utriculata*, and *T. balbisiana*, respectively, in their associated Natural Areas. Direct comparisons cannot be made because the time monitored varied and because the populations contained varying classes-sizes (small,

medium and large). Mortality rates varied between the class sizes; under normal circumstances, small bromeliads of a given species suffer much higher mortality rates than large bromeliads (Benzing 1980); however, medium and large bromeliads suffer greater mortality from *M. callizona* than do small class-sizes (see chapter 3). Figs. 6-1, 6-2 and 6-3 are included to give a description of the population for each Natural Area at the completion of monitoring, and to point out a few general observations. Table 6-1 shows the outcome for the remaining species that were included in the study in small numbers.

For all three species, FSSP had between 70% and 80% of its population remaining alive after 24 months (Figs. 1, 2 and 3). No confirmed *M. callizona* specimens were found at this study site. One dead medium class-size *T. fasciculata* had a pupal chamber found in the center, but it was assessed to be *Metamasius mosieri* Barber, Florida's only native bromeliad-eating weevil. One large *T. utriculata* (the only death in the *T. utriculata* population) died from going to seed. The remaining deaths and disappearances for all three specimens included only small and medium class-size bromeliads and were caused by catastrophic events.

In MRSP, at the end of 49 months, the *T. fasciculata* population had lost 58% of its population, of which 36.5% were killed by *M. callizona* (Fig. 6-1). Losses to the population were obvious along the edge of the population and in localized spots within the population. However, 42% of the population remained alive and, throughout the park, many large *T. fasciculata* plants were noticeable. Monitored bromeliads included only large (and some medium) class-size *T. fasciculata* because it was difficult to make an accurate identification between the medium and small *T. fasciculata* and *T. utriculata*.

Monitored *T. fasciculata* at HHSP consisted of five large plants and one medium. After 33 months, the medium plant and one large plant remained alive. *Metamasius callizona* killed one large plant and the remaining three large plants disappeared due to branch falls and parks personnel doing maintenance work (cleaning up the fallen debris). LNWR and SSSP both had roughly 60% of their monitored *T. fasciculata* alive after 28 and 17 months, respectively; both populations included all class-sizes. LNWR had a higher percentage of plants killed by *M. callizona* than by other deaths, and a lower percentage of disappearances compared to that experienced in SSSP (20% compared to 35%, respectively). SSSP also had a very low percentage of *T. fasciculata* plants killed by *M. callizona*, especially for an area that had an active infestation ongoing; weevil specimens and fallen dead bromeliads with evidence of weevil-kill were found consistently throughout the study, with the exception of the last three months. The high percentage of disappearances was caused primarily by hurricane activity in September 2004; 27 plants (10 small, 6 medium and 11 large) were removed during the storms. Six of the large plants showed possible signs of weevil infestation and this may have contributed to their dislodgement from their host. Both LNWR and SSSP had plants with signs of infestation by *M. callizona* in the remaining population.

In MRSP, at the end of 49 months, the *T. utriculata* population had lost 89% of its population, of which 19% were killed by *M. callizona* (Fig. 6-2). Other deaths (46%) were caused by going to seed, except for one plant. Disappearances (34%) were the result of catastrophic events. HHSP had a similar pattern, with a higher percentage of deaths due to *M. callizona* and fewer deaths and disappearances. FSSP, like HHSP, had a

small population of *T. utriculata*, and, as mentioned above, the one death was due to seed production and the disappearance the result of a catastrophic event.

In MRSP, at the end of 49 months, one of the two *T. balbisiana* plants died from rot and the other disappeared in flood waters (Fig. 6-3). A small percentage (5%) of *T. balbisiana* plants in LNWR was killed by *M. callizona*; none were killed by *M. callizona* in SSSP (though two *T. balbisiana* were killed by *M. mosieri*).

