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Insect Abundance In Relation To Capuchin (*Cebus capucinus*) Foraging: Fallback Foods In A Costa Rican Tropical Dry Forest

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Insect Abundance In Relation To Capuchin (*Cebus capucinus*) Foraging: Fallback Foods In A
Costa Rican Tropical Dry Forest

by

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A THESIS
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Abstract

There is a paucity of literature on tropical insect abundance, especially in tropical dry forests, and white-faced capuchin fallback foods have only recently been studied. I predicted that insects overall would be seasonal, but abundant throughout the year and hypothesized that insects are fallback foods in the capuchin diet. I measured insect abundance while simultaneously recording capuchin foraging in a tropical dry forest. I found that overall insect abundance was seasonal, although most Orders and Families that I identified were aseasonal and insects remained abundant throughout the year. Abiotic and biotic factors affected some insect Order and Family abundance patterns. Capuchins consumed insects more frequently during a period of overall food abundance and spent more time foraging extractively on pith and bromeliad leaves, which were consumed more frequently during a period of food scarcity. I conclude that white-faced capuchins likely fall back on pith and bromeliad leaves, not insects.

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Dedication

I dedicate this thesis to my parents. Thank you Mom and Dad for being unconditionally supportive in whatever I do. I would not have achieved anything without your love and willingness to drop everything anytime I needed to chat. I love you.

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Chapter One: Introduction

1.1 Project goals

Many animals, including primates, can adapt to resource abundance fluctuations by including more of a resource they would usually avoid or consume little of (MacArthur and Pianka 1966; Charnov 1976), i.e. a fallback food. Researchers have recognized the evolutionary implications of fallback foods for some time (Constantino and Wright 2009), and adaptations involving use of fallback foods have been documented across a wide array of organisms (Harrison and Marshall 2011; Lambert et al. 2004; Wright et al 2009; Robinson and Wilson 1998; Grant et al. 1985). The literature on fallback food often cites the seminal work of Peter and Rosemary Grant (e.g., Grant and Grant 1993, 1987; Grant et al. 1985). They found that in the Galapagos, average finch beak size of the species *Geospiza fortis* –highly variable in beak size- shifted towards larger beak size in future generations after a short, but severe drought depleted small seeds and left mainly large seeds. Only those finches with larger beaks could access the larger seeds that remained. The larger seeds are considered a fallback food for *G. fortis* and had a profound influence on the morphology of a population of *G. fortis*. The work of (Robinson and Wilson 1998) is also often cited; they argued that the reason for diverse feeding anatomy in African cichlids is specializations for fallback foods that the fish have evolved while still maintaining the ability to forage for preferred foods, hence broadening their environmental niche. The evolutionary implications of fallback food strategies for primates have only recently come to our attention and are in need of additional research (Constantino and Wright 2009). The present study addresses this need by examining fallback foods in the white-faced capuchin (*Cebus capucinus*) diet.

The aim of this thesis is to evaluate the interaction between insects and white-faced capuchins in a highly seasonal environment, a tropical dry forest. I evaluate whether insect abundance and seasonality patterns are related to capuchin seasonal foraging patterns. I also assess the effects that various biotic and abiotic factors have on insect abundance. Insect abundance and seasonality in tropical ecosystems is highly understudied (Wolda 1988). This study contributes to these two topics: tropical insect abundance and primate fallback foods.

1.2 Background

Optimal foraging theory suggests organisms should consume foods that are high in energy, but low in cost, therefore maximizing energy gain (MacArthur and Pianka 1966). Easily accessed and processed foods allow such maximization when they are available. However, high energy/low costs foods, such as fruit, are typically seasonal in a tropical environmental. Dry seasons can bring about very low food availability for omnivores, frugivores, folivores and insectivores (Doran-Sheehy et al. 2009; Marshall et al. 2009; Vogel et al. 2009; Lambert et al. 2004; Furuichi et al 2001; Porter 2001; Grant and Grant 1993). Extreme environmental conditions, such as severely dry seasons and resource-depleted years, can force organisms to rely more heavily on fallback foods than they would during a typical year (e.g. Grant and Grant 1987).

Seasonal environments facilitate dietary and life history adaptations more so than aseasonal environments (Gogarten et al. 2012; Lambert 2007; Janzen 2004). Tropical dry forests are highly seasonal habitats in which rain does not fall for six months of the year and then rain can fall as heavily as that in a rainforest for a few months of the year (Janzen 1988b). Such seasonality has profound impacts on many ecological processes, including dietary strategies in

capuchins (Melin et al., in press) and life history strategies in insects (Janzen 2004). Furthermore, the seasonality of insects may drive dietary strategies in capuchins (Melin et al., in press). Insect abundance data in concordance with capuchin foraging behaviour is needed to assess the interaction (at least one-way) between capuchins and insects. This study is the first to present such data.

Both capuchins and insects are affected by drastic seasonal shifts each year. For example, capuchin fruit foraging patterns tend to follow fruit abundance fluctuations (Melin et al., in press) and fruiting patterns tend to follow rainfall patterns (Levey 1988; Fleming et al 1987). Insects also tend to follow rain patterns, yet little is known about specific interactions between tropical insects, rain and other biotic and abiotic factors (Wolda 1988). Insects are a proposed fallback food in the capuchin diet (Melin et al., in press) –a seasonally important food. Animal fallback foods, such as insects, are a suggested mechanism facilitating primate range expansion into dry areas (Yamagiwa and Basabose 2009). Many fallback food adaptations have been investigated in the primate diet including both morphological and behavioural adaptations (Marshall et al. 2009). Melin et al. (in press) suggest consumption of invertebrates as fallback foods selected for extractive foraging behaviour in the capuchin diet. This study relates food abundance, including insect abundance, to capuchin foraging behaviour to gain further insight into the role insects play in the capuchin diet. My fundamental research question is: Are insects fallback foods in the capuchin diet?

1.3 Fallback food and related definitions

"Preferred" foods are often assumed "important" resulting in underestimating the value of "fallback" foods (Marshall et al. 2009). It is helpful to first understand what a preferred food is and what an important food is in order to understand what a fallback food is.

Preferred foods are typically seasonal (not always available in the environment) and are high quality foods. Quality, in this case, refers to nutrient quantity and concentration. Preferred foods tend to be patchily distributed, therefore, the forager must travel to find the food, but once located the food is easily processed and consumed. A preferred food is usually easily processed because they do not have a protective shell or defense mechanism that the consumer must overcome to ingest the edible part of the food. Fruit is usually considered a preferred food in the primate diet because it is high in sugar (a readily available energy) as well as fat and protein (high energy nutrients), is patchily distributed and is easily processed (Marshall and Wrangham 2007).

Important foods contribute to a high percentage of foraging or feeding time but are not necessarily preferred foods. A food is both important and preferred when it constitutes a large part of the diet, is high in quality, patchily distributed and seasonal.

Finally, when a food constitutes a large part of the diet during periods of low overall or preferred food abundance and is available when overall food abundance is low, it is deemed a fallback food (Harrison and Marshall 2011; Marshall and Wrangham 2007). Thus, fallback foods are never preferred, but they can be important (Marshall and Wrangham 2007). They are often uniformly distributed, but difficult to process and are usually low quality. The difficulty processing a fallback food can often select for morphological or behavioural adaptations (e.g., Makedonska et al 2012; Wright et al 2009; Lambert 2007; Marshall and Wrangham 2007;

Lambert et al. 2004; Yamakoshi 1998). The act of processing a food refers to removing or opening a protective layer (usually hard or tough in nature) or surmounting a defense mechanism that is mechanical (e.g. spines) or chemical (e.g. secondary compounds). There are two types of fallback foods, staple and filler. Staple fallback foods constitute up to 100% of the diet when preferred foods are scarce (Marshall and Wrangham 2007). Filler fallback foods do not constitute the entire diet but can supplement a diet that includes preferred foods (Marshall and Wrangham 2007). Marshall et al. (2009) suggest filler fallback foods are of higher quality than staple fallback foods, however there is overlap.

1.4 Fallback foods in the capuchin diet

Wright et al. (2009) attribute the broad niche tufted capuchins exploit to the robust jaw morphology of *Sapajus apella* and to the tool use behaviour of *S. libidinosus*. *S. libidinosus* are found in drier, more seasonal sites whereas *S. apella* are found in less variable rainforest –indeed a broad niche for a genus compared to most primates. Each species exploits different niches within each ecosystem: *S. libidinosus* is mainly terrestrial and *S. apella* is mainly arboreal. Terrestriality of *S. libidinosus*, along with their limbs of relatively intermediate length compared to other tufted and untufted capuchins, facilitate tool use. In contrast, the long limbed, untufted *Cebus olivaceus* and the short limbed, tufted *S. apella*. *S. apella*, do not use tools and, in addition to their more robust jaws, *S. apella* exhibit enhanced manual dexterity to access fallback foods in trees. All capuchin monkeys exhibit manual dexterity often in the form of extractive foraging. Untufted capuchins like *C. olivaceus* or *C. capucinus* forage extractively for embedded foods, yet do not have robust craniodental anatomy. The lack of robust morphology is presumably due to low overall dietary toughness compared to the tufted capuchin diet. Wright, et al. (2009)

conclude that this is true when comparing the diets of tufted capuchins versus the diet of *C. olivaceus*. Relative dietary comparisons with *C. capucinus* are lacking, but it is likely that their diet is similar in toughness to that of *C. olivaceus* reiterating that *C. capucinus* lack robust craniodental morphology, but do forage extractively.

The fallback foods consumed by *S. apella* and *S. libidinosus* (e.g., embedded invertebrates and palm nuts, respectively) constitute nearly 100% of the diet during times of food scarcity; therefore these foods qualify as “staple” fallback foods (Wright et al. 2009; Marshall and Wrangham 2007). Makedonska et al (2012) suggest that the robust facial and cranial morphology of *S. apella* is due to the frequent use of the face and cranium to access very tough staple fallback foods. In contrast, the untufted *C. capucinus* diet does not consist of staple fallback foods, but rather “filler” fallback foods because a single food never constitutes the entire diet (Melin et al., in press). Filler fallback foods, rather than staple fallback foods, place less selection pressure on morphological adaptations and more on behavioural adaptations (Marshall et al. 2009). *C. capucinus* do not exhibit morphological adaptations associated with their diet, but behavioural specializations have evolved, like extractive foraging, presumably due to the filler fallback foods in their diet (Melin et al., in press). The present study considers food availability and time spent processing foods to define *C. capucinus* fallback foods and not food quality.

Melin et al. (in press) suggest that extractive foraging, a manually dextrous behaviour, is a fallback food strategy in the *C. capucinus* diet. The extractive foraging behaviour exhibited by *C. capucinus* is a suggested adaptation to invertebrate fallback foods (Melin et al., in press). However, invertebrate abundance data were not previously available to assess whether capuchin insectivory fulfills a crucial element of the fallback food definition: that invertebrates are abundant during times of food scarcity. This study provides insect abundance data and examines

extractive foraging as a fallback food strategy of the untufted *C. capucinus* in a highly seasonal environment –a tropical dry forest.

1.5 Resource availability and primate insectivory

A primate can only fallback on a food if that food is available to a primate during times of food scarcity (Harrison and Marshall 2011; Marshall et al. 2009; Lambert 2007; Marshall and Wrangham 2007). Primates call fallback on a variety of resources, including palm nuts, pith, terrestrial herbaceous vegetation, and insects, depending on what is available to them in their environment (e.g., Harrison and Marshall 2011; Thorén et al. 2011; Altmann 2009; Doran-Sheehy et al. 2009; Wright et al. 2009; Fox et al. 2004; Conklin-Brittain et al. 2001; Conklin-Brittain et al. 1998; Malenky and Wrangham 1994).

An abundant source of insects available in a primate's environment allows a primate to shift their diet to those insects that are available during times of overall or preferred food scarcity (e.g. spectral tarsier (*Tarsius spectrum*) (Gursky 2000), chimpanzees (*Pan troglodytes*) (Yamagiwa and Basabose 2009; Schöning et al. 2007)). The shift to consuming insects during times of food scarcity can select for adaptive traits such as tool use in chimpanzees (McGrew 1974) or large size and efficient locomotion exhibited by patas monkeys (Isbell et al. 1998). These examples suggest that insects can be a fallback food strategy for some primates.

The importance of insects in the primate diet can vary from study to study. For example, (Tashiro 2005) found L'Hoest's monkeys (*Cercopithecus lhoesti*) spent 66% of their foraging time on insects in the Kalinzu Forest in Uganda while Tolo (2008) found the l'Hoest's monkeys, also in Kalinzu, spent more time consuming plant matter (53%) than invertebrates (47%). Such variation could be due to interannual insect abundance variation or perhaps population

differences in insectivory like that found in chimpanzee (*Pan troglodytes vellerosus*) army ant eating between Bossou, Guinea and Taï, Ivory Coast (Schöning et al. 2008). On the other hand, the environment can also influence insectivory: chimpanzees in open-spaces in Gombe National Park, Tanzania consume termites (Goodall 1963 as cited in Hladik 1988) while chimpanzees in the closed equatorial rainforests of Gabon consume ants (Hladik 1977b as cited in Hladik 1988). The variation found across studies and sites emphasizes the importance of studying insectivory regularly and across multiple groups or populations and the danger in extrapolating observations from one study to describe universal insectivory across a species.

There are few studies on primates that conclude whether insects are indeed fallback foods. Resource abundance data are lacking in published work preventing the identification of fallback foods (Constantino and Wright 2009; Lambert 2009; Marshall et al. 2009). One study on a population of chimpanzees in the seasonally dry Kahuzi-Biega National Park in the Democratic Republic of the Congo concluded the chimpanzees fallback on a variety of insects (Yamagiwa and Basabose 2009). Because capuchins can be considered similar to chimpanzees in their foraging adaptations (Sayers and Lovejoy 2008) and the capuchins in my study live in seasonally dry environment, it is possible that capuchins also use insects as fallback foods.

Dichromatic white-faced capuchins are more successful at capturing camouflaged insects on substrate surfaces while trichromatic capuchins more successful at capturing insects that require extractive foraging behaviour, suggesting insects pose selective pressure on capuchin colour vision (Melin et al. 2007). In addition, extractive foraging is thought to have evolved through capuchin insectivory – fueling the large brain to body-size ratio capuchins are so well known for (Parker and Gibson 1979, 1977). Extractive foraging for insects by capuchins increases significantly during times of overall food scarcity suggesting that insects are fallback

foods (Melin et al.). McCabe and Fedigan (2007) found that insects contain more protein than other food sources in the capuchin diet (e.g. seeds), which further supports that insects are an important resource to the capuchins –a fallback food requirement (Marshall et al. 2009). In contrast, highly nutritious caterpillars (Leug 1968 as cited in (Altmann 2009) are thought to play a preferred role in the capuchin diet as they are seasonally abundant (Janzen 1988b). Other primates have shown preference for caterpillars: (Altmann 2009) found baboons shifted their diet to primarily caterpillars when a sudden influx of caterpillars appeared in the Amboseli basin in Kenya. Capuchins in Santa Rosa shift their diet to consume more caterpillars when caterpillars are abundant (Melin et al., in press).

Insects play a variety of roles in primates diets, and there is evidence based on capuchin foraging strategies and adaptations suggesting insects are fallback foods in the capuchin diet. Insect abundance data simultaneously collected with capuchin foraging is the limiting factor missing from the literature to conclude that insects are in fact fallback foods in the capuchin diet. I measure insect abundance in this study and also assess abiotic and biotic factors that may affect insect abundance.

1.6 Factors affecting tropical insect abundance

1.6.1 Rainfall and temperature

Tropical insects are usually abundant with high rainfall (da Silva et al 2011; Andresen 2007; Murali and Sukumar 1993; Tanaka and Tanaka 1982). When assessing the effect of rainfall at the Order and Family level, however, some Orders and Families may be abundant during drier times of the year (Denlinger 1980) while others are abundant with high rainfall (da Silva et al 2011; Frith and Frith 1990; Janzen 1983). Furthermore, although insects may show a positive

correlation with rainfall, rainfall may not explain insect abundance patterns (Pinheiro et al. 2002; Wolda 1989) In addition, these patterns may vary from year to year and are not extrapolatable across sites (Wolda 1988).

Janzen and Schoener (1968) suggested a list of reasons why insects exist in drier areas, one being that both ambient temperature as well as soil temperature are too high. Otherwise, there have not been many studies demonstrating a direct effect of temperature on insect abundance in the tropics.

1.6.2 Phenology and humidity

Insect abundance patterns are not necessarily correlated with rainfall itself, but often with the general effect rainfall has on the ecosystem (Wolda 1989). Insects can be positively affected by humidity rather than actual rainfall (Janzen 1973a; Janzen and Schoener 1968).

Janzen and Schoener (1968) relate their insect abundance data to plant availability in each habitat type. Leaf phenology has been shown to have an effect on relative insect abundance across several taxa in tropical areas (Richards and Windsor 2007; Janzen 2004; Janzen 1988b; Janzen and Schoener 1968). Despite extensive research, there remain many unknowns in the effects that abiotic and biotic factors have on caterpillars in Santa Rosa (Janzen 2004).

Other studies in seasonal tropical forests have found flower phenology to have a positive effect on insect abundance (e.g., Kato et al. 2000; Pipkin et al 1966). Such relationships are likely related to pollination strategies exhibited by plants. Strategies such as that of the seed bug (*Jadera aeola*) in Panama emerging after an influx of seeds from its food source (Tanaka et al 1987) is likely a seed predation strategy by the insect. The ecological relationships between

insects and plants influence insect abundance patterns iterating the impact plant phenology might have on insect abundance studies.

1.6.3 Parasitoids

Parasitoids can drive seasonality in an aseasonal tropical environment (e.g. Lepidoptera, Godfray and Hassell 1989) as well as seasonal tropical environments (e.g. caterpillars, Janzen 1988b). In contrast, increased variability in precipitation (i.e. degree of seasonality) across different tropical ecosystems can induce a decrease in parasitism on reared caterpillars, suggesting that parasitoids are sensitive to climate as well as to host population dynamics (Stireman et al. 2005). Predation, on the other hand, can have a greater effect on their host populations in the tropics (Hawkins et al. 1997). Studying parasitism and predation on insects is particularly challenging in natural settings, therefore data, especially from the tropics, are limited.

1.6.4 Migration

Insect migration within the tropics is considered to be a small-scale version of insect migration between temperate and tropical regions (e.g. the great migrations of the monarch butterfly) (Janzen 2004). Tropical insect migrations may be driven by predator/prey interactions where insects residing in rainforests or cloud forests migrate to tropical dry forests during the rainy season when many insects preyed upon are abundant (Janzen 2004). Janzen (2004) describes these potential scenarios with empirical data from Janzen and Schoener (1968) and Janzen (1973a; 1973b). Both studies described by Janzen (2004) studied migration across rainforests, cloud forests and tropical dry forests in the Área de Conservación Guanacaste (ACG), Costa Rica.

1.7 Synopsis

Empirical studies describing tropical insect abundance and the effects of abiotic and biotic factors on insect abundance and seasonality is lacking (Wolda 1988). Studies of capuchin fallback foods are limited to comparisons between gracile and robust capuchins, usually reflecting their ability to use tools as well as the morphological adaptations associated with their diet (Wright et al 2009). White-faced capuchins in my study site do not use tools and do not exhibit morphological adaptations to their diet. In this study, I aim to measure relative insect abundance and compare it with white-faced capuchin foraging patterns to assess whether insects are fallback foods in the capuchin diet. In addition, I analyze the effect of abiotic and biotic factors against insect abundance throughout each season in a tropical dry forest. I record the effects of seasonality both on capuchins as well as insects and describe the interactions between capuchins and the insects in their diet as well as other food types.

1.8 Study species

White-faced capuchins (*Cebus capucinus*) range from Honduras to Ecuador (Rowe 1996) and this species is relatively abundant throughout their range (IUCN). Their group size ranges from 8 to over 30 individuals (Fedigan and Jack 2001). Capuchins are known to be “destructive foragers”, a behaviour that is consistent with their high quality, yet difficult-to-process diet (Wright 2009). They are omnivorous, consuming a wide array of foods opportunistically. Along with fruit, insects make up a large portion of the diet (Fragaszy et al 2004; Chapman and Fedigan 1990). Both their extractive foraging behaviour and high degree of omnivory makes capuchins an appropriate study species to investigate insects as fallback foods.

1.9 Methods

I measured insect abundance concurrently with capuchin foraging behaviour in Sector Santa Rosa in the Área de Conservación Guanacaste –a tropical dry forest situated in the northwest of Costa Rica. I measured insect abundance from June 2011 to July 2012, including all seasons, and collected data on capuchin foraging behaviour from January to July 2012, including all but the late wet season. I used malaise and pan traps to capture insects and collected behavioural data via ten minute focal sampling.

1.10 Overview

In Chapter Two, I describe insect abundance and seasonality and the effect of abiotic and biotic factors on insect abundance. I test the effect of temperature and rainfall as well as leaf, flower and fruit phenology on insect abundance.

In Chapter Three, I use the insect abundance data described in Chapter two as well as previously described fruit abundance data from my study site to define three food abundance seasons: HIGH, INTERMEDIATE and LOW. I analyze consumption frequency and time spent processing aseasonal processed foods across each of these seasons to identify a fallback food in the capuchin diet and attempt to describe the role insects play in the diet.

In Chapter Four, I synthesize my results from Chapters Two and Three and discuss the implications of my findings and limitations of my work. I conclude by suggesting hypotheses and strategies for future studies on the topic of fallback foods.

Chapter Two: Tropical insect abundance

2.1 INTRODUCTION

Most insect abundance and seasonality studies have focused on temperate ecosystems rather than tropical ecosystems (Wolda 1988). Tropical insect abundance research is limited to a few studies (e.g., da Silva et al. 2011; Grimbacher and Stork 2009; Pinheiro et al. 2002; Murali and Sukumar 1993; Wolda 1992; Frith and Frith 1990; Wolda 1989; Janzen 1988b; Wolda and Broadhead 1985; Janzen 1983; Lowman 1982; Tanaka and Tanaka 1982; Wolda and Fisk 1981; Denlinger 1980; Wolda 1978; Elton 1973; Janzen 1973a; Janzen 1973b; Fogden 1972; Dobzhansky and Pavan 1950; Bates 1945). It is well accepted among entomologists that research in the area of tropical insect abundance, seasonality and ecology is seriously lacking (Grimbacher and Stork 2009; Wolda 1988). The topic of insect abundance seemed more popular in the ‘80s (Wolda 1992; Wolda 1989; Wolda 1988; Wolda and Broadhead 1985; Wolda and Fisk 1981; Wolda 1978), whereas few studies have been conducted since (e.g., Dejean et al. 2011; Bassett et al. 2008; Missa et al. 2008). It is important to continue to monitor insect abundance given that the environment has been changing due to anthropogenic effects, including climate change (Dale et al. 2001) and such changes are affecting insect abundance (Dejean et al. 2011; Bassett et al. 2008). The need for more research is essential if we are to gain useful insights into tropical entomology. Collecting insect abundance and seasonality data can provide a baseline for understanding ecosystem processes and is important for those studying the effect of climate and especially those studying climate change (Grimbacher and Stork 2009).

It seems that tropical ecosystems provide enough diversity to result in a wide array of ecological patterns. Compared to rainforests, cloud forests or other tropical ecosystems, tropical dry forests exhibit the most extreme variation in precipitation with little variation in temperature. Although tropical dry forests do not contain as much taxonomic diversity as do other tropical forest types, they can exhibit more morphological and physiological diversity across flora and fauna (Janzen 2000). Tropical dry forests are the most endangered ecosystem on Earth comprising less than 2% remainder of the original expanse having extended from northern Mexico to Columbia (Janzen 1988a). The present study examines the effect of rainfall, temperature and plant phenology in a tropical dry forest, Sector Santa Rosa in the Área de Conservación Guanacaste (ACG), Costa Rica.

Few studies at our study site have measured insect abundance because it is difficult and time consuming to do so for an entire forest. Most studies conducted on insects in Santa Rosa have focused on caterpillars (e.g., Agosta 2007, 2008; Janzen 1988b), acacia ants (Janzen 1966) and some beetle work (Janzen 1983). Abundance has been measured for insects that live and fly between 30cm and 2m above the ground in a young tropical dry forest with vegetation only 1m and 2m high. Insect species richness and abundance decreased during the dry season (Janzen 1973b). Janzen (2004) demonstrates a comprehensive understanding of insect seasonality and life histories across several taxa in Santa Rosa, but again this work is heavily dominated by Lepidoptera (caterpillars, moths and butterflies). Comparisons across seasons within an annual cycle are lacking empirical data and data reported from the ‘60’s, ‘70’s and ‘80’s are likely outdated since Santa Rosa is a secondary forest undergoing succession and studies have shown that insect abundance is changing over time in environments with histories of anthropogenic

disturbance (e.g., Dejean et al. 2011; Basset et al. 2008). Therefore, because much has changed since published abundance data was collected, the need for recent data is apparent.

