FORAGING ACTIVITIES OF EASTERN CHIPMUNKS (*TAMIAS STRIATUS*): FOOD ACQUISITION AND CACHE DEFENSE

By Corey J Santorello

Optimal foraging theory was developed as a theoretical framework for understanding the evolution of feeding strategies. It states that animals forage in a way that will maximize their net energy intake per unit time, thereby maximizing their individual fitness. A behavior whereby animals store surplus food that potentially can be consumed later is called caching. The eastern chipmunk (*Tamias striatus*) caches food in larder hoards and scatter hoards throughout the spring, summer, and fall. During each season I would observe eastern chipmunk activities.

To construct a preliminary time budget of chipmunk food acquisition and cache defensive behaviors, I observed eastern chipmunks throughout their period of above-ground activity for several hours each day. The study was conducted on a 4-ha plot in Hartman Creek State Park located north of Hartman Lake near Waupaca, Wisconsin. I live trapped *T. striatus* from late May to early June to uniquely mark individuals for focal observations. I conducted observations on all individuals (both marked and unmarked) from early June through October during 2013 and 2014. Four behaviors that I recorded were territorial/alarm calling, foraging, expelling conspecifics from a territory, and scanning for conspecifics or predators.

Including all individuals (marked and unmarked) from both years of the study, linear analysis of categorical data revealed a difference in the distributions of behaviors across months and between years. The month*year interaction was also significant. Using the marked male and female data from the 2014 field season, I looked at the difference in distribution between behaviors for sex and month. Linear analysis of categorical data of marked individuals from 2014 revealed that there were no differences between sexes, but distributions of behaviors across months varied. There was no month*sex interaction.

Additional research on behavior needs to be implemented because caching behaviors are poorly understood and have the potential to play a fundamental role in optimal foraging by eastern chipmunks. Studying food acquisition and cache defense are critical to developing a greater understanding of optimal foraging and central place foraging theory models.

In summary, I found that foraging is the predominant behavior than cache defense, but behaviors also change over a single season and from year to year, presumably in response to environmental changes. Because of this flexibility, predicting individual behaviors is difficult without knowing the environmental cues that are used by chipmunks. Therefore, optimal foraging theory and central place foraging theory currently have utility only at a broader conceptual level. Although theorists continue to develop models that attempt to predict the behaviors of individuals, my study has shown that developing accurate utilitarian models will be difficult without knowledge of environmental influences.

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By

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Introduction

Optimal foraging theory is a body of ecological hypotheses that seeks to explain the evolution of foraging behaviors. It states that animals forage in a way that will maximize their net energy intake per unit time, thereby maximizing their individual fitness. Thus, animals behave in such a way as to find, harvest, and consume food containing the most calories while expending the least amount of time and energy possible. One way to ensure that food is available at all times (thereby maximizing intake) is to cache excess items. Caching is a behavior whereby animals store surplus food that potentially can be consumed later. This type of behavior is seen in many sciurids such as the eastern gray squirrel (*Sciurus carolinensis*) and the European red squirrel (*Sciurus vulgaris*). My study focuses on the eastern chipmunk (*Tamias striatus*), which caches food in larders (centralized caches) and scatter hoards throughout the spring, summer, and fall. Although caching behavior is critical to survival during periods of resource scarcity, the amount of time and energy budgeted by chipmunks to caching and defending larders is unknown. This species is an excellent model organism for developing time and energy budgets of foraging and larder defense because it is abundant, widely distributed, and readily observable.

Optimal foraging theory was developed by MacArthur and Pianka (1966) as a theoretical framework for understanding feeding strategies. Feeding strategies that have been observed in *T. striatus* are larder hoarding and scatter hoarding. Eastern chipmunks use these hoarding strategies to deter competitors from their resources. Central place

foraging theory, developed from optimal foraging theory, states that an individual will be influenced by factors such as conspecifics, predators, movement among patches, and load times (the amount of time an individual can collect food while at a patch). Because of such influences, theoretical models cannot presume how an individual will behave at any given time. A central place forager is where an individual collects and stores food within a territory. These individuals will defend this territory as a way to benefit themselves for future resources. By staying in one area, the central place forager must gather and defend food to survive. More behavioral studies therefore are needed to predict how an individual may behave under natural conditions, such as defending a territory, protecting offspring, and collecting sufficient food for survival and reproduction.