Of the remaining species (*Tillandsia simulata* Small, *T. variabilis* Schlechtendal), *T. paucifolia* Baker, *T. pruinosa* Swartz, and *Guzmania monostachia* L.), most of the populations were relatively stable (Table 6-1). Only one *T. paucifolia* at SSSP was killed by *M. callizona*. Both *T. paucifolia* and *T. pruinosa* lost six of their members to catastrophic events. One *G. monostachia* plant was killed by excessive foliage feeding by the fall webworm, *Hypantria cunea* (Drury) (Lepidoptera: Arctiidae).

Table 6-2 shows the number of dead bromeliads that fell from the canopy and that were collected from each Natural Area. Six hundred fifty-two dead bromeliads fell from the canopy into the study Sections in MRSP; 78% were killed by *M. callizona* and 22% were killed by other factors. In LNWR, 93 dead bromeliads were collected; 71% were killed by *M. callizona*. In HHSP, 31 dead bromeliads were collected; 77% were killed by *M. callizona*.

The percentages of dead bromeliads collected from the ground that were killed by *M. callizona* were rather consistent (within 11%) considering the different habitats and bromeliad communities from which they were collected. As well, they were relatively high (ranging from 71 to 82%), much higher than deaths observed from selected bromeliads in the canopy. This is because death caused by *M. callizona* usually results in

part of the infested plant falling to the ground due to internal chewing by the weevil larva(e) inside the plant; and because most infested plants are medium or large class-size and the fallen mass is large enough to persist.

Roughly half (66 of 129) of the dead bromeliads collected in SSSP were discovered on the initial monitoring trip in the oak hammock. All 66 were dead *T. utriculata* plants, and ranged from old, brown and dried up plants, to plants with soft tissue remaining in the center. They all showed signs of weevil damage and some contained pupal chambers (25 total were collected from the 66 plants) and live weevils (two adults and one larva). There were no remaining *T. utriculata* in the canopy within the demarcated Sections, only *T. fasciculata*. Only a small portion of the hammock was mapped (0.04 hectares); the *T. utriculata* populating the rest of the hammock had suffered the same fate and littered the ground.

Of all the bromeliads so far observed in the field, *T. utriculata* has apparently suffered the most. Situations such as that in the oak hammock in SSSP, the loss of *the T. utriculata* population in LNWR, and the obvious decline in MRSP and HHSP are not isolated events. Devastated *T. utriculata* populations have frequently been observed in south Florida (Frank 1996b). The large and medium class-size plants are being affected the greatest (Chapter 3) and their demise is interfering with *T. utriculata*'s seed production. The slow growth rate (10 to 15 years) to maturity (Benzing 1980, Isley 1987) and the reliance of *T. utriculata* on seed production to supply the following generation have profound effects on the future of this species. Because *T. utriculata* has a patchy distribution and an ephemeral nature, it may escape infestation from *M. callizona* if small patches can reach maturity and go to seed before discovery by *M.*

callizona. However, once a patch is discovered, *M. callizona* can destroy it in a year to a few years. Large patches (such as the patch that once existed in the oak hammock in SSSP) are especially vulnerable because they are more easily found, and just as easily destroyed; and because such large patches are more stable, such losses represent the loss of seed reservoirs and can have profound effects on the continuation of the species.

Tillandsia fasciculata is a more stable bromeliad species that maintains its populations through the production of vegetative offsets as well as by seed production (Benzing 1980, Isley 1987). Individual plants, as they mature and vegetatively propagate, become giant clumps. *Metamasius callizona* may take one to three years to kill an individual clump, and even longer to destroy a population (see chapter 3). It is difficult to assess the long-term outcome of *M. callizona*'s attack on *T. fasciculata*. The process is very slow, but the rate of mortality that is inflicted on the reproductive class is quite high (see chapter 3), and over time, could prove fatal to the species. A more likely outcome is that the population will become greatly reduced, yet be able to maintain a stable *M. callizona* population, from which *M. callizona* could continue to persist in the natural lands, while continuing to spread out and attack other susceptible bromeliad populations, such as those in the Everglades.