Although insect abundance studies may not be robust enough to calculate the number of insects in an ecosystem at a given time, relative insect abundance across space and time is an acceptable method to at least initiate a project that can eventually draw longer term and larger scale conclusions (Wolda 1988). Small scale studies of relative insect abundance in tropical forests have been conducted and they allow for meaningful biological conclusions (e.g., Frith and Frith 1990; Lowman 1982; Denlinger 1980). The present study also provides an example of a small scale and relative measure of insect abundance over time.

Each study site differs and data from no one site is easily extrapolated to others, therefore it is difficult to predict seasonality or the effect that certain environmental factors, such as climatic variables, might have on seasonality in a given study site (Wolda 1988). Nonetheless, I attempt to make predictions derived from patterns found in other tropical dry forests, the same forest type as that of the present study, or at least from tropical forests with similar wet and dry seasons. Most such studies found that overall insect abundance peaked during rainy months (da Silva et al. 2011; Andresen 2007; Murali and Sukumar 1993; Tanaka and Tanaka 1982). In particular, peak abundance during rainy months was found for the orders of Hymenoptera, Coleoptera, Lepidoptera and Hemiptera (da Silva et al. 2011), including dung beetles in Santa Rosa (Janzen 1983). However, Diptera was not seasonal in abundance (da Silva et al. 2011). The abundance of bees and wasps (Hymenoptera) observed in the dry season in Santa Rosa is suggested to be caused by more flowering tree species during the dry season (Janzen 1967). In addition, more individual euglossine bees were attracted to baited traps during the dry season in Santa Rosa (Janzen et al. 1982). Also in Santa Rosa, caterpillars are most abundant when new

leaves emerge since most Lepidopteran larva are herbivores (Janzen 1988b). I did not find a study conducted in a tropical dry forest reporting the effect that fruit abundance might have on insect populations, therefore I do not make a prediction with regards to fruit phenology.

I have two research questions:

- 1) Are insects seasonal in Santa Rosa, a tropical dry forest during the 14 months of my study?
- 2) What are the effects of abiotic and biotic factors on insect abundance in Santa Rosa?

I hypothesize that the extreme dry and wet seasons and deciduousness of Santa Rosa facilitate seasonality in insects I make predictions based on the previously published insect seasonality studies described above.

- a) Insects overall will be seasonal.
- b) Hymenoptera, Coleoptera, Lepidoptera and Hemiptera will be seasonal.
- c) Diptera will be aseasonal.
- d) Caterpillars will be seasonal.
- e) Insects overall will be more abundant in the early rainy season..
- f) Formicidae, Coleoptera, Lepidoptera and Hemiptera will be most abundant when rainfall is high.
- g) Bees and wasps (non-Formicidae Hymenoptera), will peak during periods of high plant flower cover and maturity.
- h) Herbivorous non-caterpillar insects will peak during periods of high plant leaf cover and maturity.
- i) Caterpillars will be most abundant with high leaf cover and maturity.

2.2 METHODS

2.2.1 Study site and length of study

Santa Rosa is a tropical dry forest in the northwest of Costa Rica and part of a larger conservation area called Área de Conservación Guanacaste (ACG) found at 10°45' to 11°00' N and 85°30' to 85° 45' W. Santa Rosa was originally the second oldest farm land in Costa Rica and is composed of patches of forest and regenerating pastures that were seasonally burned by farmers and planted with invasive African grasses. Human disturbance in the area occurred throughout different time periods and across its geographical landscape from the mid-1500's until 1971 when the original Santa Rosa National Park was established (the Área de Conservación was established in 1989). The result is a highly variable forest in successional stages with varying degrees of plant diversity and deciduousness throughout (Janzen 2000; Kalacska et al. 2004). Little to no rain falls for six months of the year (typically mid-November to May) while the rest of the year experiences the majority of the annual rainfall ranging from 915 to 2558mm per year (Campos and Fedigan 2009; Kalacska et al. 2004; Fedigan and Jack 2001; Janzen 2000). Each year can vary considerably from the next in terms of rainfall, tree phenology and the abundance of some insects such as caterpillars (Janzen 2004; Janzen 1988b; Janzen 1973a; Janzen 1966).

2.2.2 Insect Collection Methods

I used malaise and pan traps to collect arboreal and terrestrial (non-caterpillar) insects. There is evidence for variation in insect abundance in the canopy versus lower to the ground in tropical areas (Elton 1973). To account for this potential variation, I hung canopy malaise traps

in trees between approximately 1 and 10 meters from the ground to the trap bottom. I also placed traditional Townes malaise traps on the ground and refer to them here as terrestrial malaise traps. Canopy malaise traps were approximately 260cm from the bottom collection container to the top collection container and 91cm wide. Townes malaise traps were approximately 180 cm in length and 213 cm in height. Canopy malaise traps contained two 500ml collection containers –one at the top and one at the bottom of the trap- to catch insects that flew up or down when they hit the sides of the trap. Terrestrial malaise traps had one 500ml collection container at the top of the trap. All collection containers were plastic and filled approximately one quarter with 90% ethanol. All malaise traps were made of fine mesh (less than 1mm) of which the bottom panels were made of black mesh and the “roof” was made of white mesh.

I placed pan traps, blue bowls of approximately 10cm in diameter and 5cm deep, flush with the forest floor and filled each with ethanol until about two centimeters from the bottom of the trap. Although yellow pan traps are known to collect more insects on the whole (Danks 1996), I had difficulties finding yellow bowls of the same size and shape to place in each habitat. All blue pan traps were the same size and shape and since I was collecting relative insect abundance across space and time (as opposed to absolute insect numbers in the environment), as long as the traps were the same across habitats, it did not matter whether the pan trap was yellow or blue. I placed a tarp over each pan trap to keep rain and falling leaves from overfilling the trap and facilitating the escape of trapped insects or causing them to rot with diluted ethanol. I emptied each trap from all four habitats every two to three days in an attempt to minimize the variation in insect abundance found between days and weeks by Wolda (1978), and I replaced the ethanol at that time. I counted all insects larger than 4mm.

I used frass traps to collect caterpillar frass as a proxy to measure caterpillar abundance, a reliable method (Mizutani and Hijii 2001). Traps were made of canvas material attached to a square rebar frame. I used canvas to allow rain water to move through the material, but keep all sizes of caterpillar frass in the trap. Rain water did occasionally flood the traps (see Results below). I placed twenty-five frass traps in each of four habitats (100 traps in total). I collected the frass from each trap in each habitat every two to three days. I brought the frass back to the lab where I dried it in a dehydrator for 48 hours. I then weighed the frass to obtain a dry weight.

One of each of the three trap types was placed in each of the four habitat types found in Table 2.1. Forest ages are based on Enquist & Enquist (2011) and Sorensen & Fedigan (2000). All habitat types were within two kilometres of each other and alternated on either side of a paved road. See map in Figure 2.1 for the location of each study habitat within Sector Santa Rosa. Habitat CP had a very low canopy (lowest canopy height could be as low as 3 meters and sometimes grassland) whereas the other three habitats range between approximately 15 and 25 meters, although canopy height was not a measured variable in the present study. All four habitats are near minor dirt roads as well as the main paved road, but CP is near a campground where tourists are seasonally abundant during the dry season. Each Townes malaise trap faced either North or East. Traps at the Viejo habitat were on a hill approximately 10m higher than each of the other three habitats.

Table 2.1 The name, age and average height of four habitat types where one of each trap type was placed.

Local Name	Age (years)	Description
Viejo	160	Tall canopy (approx. 25m)
Borrachos	110	Intermediate canopy (approx. 15m)
Cafetal	105	Tall canopy (approx. 20m)
CP	70	Short canopy, minimum 3m

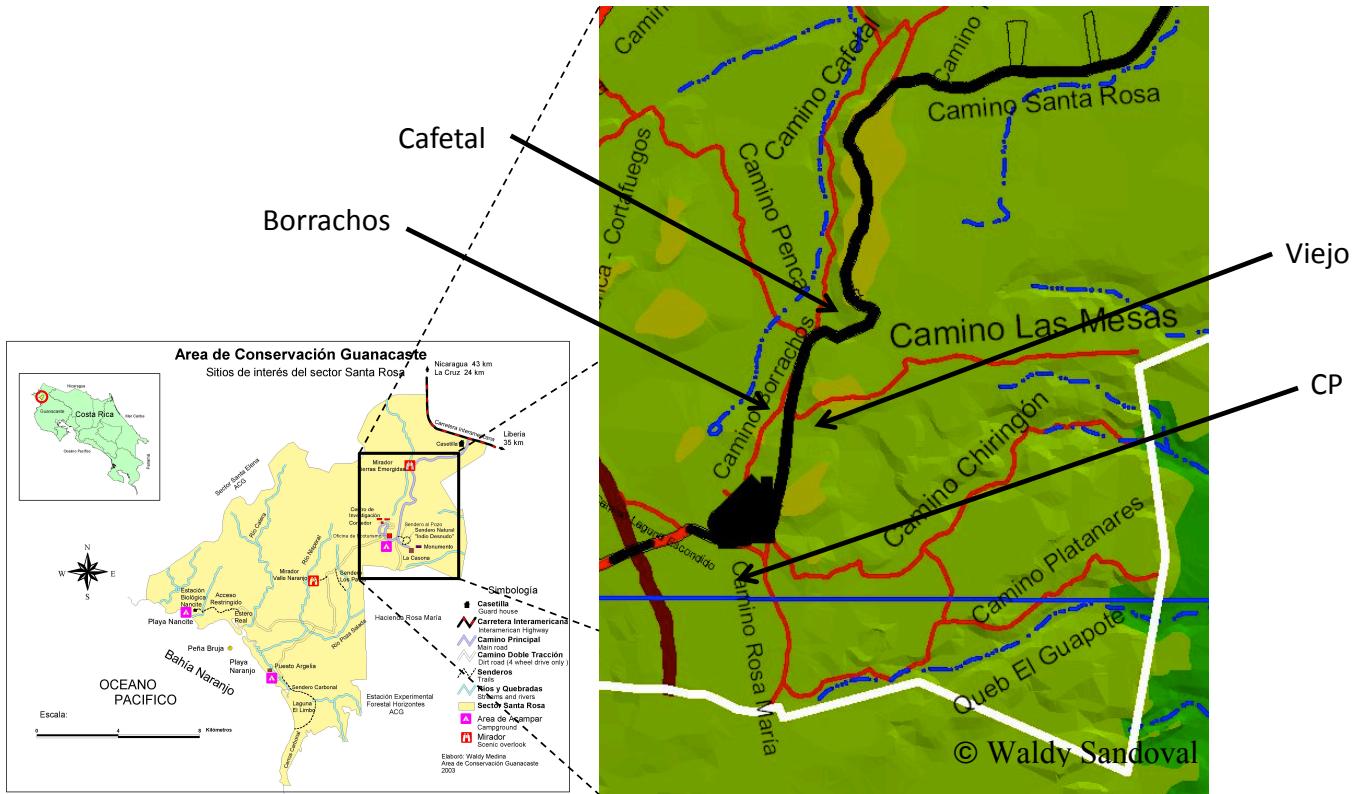


Figure 2.1 Map of Sector Santa Rosa within the ACG. Black arrows show the location of each habitat site where insect traps were set-up: CP, Viejo, Cafetal and Borrachos. All traps were within 2km of each other. The thick black line going north to south is the main paved road. The light green colour in the expanded map refers to elevation between 200 to 300m colour yellow refers to elevation between 300 and 400m. Red lines refer to roads while blue lines refer to rivers. The black house refers to the research station in the middle of the park administrative area.

2.2.3 Weather Data Collection

I used standard rain gauges placed vertically approximately 10cm above the ground and secured on sticks with flagging tape. Each rain gauge ranged from 0 to 25mm and rain could overflow into a surrounding container up until approximately 100mm. I placed one gauge per habitat type, therefore four in total and emptied and recorded from them each day it rained.

I used a Kestrel weather station to record daily maximum and minimum temperatures. This weather station is placed in one place at the research base rather than in each habitat. For this reason and because I collected phenology data only once a month, I averaged both the maximum and then the minimum daily temperatures as well as rainfall to obtain one mean value per month of each of these variables..

2.2.4 Analyses

2.2.4.1 Average insect abundance and seasonality

I used circular statistics to assess whether insects overall as well as Orders and Families demonstrated seasonality. I performed circular analyses in Oriana, a statistical program that uses a Rayleigh Uniformity test to generate a p-value indicating whether the data diverge from linearity (Carnegie et al. 2011; Morellato et al. 2009; Batschelet 1981). Overall, Order and Family level insect count were averaged across each month and these values were used in each circular analysis.

2.2.4.2 Weather and phenological effects on insect abundance

Phenology data were collected at the beginning of each month between January 2011 and July 2012. A score of 0 to 4 was used to assess cover and maturity where 0 is 0%, 1 is 1-24%, 25% to 74%, 75% to 100% of the tree covered or full of mature fruit, flowers or leaves. These data were collected as part of a long-term study in Santa Rosa by Dr. Linda Fedigan (see Melin et al., in press). I calculated a percentage of monthly cover and maturity for each fruit, flowers and leaves for each of 43 tree species by multiplying the percent cover by the percent maturity and multiplying by 100. I then took the average value for cover and maturity across the 43 species to gain one value for cover and maturity per month.

I also used a GLMM to assess the effects of climate factors averaged per month (rain, maximum temperature (Tmax) and minimum temperature (Tmin)) and phenology factors (fruit, flowers and leaves) on insect Orders and Families trapped and reliably identified. Insect count was my response variable, the climate and phenology data were my explanatory variables and trap type nested in site was my random variable. Each climate and phenology factor was fixed except Tmax and Tmin, which were interaction factors.

2.3 RESULTS

2.3.1 *Weather and phenology*

Patterns of rain and temperature as well as fruit, flower and leaf phenology were similar to those of previous years in Santa Rosa. Rainfall began in April with only a few showers and gradually increased through October where rainfall spiked and gradually decreased until December with virtually no rain from January through March (Figure 2.2). Maximum and minimum temperature

did not fluctuate (Figure 2.3 and Figure 2.4), however a slight increase in maximum temperature occurred in March and April (Figure 2.3). Fruit phenology followed closely with the results found in (Melin et al., in press; Carnegie et al. 2011) who studied fruit abundance in Santa Rosa across many years. Peak fruit abundance was in May and June, fruit was most abundant from April through July and low from August through March (Figure 2.5). Flowers were abundant from February through June as shown in Figure 2.6. Leaves peaked in abundance from June through December following rainfall, a common pattern in Santa Rosa (Figure 2.7).

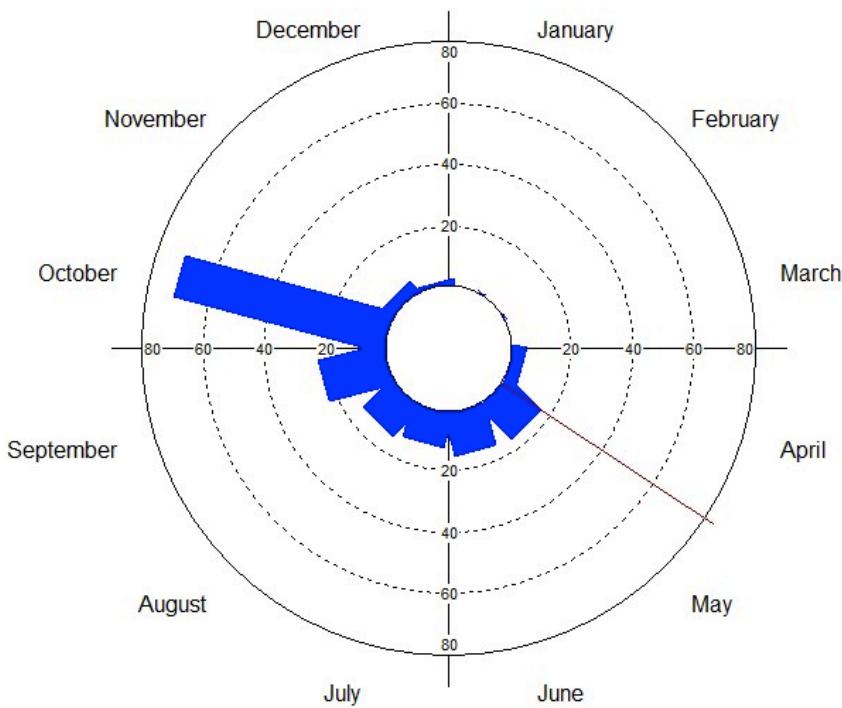


Figure 2.2 A circular graph with months of the year around the circumference and average rainfall (mm) on the inner circular axis with the inner-most circle being zero mm. Each bar represents average rainfall per month from May 25, 2011 through July 10, 2012.

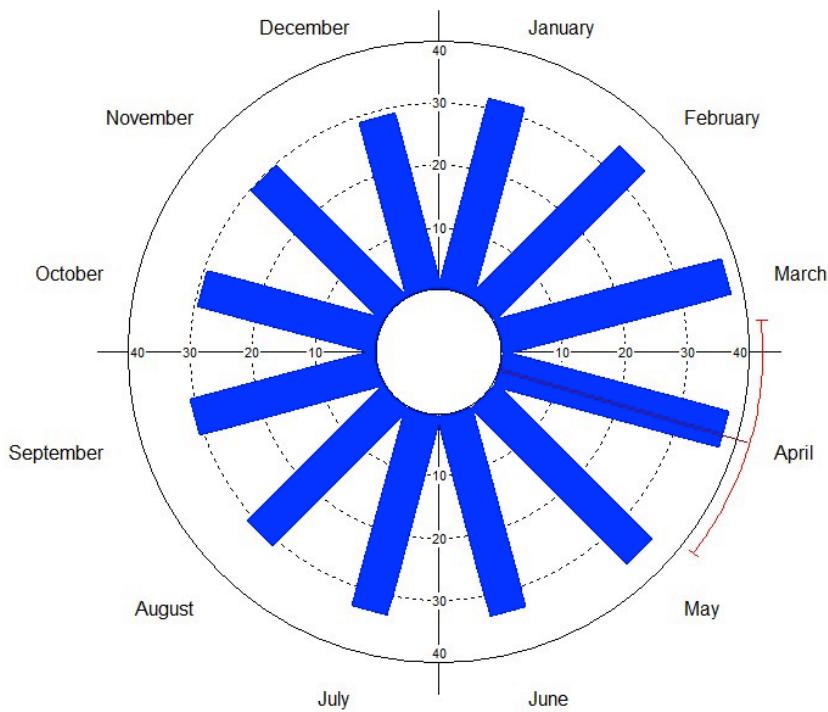


Figure 2.3 A circular graph of maximum temperature in Santa Rosa from May 25, 2011 to July 10, 2012. The outer circumference shows the months of the years and the inner circles represent degrees Celsius with the inner-most circle being zero degrees Celsius. The red line starting at the inner-most circle and moving outwards at the month of April represents the mean and the red line spanning from May to March on the outside of the circumference represents the standard error.

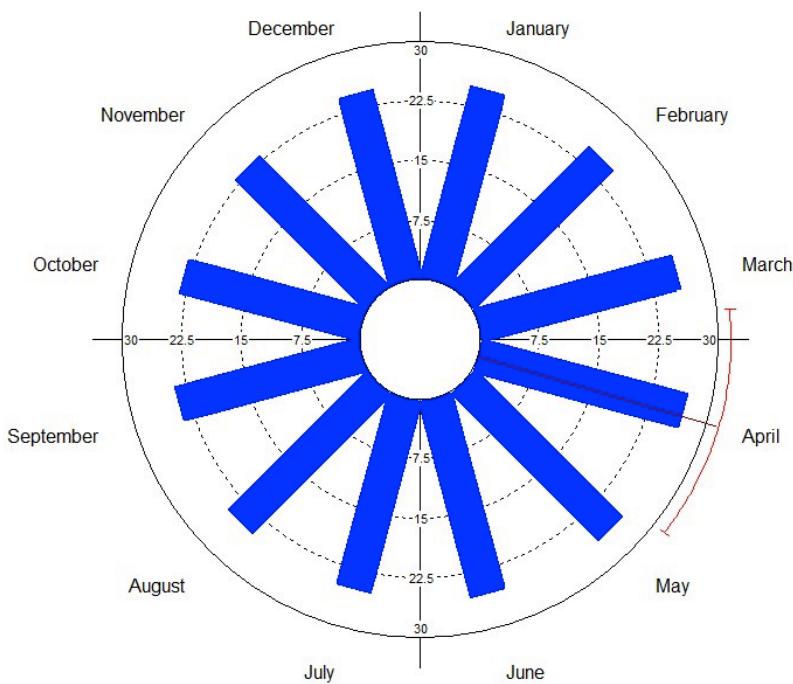


Figure 2.4 A circular graph of minimum temperature in Santa Rosa from May 25, 2011 to July 10, 2012. The outer circumference shows the months of the years and the inner circles represent degrees Celsius with the inner-most circle being zero degrees Celsius. The red line starting at the inner-most circle and moving outwards at the month of April represents the mean and the red line spanning from May to March on the outside of the circumference represents the standard error.

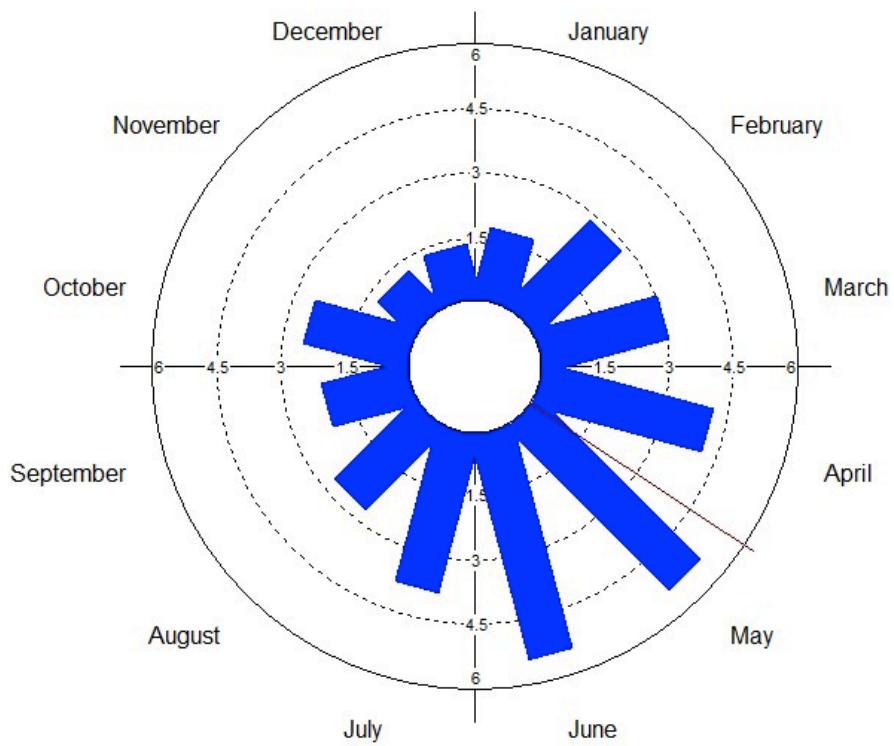


Figure 2.5 A circular graph of percent fruit phenology from January 2011 through June 2012. I multiplied percent cover and percent maturity to gain an overall fruit phenology percentage, averaged these values across plant species per month. This fruit phenology percentage value is shown on the inner circular axes with months of the year around the outer edge of the graph.