Larder hoarding is advantageous because food resources are stored in one centralized area that can be accessed at any time. However, by storing food in one area, the individual must be able to defend its hoard. One defensive strategy employed by chipmunks is to emit a territorial call that will notify competitors that the individual defending the area is present. If the pilfering individual does not leave that area, the chipmunk emitting the call will then actively chase the intruder from its territory. Adult males are more likely than adult females to defend a larder hoard because they are typically larger in size when compared to females (Schoener 1971; Yahner 1977; Smith and Reichman 1984; Vander Wall 1990; Clarke and Kramer 1994; Chang *et al*. 2010; Penner and Davenport 2011; Zhang *et al*. 2013). Thus, males are more likely to actively defend their hoard through vigilance, territorial calling, and physically expelling competitors.

Males can also scatter hoard their food; however, scatter hoarding increases the risk of finding fewer food resources away from a centralized location (Vander Wall 1990; Clarke and Kramer 1994). The advantage to scatter hoarding is that food is distributed unevenly over space and time and cache locations are known only to the individual that makes the caches. Any conspecific intruder most likely will find a cached item strictly by chance. By scatter hoarding food, an individual therefore will be able to devote more time and energy to foraging because competitors are unaware of that individual's cached items. The pilfering individuals consequently will have to spend additional time searching for cached items. By scatter hoarding its food resources, the caching individual can spend more time foraging rather than being vigilant and expelling intruders. Adult females and juveniles are more likely to scatter hoard their food because they tend to be smaller than adult males and are less able than males to defend a larder hoard (Schoener 1971; Yahner 1977; Smith and Reichman 1984; Vander Wall 1990; Clarke and Kramer 1994; Vander Wall and Jenkins 2003; Moore *et al*. 2007; Chang *et al*. 2010; Penner and Davenport 2011). Thus, previous studies state that females are expected to spend more time foraging for food rather than scanning for intruders, emitting territorial calls, and expelling conspecifics.

Elliot (1978) was the first to publish detailed observations of eastern chipmunks that focused on intraspecific interactions and how such interactions changed seasonally. During March, an eastern chipmunk's activity begins as it emerges from a torpid state and copulates, initiating the first of two breeding seasons. Fruit production in plants begins during April and May; until fruits are ripe, eastern chipmunks will consume food

from their winter hoards. As daily temperatures rise during the spring months, above-ground activity begins. Eastern chipmunks are particularly active above ground from June through September because new individuals are recruited into a population, territories are defended, and resource caching accelerates for the coming winter. According to Yahner (1977), eastern chipmunks experience a summer lull when activity is reduced because chipmunks are producing a second litter. Yahner's research was conducted in southeastern Ohio and may not represent all populations. More research is needed to identify summer lulls within eastern chipmunk populations. Finally, in October and November, eastern chipmunks finish their hoarding and enter periodic states of torpor until spring, when new food resources are once again appearing.

Although controlled experiments are ultimately necessary for testing hypotheses of optimal foraging theory, non-manipulative observations are a necessary first step. Such observations provide the basis for more rigorous hypothesis-testing, either in a laboratory or field setting. My goal was therefore to collect observational data to construct a preliminary time budget of chipmunk foraging and defensive behaviors. This budget will provide greater detail of eastern chipmunk behavioral activities for future optimal foraging theory studies. I accomplished this goal by observing chipmunks for several hours each day throughout their period of above-ground activity. Because eastern chipmunks are not sexually dimorphic (other than slight size differences) and frequently interact with multiple conspecifics, I needed to trap and uniquely mark a subset of individuals for more detailed focal observations. Those marked individuals therefore provided a sample on which I could search for gender-based differences in behaviors.