Metamasius callizona has been sighted only once, in March 2002, in FSSP, and has since been spotted several times in the Big Cypress National Preserve (Frank 1996b). That *M. callizona* was not found in the study site in FSSP demonstrates only that *M. callizona* has not yet found that very small area within the greater area. FSSP, as well as the Everglades in general, has the highest diversity of Florida's native bromeliads; most are patchily distributed, and many are rare (Benzing 1980). The arrival of *M. callizona*

into this area heralds the potential for the loss of numerous species of bromeliads (Frank and Cave 2005).

Part of the difficulty in determining the future outcome of Florida's native bromeliads in response to *M. callizona* is caused by the number (12) of species that are affected, and the different habitats and life strategies these species have. Factors that will determine the long-term survivability for a particular species of bromeliad include 1) the increased rate of mortality caused by *M. callizona* in relation to the species' ability to outgrow or outrun *M. callizona* attack, 2) the range and rarity of the species, and 3) the distribution of the bromeliad patches.

Survival analysis has shown that *M. callizona* has a great effect on the mortality rate of *T. fasciculata* and *T. utriculata*, but in different ways. The weevil consumes *T. fasciculata* slowly, and the infestation is a long process because of the large biomass and quick growth rate of the vegetative offsets produced by *T. fasciculata*, and because *T. fasciculata* has coriaceous leaves that would be hard to consume and digest (Benzing 1980). In order to survive, *T. fasciculata* must outgrow the weevil. *Tillandsia utriculata*, because it has an ephemeral life style and dies upon going to seed, must outrun the weevil. Infestations move quickly in a patch of *Tillandsia utriculata* because, despite the large body size, the plant has soft, easily consumed leaves and produces no offsets to replace eaten tissue.

It is possible that *M. callizona* exhibits seasonal population increases on *T. utriculata* (in the spring; see chapter 3). This could complicate understanding how *M. callizona* would shift geographically, and how the distribution of bromeliad patches may affect the survivability of some of the patches. While large *T. fasciculata* populations

may support a long-term population of *M. callizona* in a geographic spot, as *T. utriculata* patches move from one location to another, small, localized, and ephemeral outbreaks of *M. callizona* could arise near other bromeliad patches.

This thesis has only examined *T. fasciculata* and *T. utriculata* in great detail, and one can only speculate on how the other species will respond to the weevil infestation. *Guzmania monostachia* (Larson 2000c) is a large bromeliad that reproduces both vegetatively and by seed; its range is restricted to the lower tip of the peninsula, but large populations can be found. Individual plants grow as giant clumps, much like *T. fasciculata*; however, *G. monostachia* has soft leaves, softer than *T. utriculata*. *Guzmania monostachia*, with such large populations, may not be able to outrun *M. callizona*; will it be able to outgrow the weevil, or will the weevil be able to quickly consume the plant's soft tissue?

Tillandsia pruinosa is a very rare plant with a range limited to Collier County in the southern end of the peninsula (Larson 2000c). It is a small plant, only reaching about 25 cm long and it has tough leaves; it grows in small patches both by vegetative offsets and by seed. It is unknown how this plant will react to an attack by *M. callizona*; however, the very rarity of the species and the small patches make this plant vulnerable to any added stresses. *Metamasius callizona* has not been observed attacking *M. pruinosa* (Frank and Cave 2005), however it is a safe assumption that *T. pruinosa* would be susceptible to attack by *M. callizona* because the plant has enough biomass to support larval growth and because *M. callizona* has been observed attacking a similar, wider ranging species, *T. paucifolia*.