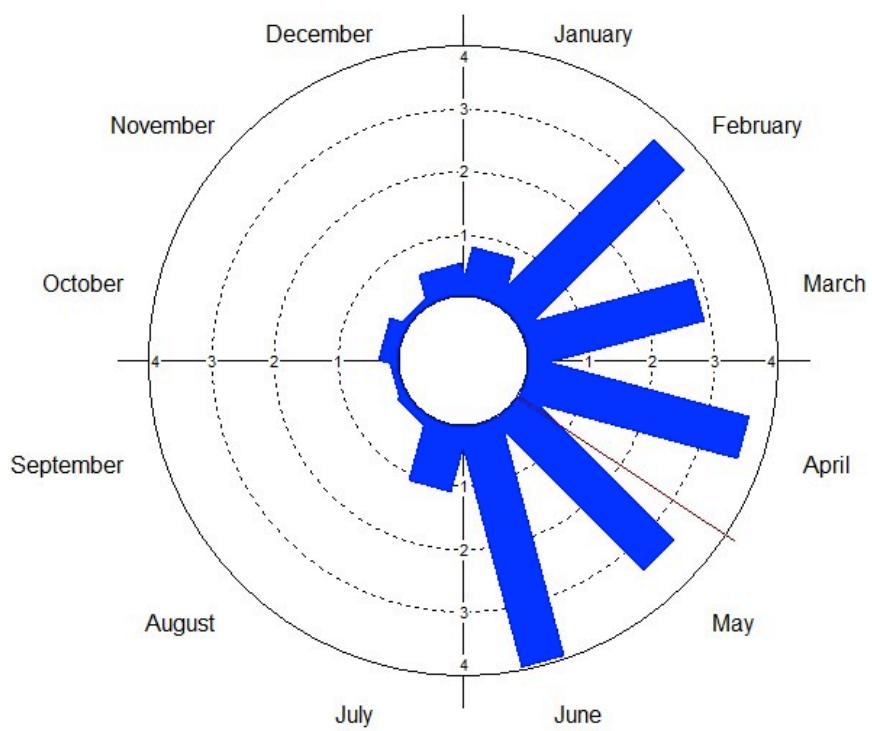


Figure 2.6 Flower phenology from January 2011 through June 2012. Flower percent cover and maturity was clearly abundant from February through June. I calculated flower phenology percentage by the same means described for fruit. Percentages on the inner circular axes are average values across plant species and month.

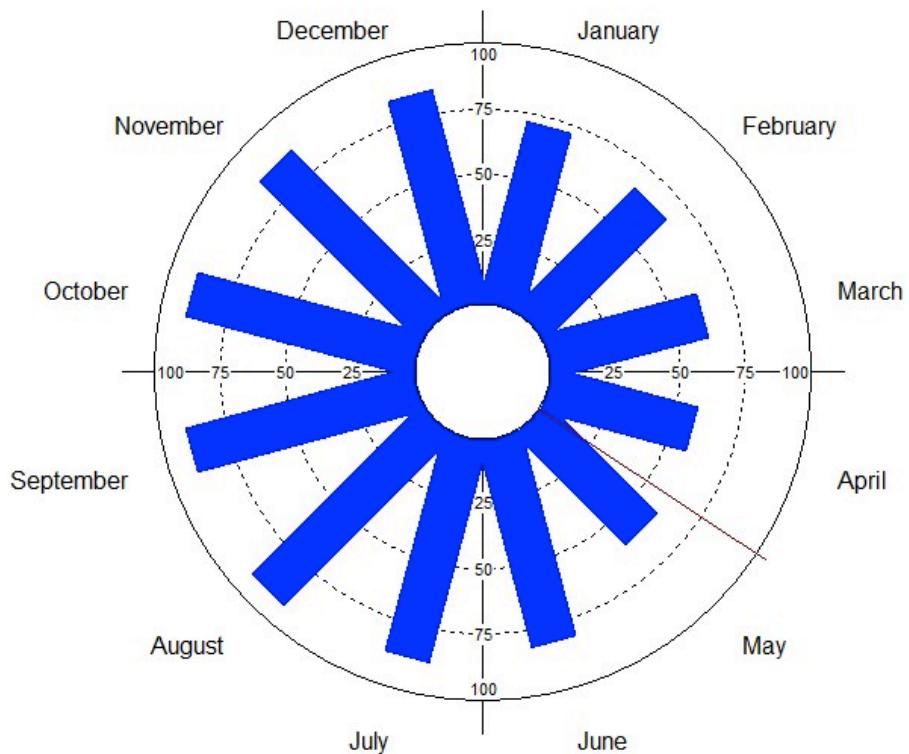


Figure 2.7 Leaf phenology from January 2011 through June 2012 calculated in the same manner as that described for fruit. Leaves were most abundant from June through December.

2.3.2 Average insect abundance and seasonality across all study months

2.3.2.1 Non-caterpillar insects

I collected a total of 28,236 non-caterpillar (nc) insects over the course of 14 months. While the range of samples collected per month was 83 to 175, I counted only 14 samples in August. This, however, does not effect any of my results because the number of samples per month (i.e. sampling effort) was accounted for in each month by averaging the number of insects per sample

each month when analyzing for seasonality as well as using trap type as a random variable when analyzing for climatic and phenological effects.

I found overall abundance of nc insects to be seasonal (Raleigh: N=14,100, Z=14,100, p<0.0001) due to an abundance peak in April and May. Although overall insect abundance peaks, insects were never sparse and remained abundant throughout the year, see Figure 2.8.

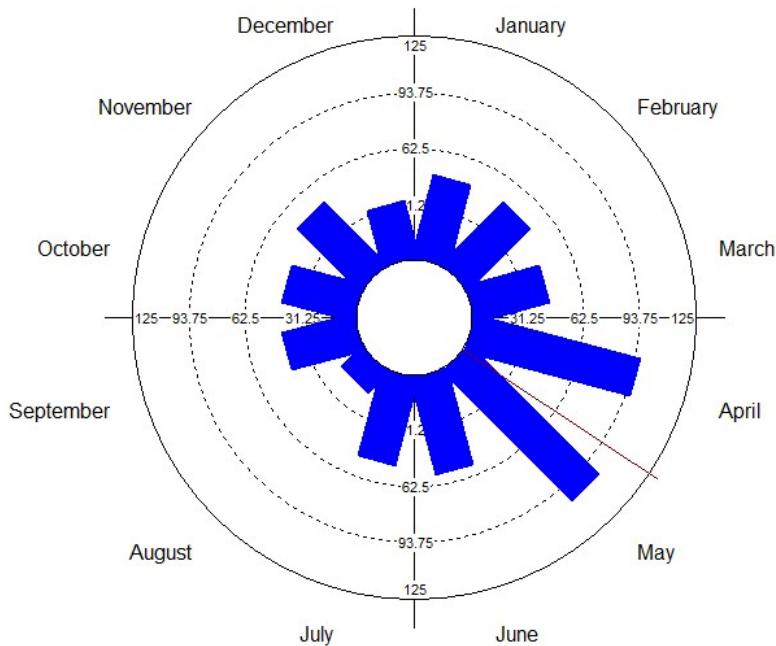


Figure 2.8 Overall non-caterpillar insect abundance averaged across each month. Outer circumference represents one year and is labelled by month. Inner dotted circles represent the response variable: insect count where zero is at the center and the maximum count is at the outer edge of the graph.

I found many Orders and Families in the insect traps, but analyzed only the most consistently identified (N= 12,717; 45.9%) for seasonality. See Table 2.2 listing nine Orders and 11 Families used in the analyses. Some Orders were not represented by consistently counted

Families and are labelled as “NA” in the “Family” column of Table 2.2. I did not identify any Family within the Order Hymenoptera other than Formicidae consistently through my study, therefore I pooled all Families within the order Hymenoptera that were not Formicidae, such as bees and wasps and called this group of insects “Non-Formicidae Hymenoptera”, which I included in the Family column in Table 2.2. Of all of the insect Orders identified and counted I found Insecta Blattodea to be the only significantly seasonal Order (Rayleigh test; N=26, Z=3.49, p=0.029) (See Figure 2.9). All other insect Orders found in my traps were aseasonal. Of the insect Families identified and counted I found Curculionidae to be statistically seasonal (Raleigh: N=25, Z=5.018, p=0.006) as well as Formicidae (N=33, Z=5.72, p=0.003) (Figure 2.10 and Figure 2.11, respectively).

Table 2.2 List of consistently counted Orders and Families

Order	Family	Common Name
Blattodea	NA	Cockroach
Coleoptera	Curculionidae	Weevil
Coleoptera	Lampyridae	Firefly
Coleoptera	Elateridae	Click beetle
Coleoptera	Scarabaeidae	Scarab beetle
Coleoptera	Cleridae	Checkered beetle
Diptera	NA	Fly
Hemiptera	Cicadidae	Cicada
Hemiptera	Pentatomidae	Stink bug
Hemiptera	Membracidae	Tree hopper
Hymenoptera	Formicidae	Ant
Hymenoptera	Non-Formicidae	
	Hymenoptera	Bees, wasps, etc.
Lepidoptera	NA	Butterflies and moths
Mantodea	Mantidae	Praying mantis
Orthoptera	NA	Grasshopper, cricket, etc.
Orthoptera	Tettigoniidae	Katydid

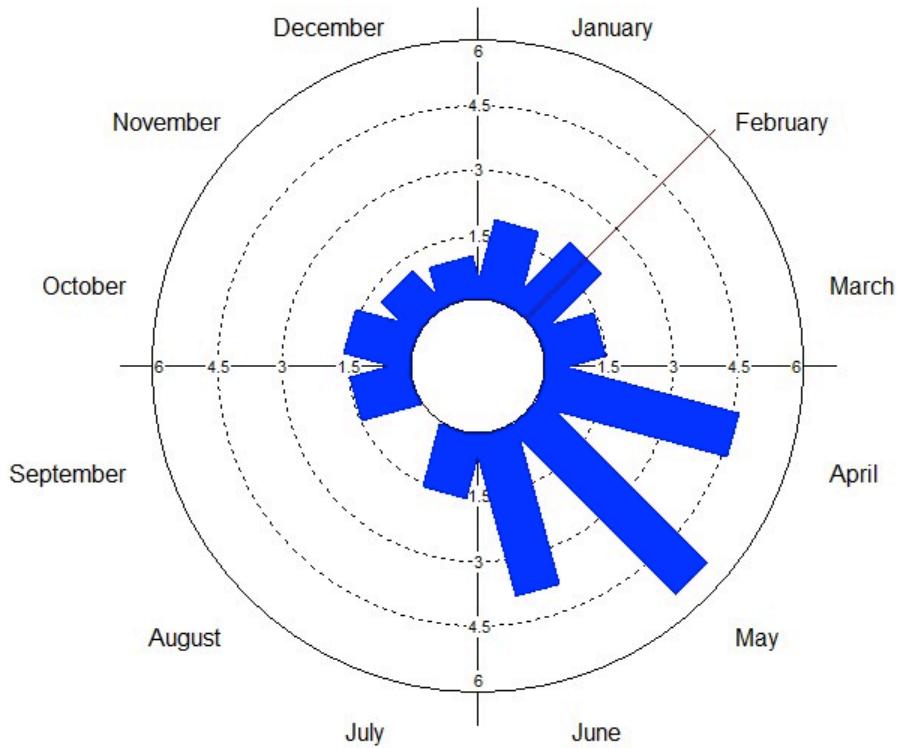


Figure 2.9 Average Blattodea count per month combining all trap types and habitats.

Outer circumference represents one year and is labelled by month. Inner dotted circles represent the response variable: insect count where zero is at the center and the maximum count is at the outer edge of the graph.

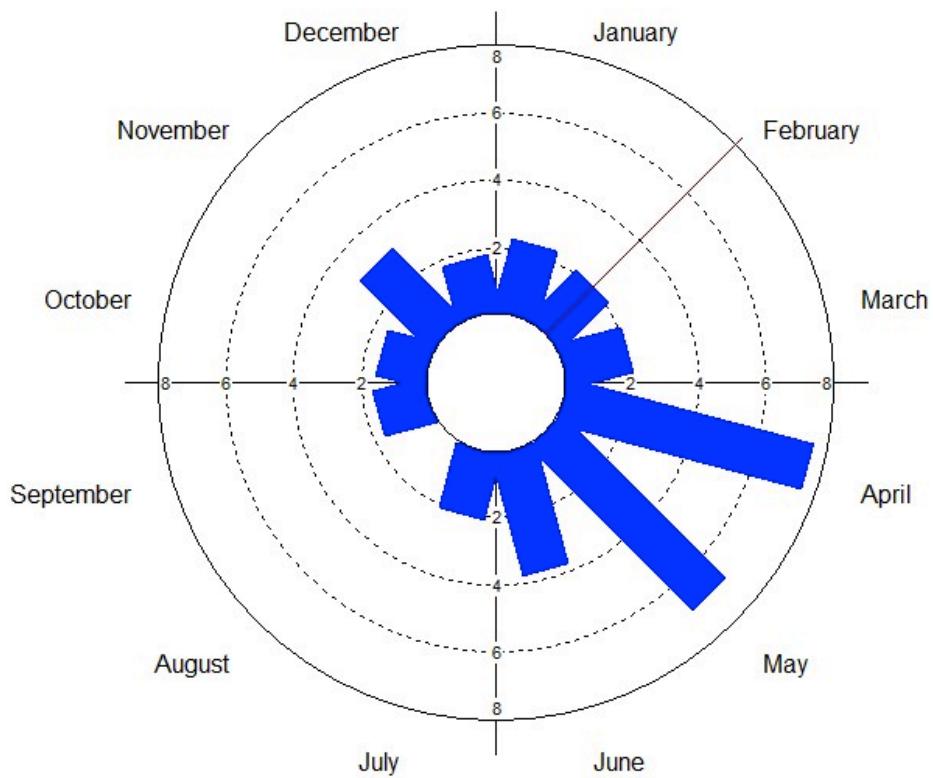


Figure 2.10 Average Curculionidae count per month combining all trap types and habitats.

Outer circumference represents one year and is labelled by month. Inner dotted circles represent the response variable: insect count where zero is at the center and the maximum count is at the outer edge of the graph.

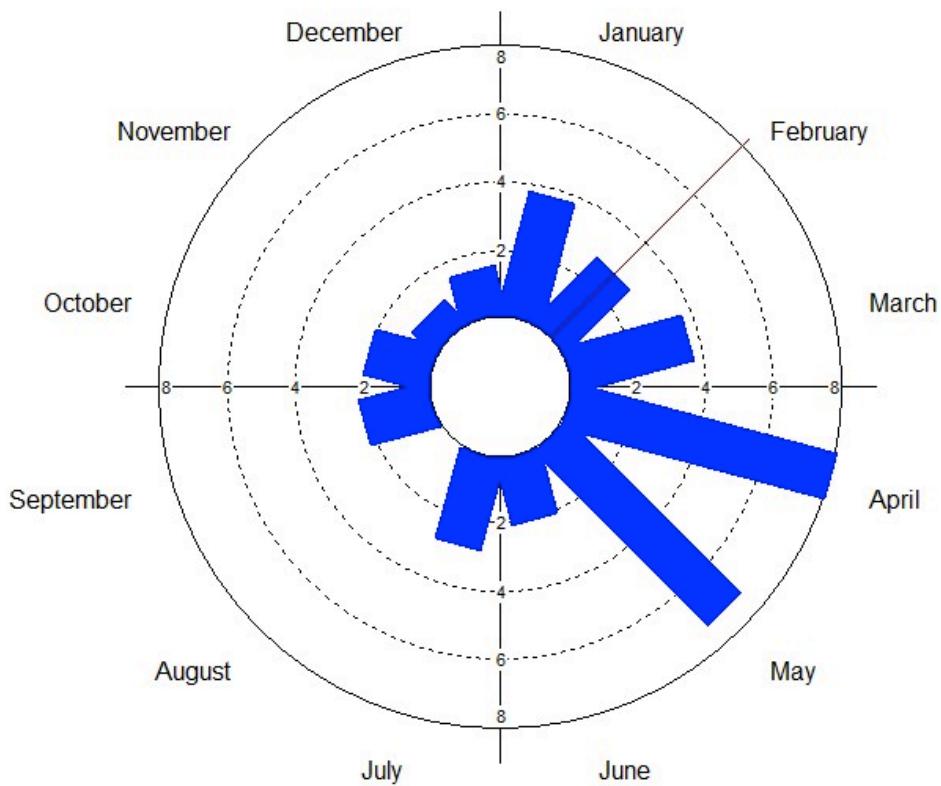


Figure 2.11 Average number of Formicidae per month combining all trap types and habitats. Outer circumference represents one year and is labelled by month. Inner dotted circles represent the response variable: insect count where zero is at the center and the maximum count is at the outer edge of the graph.

2.3.2.2 Caterpillar frass

Between mid-July 2011 and end of July 2012, I found that caterpillar frass dry weight peaked in September and November. However, I could not collect data in October due to very heavy rain flooding the frass traps. Because I did not have a full-year's worth of data, I could not perform

circular statistical analyses in order to analyse for seasonality. However, seasonality in caterpillar abundance is quite obvious in Figure 2.12

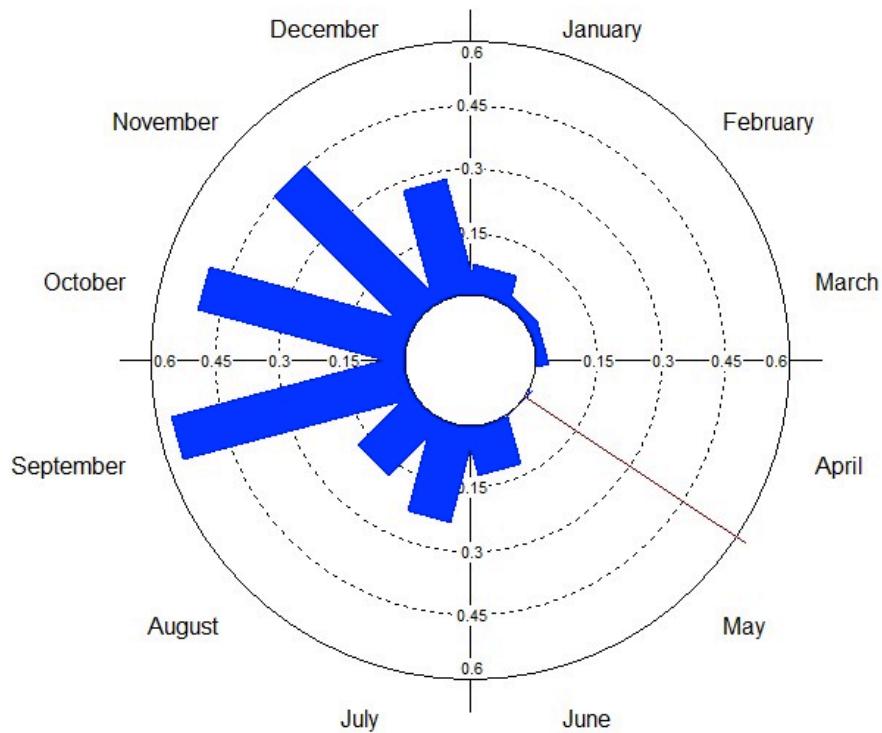


Figure 2.12 A circular graph with months in a year around the outer axis and average dry caterpillar frass weight in grams on the inner axes. Note that the October value (0.5g) is not data from the field, but an assumed value based on the obvious trend in September and November. We know caterpillars are seasonally abundant once a year (i.e. not bimodality abundant), therefore abundance was most likely maintained in October. There are no data for the month of October due to heavy rainfall preventing frass collection. The red line coming from the center for the graph to the outer edge is the mean dry caterpillar frass weight and the red lines on the outer edge of the graph is the standard error.

2.3.3 Climatic and phenological effects on insect abundance

2.3.3.1 Blattodea and Mantodea

I found significantly more Blattodea when percent flower cover and maturity was high ($B=2.71e^{-01}$, $SE=7.16e^{-02}$, $z=3.78$, $p=0.00016$) and a significant fewer Blattodea when percent leaf cover and maturity were high ($B=-6.37e^{-02}$, $SE=9.06e^{-03}$, $z=-7.028$, $p<0.0001$) as well as when fruit cover and maturity were high ($B=-4.35e^{-01}$, $SE=8.74e^{-02}$, $z=-4.98$, $p<0.0001$). Neither climate factor, rain or temperature, had a significant effect on Blattodea count. See Figure 2.13.

I found significantly more mantids when average leaf percent cover was high (GLMM: $B=-0.069$, $SE=0.030$, $z=-2.27$, $p=0.024$), however, Figure 2.14 shows that this result is driven by the high mantid count in December only. None of the other variables had a significant effect on Mantodea count.

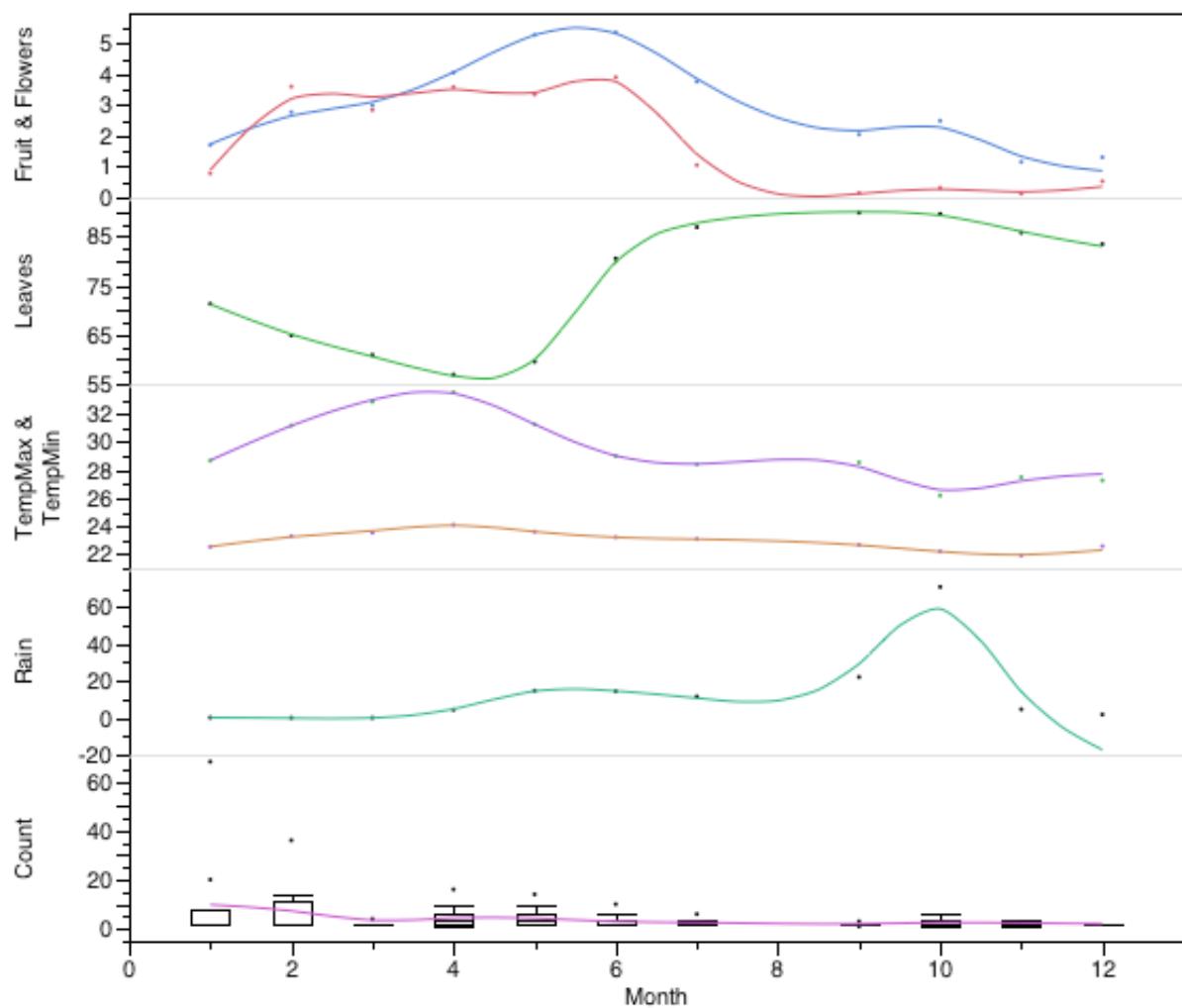


Figure 2.13 Average Blattodea count, rainfall, Tmax, Tmin per month as well as average percent leaf, fruit and flower cover and maturity. The count variable is presented as boxplots at the base of the figure where the bottom and top of the box represents the 25th and 75th percent quantiles, respectively, the whiskers represent the 75th quantile + 0.5*(interquantile range), the horizontal line is the median and the smoother represents the mean. Total number of insects = 833.