There are several other bromeliads that are rare and that grow in small patches, including three *Catopsis* species and *T. variabilis*; as well as some with wider ranges, including *T. simulata*, Florida's only precinctive species of bromeliad (Larson 2000c). Canopy scientists have broadened our understanding of canopy ecosystems, and biological control has increased our understanding of invasive species, but there is still much to learn about both of these topics. The lack of information available on bromeliads in general, on Florida's bromeliads in particular, and on bromeliad-eating weevils is pronounced. The weevil infestation in Florida is unfortunate; however, it has opened an opportunity and a need to learn more about Florida's native bromeliads and about bromeliad-eating weevils. The more urgent tasks are to continue research on the potential biological control agent, the tachinid fly *Lixadmontia franki* Wood and Cave, which is in quarantine at the UF-IFAS Biological Control Research and Containment Laboratory in Ft. Pierce. The objective is to rear the fly in great enough quantity that it can be released into natural areas, become established, and reduce the *M. callizona* population by parasitizing the weevil larvae. Post-monitoring will be necessary to know the results of this process.
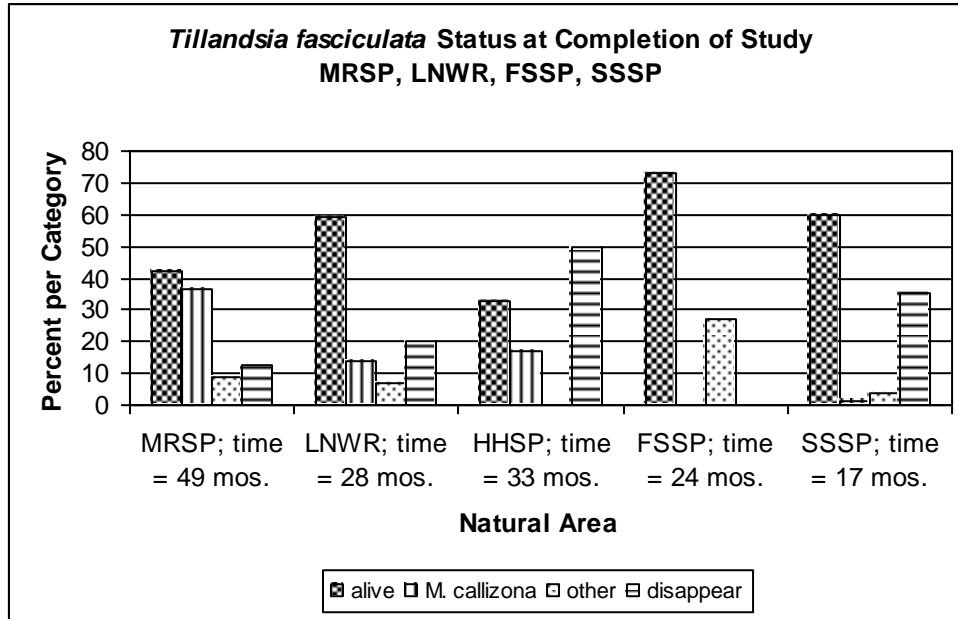
Figure 6-1: Status of *Tillandsia fasciculata* bromeliads (given as a percentage in the following categories: Alive; killed by *M. callizona*; killed by cause other than *M. callizona*; or disappeared) in MRSP, LNWR, HHSP, FSSP, and SSSP.
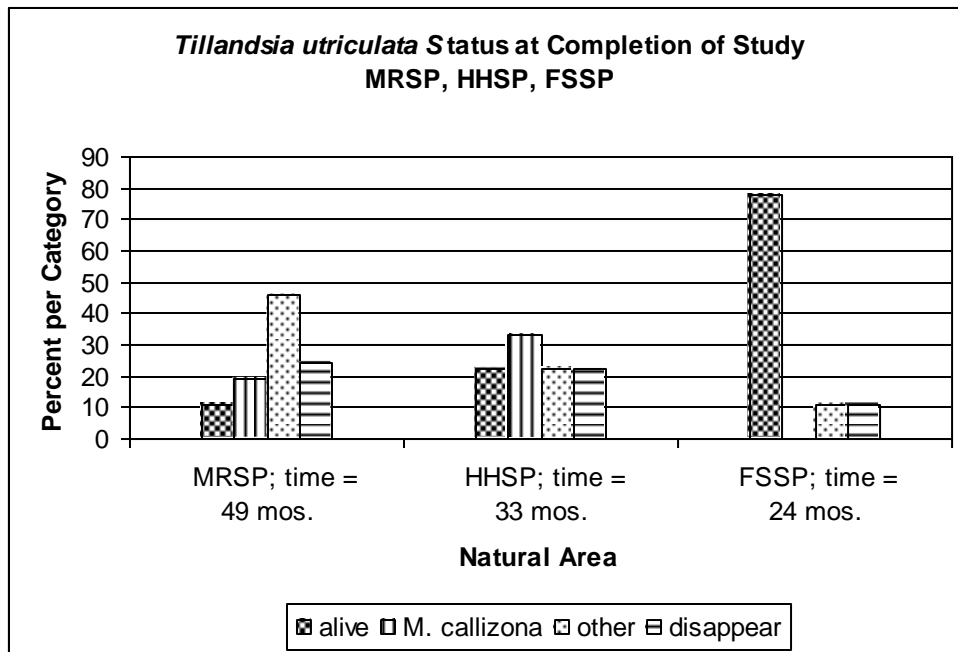
Figure 6-2: Status of *Tillandsia utriculata* bromeliads (given as a percentage in the following categories: Alive; killed by *M. callizona*; killed by cause other than *M. callizona*; or disappeared) in MRSP, HHSP, and FSSP.
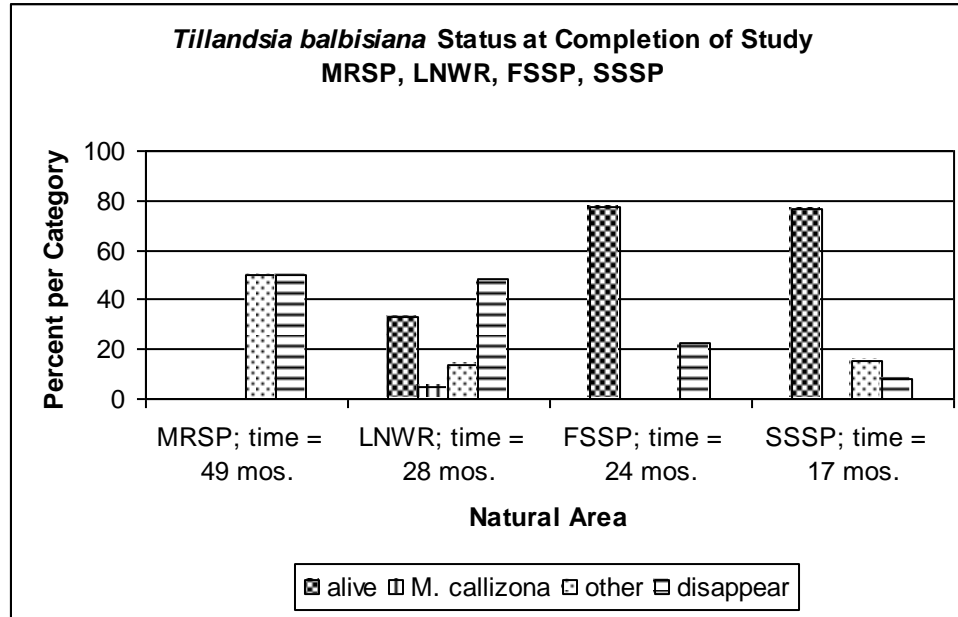
Figure 6-3: Status of *Tillandsia balbisiana* bromeliads (given as a percentage in the
following categories: Alive; killed by *M. callizona*; killed by cause other than
M. callizona; or disappeared) in MRSP, LNWR, FSSP, and SSSP.