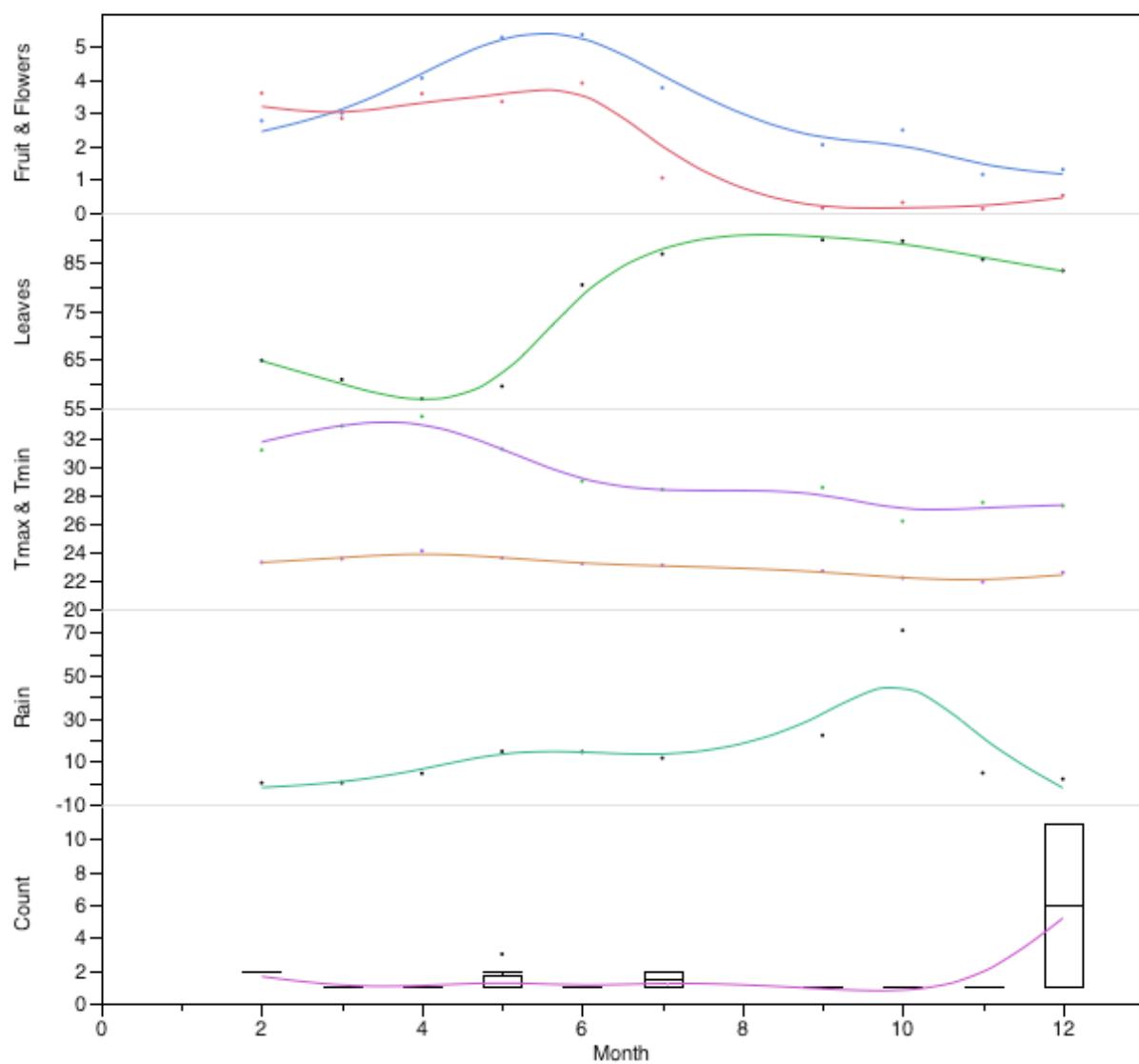


Figure 2.14 The number of mantids found across months contrasted with average Rain, Tmax, Tmin per month as well as average percent leaf, fruit (blue smoother) and flower (red smoother) cover and maturity. The count variable is presented as boxplots at the base of the figure where the bottom and top of the box represents the 25th and 75th percent quantiles, respectively, the whiskers represent the 75th quantile + 0.5*(interquantile range), the horizontal line is the median and the smoother represents the mean. Total number of insects = 55.

2.3.3.2 Formicidae

I found significantly more Formicidae when the interaction between Tmax and Tmin was high ($B=-1.32$, $SE=5.23e^{-01}$, $z=-2.52$, $p=0.012$) as well as when Rain was low and Tmin was high ($B=-5.53$, $SE=2.40$, $z=-2.31$, $p=0.021$) (Figure 2.15). However, I did not find a significant interaction effect on Formicidae count between Rain and Tmax or between Rain, Tmax and Tmin. I found significantly less Formicidae count when the peak percent leaf cover and maturity was high ($B=-4.65e-01$, $SE=2.29e-01$, $z=-2.04$, $p=0.042$) and fruit peak percent maturity and cover was high ($B=1.74$, $SE=7.02$, $z=2.48$, $p=0.013$). In contrast, I found significantly more Formicidae when flower cover and maturity was high ($B=-6.04$, $SE=2.40$, $z=-2.52$, $p=0.012$). In summary, ants tended to be most abundant at the end of the dry season and beginning of the wet season when temperatures were highest, flowers were abundant and fruit and leaves were becoming abundant.

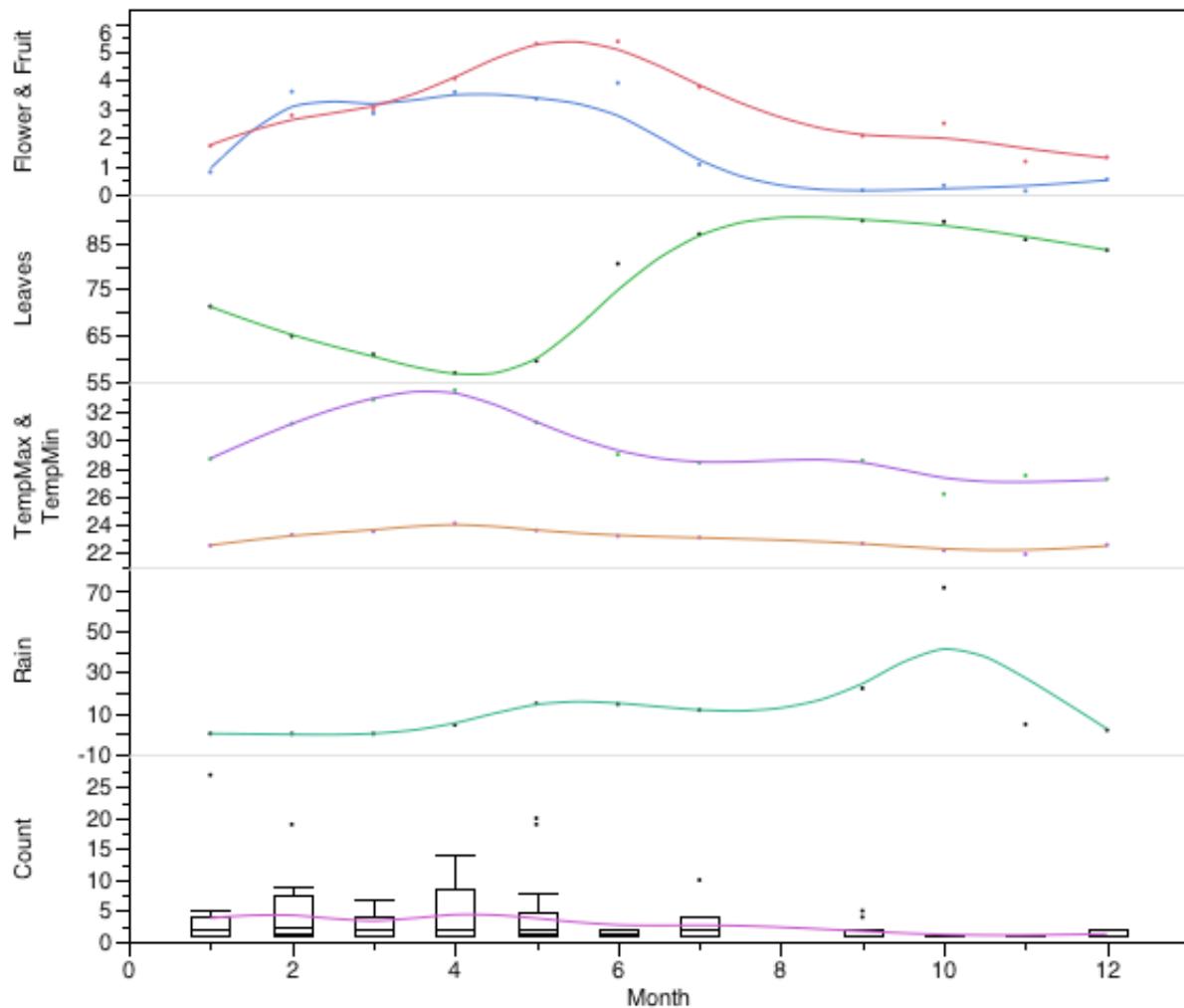


Figure 2.15 The average number of Formicidae individuals found in traps across each study month (Count) contrasted with climatic and phenological variables: Average rain, Tmax, Tmin per month as well as average leaf, fruit (red smoother) and flower (blue smoother) percent cover. The count variable is presented as boxplots at the base of the figure where the bottom and top of the box represents the 25th and 75th percent quantiles, respectively, the whiskers represent the 75th quantile + 0.5*(interquantile range), the horizontal line is the median and the smoother represents the mean. Total number of insects =407.

2.3.3.3 Non-Formicidae Hymenoptera

I found significantly more non-Formicidae Hymenopterans when Tmax and Tmin were both high ($B=0.16$, $SE=0.014$, $z=11.11$, $p<0.0001$). I found significantly fewer non-Formicidae Hymenopterans when rainfall was high (GLMM: $B=-0.014$, $SE=0.0011$, $z=-12.18$, $p<0.0001$) as well as when percent leaf cover was high ($B=-0.021$, $SE=0.0026$, $z=-8.065$, $p<0.0001$). I found significantly more non-Formicidae Hymenopterans when percent flower cover and maturity ($B=-0.13$, $SE=0.025$, $z=-5.24$, $p<0.0001$) and percent fruit cover and maturity was high ($B=0.32$, $SE=0.025$, $z=12.48$, $p<0.0001$). See Figure 2.16 showing all factors involved in this analysis.

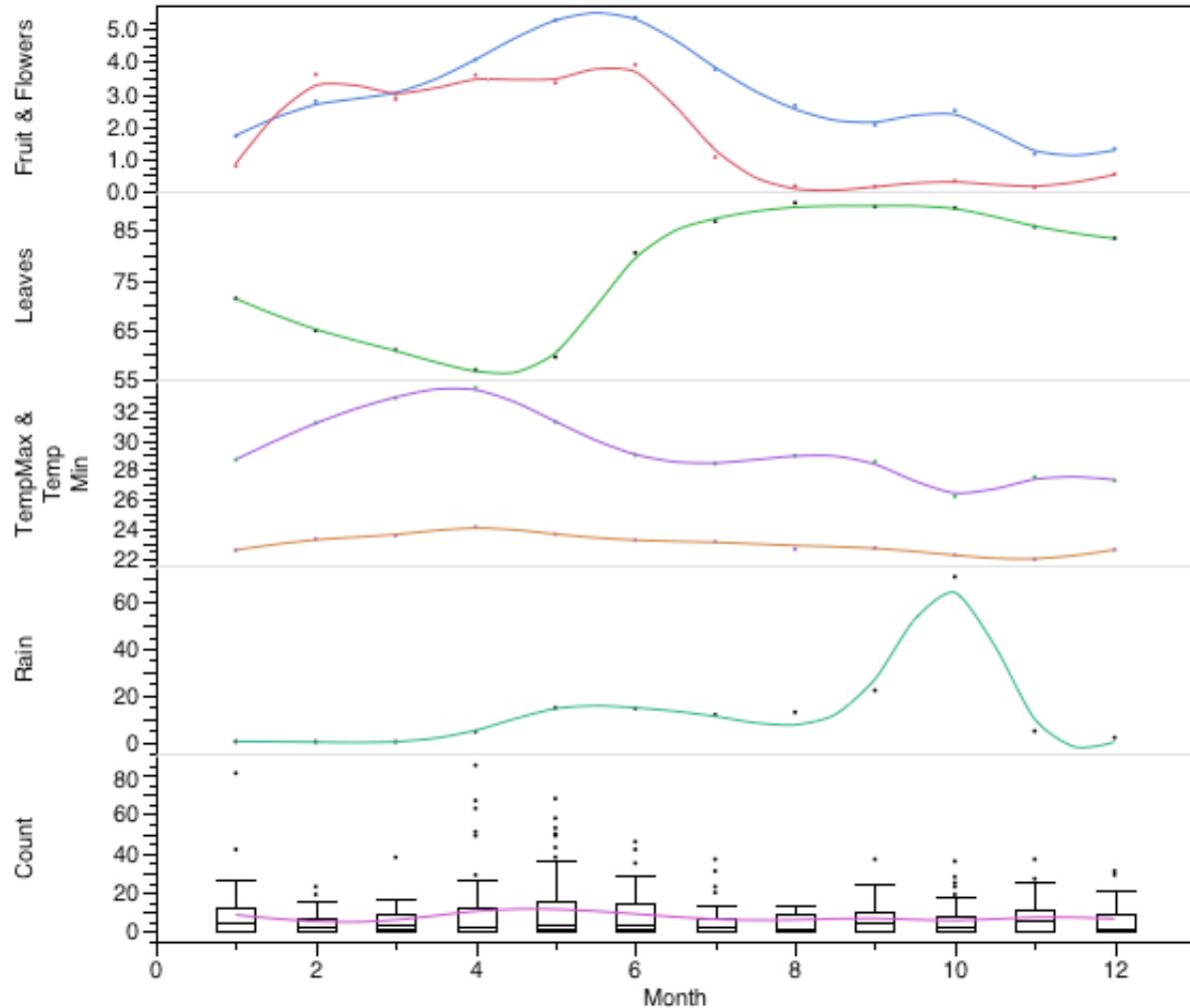


Figure 2.16 The number of non-Formicidae Hymenopterans found for each study month from June 2011 to July 2012 and corresponding average rainfall, fruit (purple smoother), flower (orange smoother) and leaf phenology as well as maximum (blue smoother) and minimum temperature (red smoother) per month. The count variable is presented as boxplots at the base of the figure where the bottom and top of the box represents the 25th and 75th percent quantiles, respectively, the whiskers represent the 75th quantile + 0.5*(interquantile range), the horizontal line is the median and the smoother represents the mean. Total number of insects = 6115.

2.3.3.4 Caterpillar frass

I found significantly more frass dry weight when rainfall was high and Tmax was low (GLMM: $B=-0.089$, $SE=0.021$, $z=-4.27$, $p<0.0001$). I found significantly less frass dry weight when percent fruit cover and maturity was high ($B=-0.24$, $SE=0.011$, $z=-2.12$, $p=0.034$). In contrast, I found significantly more frass dry weight with high percent leaf cover and maturity ($B=0.060$, $SE=0.020$, $z=-4.27$, $p<0.0001$). See Figure 2.17.

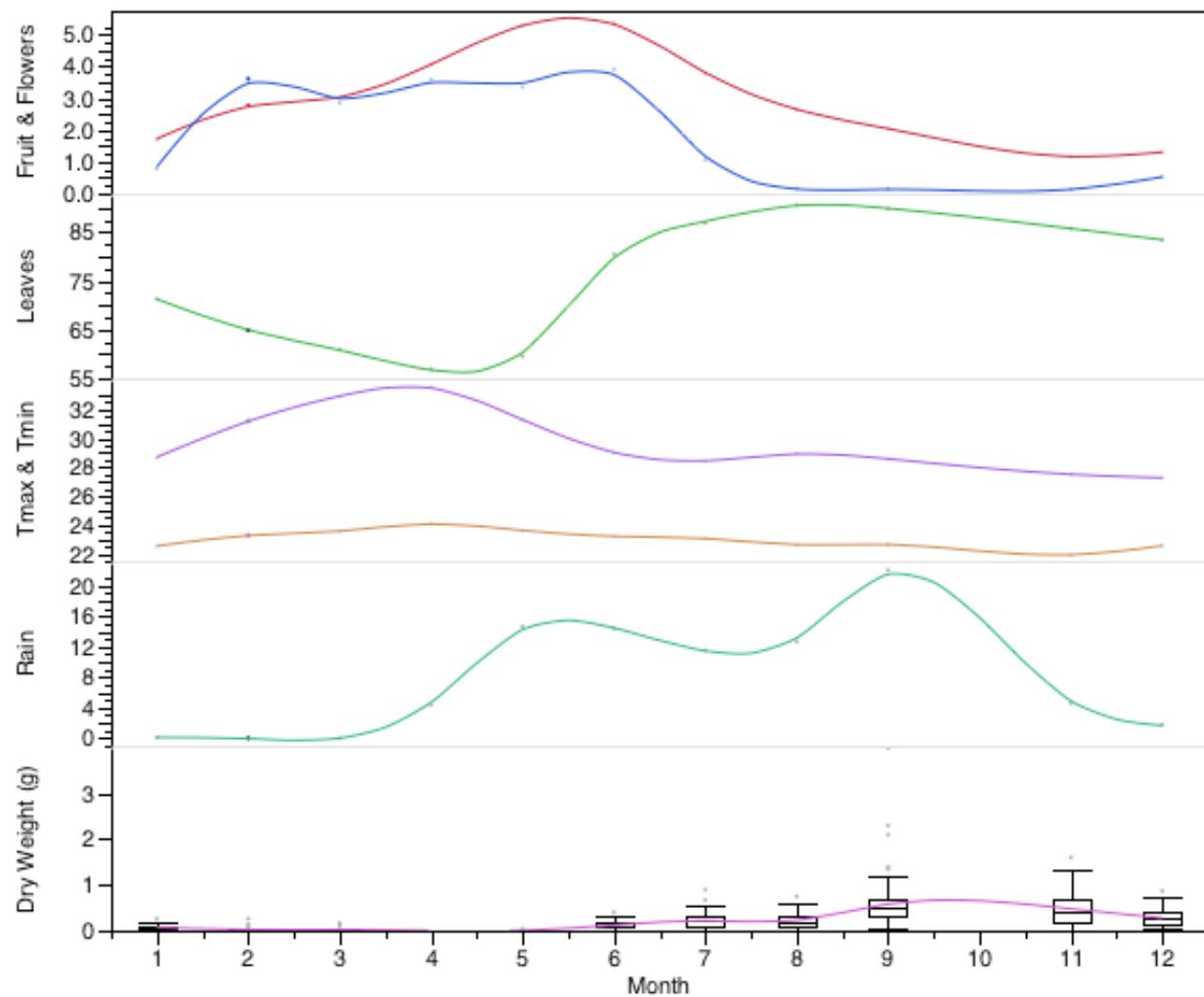


Figure 2.17 Dry caterpillar frass weight averaged across sites and traps per month.

Average rain, Tmax, Tmin per month as well average leaf, fruit and flower cover and maturity per month. Number of samples = 3826.

I did not find a significant effect of temperature, rain or plant phenology on any Coleopteran Family (Curculionidae, Elateridae, Lampyridae or Scarabaeidae) nor on Pentatomidae, Tettigoniidae and Membracidae.

2.4 DISCUSSION

2.4.1 Average insect abundance and seasonality across all study months

I predicted that non-caterpillar insects overall are seasonal and found support for this prediction. On the other hand, my prediction stating Hymenoptera, Coleoptera, Lepidoptera and Hemiptera will be seasonal was only partially fulfilled. Of the insects that I was able to identify to taxa, one out of nine Orders, (Blattodea), and two (Curculionidae and Formicidae) out of 11 Families were seasonally abundant. In contrast, (da Silva et al. 2011) found all 19 of their study insect Orders to be seasonal in the Brazilian “Cerrado” –a different ecosystem in that it is mostly savannah-like vegetation, however, the drastic seasonal changes are similar to those of Santa Rosa. I predicted Diptera would be aseasonal, which was supported in the present study as well as another study in the Brazilian “Cerrado” where Pinheiro et al. (2002) demonstrated seasonality in Coleoptera and Hemiptera, but aseasonality in the remaining 13 Orders studied. The low percentage of studied seasonal taxa in the present study begs the question: what is driving overall insect seasonality in Santa Rosa if most insect taxa that I identified and analyzed at the Order and Family level are aseasonal? One explanation may be the fact that I could not identify 54.1% of the insects captured that went into the “overall” analysis and some of those unidentified insects may be seasonal. I could not identify these insects because I did not have access to a microscope in the field and was identifying all insects without equipment. In addition, the three insect taxa that proved to be significantly seasonal all peaked in abundance in April and May, which is the same as the “overall insect” pattern. Therefore, these taxa may constitute what is driving the overall seasonality pattern of insect abundance. On the other hand, insects remained abundant throughout the year even though overall insect abundance was statistically seasonal and peaked

in April and May. This is to say that while I may not have caught as many insects during the rest of the year (June through March) compared to April and May, I caught an abundance of insects throughout each study month. The peak in April and May is an increase in insect abundance from an already abundant population rather than from a scarce population. This point may be further explained by comparing insects to flower and fruit abundance data. Flower and fruit abundance are seasonal and peak during certain months of the year, but there are next to no flowers or fruit throughout the remainder of the year –contrary to insect abundance.

My findings that overall insect abundance peaks in April and May support my prediction based on Janzen (2004) who described many insects that emerge just before and during the rains in Santa Rosa. Janzen (2004) also describes various situations in which the reproductive ecology of the insects necessitates their active existence during the dry season in Santa Rosa. Given that my research does not include data collection on every insect taxon, some of the unidentified insect taxa may in fact peak at other times of year besides April and May, but these insects may not exist in large enough numbers to influence the overall pattern of abundance, instead they may explain the maintenance of insect abundance during periods of the year when overall insect abundance did not peak. For instance, some beetles oviposit in the open terminal branches that have broken due to the harsh winds characteristic of the dry season, and some bees and wasps breed during the dry season because this is when the majority of flowers are in bloom (Janzen 2004). These dry-season active insects may be some of those that I was unable to identify and may occur in relatively small numbers, thus may at least partially explain why overall insect abundance is maintained throughout the year.

In accordance with my prediction, caterpillars were seasonal and abundant during a period of high leaf abundance. Although caterpillar frass abundance data were lacking for the

month of October, therefore hindering my ability to perform circular statistics, caterpillars have long been understood to be seasonal in Santa Rosa (Janzen 1988b). The lack of frass data in October is particularly unfortunate since this would have been, arguably, the most interesting month to contrast with weather factors since that October was the month with heaviest rainfall. It is likely that average dry weight was high in October because I collected high amounts of dry frass in September and November and dry weight increased relatively steadily from June through November. I do not make this assumption in my analyses, but this likely would have enhanced the effects of weather factors on caterpillar frass abundance.

2.4.2 Weather and phenological effects on insect abundance

Although I found seasonality in the abundance of two Families out of 11, climate and phenology did not necessarily play a role in peak abundance of these two Families. Curculionidae, a seasonal insect Family in the present study, was not significantly affected by the climatic and phenological variables examined. And while the seasonal Formicidae was found in lower quantities when leaf production was high, I also found that the aseasonal non-Formicidae Hymenopterans exhibited the same correspondence to leaf production. I found more non-Formicidae Hymenopterans when there were more flowers in the environment, confirming my prediction based on Janzen (1967), who observed many bees and wasps when flowers were in full bloom in Santa Rosa, but did not compare across seasons. Blattodea, cockroaches, were also found in abundance when flowers were in bloom in the present study. In contrast, flower phenology did not have an effect on Coleoptera (beetles). These results are in contrast to beetles in South East Asia (Corlett 2004) as well as Mexico (Aguirre and Dirzo 2008) that are often thought of as more frequent flower-visitors than Blattodea and beetle abundance fluctuates

largely with flower phenology in a tropical forest in south east Asia (Kato et al. 2000). To my knowledge, Coleoptera and Blattodea associations with flowers have not been studied in tropical dry forests. Vasconcellos et al (2010) found Blattodea was more abundant during the dry season in the seasonal, deciduous forest of Caatinga, Brazil, a similar result to that found in the present study (flowers bloom in the dry season in Santa Rosa), however Vasconcellos et al (2010) did not measure flower phenology. Vasconcellos et al (2010) mentioned other studies that found most flowering plant species in the Caatinga were in bloom during the rainy season, contrary to the patterns found in Santa Rosa. Therefore, there may be another mechanism other than flower phenology behind Blattodea abundance in the Caatinga. The authors do suggest that insect abundance patterns found in the Caatinga may be a product of biotic factors associated with rainfall, such as parasitoids, migration, soil moisture, but these factors were not measured in their study. Blattodea may be abundant in Santa Rosa when flowers are abundant for reasons other than the abundance of flowers themselves. Insects can peak due to the general effect that rainfall has on the environment rather than direct climate and phenological effects on insect abundance (Wolda 1989). Future studies should include parasitoids, migration, soil moisture, photoperiod and other factors not studied here to gain a more complete spectrum of factors with potential influence on insect abundance, which could allow for more concrete conclusions on the effects abiotic and biotic factors have on insect abundance.

I found significantly more mantids when percent leaf cover and maturity was high. However mantids are known predators, not herbivores suggesting other factors associated with high leaf cover and maturity, such as prey abundance, may affect Mantodea in Santa Rosa. The present study did not identify potential mantid prey, specifically, therefore I cannot conclude that there is a clear predator-prey relationship that drives mantid abundance fluctuations in

accordance with leaf phenology. However, this could be a useful hypothesis for future studies. Assessing insects within specific guilds such as herbivores, carnivores, detrivores, etc, may provide further insights into the effect climate and phenological variables have on insect ecology.

The present study found both rain as well as leaf production to have a positive effect on caterpillar frass, whereas fruit production had a negative effect. This is in accordance with my prediction and is not surprising given that Janzen (1988b) described the intense herbivory of most Santa Rosa caterpillars in detail. Janzen (1988b) found caterpillars to exhibit very large intra-annual variation in the timing and capacity of caterpillar abundance. Therefore, not only is it important to study tropical insects across every tropical ecosystem, but also over the course of longitudinal projects.

2.4.3 Potential caveats, future directions and significance

Phenological data in the current study is limited to 43 tree species and does not include lianas, grasses or cacti –all plausible food sources or habitat for the insects captured and analyzed in this study. Non-tree plants can flower during the wet season (Frankie et al. 2004) as opposed to the tree species in the present study, which flowered mostly in the dry season (but also at the beginning of the wet season). Furthermore, phenology data are limited to two of the four habitats measured for insect abundance. Although habitats were only two kilometers apart, there are differences in canopy height and age (i.e. successional stage) suggesting there is potential for variation in plant species composition across habitats. Future studies should incorporate phenology for more plant species and across broader habitat.

I studied insects at the Order and Family levels, not at the species level, therefore I cannot make inferences about life-cycle seasonality, for example dormancy versus emergence, -a typical

approach to studying insect seasonality at the species level (e.g., Grimbacher and Stork 2009; Wolda 1989). Although I cannot make inferences about species-level ecology, Timms et al (2012) found that species level identification is not always necessary in making biologically meaningful conclusions and that higher taxonomic levels, like Family level, can be sufficient. This is not to say that studying at the species level is not important. The tropics provide researchers with a large and perhaps unattainable goal of knowing all the diversity tropical ecosystems have to offer. Occasionally it is necessary to at least start a project at a coarse level and include more detailed analyses in the future.

The present study is limited in that I have only a little over a year's worth of data. Tropical insects can vary in seasonality patterns from year to year (Wolda 1988). Multi-year datasets are the only way to conclude seasonality patterns in the tropics. Patterns found in the present study cannot be extrapolated to other tropical climates, including tropical dry forests. However, studies such as mine can be viewed as providing two contributions: 1) fourteen months of data to compare to future studies on the same subject and add to, hopefully, future long term studies on tropical dry forest insect abundance and seasonality and 2) insect abundance patterns according to specific climate and phenological conditions from June 2011 to July 2012. Small-scale studies such as this one can benefit when building upon each other to find long-term patterns.

Long-term patterns are important when advising land management decisions. Such decisions are sometimes made unexpectedly, it is important to be prepared with useful information, like that present in this study to inform decision makers. Climate change will increase temperatures and create a drier environment for those insects currently living in Santa Rosa, therefore, it is important to document basal insect abundance and seasonality patterns now

while the forest is on a trajectory towards “old-growth status” (Janzen 2004) and while the insects continue to thrive.

Chapter Three: Capuchin insectivory and fallback foods

3.1 INTRODUCTION

Omnivores are able to consume many types of foods and can alter their diet when one food source is depleted and another becomes abundant (Castellarini et al. 2003; Chapman 1987). The importance and evolutionary implications of variation in food availability to the omnivore and diet during periods of food scarcity, or fallback foods, has become a hot-topic among researchers (Harrison and Marshall 2011; Lambert 2007; Marshall and Wrangham 2007; Lambert et al. 2004). Fallback foods are a resource that an animal relies on because it is one of very few resources available during times of overall or preferred food scarcity. Thus, fallback foods are imperative to survival in many cases, which is why many adaptive strategies have evolved in order to exploit fallback foods (e.g., Darwin's finches: Grant and Grant 1993, 1987; Grant et al. 1985; Abbott 1977). Primates have demonstrated many adaptations to exploit fallback foods when preferred foods are not available (Terborgh 1983) and recent research found various fallback food strategies, both morphological and behavioural, in primates around the world (Makedonska, Wright, and Strait 2012; Harrison and Marshall 2011; Wright, et al. 2009; Lambert 2007; Marshall and Wrangham 2007; Lambert et al. 2004; Yamakoshi 1998).

White-faced capuchins (*Cebus capucinus*) are omnivores who spend between 50% and 80% of their feeding time on fruit (Chapman and Fedigan 1990), and approximately 20% to 50% on invertebrates and consume small vertebrates occasionally. Some capuchin groups spend more feeding time on fruit than others, however foraging times are consistent across groups: approximately 25% of scans are spent foraging for fruit and 75% of scans are spent foraging for insects (Melin, AM unpub. data). From these data, we can also see that even though the majority

of time is spent foraging (e.g. visually foraging) for insects, the majority of feeding time (i.e. ingestion) is spent on fruit. In addition, white-faced capuchins spend a lot of time extractive foraging for invertebrates during times of food scarcity (Melin et al., in press). Insects, therefore, meet multiple fallback food criteria - they are difficult to process or find and are consumed during times of overall and preferred food scarcity. Recent literature suggests fallback foods have implications for morphological and behavioural adaptations for processing foods (Marshall et al. 2009). White-faced capuchins do not exhibit morphology adapted to their diet (Janson and Boinski 1992), instead they are suggested to have adapted behaviourally to their insect diet (Melin et al., in press). However the role that insects play in the capuchin diet is uncertain because resource abundance data is incomplete. Measuring insect abundance is critical in order to identify insects as fallback foods in the capuchin diet. Few studies at our site have measured insect abundance because it is difficult and time consuming to do so for an entire forest. I measured relative insect abundance across four capuchin habitats and reported the results in the previous chapter. The current chapter relates this insect abundance measure to patterns of capuchin insect foraging and fruit abundance. My fundamental research question is: Are insects fallback foods in the white-faced capuchin diet? To address my research question, I assessed when white-faced capuchins consumed processed, aseasonal or consistently abundant foods in relation to food abundance derived from fruit and insect abundance data. Capuchins consume a few non-insect invertebrates as well as insects and I treat the former as having similar dietary roles in the capuchin diet. Therefore, I refer to fallback foods in relation to invertebrates rather than simply insects. I also refer to invertebrates that capuchins consume and exclude caterpillars from this term because invertebrates are quantified with different units compared to caterpillars

due to different collection techniques (i.e. insect traps versus frass traps). I refer to invertebrates as “non-caterpillar invertebrates” and “caterpillars” as separate terms.

3.1.1 Insects in the primate diet

Insects constitute the majority of animal matter found in the primate diet (Lambert 1998). Many primates supplement their diet with insects, including mainly frugivorous spider monkeys, mainly herbivorous gorillas and omnivorous chimpanzees (Deblauwe et al. 2003; Chapman 1987; Suzuki 1966). According to Harding (1981), 65% of primate species consume invertebrates and some may seek out insects within fruit (Redford et al. 1984). Other primates, such as yellow baboons in East Africa, can focus their diet entirely on insects (in this case, caterpillars) when insects are seasonally abundant (Altmann 2009). This suggests that insects may be more important in the primate diet than previously realized.

Insects provide the majority of protein, an essential nutrient, to the capuchin diet, and are second to seeds in the proportion of fat provided to the capuchins (McCabe and Fedigan 2007). We know that white-faced capuchins eat various insect species from about six orders (Melin et al. 2007): three families of Hemiptera (true bugs), five families of Lepidoptera (moths and butterflies), seven families of Coleoptera (beetles), and four families of Hymenoptera (ants and wasp larvae), Orthoptera and Blattodea. This includes several species of acacia ant, and various other insect species, some of which have been definitively identified in the capuchin diet and others which have not (Young et al. 2007; Young 2005). We also know that capuchins eat insects throughout most seasons, peaking in June and July, presumably due to the consumption of congregated caterpillars, and decreasing noticeably during the late wet season (Melin et al., in press). This feeding pattern suggests that insect abundance may vary across seasons. As with

fruit feeding, some capuchin groups spend more time feeding on insects than others, which suggests variation in insect abundance across habitats (Chapman and Fedigan 1990; Chapman 1987). Chapman (1987) found that capuchins spent 17% of their foraging time on insects, however, he studied one group of capuchins in an older (“primary”) forest with many capuchin food trees. Melin, AM (unpub. data) studied four capuchin groups living in variable habitats and found that the majority of capuchin foraging time was spent on insects, suggesting that foraging time spent on insects can vary across studies. Such variation also may be a consequence of large interannual variation in resource abundance, which I discuss later in the chapter.

3.1.2 Fallback foods and seasonality

The importance and intensity of selection on dietary strategy is enhanced the more seasonal the environment or preferred food source (Gogarten et al. 2012; Lambert 2007). Potts (2004) suggests seasonal environments impose the necessity for including fallback foods in the primate diet. Primates may consume more fallback foods and fewer preferred foods during times of overall food paucity when their environment is highly seasonal (Harrison and Marshall 2011). We know fruit is highly seasonal at our study site in Santa Rosa (Melin et al., in press; Carnegie et al. 2011) and in general, fruit is strongly affected by climatic variables, especially rain (Levey 1988; Fleming et al. 1987). Santa Rosa is a tropical dry forest –a highly seasonal environment-- where it does not rain for up to 6 months of the year (Campos and Fedigan 2009; Fedigan and Jack 2001). This has a great effect not only on fruit abundance, but on all flora and fauna. Although temperature does not vary as much as rainfall throughout an annual cycle in Santa Rosa, temperature is statistically seasonal (Melin et al., in press). Fallback foods are important

during food scarcity in seasonal environments where, in some cases, an animal may not survive if such foods were not available.

Some authors (e.g., Yamagiwa and Basabose 2009; Wrangham et al. 1998) distinguish fallback foods from preferred foods in various primate diets by using a consumption to abundance ratio. The assumption is that preferred foods are consumed in higher quantities than expected from their abundance in the environment (“overselected”) whereas fallback foods are consumed at lower than expected amounts (“underselected”) compared to their abundance. I suggest that this method is too subjective given that researchers must decide what is a small versus large ratio in order to conclude what is a fallback food and what is preferred. Furthermore “intermediate” ratios may occur that do not fall into either category. The present study defined seasons based on food abundance and then compared capuchin foraging frequencies on various foods across those seasons.

Fallback foods are important in the primate diet during times of overall and preferred food scarcity, as a result they can impose strong selective forces on evolutionary adaptations (Marshall et al. 2009; Lambert 2007; Marshall and Wrangham 2007). Such adaptations can be morphological, in order to physically overcome tough fallback foods, (see Lambert et al 2004) or cognitive, such as tool use in chimpanzees (e.g. Yamakoshi 1998). Summarizing this definition, which has been constructed over time by various authors (Harrison and Marshall 2011; Marshall et al. 2009; Lambert 2007; Marshall and Wrangham 2007), I analyze my data using this fallback food definition: foods that require processing time and are either aseasonal or are available during times of overall and preferred food paucity.

3.1.3 Fallback foods and processing adaptations

Fallback foods are thought to play a role in the evolution of harvesting and processing adaptations in primates (Harrison and Marshall 2011; Marshall et al. 2009; Lambert 2007; Marshall and Wrangham 2007). Processing adaptations are defined by Harrison and Marshall (2011) as “traits that facilitate the exploitation of (fallback) foods that are difficult to process”. These traits can be morphological adaptations, such as large jaws or thick tooth enamel, or behavioural adaptations, such as extractive foraging -facilitating the exploitation of fallback foods (Marshall et al. 2009).

Some capuchin monkeys have morphological features associated with processing adaptations, the most apparent being the robust jaws possessed by *Sapajus apella* to open hard palm nuts (Wright et al. 2009) as well as to obtain insects from within branches (Janson and Boinski 1992; Terborgh 1983). Although capuchins overall have thicker tooth enamel than most primate species (Kay 1981), white-faced capuchins are not considered to exhibit morphological adaptations associated with food (Janson and Boinski 1992), and they do not use tools as do tufted capuchins (Wright et al. 2009; Moura and Lee 2004). Melin et al (in press) suggest the evolution of the large brain-to-body ratio of white-faced capuchins facilitated enhanced sensorimotor intelligence (a term defined by Parker and Gibson 1977) and, in turn, processing ability –specifically extractive foraging behaviour. All capuchins exhibit a behavioural pattern called extractive foraging that is thought to be a processing adaptation (Janson and Boinski 1992; Melin et al.) and a product of the large brain to body size ratio of the capuchin (Parker and Gibson 1979; 1977). Extractive foraging consists of breaking apart tough materials such as bark, whole branches, hard fruit shells, etc. to access the food beneath these protective materials. A large proportion of the capuchin activity budget is spent on extractive foraging and recent

evidence shows white-faced capuchins practice extractive foraging most often during times of preferred food scarcity (Melin et al., in press).

Extractive foraging is the most plausible adaptation to fallback foods in the white-faced capuchin diet because they are considered primarily frugivorous rather than folivorous (Fragaszy and Visalberghi 2004). Frugivores are known to have enlarged brains and fall back on either vegetative foods that require morphological adaptations or extractive foods that require manual dexterity and sensorimotor intelligence (Melin et al., in press). White-faced capuchins do not possess morphological adaptations to their digestive or masticatory systems, whereas they are known for their manual dexterity and ability to forage extractively, suggesting their fallback food should impose increased processing effort via extractive foraging (rather than through digestion). Melin et al. (in press) focused their paper on capuchins extractive foraging for invertebrates found in branches and under bark. I recorded extractive foraging behaviour, insectivory and other food feeding on the same study animals. I included any invertebrates, plant pith, bromeliad leaves and other foods that required extractive foraging and were consistently available in the capuchin environment throughout each season. See Table 3.1 for a list of all foods that required extractive foraging.

Table 3.1 Capuchin foods that required processing time

Food Category	Food Source
Invertebrate	Unknown insect –gleaned
Invertebrate	Small insects in branches/bark
Invertebrate	Unknown insects in bird nest
Invertebrate	Unknown insects in bird nest on acacia tree
Invertebrate	Unknown invertebrate
Invertebrate	Acacia ant*
Invertebrate	Orthopteran sp.
Invertebrate	Unknown Insect in Byrsionima crassifolia leaves (cecidozoa)
Pith & Bromeliads	Bromeliad leaf
Pith & Bromeliads	Bromiliad plumieri leaf
Pith & Bromeliads	Bursera simaruba pith
Pith & Bromeliads	Unknown pith
Unknown	Unknown species

*Janzen 1966

3.1.4 Insects as fallback foods

Researchers previously thought that insects (as opposed to leaves) were fallback foods for New World monkeys; because leaves and fruit occur in abundance during roughly the same seasons in the New World, therefore leaves would not be available as fallback foods when fruit-a preferred food- is not available (i.e. when fallback foods are needed by the consumer) (Lambert 1998). However, recent studies suggest that leaf and fruit phenology are not necessarily synchronized in the New World (Lambert 1998), and further insights into whether insects are fallback foods in New World monkey diets are lacking. Wright et al (2009) compared the food use patterns of New World tufted capuchins species *S. libidinosus* and *S. apella* and found *S. apella* used embedded colonial insects as well as woody legume pods as fallback foods whereas *S. libidinosus* used palm nuts as fallback foods. Wright et al. (2009) studied *S. apella* in a

tropical forest, whereas *S. libidinosus* resided in a dry open savannah, suggesting different environments are conducive to different fallback food strategies. Melin et al. (in press) studied white-faced capuchins in a tropical dry forest and found that the capuchins spent more time consuming embedded invertebrates during a period of low fruit abundance. This suggests that, similar to what has been observed with the closely related *S. apella*, invertebrates may be fallback foods in the white-faced capuchin diet.

Old World primates also use insects as fallback foods. Chimpanzees use honey bees, ants, termites and other animal foods as fallback foods and have the ability to access such foods using tools (Yamagiwa and Basabose 2009). Animal matter protein is more easily digested than plant protein (Carpenter 1994, 1986 as cited in Milton 2003) and protein is essential to brain development (Bourre 2006) implying insects are a high quality food source. Milton (2003) suggests the high energy requirements large brains impose on primates is satisfied by animal protein, such as protein from insects. Capuchins obtain most of their dietary protein from insects (Terborgh 1983), further supporting Melin et al's (in press) proposal. Animal fallback foods are a suggested mechanism that may facilitate animals expanding their ranges into dry areas (whereas herbs facilitated smaller home ranges) (Yamagiwa and Basabose 2009). Hominoids with large brains in seasonal environments used tools to forage for animal protein (Fleagle 1999 as cited in Milton 2003), similar to the strategy exhibited by chimpanzees living in the seasonal environment of in Kahuzi-Biega National Park, Democratic Republic of Congo that includes a severe dry season (Yamagiwa and Basabose 2009). The capuchins of Santa Rosa experience a very long and dry season each year and if insects are fallback foods then capuchin ability to forage for insects, i.e. extractive foraging, may be adaptive to their dry environment.

Tool use is said to be correlated with large brain to body size ratios (Reader and Laland

2002), such as that found in capuchins. Although the white-faced capuchins in Santa Rosa do not use tools, the correlation between tool use and large brains in primates as well as the important source of protein that insects provide further supports the prediction that insects are fallback foods. High quality fallback foods select for the evolution of behavioural adaptations to process such foods (Marshall et al. 2009). Capuchins living in seasonal Santa Rosa forage extractively, a behavioural adaptation proposed to be facilitated by their large brain to body ratio and that allows them to access insects as fallback foods (Melin et al., in press). The present study attempts to confirm this proposal.

3.1.5 Fallback foods in the capuchin diet

According to Wright et al (2009), capuchins are the best primate group to study fallback foods since they are found in a wide range of habitat types and are able to exploit these habitats via morphological and behavioural adaptations. I would also argue that capuchins are an appropriate study subject to understand the importance of fallback foods in an ecosystem because they are known to be opportunistic foragers, and they will try to access any food resource available to them (Fragaszy and Visalberghi 2004). Therefore, one can predict that their diet might change with food abundance fluctuations –a necessary component to study fallback foods.

Capuchins can supplement and sometimes substitute the fruit part of their diet with insects, even though fruits are considered preferred (Chapman 1987). This implies that insects can provide for capuchin nutritional needs during periods of fruit scarcity (Marshall and Wrangham 2007). Capuchins consume invertebrates throughout the year, including during a period of low overall food abundance when they also forage extractively for invertebrates (Melin

et al., in press). To determine if invertebrates are fallback foods in the capuchin diet, we need to record the availability of preferred and potential fallback foods simultaneously with capuchin feeding and processing behaviour patterns. For example, Harrison and Marshall (2011) could not confirm that figs are fallback foods in the bonobo diet because fig availability data versus fig consumption data were lacking. Marshall et al (2009) found a paucity of published resource abundance data across primate foraging studies, which made it difficult to assess fallback food strategies across taxa. We know capuchins visit fruit trees more frequently when fruit is abundant than when fruit is not abundant and that capuchins spend a large amount of time consuming caterpillars when they are available, suggesting fruit and caterpillars are preferred foods and not a fallback food (Melin et al., in press). A final key piece of the present puzzle is to have data on invertebrate abundance throughout the year.

3.1.6 Research question, hypothesis and predictions

My overarching research question is: Are non-caterpillar invertebrates fallback foods in the capuchin diet? My general hypothesis and predictions (as an “if/then” statement) are as follows: If invertebrates are fallback foods, then 1) capuchins should consume significantly more invertebrates during times of overall and preferred food scarcity (i.e. fruit and caterpillars), than when preferred and overall food abundance is high; and 2) capuchins should spend more time processing invertebrates than other aseasonal foods (e.g., pith).

More specifically, I analyzed my data to answer the following research questions:

- 1) Do capuchins consume invertebrates more frequently during a season with low preferred and overall food abundance?

- 2) Do capuchins spend more time processing invertebrates than other aseasonal processed foods?

3.2 Methods

3.2.1 Study site

I conducted my research in Sector Santa Rosa in the Área de Conservación Guanacaste (ACG) in Costa Rica. Santa Rosa is highly seasonal with a six month dry period (mid-November to mid-May) and a six month rainy season when rainfall gradually increases as the season progresses. Further study site details can be found in Chapter One and Two.

3.2.2 Insect abundance measures

Although insects are an important part of the capuchin diet, few studies have attempted to understand the ecological relationship that capuchins have with insects. Young (2005) studied the role of insects in the capuchin diet, how capuchins foraged for insects, and how capuchins select insect types in relation to their abundance. However, insect abundance measures were limited in her study and were collected over a total of only four days using leaf litter sampling, tree beating, twig sampling and pitfall trapping. The present study measured insect abundance over a period of 14 months using various insect trapping methods.

The previous chapter described insect abundance patterns from June 2011 through July 2012. Overall abundance was statistically seasonal with a peak in abundance in April and May. I also found Formicidae (ants), Curculionidae (weevils, a type of beetle) and Blattodea (cockroaches) to peak in abundance in April and May. Caterpillar abundance peaked in September, however, I did not study capuchin foraging behaviour between the months of

September and December. I found that during the period of my foraging study (January-July), capuchin feeding on caterpillars peaked in June and July –a period of overall and preferred food (i.e. fruit) abundance. Because fallback foods are defined as being consistently available, especially during times of food scarcity, I do not consider caterpillars (which are seasonally abundant when fruit is also abundant) as fallback foods in the present study.

Although I identified to taxon and analyzed less than half of the overall insects that I collected and counted to determine my food abundance seasons, I did include a wide-range of Orders and Families, encompassing a wide variety of ecologies and life strategies. Of the nine Orders and 11 Families that I analyzed, I found only one Order and two Families to be seasonal.

3.2.3 Study subjects and collection of foraging data

I collected behavioural data on white-faced capuchins from January through July 2012. I did not collect behavioural data on them during the雨iest time of year (September to December), although sampling of insects continued during those months. I used focal follows as suggested by Altmann (1974) to collect foraging behaviour from 72 individuals in four groups. I was able to identify each individual by scars and facial markings. I collected data on adults and large immatures of both sexes as well as subadult males (Table 3.2). Foraging for particular food types does not differ across age-sex class (Melin & Young, unpub. data). Therefore, I do not consider variation across age-sex class to be a confounding factor in the present study, particularly as I did not include infants and small immatures who may still be dependent on their mothers and not foraging independently.

Each focal follow was ten minutes in length, during which I recorded every instance of foraging on all aseasonal and processed foods. I recorded and analyzed consumption frequency

and food processing duration (i.e. extractive foraging) for each food item consumed and processed by the capuchin.

Table 3.2 The number of focal animals in each age/sex class

Age	Female	Male
Adult	31	7
Subadult	NA	8
Large	10	16
Immature		

3.2.4 Food abundance data collection and capuchin foraging (addressing research question one from above)

I measured both fruit as well as insect abundance concurrently with capuchin foraging data collection. Fruit phenology is collected as part of the larger ongoing primate research project in Santa Rosa and we know that fruit is a highly seasonal resource for the capuchins. Collected transect data to sample the abundance of each food species across different capuchin habitats confirms that fruit is highly seasonal and most abundant during the early rainy season in Santa Rosa (Carnegie et al. 2011).