Table 6-1: Other species of bromeliads monitored in HHSP, FSSP and SSSP and
condition at end of monitoring period.

Species	HHSP (at 33 months)	FSSP (at 24 months)	SSSP (at 17 months)
Tillandsia simulata	2 (alive)	--	2 (alive)
Tillandsia variabilis	--	2 (alive)	--
Tillandsia paucifolia	--	--	6 (alive) 1 (*M. callizona*) 6 (disappear)
Tillandsia pruinosa	--	16 (alive) 6 (disappear)	--
Guzmania monostachia	--	10 (alive) 1 (other)	--

Table 6-2: Total number of dead bromeliads fallen from canopy into mapped Sections, collected, and categorized as percent killed by *M. callizona* or killed by cause other than *M. callizona*.

Natural Area	Months monitored	Total Number Fallout	% - *M. callizona*	% - other
MRSP	49	652	78%	22%
LNWR	28	93	71%	29%
HHSP	33	31	77%	23%
FSSP	24	9	0%	100%
SSSP	17	158	82%	18%

APPENDIX A
METHOD TIERS

Table A-1: Description and parameters for the five tiers used to define demarcated
Sections and Bromeliad Hosts.

Tier	Description	Parameters
I Natural Areas	State and Federal Parks and Refuges.	Bromeliad-supporting habitat present.
II Region	Bromeliad-supporting habitat in the Natural Areas.	At least 10 bromeliad hosts must make up this tier at the initial mapping; there is no upper limit.
III Area	Regions were divided into Areas based on bromeliad host density and local landmarks that defined the Area. A Region could have 1 or more Areas; upper limit was defined by the habitat, or by limitations in resources and time.	10 – 100 bromeliad hosts per Area must be present in an area at the initial mapping.
IV Section	Areas were divided into sections based on bromeliad host density. An Area could have 3 to 10 Sections. Of these Sections, half (or half of the Sections + 0.5, if there was an odd number of Sections) were randomly selected for monitoring – collecting weevil specimens from dead bromeliads monthly.	3-10 bromeliad hosts per Section must be present in a Section at the initial mapping.
V Bromeliad host	Each Section contained 3 to 10 bromeliad hosts; of these bromeliad hosts, half (or half of the bromeliad hosts + 0.5, if there was an odd number of Sections) were randomly selected for monitoring. Bromeliad hosts were sketched from a particular direction and the bromeliads growing on the host were indicated on the sketch; these are the bromeliads that were monitored monthly.	Bromeliads included in the sketch were selected based on apparency, that is, those that were most obvious. If the bromeliad host were covered with numerous bromeliads, then up to 15 were included. If these bromeliads died or disappeared, then the bromeliad host would be examined for any other bromeliads; if any were found, they replaced the lost bromeliads and were monitored; if no other bromeliads could be found on the host, then another bromeliad host in the Section was randomly selected for monitoring. Updates to replace lost or dead bromeliads were made every six months.

APPENDIX B
MAPPING SCHEDULE

Table B-1: Total hectarage mapped for each Natural Area, mapping and monitoring schedules, and bromeliad species susceptible to weevil attack present for each of the five Natural Areas.

Natural Area	Hectares mapped	Mapping schedule	Bromeliad species
MRSP	2.98	June 2001 – Initial mapping; began monitoring. December 2001 – Added five new Areas. February 2002 – Added 1 new Region and 1 new Area. June 2005 – Ended study.	*Tillandsia fasciculata* Swartz *Tillandsia utriculata* Linnaeus *Tillandsia balbisiana* Schultes
LNWR	0.05	April 2002 – Initial mapping; begin monitoring. March 2003 – Added 1 new Region. February 2005 – Ended monitoring.	*Tillandsia fasciculata* Swartz *Tillandsia balbisiana* Schultes
HHSP	0.45	August 2002 – Initial mapping; began monitoring. September 2002 – Added 1 new Region. April 2005 – Ended monitoring.	*Tillandsia fasciculata* Swartz *Tillandsia utriculata* Linnaeus *Tillandsia balbisiana* Schultes *Tillandsia simulata* Small
FSSP	0.04	March 2003 – Initial mapping; began monitoring. March 2005 – Ended monitoring	*Tillandsia fasciculata* Swartz *Tillandsia utriculata* Linnaeus *Tillandsia balbisiana* Schultes *Tillandsia variabilis* Schlechtendal *Guzmania monostachia* (Linnaeus) *Tillandsia pruinosa* Swartz
SSSP	0.57	November 2003 - Initial mapping; began monitoring. March 2005 – Ended monitoring.	*Tillandsia fasciculata* Swartz *Tillandsia utriculata* Linnaeus *Tillandsia balbisiana* Schultes *Tillandsia paucifolia* Baker