I used insect abundance data collected during the present study period as well as the fruit phenology patterns from data collected in the present study as well as those presented in (Carnegie et al. 2011) to establish seasons based on capuchin food abundance. Please see Chapter Two for insect collection methodology. Fruit and caterpillars are both patchily distributed, high quality food sources that generally require little processing, making them likely to be preferred foods. Formicidae, Blattodea and Curculionidae either do not exhibit these characteristics or not enough is known about them to assume their ecology is similar to that of

caterpillars. Therefore, I consider Formicidae, Blattodea and Curculionidae (henceforth referred to as “Non-Caterpillar Insects”) separately from caterpillars when defining the following seasons found in Table 3.3: Low Fruit/Low Non-Caterpillar Insects/Low Caterpillar (LOW) season (January through March); High Fruit/High Non-Caterpillar Insects/Low Caterpillar (INTERMEDIATE) season (April and May), and High Fruit/Low Non-Caterpillar Insects/High Caterpillar (HIGH) season (June through August). In short, the LOW season refers to a low overall food abundance season, during which I predict that capuchins will consume fallback foods. The INTERMEDIATE season refers to a period when fruit (believed by capuchin researchers to be a preferred food, Melin et al, in press), is high in abundance and Non-Caterpillar Insects are also abundant whereas caterpillars (also believed to be preferred), are low in abundance. The HIGH season refers to a period when fruit and caterpillars are high in abundance and Non-Caterpillar Insect abundance is low.

Overall insect abundance was seasonal, peaking in April and May. However, many aseasonal insects continue to be available throughout the whole year, therefore capuchins can readily fallback on them. Given that there are clear seasons composed of capuchin foods demonstrating periods of high low abundances , it is reasonable to predict that if capuchins are to fall back on a food, they will do so during the LOW season.

The second “INTERMEDIATE” season described in Table 3.3 occurred from September to December, a period when I collected insect abundance data, but did not collect capuchin behavioural data. I do not include this season in my behavioural analyses, but I discuss our knowledge about capuchin foraging during this season in the discussion section.

I recorded each time a capuchin consumed one food item within a ten minute focal follow. I used the frequency of each consumption record on available and processed foods to compare consumption frequency across food abundance seasons.

Table 3.3 Food abundance seasons

Season	Fruit	Caterpillars	Seasonal Non-Caterpillar Insects	Month range
LOW	Low	Low	Low	January-March
INTERMEDIATE	High	Low	High	April & May
HIGH	High	High	Low	June-August
INTERMEDIATE (Caterpillar High)	Low	High	Low	September-December

3.2.5 Food processing (addressing research question two from above)

I recorded when capuchins demonstrated extractive foraging and other processing behaviours. Food processing involved extractive foraging where opening of a substrate, plant part or insect part took place before, during or after consumption. Extractive foraging behaviour was always durational and recorded in seconds.

I used both abundance data as well as capuchin behavioural data to categorize foods that were aseasonal or always available in the environment. I then used behavioural data to determine what foods required time to process. Processed foods that are always available in the environment are potential fallback foods according to definitions discussed above. These are the only foods I analyzed. I categorized all major food types into what I call from now on “Fallback Food Categories” (see Table 3.1). I defined each Fallback Food Category by clumping together similar food items I observed the capuchins to eat. Capuchins consume a few non-insect invertebrates (e.g. spiders and snails), but not enough to merit a category of their own. I,

therefore, included both non-insects and insects in the Fallback Food Category “Invertebrate”. In addition to the Fallback Food Category “Invertebrate”, I defined “Pith & Bromeliads” and “Unknown”. The category “Pith & Bromeliads” refers mostly to pith, a woody substance found in the center of some tree branches, as capuchins only rarely consumed bromeliad leaves. Although I did not measure pith and bromeliad leaf abundance, both are always available in capuchin home ranges in Santa Rosa (Melin, unpub. data), therefore I chose to include pith and bromeliads when analyzing my data. The Fallback Food Category “Unknown” consists of unidentifiable foods consumed by capuchins. Table 3.1 provides a list of “Food Sources” within each Fallback Food Category. I did not analyze food down to this Food Source level because I did not have enough data points per Food Source. However, I list them in the table to give the reader a better idea of what constitutes “foods requiring processing”. Many Invertebrate Food Sources consumed by the capuchins are unknown in abundance; however, because I found invertebrates to always be abundant in the environment through insect trapping methods, I assumed unknown Invertebrates consumed by capuchins were abundant regardless of the season.

3.2.6 Statistical analyses

Marshall and Wrangham (2007) emphasize the importance of collecting and analyzing foraging data while ensuring independence. I chose to use Generalized Linear Mixed Models (GLMMs) to analyze my data because this is the best method available to account for repeated measures on the same individuals over time. Since I followed the same capuchin individuals multiple times throughout my study, I needed to account for this in my analyses to avoid biasing my results. GLMMs are “mixed” models because they include both fixed as well as random factors. Fixed factors are variables the researcher would like to test in order to answer their

research question (e.g. Fallback Food Category). Random factors are variables with repeated measures as well as unequal sampling effort that need to be accounted for (e.g. the individual capuchin). I explain how I constructed a GLMM for each research question below.

3.2.6.1 Food consumption frequency across seasons (addressing research question 1)

I used a Generalized Linear Mixed Model (GLMM) with a Poisson distribution, the most appropriate distribution for count response variables (i.e. consumption frequency). I considered each consumption event, the unit of analysis, to be independent from each other. I used the lmer() function from the “lme4” package (Bates et al 2012) in the statistical program R (R Core Development Team 2012). I included Food Category and Season as the explanatory variables with an interaction and as individual effects. I nested the individual focal animal within capuchin group as random effects to account for repeated measures and unequal sampling effort across individuals (Crawley 2007; Zuur 2009; Zuur et al. 2009; Zuur et al. 2007).

To assess resulting significant interactions, I used testInteractions() from the “phia” package in R (De Rosario-Martinez 2012). Contrast sums are used to detect significant interactions in a simple effects test when using the testInteractions() function. This means a difference is calculated between treatments within each variable involved in the interaction (e.g. Pith & Bromeliads and Invertebrates within the variable Fallback Food Category). The resulting differences are subtracted from each other and a Chi-square output is produced (De Rosario-Martinez 2012). The results I report are from the Chi-square (χ^2) output.

3.2.6.2 Food processing duration across food categories (addressing research question 2)

To assess the difference in amount of time, in seconds, capuchins spent processing different Fallback Food Categories, I used a GLMM in R. Processing duration was the response variable and Fallback Food Category was the explanatory variable. I nested capuchin individual in capuchin group as random effects to account for repeated measures.

3.3 RESULTS

3.3.1 *Food consumption frequency across seasons*

Mean Invertebrate consumption frequency in the capuchin diet was higher during the HIGH season than the LOW season ($\chi^2=2, N=1187$)=42.96, $p<0.0001$). This is apparent in Figure 3.1. Pith & Bromeliads and Unknowns did not exhibit a significant difference in consumption frequency across seasons. But across food types, Invertebrate, Pith & Bromeliads and Unknown consumption frequency differed from each other in all three seasons HIGH: ($\chi^2=59.96, df=2, N=1187, p<0.0001$); INTERMEDIATE: ($\chi^2=12.39, df=2, N=1187, p<0.0001$); LOW: ($\chi^2=33.18, df=2, N=1187, p<0.0001$). This is because Invertebrate consumption frequency is higher than Pith & Bromeliad as well as Unknown during the HIGH season, but changes in the INTERMEDIATE and LOW seasons when Pith & Bromeliad consumption frequency is higher than Invertebrate and Unknown (Figure 3.1).

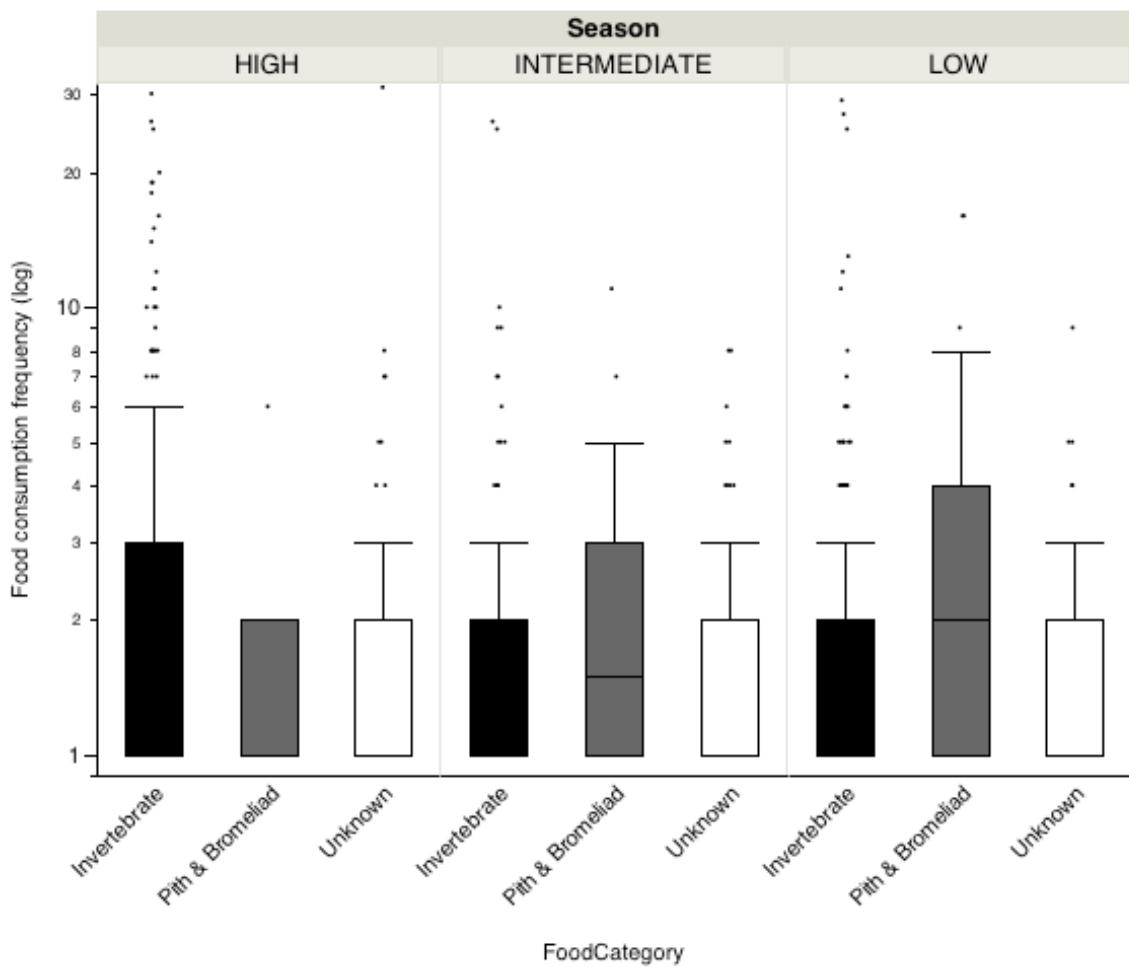


Figure 3.1 The number of aseasonal processed food items consumed (log-transformed) by capuchins across the HIGH, INTERMEDIATE and LOW seasons. Invertebrates are represented by black box plots, Pith & Bromeliads by grey box plots and Unknowns by white box plots. The upper and lower edge of each box represents the 75th and 25th quantile, respectively, the horizontal bar found in some boxes is the sample median (some are not apparent because they are either right at the 75th or 25th quantile), the whiskers represent the 75th quantile + 0.5*(interquantile range). The terminal or angled point in each of the three independent, light coloured lines represent the mean consumption frequency value for each Food Category.

3.3.2 Time spent processing foods

Capuchins spent significantly more time processing Invertebrates during the LOW season than during the other seasons ($\chi^2=41.29$, $df=2$, $N=2532$, $p<0.0001$; Figure 3.2). I did not find significant results across seasons for Pith & Bromeliads or Unknown foods, suggesting capuchins spent a consistent amount of time processing Pith & Bromeliads and Unknowns per processing event across each season. However, note that there is only one processing event (or data point) for Unknowns during the LOW season in Figure 3.2. Within each season and across Fallback Food Categories, capuchins spent significantly more time processing Pith & Bromeliads than Invertebrates or Unknowns during the HIGH season ($\chi^2=7.76$, $df=2$, $N=2532$, $p=0.037$) the INTERMEDIATE season ($\chi^2=8.77$, $df=2$, $N=2532$, $p=0.037$) as well as during the LOW season ($\chi^2=8.37$, $df=2$, $N=2532$, $p=0.037$).

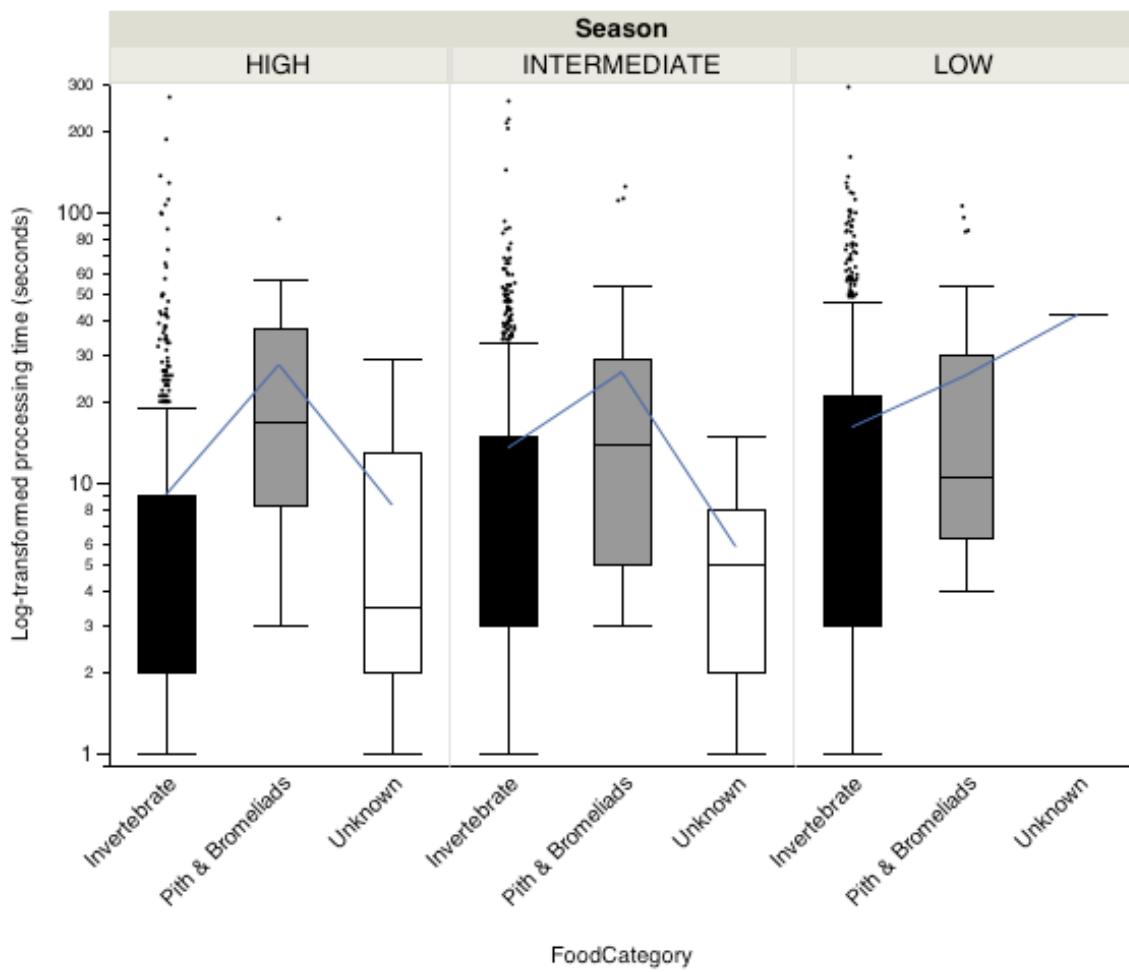


Figure 3.2 The amount of processing time in seconds (log-transformed) spent by capuchins foraging on aseasonal Pith & Bromeliads, Unknown and Invertebrate Food Categories.

Invertebrates are represented by black box plots, Pith & Bromeliads by grey box plots and Unknowns by white box plots. The upper and lower edge of each box represents the 75th and 25th quantile, respectively, the horizontal bar found in some boxes is the sample median (some are not apparent because they are either right at the 75th or 25th quantile), the whiskers represent the 75th quantile + 0.5*(interquantile range). The terminal or angled point in each of the three independent, light coloured lines represent the mean consumption frequency value for each Food Category.

3.4 DISCUSSION

3.4.1 Are invertebrates fallback foods?

Capuchins consumed Invertebrates at higher frequencies during the season of highest overall food abundance rather than when food availability was low. These results contradict my prediction that capuchins would consume Invertebrates at higher frequency during the LOW food abundance season, which would have confirmed Invertebrates as fallback foods. Fallback foods are foods that are consumed during times of overall and preferred food scarcity, whereas capuchins consumed Invertebrates when preferred foods and food overall were abundant. However, capuchins did spend more time processing Invertebrates during the LOW food abundance season, suggesting that certain Invertebrates may be fallback foods. Had I had enough data to analyze independent capuchin consumption frequencies for Invertebrates that they spent more time processing I might have found capuchins consume them more when overall food abundance is low, fitting the definition of a fallback food.

Pith and bromeliad leaves are likely fallback foods since capuchins consumed Pith & Bromeliads at a significantly higher frequency than Invertebrates and Unknowns during the LOW food abundance season, and they also spent significantly more time processing Pith & Bromeliads than either other Fallback Food Category during each season. Although the present study did not measure pith or bromeliad leaf abundance, we know both are abundant throughout the year and throughout each capuchin habitat in Santa Rosa (Melin, unpub. data). Melin (unpub. data) collected data on tree abundance for popular species capuchins consume. Pith & Bromeliads meet each fallback food requirement –they are processed more than other foods, are

consumed more during overall and preferred food scarcity and are abundant during times of overall and preferred food scarcity.

These results make sense in light of fallback food studies on chimpanzees, a large-brained primate with which capuchins are often compared. Wrangham et al (1998) and Malenky & Wrangham (1994) found chimpanzees ate pith or leaves significantly more during times of fruit scarcity than when fruit was abundant. Basabose et al (2002) found similar results, also reporting that chimpanzees included small amounts of insect matter during the same period of fruit scarcity. Capuchins in the present study continued to consume invertebrates while falling back on pith during periods of low food abundance, suggesting invertebrates may continue to fulfill protein requirements in the capuchin diet. Yamakoshi (1998) found chimpanzees in Bossou, Guinea used pestles to extract pith as a fallback food. Pith is higher in quality than some plant fallback foods such as leaves (Lambert 2007). High quality palm nut fallback foods in *Sapajus* diet selected for tool use and pith may have acted as a strong selection pressure on the evolution of tool use in chimpanzees and perhaps the extractive foraging behaviour in white-faced capuchins.

3.4.2 Potential caveats and future directions

The present study focuses on one population of *C. capucinus* in a tropical dry forest. Other ecosystems provide different resources and resource abundance patterns, therefore it is likely that capuchins in other environments do not necessarily fallback on pith and bromeliads as do the capuchins in Santa Rosa. Future research should continue to explore various fallback foods in the *C. capucinus* diet across each ecosystem that this species inhabits.

The present study supports a previous finding that white-faced capuchins in Santa Rosa forage extractively for embedded invertebrates more so during a time of overall food scarcity (Melin et al., in press). Although I was able to measure relative adult and caterpillar insect abundance or activity over time, I was not able to measure embedded invertebrate abundance. Such data would help in understanding the role insects play in the capuchin diet, however methodologies to measure embedded invertebrates are limited and were unsuccessful in the present study.

The present study considered only one possible adaptation to dealing with periods of low food abundance –food processing (i.e. extractive foraging). Capuchins foraged extractively for Invertebrates more when overall food was low in abundance and they foraged extractively for Pith & Bromeliads more than for Invertebrates. These results support an idea posited by Melin et al (in press), that extractive foraging is an important behaviour that allows *C. capucinus* to access foods during times of low food availability. However, Melin et al (in press) did not present extractive foraging behavioural data, but rather foraging behaviour on embedded insects, therefore the authors did not consider other processed foods as potential fallback foods. In contrast, grey snub-nosed monkeys, recently recognized as extractive foragers, do not rely on extractive foraging during times of food paucity (Xiang et al. 2013), suggesting there are alternative strategies for accessing fallback foods among primates that forage extractively. Many traits can be associated with fallback food adaptations, such as differences in gut morphology, food retention, etc (Harrison and Marshall 2011). Gut morphology and physiological responses in the capuchin body are nearly impossible to study unless extremely invasive methods are applied. Frugivorous primates are more likely to evolve behavioural adaptations to their diet, such as extractive foraging, rather than complex morphological adaptations, such as changes to

the digestive system (Reader and Laland 2002; Keverne et al. 1996). Being that capuchins are primarily frugivorous, it is unlikely they have a digestive adaptation to fallback foods.

Nevertheless, future studies should build on the list of potential adaptations to fallback foods as there are many strategies among primates and other animals.

Capuchins include many flowers in their diet during periods of overall food scarcity. Flowers in Santa Rosa are, for the most part, seasonal and hence were not included in the present study. However, because they constitute a large portion of the capuchin diet during the LOW season, they may be a fallback food. Flowers, though, do not generally require a capuchin in Santa Rosa to forage extractively and little is known about capuchin flower foraging compared to flower abundance. Research on the role flowers play in the capuchin diet is currently underway.

The present study is the first to describe identifiable fallback foods in the *C. capucinus* diet. This research is important because fallback foods are foods that primates rely on and capuchins could very well perish if fallback foods like pith and bromeliads were to become extinct in the capuchin environment. Such information can be useful in conservation and land management decision-making –a common necessity in today’s world of constant and rapid human population expansion and resource use resulting in encroachment and, in turn, species extinction.

Chapter Four: Discussion

Tropical insect abundance data are sparse in the literature and patterns found at one research site may not be translatable to another research site. Similarly, insect abundance patterns may vary interannually within the same research site. My study presents insect abundance patterns found from June 2011 to July 2012 in Santa Rosa, a tropical dry forest. My results indicate divergent insect abundance patterns when comparing my findings to published data from other sites with similar ecosystems (i.e., highly seasonal with a long dry season). This variation across space and time underscores the importance of continued research on tropical insect abundance –a neglected field of research.

Along the same lines, the present study identified fallback foods for one white-faced capuchin population residing in one type of ecosystem –a tropical dry forest. White-faced capuchins from other ecosystems are likely faced with different resource availability patterns and may fall back on different foods depending on what is available in the environment. My findings are likely not applicable to other capuchin populations residing in other environments.

Identifying and understanding the role that fallback foods have in the primate diet has been influential in our understanding of evolved traits in primates. Studies have shown that fallback foods can shape morphological adaptations as well as behavioural adaptations (Marshall et al. 2009; Marshall and Wrangham 2007). White-faced capuchins in the present study demonstrate a reliance on extractive foraging behaviour to access fallback foods, pith and bromeliad leaves. In addition, capuchins are known for their large brain to body size ratio, said to

have coincided with the evolution of extractive foraging in capuchins in order to access fallback foods (Melin et al., in press). The present study supports the idea that extractive foraging is a mechanism by which white-faced capuchins access fallback foods, a resource known to have strong selection forces on primate morphological and behavioural traits like those exhibited by large brain to body ratios.

Most research on fallback foods conducted on capuchins focuses on tufted capuchins (e.g., Wright et al 2009) presumably because they exhibit the most obvious morphological adaptations to fallback foods: tool use and robust craniodontal morphology. Gracile capuchins on the other hand have been virtually ignored with regards to the topic of fallback foods (but see Wright et al. 2009) perhaps because they typically do not use tools, at least not in the traditional sense, and they do not exhibit morphological adaptations for feeding. The present study attempts to build on the limited available literature by focusing on the gracile *Cebus capucinus*, a species that does not use tools nor does it exhibit morphological adaptations for feeding, but rather behavioural adaptations.

A major limitation to past capuchin fallback food studies has been the lack of food abundance data, specifically insect abundance data collected simultaneously with capuchin foraging data (see Melin et al., in press). The present study measured insect abundance as well as capuchin feeding and foraging data to assess the effects of seasonal resource abundance on capuchin feeding and extractive foraging behaviours.

4.1 Project summary and synthesis

In order to determine what might constitute fallback foods for white-faced capuchins, I collected data on their foraging behaviour simultaneously with data collection on fruit and insect

availability, since together these two resources represent the majority of the capuchin diet. In Chapter Two I presented insect abundance data as well as examined climatic and plant phenology effects on insect abundance in a tropical dry forest. I found that most insects identified to Order and Family were aseasonal in abundance, even though overall insect abundance was seasonal and peaked in April and May. These findings supported my prediction that overall insect abundance would be seasonal. I also predicted that Coleoptera, Lepidoptera, Hemiptera would be seasonal based on previous work done in a seasonal tropical environment (da Silva et al. 2011). However, I found that only one Coleopteran Family, Curculionidae was seasonal, whereas the rest of the Coleopteran Families as well as Lepidoptera and Hemiptera were aseasonal. Formicidae and Blattodea also peaked in April and May, but unfortunately, information on Formicidae and Blattodea abundance in tropical dry or seasonal environments was not available to make predictions on these taxa (besides acacia ants, see Janzen 1966).

In support of my predictions about the effects of weather and phenological variables (based on Janzen 1967), I found that when temperatures and flower abundance were high (and when rainfall, fruit and leaf abundance were low), both Formicidae and non-Formicidae Hymenoptera were abundant. I found similar phenological effects on Blattodea abundance, although neither temperature or rainfall affected Blattodea abundance. Literature for the abundance of Blattodea as well as Mantodea in a tropical dry forest (or a similarly seasonal environment) is lacking, therefore I did not make specific predictions based on these taxa. Leaf cover positively affected Mantodea abundance, however, there was an inexplicably large number of mantids caught in December while relatively few throughout the rest of the study months. Mantids are predatory insects, therefore it is possible that they increased in abundance in

December in reaction to prey influx. However, I do not have ecological data on mantid prey to support this hypothesis.

Caterpillar abundance followed predicted and previously demonstrated patterns in that they increased in abundance with rainfall as well as with leaf phenology (Janzen 1988b). Heavy rain, unfortunately, prevented caterpillar frass collection during the entire month of October. I proposed that caterpillar abundance maintains a trend of increasing abundance during this time of year since I found high levels of frass in September as well as November. Caterpillar abundance and seasonality (as well as caterpillar biology) is well studied in Santa Rosa (Janzen 1988b) and these invertebrates tend to increase steadily to a single peak once during the year, that is, they do not show multiple peaks in a year, further supporting my assumption that caterpillars were likely abundant in October during the present study period. Although past studies on caterpillar abundance provide a good source of information, I decided to measure caterpillar abundance in the present study because it varies substantially from year to year in both emergence timing as well as density.

In Chapter Two I draw attention to the fact that insect abundance peaks in April and May, yet the majority of insect taxa that I identified were aseasonal. I provide two possible explanations. First, I was unable to identify approximately 54% of the insects in my traps, therefore many of the unidentified taxa could be seasonal. Had I been able to identify these unknown taxa, I might have found that they belong to the seasonal taxa that I did identify (e.g., Blattodea, Curculionidae, and Formicidae). Also, the nature of aseasonal insects is that they are found throughout all months of the year. I found insects, overall, were abundant throughout the year and peaked during April and May. The peak, although significant, is not representative of a

change in abundance from few insects to many insects, rather the peak represents an increase in abundance from an already abundant population.

Fallback foods are consumed when overall or preferred foods are scarce (Lambert 2007). In Chapter Three, I predicted that capuchins would consume invertebrates during times of fruit paucity. I discovered the opposite; capuchins consumed invertebrates significantly more frequently during a period of overall and preferred food abundance. It would therefore be inappropriate to conclude that invertebrates in general are fallback foods in the capuchin diet. However, capuchins did spend more time foraging extractively for and consuming pith and bromeliad leaves during times of overall and preferred food paucity, which suggests that pith and bromeliad leaves do function as fallback foods. As described in Chapter Three, pith and bromeliad leaves are available throughout the year in Santa Rosa (Melin, unpub. data). This means that these food sources fulfill both aspects of the fallback food definition used in the current study: they are difficult to process and are available during times of overall and preferred food scarcity.

Furthermore, pith is a known fallback food for some chimpanzees (Wrangham et al. 1998; Yamakoshi 1998). Chimpanzees and capuchins share a convergent trait –they have large brains compared to their body size. Chimpanzees are known for their tool use (Yamakoshi 1998; McGrew 1974) and cognitive abilities in general. Since both chimpanzees as well as capuchins share some of these traits, it may be that pith acting as a fallback food selects for the evolution of tool use and cognitive skills. While white-faced capuchins do not use tools, other capuchin species do and such traits are thought to have evolved to broaden the capuchin niche, which is indeed very broad compared to other primate genera (Wright et al. 2009). Why some large brained primates use tools and others do not remains a mystery, however it is arguably the suite

of traits that require manual dexterity, such as tool use and extractive foraging, that are associated with large brain to body size ratio (Melin et al., in press). There are many theories behind the evolution of cognition and large brain size and no one theory is conclusive. The present study may assist in drawing us nearer to an understanding of the evolution of large brain size and cognition in primates like chimpanzees, capuchins and humans.

Although I did not find capuchins to spend more time consuming all types of invertebrates during periods of overall food paucity, capuchins did spend more time foraging extractively for invertebrates during these periods. My findings confirm prior research on the same population of capuchins (Melin et al., in press). Some non-caterpillar invertebrates may act as a fallback food role in the capuchin diet whereas other non-caterpillar invertebrates may be preferred foods. The present study did not collect enough data per invertebrate type consumed by capuchins. These data would have allowed me to evaluate the role each invertebrate type might have in the capuchin diet. There is a possibility that capuchins spend more time foraging extractively for some invertebrates than others, which would suggest that some invertebrates (i.e., those that require extraction) are fallback foods. Future research should include finer-scale food categories to identify any preference differences that capuchins may have between embedded versus gleaned invertebrates.

4.1.1 Potential caveats

As mentioned in Chapter Two, I identified insects to the Order and Family level only, therefore I could not draw inferences on the biology of an insect species in relation to weather and phenology. Having said this, species-level is not always necessary when studying invertebrates

Timms et al (2012) showed that meaningful conclusions could be drawn from higher taxonomic levels.

It is important to note that malaise traps capture active insects only and active insects can come from neighbouring or distant habitats from that in which the trap is set-up. Therefore, malaise traps do not measure true insect abundance. As mentioned in Chapter Two, measuring insect abundance using traps can be interpreted as measuring insect activity. Insects vary in their life stages, life cycles, sexual dimorphisms, etc, which can have an affect on insect abundance measurements. For example, Formicidae (ants) are social insects with different castes, some of which possess wings while other do not. The traps that I used would have only caught the winged individuals –sexual life stage- and very few without wings. The peak Formicidae abundance in April and May may simply imply that ants breed during the months of April and May, not that they are necessarily more abundant.

Malaise traps are known amongst entomologists as a reliable tool to capture insects for research (e.g., Hutcheson 1990). Kitching et al (2001) demonstrated accuracy in capture rate across habitats resulting in the most consistent insect numbers compared to other trap types. Therefore, I trust that I provide meaningful results for understanding temporal insect abundance and the effect abiotic and biotic factors have on captured insects.

As mentioned in Chapter Two, phenology data was limited to 43 plant species in two of the four habitat types studied. Lianas, bromeliads and grasses were not included in the phenology even though these plant types can likely affect insect abundance as well as capuchin foraging habits. In addition, habitats in the present study vary in age and canopy height suggesting variation in plant species composition. Future research should include a wider range of plant species and types to evaluate their effect on insects as well as capuchins.

Wolda (1989) demonstrated that rainfall had little to do with insect seasonality in Barro Colorado Island, Panama and suggested that photoperiod has more of an effect on insect abundance. Photoperiod is said to play an important role in insect seasonality and is closely linked to phenology (Burke et al. 2005; Musolin and Numata 2003; Masaki 1972). The present study did not include photoperiod, predation, migration, humidity, parasitoids –all of which are proposed to have effects on insect abundance. Although the present study collected insects from four habitat types, these habitats were within two kilometers of each other –a distance that likely would not reveal insect migration effects. Humidity, as a separate variable to rainfall, can affect tropical insect abundance patterns (e.g., Shapiro and Pickering 2000), however I measured rainfall not humidity in the present study. As pointed out by Kato (2000), “internal” factors or natural enemies, such as parasitoids, can largely influence insect abundance and seasonality (Morais et al. 1999). Measuring parasitoid prevalence is a very involved task that the present study was not equipped for, however, future studies should consider rearing various insects and using other methodologies to account for parasitoid prevalence across different seasons in Santa Rosa.

It is unfortunate that I was not able to take behavioural data on the capuchins during the雨季 season from September to December. However, resource abundance data are known for this time of year with even lower fruit availability than January through March (Carnegie et al. 2011), consistent insect availability similar to that of January through March (present study) and pith and bromeliad leaves are consistently available throughout the year (Melin, unpub. data). We also know that capuchins forage for pith throughout this season (Melin, unpub. data). Together, these data support the findings of the present study that pith and bromeliad leaves are capuchin fallback foods.

Interannual variability exists for both fruit and (Fleming et al. 1987) caterpillar abundance patterns (Janzen 1988b; Powers unpub. data). The data I present in the current study is not necessarily meant to represent long-term seasonal patterns, but rather to demonstrate what patterns *can* exist and hopefully emphasize the need for more long-term insect abundance studies. Longitudinal ecological pattern information is essential for land management, conservation, political decision-making, etc. Building upon preliminary data, such as those presented here, is a necessary step towards understanding an ecosystem and, therefore, enhancing our ability to manage it.

4.1.2 Future directions

Although nutritional analyses would have been a valuable data source in assessing food preference and importance in the capuchin diet, it was not possible during this study. An enormous amount of effort is required in order to properly assess the nutritional quality of a food not only because the quantity of each food necessary to detect a nutrient is large (about 20g per food item), but also because there is potential for variation in nutritional quality of a particular food throughout space and time (O'Driscoll Worman and Chapman 2005). Therefore, collecting food in large enough quantities and consistently enough to obtain meaningful results would have taken an entire project in itself. Having said this, the Fedigan lab has researched the nutritional composition of some foods as part of another study. More foraging data is needed per capuchin food species before associations between food nutrition and fallback foods can be made. According to Marshall et al (2009), however, nutritional data is not necessary when identifying fallback foods in a primate diet.

4.1.3 Significance

Data on insect abundance and seasonality is so sparse that “almost any study of seasonal patterns is a welcome addition to our knowledge” (Wolda 1988). The present study offers information on insect abundance patterns over fourteen months in a tropical dry forest. This information, along with weather and phenology data, can be referred to in the future when management decisions are to be made or future studies conducted.

Fallback foods, similar to keystone species, are highly important resources for the maintenance of a species and are thought to be an important selective force in the evolution of non-human primates (Marshall et al. 2009; Lambert et al. 2004) as well as humans (Harrison and Marshall 2011; Marshall et al. 2009; Hladik et al. 1999). Researchers have the opportunity to gain insight into human evolution by continuing to study fallback foods in extant primate diets. Such insights enable researchers to trace back to our common ancestry among extant primates.

Since fallback foods often supplement an animal’s diet during times of food scarcity, an animal can perish without them (Milton & Giacalone 2012 as cited in Melin et al., in press). By knowing what is likely to be consumed by an animal and what foods are closely tied to the evolution of the consumer, researchers and conservationists can make useful decisions regarding the effects of human encroachment on natural habitat. With the rate of present day habitat loss being the number one cause of extinction, choosing which habitat to preserve is crucial to maximizing the number of species that can coexist with humans in the future.

Conservation decisions are often made based on the number of species present in an ecosystem. Although tropical dry forests house fewer species than rainforests they house important interactions among species (Janzen 1986). Such interactions should be the focus of conservation efforts, not necessarily the number of species (Janzen 1988b). Biological

information about ecological interactions is a large part of the restoration process of a tropical dry forest (Janzen 1988b). The present study describes interactions between white-faced capuchins and their foods, which cover a diverse array of organisms, in a tropical dry forest. Capuchins may very well be negatively affected if pith and bromeliad leaves declined in abundance.. The present study reports a dietary shift during a seasonally hot and dry period and the importance of certain plants and animals as foods for capuchins. With average temperatures rising in the tropics due to climate change and the phenomenon of global desertification, it is important to understand how ecosystems may shift during seasonally hot and dry periods.

4.1.4 Conclusion

My study speaks to recent of the importance and usefulness in studying fallback foods as well as the recognized paucity of tropical insect abundance and seasonality studies. By integrating these two topics that are in need of research and information, my thesis project contributes to the recently growing literature on fallback foods as well as the seemingly forgotten realm of tropical insect abundance and seasonality.

The insects that I studied demonstrated an array of reactions to weather and phenology effects. Overall insect abundance peaked in April and May when the rainy season began. Pollinators seemed to be influenced by flower phenology whereas herbivorous insects were influenced by leaf phenology patterns. Some insects, like Coleoptera, did not follow predictable patterns, likely because beetles are highly diverse and range across most dietary niches.

What constitutes a fallback food in an animal's diet varies from species to species. While invertebrates may still play a fallback food role for some capuchin individuals, pith and bromeliad leaves better fit the definition of fallback food for my study animals. Capuchins spent

more time processing pith and bromeliad leaves than invertebrates (and unknown foods) and consumed pith and bromeliad leaves more frequently during times of overall food scarcity.

Although not measured in the present study, pith and bromeliad leaves are abundant throughout the year, including times of food scarcity –fulfilling the fallback food definition.

Continuing to study tropical insect abundance will always be beneficial as information is limited. And continuing to study potential fallback foods in the capuchin diet in a highly seasonal environment may help to answer questions regarding the evolution of extractive foraging and other capuchin traits such as enhanced manual dexterity and polymorphic color vision. Finding these answers brings researchers one step closer to understanding primate evolutionary patterns and, in turn, our own evolution as a species of primate.

References

- Abbott, Ian, L K Abbott, and P R Grant. 1977. "Comparative Ecology of Galapagos Ground Finches (*Geospiza Gouldi*): Evaluation of the Importance of Floristic Diversity and Interspecific Competition." *Ecological Monographs*: 151–184.
- Agosta, Salvatore J. 2008. "Fitness Consequences of Host Use in the Field: Temporal Variation in Performance and a Life History Tradeoff in the Moth *Rothschildia Lebeau* (Saturniidae)." *Oecologia* 157 (1) (May 21): 69–82. doi:10.1007/s00442-008-1059-1.
- Aguirre, Armando, and Rodolfo Dirzo. 2008. "Effects of Fragmentation on Pollinator Abundance and Fruit Set of an Abundant Understory Palm in a Mexican Tropical Forest." *Biological Conservation* 141 (2) (February): 375–384. doi:10.1016/j.biocon.2007.09.014.
- Altmann, Jeanne. 1974. "Observational Study of Behavior: Sampling Methods." *Behaviour*: 227–267.
- Altmann, S A. 2009. "Fallback Foods, Eclectic Omnivores, and the Packaging Problem." *American Journal of Physical Anthropology* 140 (4) (December): 615–629. doi:10.1002/ajpa.21097.
- Andresen, Ellen. 2007. "Dung Beetle Assemblages in Primary Forest and Disturbed Habitats in a Tropical Dry Forest Landscape in Western Mexico." *Journal of Insect Conservation* 12 (6) (July 27): 639–650. doi:10.1007/s10841-007-9100-y.
- Basabose, A Kanyunyi. 2002. "Diet Composition of Chimpanzees Inhabiting the Montane Forest of Kahuzi, Democratic Republic of Congo" 58 (1) (September 25): 1–21. doi:10.1002/ajp.10049.
- Basset, Yves, Olivier Missa, Alfonso Alonso, Scott E Miller, Gianfranco Curletti, MARC DE MEYER, Connal Eardley, et al. 2008. "Changes in Arthropod Assemblages Along a Wide Gradient of Disturbance in Gabon." *Conservation Biology* 22 (6) (December): 1552–1563. doi:10.1111/j.1523-1739.2008.01017.x.
- Douglas Bates, Martin Maechler and Ben Bolker (2012). lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-0.
<http://CRAN.R-project.org/package=lme4>
- Bates, Marston. 1945. "Observations on Climate and Seasonal Distribution of Mosquitoes in Eastern Colombia." *The Journal of Animal Ecology*: 17–25.
- Batschelet, Edward. 1981. "Circular Statistics in Biology." *Academic Press, 111 Fifth Ave., New York, Ny 10003, 1981*, 388.
- Burke, Steve, Andrew S Pullin, Robert J Wilson, and Chris D Thomas. 2005. "Selection for Discontinuous Life-History Traits Along a Continuous Thermal Gradient in the Butterfly *Aricia Agestis*." *Ecological Entomology* 30 (6): 613–619.
- Campos, Fernando A, and Linda M Fedigan. 2009. "Behavioral Adaptations to Heat Stress and Water Scarcity in White-Faced Capuchins (*Cebus Capucinus*) in Santa Rosa National Park, Costa Rica." *American Journal of Physical Anthropology* 138 (1) (January): 101–111. doi:10.1002/ajpa.20908.
- Carpenter, K. J. (1986) The History of Enthusiasm for Protein. American Institute of Nutrition

- publication. *Presented as part of the History of Nutrition symposium given by the American Institute of Nutrition at the 69th Annual Meeting of the Federation of American Societies for Experimental Biology*, Anaheim, CA.
- (1994) Protein and Energy: A Study of Changing Ideas in Nutrition. UK: Cambridge University Press.
- Carnegie, Sarah D, Linda M Fedigan, and Amanda D Melin. 2011. "Reproductive Seasonality in Female Capuchins (*Cebus Capucinus*) in Santa Rosa (Area De Conservación Guanacaste), Costa Rica." *International Journal of Primatology* 32 (5) (May 3): 1076–1090. doi:10.1007/s10764-011-9523-x.
- Castellarini, Fabiana, Claudia Dellafiore, and J Polop. 2003. "Feeding Habits of Small Mammals in Agroecosystems of Central Argentina." *Mammalian Biology-Zeitschrift Für Säugetierkunde* 68 (2): 91–101.
- Chapman, Colin. 1987. "Flexibility in Diets of Three Species of Costa Rican Primates." *Folia Primatologica* 49 (2): 90–105.
- Chapman, Colin A, and Linda M Fedigan. 1990. "Dietary Differences Between Neighboring *Cebus Capucinus* Groups: Local Traditions, Food Availability or Responses to Food Profitability?" *Folia Primatologica* 54 (3-4): 177–186.
- Charnov, E L. 1976. "Optimal Foraging, the Marginal Value Theorem.." *Theoretical Population Biology* 9 (2) (April): 129–136.
- Conklin-Brittain, Nancy L, Cheryl D Knott, and Richard W Wrangham. 2001. "The Feeding Ecology of Apes." *The Apes: Challenges for the 21st Century*: 167–174.
- Conklin-Brittain, Nancy Lou, Richard W Wrangham, and Kevin D Hunt. 1998. "Dietary Response of Chimpanzees and Cercopithecines to Seasonal Variation in Fruit Abundance. II. Macronutrients." *International Journal of Primatology* 19 (6): 971–998.
- Constantino, Paul J, and Barth W Wright. 2009. "The Importance of Fallback Foods in Primate Ecology and Evolution." *American Journal of Physical Anthropology* 140 (4) (December): 599–602. doi:10.1002/ajpa.20978.
- Corlett, Richard T. 2004. "Flower Visitors and Pollination in the Oriental (Indomalayan) Region." *Biological Reviews of the Cambridge Philosophical Society* 79 (3) (August): 497–532.
- Crawley, Michael J. 2007. *The R Book*. UK: John Wiley & Sons Ltd.
- da Silva, N A, M R Frizzas, and M de Oliveira. 2011. "Seasonality in Insect Abundance in the 'Cerrado' of Goiás State, Brazil." *Revista Brasileira De Entomologia* 55 (1): 79–87.
- Dale, Virginia H, Linda A Joyce, Steve McNulty, Ronald P Neilson, Matthew P Ayres, Michael D Flannigan, Paul J Hanson, Lloyd C Irland, Ariel E Lugo, and Chris J Peterson. 2001. "Climate Change and Forest Disturbances: Climate Change Can Affect Forests by Altering the Frequency, Intensity, Duration, and Timing of Fire, Drought, Introduced Species, Insect and Pathogen Outbreaks, Hurricanes, Windstorms, Ice Storms, or Landslides." *BioScience* 51 (9): 723–734.
- Danks, H V. 1996. "How to Assess Insect Biodiversity Without Wasting Your Time." *Biological Survey of Canada Terrestrial Arthropods*.
- Deblauwe, Isra, J Dupain, G M Nguenang, D Werdenich, and Linda Van Elsacker. 2003. "Insectivory by Gorilla Gorilla Gorilla in Southeast Cameroon." *International Journal of Primatology* 24 (3): 493–502.
- Dejean, Alain, Régis Céréghino, James M Carpenter, Bruno Corbara, Bruno Hérault, Vivien

- Rossi, Maurice Leponce, Jérôme Orivel, and Damien Bonal. 2011. "Climate Change Impact on Neotropical Social Wasps." Edited by Nicolas Salamin. *PLoS ONE* 6 (11) (November 2): e27004. doi:10.1371/journal.pone.0027004.s005.
- Denlinger, David L. 1980. "Seasonal and Annual Variation of Insect Abundance in the Nairobi National Park, Kenya." *Biotropica*: 100–106.
<http://www.jstor.org.ezproxy.lib.ucalgary.ca/stable/pdfplus/2387725.pdf?acceptTC=true>.
- Dobzhansky, Theodosius, and Crodowaldo Pavan. 1950. "Local and Seasonal Variations in Relative Frequencies of Species of Drosophila in Brazil." *The Journal of Animal Ecology*: 1–14.
- Doran-Sheehy, D, P Mongo, J Lodwick, and N L Conklin-Brittain. 2009. "Male and Female Western Gorilla Diet: Preferred Foods, Use of Fallback Resources, and Implications for Ape Versus Old World Monkey Foraging Strategies." *American Journal of Physical Anthropology* 140 (4) (December): 727–738. doi:10.1002/ajpa.21118.
- Elton, Charles S. 1973. "The Structure of Invertebrate Populations Inside Neotropical Rain Forest." *The Journal of Animal Ecology*: 55–104.
- Fedigan, Linda Marie, and Katharine Jack. 2001. "Neotropical Primates in a Regenerating Costa Rican Dry Forest: a Comparison of Howler and Capuchin Population Patterns." *International Journal of Primatology* 22 (5): 689–713.
- Fleming, Theodore H, Randall Breitwisch, and George H Whitesides. 1987. "Patterns of Tropical Vertebrate Frugivore Diversity." *Annual Review of Ecology and Systematics*: 91–109.
<http://www.jstor.org.ezproxy.lib.ucalgary.ca/stable/pdfplus/2097126.pdf?acceptTC=true>.
- Fogden, MPL. 1972. "The Seasonality and Population Dynamics of Equatorial Forest Birds Est Sarawak." *Ibis* 114 (3): 307–343.
- Fox, ElizaBeth A, Carel P van Schaik, Arnold Sitompul, and Donielle N Wright. 2004. "Intra- and Interpopulational Differences in Orangutan (*Pongo Pygmaeus*) Activity and Diet: Implications for the Invention of Tool Use." *American Journal of Physical Anthropology* 125 (2): 162–174. doi:10.1002/ajpa.10386.
- Fragaszy, Dorothy M, and Elisabetta Visalberghi. 2004. "The Complete Capuchin: the Biology of the Genus *Cebus*."
- Frankie, G W, W A Haber, S B Vinson, K S Bawa, P S Ronchi, and N Zamora. 2004. "Flowering Phenology and Pollination Systems Diversity in the Seasonal Dry Forest." *Biodiversity Conservation in Costa Rica: Learning the Lessons in a Seasonal Dry Forest*: 17–29.
- Frith, Dawn, and Clifford Frith. 1990. "Seasonality of Litter Invertebrate Populations in an Australian Upland Tropical Rain Forest." *Biotropica*: 181–190.
- Furuichi, T, C Hashimoto, and Y Tashiro. 2001. "Fruit Availability and Habitat Use by Chimpanzees in the Kalinzu Forest, Uganda: Examination of Fallback Foods." *International Journal of Primatology* 22 (6): 929–945.
- Godfray, HCJ, and M P Hassell. 1989. "Discrete and Continuous Insect Populations in Tropical Environments." *The Journal of Animal Ecology*: 153–174.
- Gogarten, Jan F, Leone M Brown, Colin A Chapman, Marina Cords, Diane Doran-Sheehy, Linda M Fedigan, Frederick E Grine, et al. 2012. "Seasonal Mortality Patterns in Non-Human Primates: Implications for Variation in Selection Pressures Across Environments." *Evolution* 66 (10) (May 14): 3252–3266. doi:10.1111/j.1558-5646.2012.01668.x.