APPENDIX C
LONGEST LEAF LENGTH

Table C-1: Size classifications, defined by longest leaf length, for the bromeliad species
in this study.

Longest Leaf Size Categories (cm)			
Species	Small	Medium	Large
Tillandsia fasciculata	≤ 15	15-60	> 60
Tillandsia utriculata	≤ 15	15-60	> 60
Tillandsia balbisiana	≤ 5	5-15	> 15
Tillandsia simulata	≤ 5	5-15	> 15
Tillandsia variabilis	≤ 10	10-30	> 30
Guzmania monostachia	≤ 15	15-60	> 60
Tillandsia paucifolia	≤ 2.5	2.5-5	> 5
Tillandsia pruinosa	≤ 2.5	2.5-5	> 5

APPENDIX D
HEALTH RATINGS

Table D-1: Health rating chart showing the classifications for the four quarters of the physiological condition scale.

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3.0 ┌──────────────────────────────────────────────────────┐
    │  First quarter (healthy):                            │
    │  At 3.0, the bromeliad has good, strong green color  │
    │  and no discoloration; no obvious injuries; and      │
    │  turgid leaves.  As the health rating falls to 2.5,  │
    │  there may be a few injuries or minor discoloration, │
    │  but nothing serious.                                │
2.5 │  ──    ──    ──    ──    ──    ──                     │
    │                                                      │
    │  Second quarter (moderately stressed):               │
    │  Outward stresses are more apparent; leaves chewed,  │
    │  moderate discoloration; slight desiccation or       │
    │  freeze trauma.  If the stresses were removed, the   │
    │  plant would likely recover.                         │
2.0 ├──────────────────────────────────────────────────────┤
    │                                                      │
    │  Third quarter (heavily stressed):                   │
    │  Heavy injury, major discoloration or browning of    │
    │  leaves covering up to half of the plant's biomass;  │
    │  core leaves falling out; severe frost or drought    │
    │  damage.  If the stress or injuries were removed,    │
    │  the plant might recover, but would suffer long-term │
    │  consequences from the experience.                   │
1.5 │  ──    ──    ──    ──    ──    ──                     │
    │  Fourth quarter (seriously stressed):                │
    │  Very poor health; heavy injury and/or loss of       │
    │  leaves affecting more than half of the plant's      │
    │  biomass; core missing; severe discoloration.        │
    │  Death = 1.0 = no green tissue on plant.             │
1.0 └──────────────────────────────────────────────────────┘
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BIOGRAPHICAL SKETCH

Teresa M. Cooper was born in Rhode Island, USA, in 1966. She attended Eastern Kentucky University (Richmond, Kentucky) from September 1990 to December 1992. She moved to Florida in the spring of 1993 and graduated from Santa Fe Community College (Gainesville, Florida) in 1995 with an Associate of Science in environmental science. In 2002, she received her Bachelor of Science in entomology, specializing in plant protection, from the University of Florida (Gainesville, Florida). During her undergraduate years, she started field research monitoring an invasive bromeliad-eating weevil that was attacking Florida's native bromeliads; she carried this research into her graduate studies at the Entomology and Nematology Department in the University of Florida, and it has culminated in this thesis.