- Goodall, Jane. 1963. "Feeding Behaviour of Wild Chimpanzees: a Preliminary Report." *Symposium of the Zoological Society of London* 10: 39–48.
- Grant, B Rosemary, and Peter R Grant. 1993. "Evolution of Darwin's Finches Caused by a Rare Climatic Event." *Proceedings. Biological Sciences / the Royal Society* 251 (1331): 111–117.
- Grant, P R, I Abbott, D Schluter, R L Curry, and L K Abbott. 1985. "Variation in the Size and Shape of Darwin's Finches." *Biological Journal of the Linnean Society* 25 (1): 1–39.
- Grant, Peter R, and B Rosemary Grant. 1987. "The Extraordinary El Niño Event of 1982-83: Effects on Darwin's Finches on Isla Genovesa, Galápagos." *Oikos*: 55–66.
- Grimbacher, Peter S, and Nigel E Stork. 2009. "Seasonality of a Diverse Beetle Assemblage Inhabiting Lowland Tropical Rain Forest in Australia." *Biotropica* 41 (3): 328–337. doi:10.1111/j.1744-7429.2008.00477.x.
- Gursky, Sharon. 2000. "Effect of Seasonality on the Behavior of an Insectivorous Primate, *Tarsius Spectrum*." *International Journal of Primatology* 21 (3): 477–495.
- Harding, Robert SO. 1981. "An Order of Omnivores: Nonhuman Primate Diets in the Wild." *Omnivorous Primates: Gathering and Hunting in Human Evolution*: 191–214.
- Harrison, Mark E, and Andrew J Marshall. 2011. "Strategies for the Use of Fallback Foods in Apes." *International Journal of Primatology* 32 (3) (January 7): 531–565. doi:10.1007/s10764-010-9487-2.
- Hawkins, Bradford A, Howard V Cornell, and Michael E Hochberg. 1997. "Predators, Parasitoids, and Pathogens as Mortality Agents in Phytophagous Insect Populations." *Ecology* 78 (7): 2145–2152.
- Hladik, C M, D J Chivers, and P Pasquet. 1999. "On Diet and Gut Size in Non-Human Primates and Humans: Is There a Relationship to Brain Size?" *Current Anthropology* 40 (5) (December): 695–697. doi:10.1086/300099.
- Hladik, Claude Marcel. 1988. "Seasonal Variations in Food Supply for Wild Primates." *Coping with Uncertainty in Food Supply*: 1–25.
- Hutcheson, John. 1990. "Characterization of Terrestrial Insect Communities Using Quantified, Malaise-Trapped Coleoptera." *Ecological Entomology* 15 (2): 143–151.
- Isbell, Lynne A, Jill D Pruetz, and Truman P Young. 1998. "Movements of Vervets (*Cercopithecus Aethiops*) and Patas Monkeys (*Erythrocebus Patas*) as Estimators of Food Resource Size, Density, and Distribution." *Behavioral Ecology and Sociobiology* 42 (2): 123–133.
- Janson, C H, and S Boinski. 1992. "Morphological and Behavioral Adaptations for Foraging in Generalist Primates: the Case of the Cebines.." *American Journal of Physical Anthropology* 88 (4) (August): 483–498. doi:10.1002/ajpa.1330880405.
- Janzen, Daniel H. 1966. "Coevolution of Mutualism Between Ants and Acacias in Central America." *Evolution* 20 (3): 249–275.
- 1967. "Synchronization of Sexual Reproduction of Trees Within the Dry Season in Central America." *Evolution*: 620–637.
- 1973a. "Sweep Samples of Tropical Foliage Insects: Effects of Seasons, Vegetation Types, Elevation, Time of Day, and Insularity." *Ecology*: 687–708.
- 1973b. "Sweep Samples of Tropical Foliage Insects: Description of Study Sites, with Data on Species Abundances and Size Distributions." *Ecology*: 659–686.
- 1983. "Seasonal Change in Abundance of Large Nocturnal Dung Beetles (Scarabaeidae) in a Costa Rican Deciduous Forest and Adjacent Horse Pasture." *Oikos*: 274–283.

- 1986. "The Future of Tropical Ecology." *Annual Review of Ecology and Systematics*: 305–324.
- 1988a. "Tropical Dry Forests." *Biodiversity*: 130.
- 1988b. "Ecological Characterization of a Costa Rican Dry Forest Caterpillar Fauna." *Biotropica*: 120–135.
- 2000. "Costa Rica's Area De Conservación Guanacaste: a Long March to Survival Through Non-Damaging Biodevelopment." *Biodiversity* 1 (2) (May): 7–20. doi:10.1080/14888386.2000.9712501.
- 2004. "Ecology of Dry-Forest Wildland Insects in the Area De Conservación Guanacaste." *Biodiversity Conservation in Costa Rica: Learning the Lessons in a Seasonal Dry Forest* (GW Frankie, a Mata, and SB Vinson, Eds.). University of California Press, Berkeley, California: 80–96.
- Janzen, Daniel H, and Thomas W Schoener. 1968. "Differences in Insect Abundance and Diversity Between Wetter and Drier Sites During a Tropical Dry Season." *Ecology*: 96–110.
- Janzen, Daniel H, Philip J DeVries, M L Higgins, and Lynn S Kimsey. 1982. "Seasonal and Site Variation in Costa Rican Euglossine Bees at Chemical Baits in Lowland Deciduous and Evergreen Forests." *Ecology*: 66–74.
- Kalacska, M, G A Sanchez-Azofeifa, J C Calvo-Alvarado, M Quesada, B Rivard, and D H Janzen. 2004. "Species Composition, Similarity and Diversity in Three Successional Stages of a Seasonally Dry Tropical Forest." *Forest Ecology and Management* 200 (1-3) (October): 227–247. doi:10.1016/j.foreco.2004.07.001.
- Kato, Makoto, Takao Itioka, Shoko Sakai, Kuniyasu Momose, Seiki Yamane, Abang Abdul Hamid, and Tamiji Inoue. 2000. "Various Population Fluctuation Patterns of Light-Attracted Beetles in a Tropical Lowland Dipterocarp Forest in Sarawak." *Population Ecology* 42 (1): 97–104.
- Kay, Richard F. 1981. "The Nut-Crackers—a New Theory of the Adaptations of the Ramapithecinae." *American Journal of Physical Anthropology* 55 (2): 141–151.
- Keverne, E B, F L Martel, and C M Nevison. 1996. "Primate Brain Evolution: Genetic and Functional Considerations.." *Proceedings. Biological Sciences / the Royal Society* 263 (1371) (June 22): 689–696. doi:10.1098/rspb.1996.0103.
- Kitching, R L, Daiqin Li, and Nigel E Stork. 2001. "Assessing Biodiversity 'Sampling Packages': How Similar Are Arthropod Assemblages in Different Tropical Rainforests?" *Biodiversity & Conservation* 10 (5): 793–813.
- Lambert, J E. 1998. "Primate Digestion: Interactions Among Anatomy, Physiology, and Feeding Ecology." *Evolutionary Anthropology: Issues, News, and Reviews* 7 (1): 8–20.
- 2007. "Seasonality, Fallback Strategies, and Natural Selection: a Chimpanzee and Cercopithecoid Model for Interpreting the Evolution of the Hominin Diet." *Evolution of the Human Diet: the Known, the Unknown, and the Unknowable*. Oxford: Oxford University Press. P: 324–343.
- 2009. "Summary to the Symposium Issue: Primate Fallback Strategies as Adaptive Phenotypic Plasticity—Scale, Pattern, and Process." *American Journal of Physical Anthropology* 140 (4): 759–766.
- Lambert, Joanna E, Colin A Chapman, Richard W Wrangham, and Nancy Lou Conklin-Brittain. 2004. "Hardness of Cercopithecine Foods: Implications for the Critical Function of Enamel Thickness in Exploiting Fallback Foods." *American Journal of Physical Anthropology* 125

- (4): 363–368. doi:10.1002/ajpa.10403.
- Leung, W W. 1968. "Food Composition Table for Use In Africa: a Research Project Sponsored Jointly by U.S. Dept. of Health, Education, And Welfare, Nutrition Program, And Food Consumption And Planning Branch, Food And Agriculture Organization of the United Nations". *Nutrition Program. United States*: Bethesda, Md.
- Levey, Douglas J. 1988. "Spatial and Temporal Variation in Costa Rican Fruit and Fruit-Eating Bird Abundance." *Ecological Monographs*: 251–269.
<http://www.jstor.org.ezproxy.lib.ucalgary.ca/stable/pdfplus/1942539.pdf>.
- Lowman, M D. 1982. "Seasonal Variation in Insect Abundance Among Three Australian Rain Forests, with Particular Reference to Phytophagous Types." *Australian Journal of Ecology* 7 (4): 353–361.
- MacArthur, Robert H, and Eric R Pianka. 1966a. "On Optimal Use of a Patchy Environment." *American Naturalist*: 603–609.
- Makedonska, Jana, Barth W Wright, and David S Strait. 2012. "The Effect of Dietary Adaption on Cranial Morphological Integration in Capuchins (Order Primates, Genus Cebus)." Edited by Sharon Gursky-Doyen. *PLoS ONE* 7 (10) (October 26): e40398.
doi:10.1371/journal.pone.0040398.t016.
- Malenky, Richard K, and Richard W Wrangham. 1994. "A Quantitative Comparison of Terrestrial Herbaceous Food Consumption by Pan Paniscus in the Lomako Forest, Zaire, and Pan Troglodytes in the Kibale Forest, Uganda" 32 (1): 1–12.
http://onlinelibrary.wiley.com.ezproxy.lib.ucalgary.ca/store/10.1002/ajp.1350320102/asset/1350320102_ftp.pdf?v=1&t=heq6xxyz&s=a203ed0c3f9087fc04c0e4865ec3848c079186f9.
- Marshall, Andrew J, and Richard W Wrangham. 2007. "Evolutionary Consequences of Fallback Foods." *International Journal of Primatology* 28 (6) (December 4): 1219–1235.
doi:10.1007/s10764-007-9218-5.
- Marshall, Andrew J, Corin M Boyko, Katie L Feilen, Ryan H Boyko, and Mark Leighton. 2009. "Defining Fallback Foods and Assessing Their Importance in Primate Ecology and Evolution." *American Journal of Physical Anthropology* 140 (4) (December): 603–614.
doi:10.1002/ajpa.21082.
- Masaki, Sinzo. 1972. "Climatic Adaptation and Photoperiodic Response in the Band-Legged Ground Cricket." *Evolution*: 587–600.
- McCabe, Gráinne Michelle, and Linda Marie Fedigan. 2007. "Effects of Reproductive Status on Energy Intake, Ingestion Rates, and Dietary Composition of Female Cebus Capucinus at Santa Rosa, Costa Rica." *International Journal of Primatology* 28 (4) (July 20): 837–851.
doi:10.1007/s10764-007-9159-z.
- McGrew, William C. 1974. "Tool Use by Wild Chimpanzees in Feeding Upon Driver Ants." *Journal of Human Evolution* 3 (6): 501–508.
- Melin, Amanda D, Hilary C Young, Krisztina Mosdossy, and Linda M Fedigan. In Press. "Seasonality, Extractive Foraging and the Evolution of Primate Sensorimotor Intelligence." *Journal of Human Evolution*.
- Melin, Amanda D, Linda M Fedigan, C Hiramatsu, C Sendall, and S Kawamura. 2007. "Effects of Colour Vision Phenotype on Insect Capture by a Free-Ranging Population of White-Faced Capuchins, *Cebus Capucinus*." *Animal Behaviour* 73 (1) (January): 205–214.
doi:10.1016/j.anbehav.2006.07.003.
- Milton, Katharine. 2003. "The Critical Role Played by Animal Source Foods in Human (Homo)

- Evolution." *The Journal of Nutrition* 133 (11): 3886S–3892S.
- Miss, Olivier, Yves Basset, Alfonso Alonso, Scott E Miller, Gianfranco Curletti, Marc Meyer, Connal Eardley, Mervyn W Mansell, and Thomas Wagner. 2008. "Monitoring Arthropods in a Tropical Landscape: Relative Effects of Sampling Methods and Habitat Types on Trap Catches." *Journal of Insect Conservation* 13 (1) (January 11): 103–118. doi:10.1007/s10841-007-9130-5.
- Mizutani, Mizuki, and Naoki Hijii. 2001. "Mensuration of Frass Drop for Evaluating Arthropod Biomass in Canopies: a Comparison Among Cryptomeria Japonica, Larix Kaempferi, and Deciduous Broad-Leaved Trees." *Forest Ecology and Management* 154 (1): 327–335.
- Morais, Helena C, Ivone R Diniz, and Delano Silva. 1999. "Caterpillar Seasonality in a Central Brazilian Cerrado." *Revista De Biologia Tropical* 47 (4): 1025–1033.
- Morellato, L Patricia C, L F Alberti, and Irene L Hudson. 2009. "Applications of Circular Statistics in Plant Phenology: a Case Studies Approach." In, 339–359. Dordrecht: Springer Netherlands. doi:10.1007/978-90-481-3335-2_16.
- Moura, A C de A, and P C Lee. 2004. "Capuchin Stone Tool Use in Caatinga Dry Forest.." *Science* 306 (5703) (December 10): 1909. doi:10.1126/science.1102558.
- Murali, K S, and R Sukumar. 1993. "Leaf Flushing Phenology and Herbivory in a Tropical Dry Deciduous Forest, Southern India." *Oecologia* 94 (1): 114–119.
- Musolin, Dmitry L, and Hideharu Numata. 2003. "Photoperiodic and Temperature Control of Diapause Induction and Colour Change in the Southern Green Stink Bug *Nezara Viridula*." *Physiological Entomology* 28 (2): 65–74.
- O'Driscoll Worman, Cedric, and Colin A Chapman. 2005. "Seasonal Variation in the Quality of a Tropical Ripe Fruit and the Response of Three Frugivores." *Journal of Tropical Ecology* 21 (06) (October 19): 689. doi:10.1017/S0266467405002725.
- Parker, Sue Taylor, and Kathleen R Gibson. 1977. "Object Manipulation, Tool Use and Sensorimotor Intelligence as Feeding Adaptations in *Cebus* Monkeys and Great Apes." *Journal of Human Evolution* 6 (7): 623–641.
- 1979. "A Develo." *The Behavioral and Brain Sciences* 2: 367–408.
- Pinheiro, F, I R Diniz, D Coelho, and MPS Bandeira. 2002. "Seasonal Pattern of Insect Abundance in the Brazilian Cerrado." *Australian Journal of Ecology* 27 (2): 132–136.
- Pipkin, Sarah Bedichek, Rafael L Rodriguez, and Jorge Leon. 1966. "Plant Host Specificity Among Flower-Feeding Neotropical *Drosophila* (Diptera: Drosophilidae)." *American Naturalist*: 135–156.
- Porter, Leila M. 2001. "Dietary Differences Among Sympatric Callitrichinae in Northern Bolivia: *Callimico Goeldii*, *Saguinus Fuscicollis* and *S. Labiatus*." *International Journal of Primatology* 22 (6): 961–992.
- Potts, Richard. 2004. "Paleoenvironmental Basis of Cognitive Evolution in Great Apes" 62 (3): 209–228.
- Reader, Simon M, and Kevin N Laland. 2002. "Social Intelligence, Innovation, and Enhanced Brain Size in Primates.." *Proceedings of the National Academy of Sciences of the United States of America* 99 (7) (April 2): 4436–4441. doi:10.1073/pnas.062041299.
- Redford, Kent H, Gustavo A Bouchardet da Fonseca, and Thomas E Lacher Jr. 1984. "The Relationship Between Frugivory and Insectivory in Primates." *Primates* 25 (4): 433–440.
- Richards, Lora A, and Donald M Windsor. 2007. "Seasonal Variation of Arthropod Abundance in Gaps and the Understorey of a Lowland Moist Forest in Panama." *Journal of Tropical*

- Ecology* 23 (02) (March 5): 169. doi:10.1017/S0266467406003907.
- Robinson, Beren W, and David Sloan Wilson. 1998. "Optimal Foraging, Specialization, and a Solution to Liem's Paradox." *The American Naturalist* 151 (3) (March): 223–235. doi:10.1086/286113.
- Rowe, N. 1996. "The Pictorial Guide to the Living Primates."
- Sayers, Ken, and C Owen Lovejoy. 2008. "The Chimpanzee Has No Clothes: a Critical Examination of Pan Troglodytesin Models of Human Evolution." *Current Anthropology* 49 (1) (February): 87–114. doi:10.1086/523675.
- Schöning, C, D Ellis, A Fowler, and V Sommer. 2007. "Army Ant Prey Availability and Consumption by Chimpanzees (Pan Troglodytes Vellerosus) at Gashaka (Nigeria)." *Journal of Zoology* 271 (2) (February): 125–133. doi:10.1111/j.1469-7998.2006.00177.x.
- Schöning, Caspar, Tatyana Humle, Yasmin Möbius, and W C McGrew. 2008. "The Nature of Culture: Technological Variation in Chimpanzee Predation on Army Ants Revisited." *Journal of Human Evolution* 55 (1) (July): 48–59. doi:10.1016/j.jhevol.2007.12.002.
- Shapiro, B A, and John Pickering. 2000. "Rainfall and Parasitic Wasp (Hymenoptera: Ichneumonoidea) Activity in Successional Forest Stages at Barro Colorado Nature Monument, Panama, and La Selva Biological Station, Costa Rica." *Agricultural and Forest Entomology* 2 (1): 39–47.
- Stireman, J O, L A Dyer, D H Janzen, M S Singer, J T Lill, R J Marquis, R E Ricklefs, et al. 2005. "Climatic Unpredictability and Parasitism of Caterpillars: Implications of Global Warming.." *Proceedings of the National Academy of Sciences of the United States of America* 102 (48) (November 29): 17384–17387. doi:10.1073/pnas.0508839102.
- Suzuki, Akira. 1966. "On the Insect-Eating Habits Among Wild Chimpanzees Living in the Savanna Woodland of Western Tanzania." *Primates* 7 (4): 481–487.
- Tanaka, L K, and S K Tanaka. 1982. "Rainfall and Seasonal Changes in Arthropod Abundance on a Tropical Oceanic Island." *Biotropica*: 114–123.
- Tanaka, Seiji, Henk Wolda, and David L Denlinger. 1987. "Seasonality and Its Physiological Regulation in Three Neotropical Insect Taxa From Barro Colorado Island, Panama.." *Insect Science and Its Application* 8 (4): 507–514.
- Tashiro, Yasuko. 2005. "Frequent Insectivory by Two Guenons (*Cercopithecus Lhoesti* and *Cercopithecus Mitis*) in the Kalinzu Forest, Uganda." *Primates* 47 (2) (October 7): 170–173. doi:10.1007/s10329-005-0160-x.
- Terborgh, John. 1983. "Five New World Primates: a Study in Comparative Ecology.." *Princeton University Press, Princeton, Nj(Usa)*. 1983.
- Thorén, Sandra, Franziska Quietzsch, Doreen Schwochow, Lalandy Sehen, Christopher Meusel, Kate Meares, and Ute Radespiel. 2011. "Seasonal Changes in Feeding Ecology and Activity Patterns of Two Sympatric Mouse Lemur Species, the Gray Mouse Lemur (*Microcebus Murinus*) and the Golden-Brown Mouse Lemur (*M. Ravelobensis*), in Northwestern Madagascar." *International Journal of Primatology* 32 (3) (January 13): 566–586. doi:10.1007/s10764-010-9488-1.
- Timms, Laura L, Joseph J Bowden, Keith S Summerville, and Chris M Buddle. 2012. "Does Species-Level Resolution Matter? Taxonomic Sufficiency in Terrestrial Arthropod Biodiversity Studies." Edited by Raphael Didham and Yves Basset. *Insect Conservation and Diversity* (November 1): n/a–n/a. doi:10.1111/icad.12004.
- Tolo, C U, J Baranga, and G Kagoro-Rugunda. 2008. "Dietary Selection of L'Hoest Monkeys in

- Kalinzu Forest Reserve, Southwestern Uganda." *African Journal of Ecology* 46 (2): 149–157.
- Vasconcellos, Alexandre, Ricardo Andreatze, Adriana M Almeida, Helder FP Araujo, Eduardo S Oliveira, and Uirandé Oliveira. 2010. "Seasonality of Insects in the Semi-Arid Caatinga of Northeastern Brazil." *Revista Brasileira De Entomologia* 54 (3): 471–476.
- Vogel, Erin R, Livia Haag, Tatang Mitra-Setia, Carel P van Schaik, and Nathaniel J Dominy. 2009. "Foraging and Ranging Behavior During a Fallback Episode: Hylobates Albibarbis and Pongo Pygmaeus Wurmbii compared." *American Journal of Physical Anthropology* 140 (4) (December): 716–726. doi:10.1002/ajpa.21119.
- Wolda, Henk. 1978. "Seasonal Fluctuations in Rainfall, Food and Abundance of Tropical Insects." *The Journal of Animal Ecology*: 369–381.
- 1988. "Insect Seasonality: Why?" *Annual Review of Ecology and Systematics* 19: 1–18.
- 1989. "Seasonal Cues in Tropical Organisms. Rainfall? Not Necessarily!." *Oecologia* 80 (4): 437–442.
- 1992. "Trends in Abundance of Tropical Forest Insects." *Oecologia* 89 (1): 47–52.
- Wolda, H, and E Broadhead. 1985. "Seasonality of Psocoptera in Two Tropical Forests in Panama." *The Journal of Animal Ecology*: 519–530.
- Wolda, Henk, and Frank W Fisk. 1981. "Seasonality of Tropical Insects. II. Blattaria in Panama." *The Journal of Animal Ecology*: 827–838.
- Wrangham, Richard W, Nancy Lou Conklin-Brittain, and Kevin D Hunt. 1998. "Dietary Response of Chimpanzees and Cercopithecines to Seasonal Variation in Fruit Abundance. I. Antifeedants." *International Journal of Primatology* 19 (6): 949–970.
- Wright, Barth W, Kristin A Wright, Janine Chalk, Michele P Verderane, Dorothy Fragaszy, Elisabetta Visalberghi, Patricia Izar, Eduardo B Ottoni, Paul Constantino, and Christopher Vinyard. 2009. "Fallback Foraging as a Way of Life: Using Dietary Toughness to Compare the Fallback Signal Among Capuchins and Implications for Interpreting Morphological Variation." *American Journal of Physical Anthropology* 140 (4) (December): 687–699. doi:10.1002/ajpa.21116.
- Xiang, Zuofu, Wenbin Liang, Shuaiguo Nie, and Ming Li. 2013. "Short Notes on Extractive Foraging Behavior in Gray Snub-Nosed Monkeys." *Integrative Zoology*.
- Yamagiwa, Juichi, and Augustin Kanyunyi Basabose. 2009. "Fallback Foods and Dietary Partitioning Among Pan and Gorilla." *American Journal of Physical Anthropology* 140 (4) (December): 739–750. doi:10.1002/ajpa.21102.
- Yamakoshi, G. 1998. "Dietary Responses to Fruit Scarcity of Wild Chimpanzees at Bossou, Guinea: Possible Implications for Ecological Importance of Tool Use.." *American Journal of Physical Anthropology* 106 (3) (July): 283–295. doi:10.1002/(SICI)1096-8644(199807)106:3<283::AID-AJPA2>3.0.CO;2-O.
- Young, H C. 2005. "Sharp Spines and Toxic Stings: How White-Faced Capuchins (*Cebus Capucinus*) Overcome the Defense Mechanisms of Invertebrates in Costa Rica". *Masters Thesis*.
- Young, Hilary, Linda M Fedigan, and John F Addicott. 2007. "Look Before Leaping: Foraging Selectivity of Capuchin Monkeys on Acacia Trees in Costa Rica." *Oecologia* 155 (1) (October 27): 85–92. doi:10.1007/s00442-007-0883-z.
- Zuur, Alain F. 2009. "Mixed Effects Models and Extensions in Ecology with R."
- Zuur, Alain F, Elena N Ieno, and Erik Meesters. 2009. "A Beginner's Guide to R."

Zuur, Alain F, Elena N Ieno, and Graham M Smith. 2007. "Analysing Ecological Data" 680. "Selection on Offspring Size Varies Within and Among Families in Relation to Host Nutritional Quality." 2007. "Selection on Offspring Size Varies Within and Among Families in Relation to Host Nutritional Quality" 22 (1) (February 24): 71–83. doi:10.1007/s10682-007-9159-7. <http://link.springer.com/10.1007/s10682-007-9159-7>.