My study was conducted at Hartman Creek State Park in Waupaca County, Wisconsin and spanned two years of above-ground chipmunk activity. After two years of data collection, I am able to assess whether eastern chipmunks optimally forage and conform to predictions for central-place foragers. I predicted foraging will be the predominant observed behavior over cache defense (territorial/alarm calling, expelling competition from home range, and scanning). Although defending hoards is essential, *T. striatus* will devote more time to caching discovered resources. This research may lead to increased knowledge not only of eastern chipmunks but also other mammals and their foraging behaviors within the framework of optimal foraging theory and central place foraging theory.

Chapter I

Foraging Activities of Eastern Chipmunks (*Tamias striatus*): Food Acquisition and Cache Defense

Abstract

Optimal foraging theory was developed as a theoretical framework for understanding feeding strategies and is a body of ecological hypotheses that explain the evolution of foraging behaviors. It states that animals forage in a way that will maximize their net energy intake per unit time, thereby maximizing their individual fitness. Caching is a behavior whereby animals store surplus food that potentially can be consumed later. The eastern chipmunk (*Tamias striatus*) exhibits this type of behavior because it caches food in larder hoards and scatter hoards throughout the spring, summer, and fall.

My goal was to collect observational data to construct a preliminary time budget of chipmunk foraging and defensive behaviors. I accomplished this goal by observing chipmunks for several hours each day throughout their period of above-ground activity. The study was conducted on a 4-ha plot in Hartman Creek State Park located north of Hartman Lake near Waupaca, Wisconsin. I live trapped *T. striatus* from late May to early June to mark individuals for identification and conducted observations from early June through October in 2013 and 2014. Four behaviors that I recorded were territorial/alarm calling, foraging, expelling conspecifics from a territory, and scanning for conspecifics or predators.

Including all individuals (marked and unmarked) from both years of the study, linear analysis of categorical data revealed a difference in the distributions of behaviors across months and between years. The month*year interaction was also significant. Although there are changes in behavior, foraging remained the predominant single behavior across months and between years. Using the marked male and female data from the 2014 field season, I searched for a difference in the distribution of behaviors according to sex and month. Linear analysis of marked individuals from 2014 revealed that there were no differences between sexes, but distributions of behaviors varied across months. There was no month*sex interaction.

My prediction that chipmunks would spend more time on food acquisition over cache defense was supported. When comparing genders, my prediction was not supported, as males and females did not show a difference in behaviors. Caching behaviors are poorly understood; however, they have the potential to play an important role not only within eastern chipmunk populations but also within their communities. Studying food acquisition, hoarding, and cache defense is critical to developing a greater understanding of optimal foraging and central place foraging theory.

Introduction

Feeding strategies were first formalized within a theoretical framework by MacArthur and Pianka (1966), who developed optimal foraging theory. Schoener (1971) further developed theories of foraging strategies. Optimal foraging theory states that

organisms forage to maximize their net energy gains. Studies on ants (*Pogonomyrmex*, Morehead and Feener 1998), Edward's long-tailed rat (Chang *et al.* 2010) and Brant's whistling rat (Jackson 2001) support the predictions of optimal foraging theory.

Charnov (1976) proposed the marginal value theorem. This theorem was developed under the assumption that animals optimized their foraging strategies. The marginal value theorem applies to individuals as they consume food and travel between patches. The theorem, however, is not entirely accurate because there are discrepancies when comparing different types of animals such as carnivores, herbivores, frugivores, and granivores. Subsequent studies by Orians and Pearson (1979), Giraldeau and Kramer (1982) and Jackson (2001) found mathematical errors with different terms, such as time spent in a patch, handling times within a patch, traveling times between patches, predation, and the size of a food item an individual may have in its possession. These terms are different with every type of animal. Because animals react differently in their environment whether they are a primary or secondary producer or an apex predator, researchers molded the marginal value theorem into the central place foraging theory. This theory states that an individual will be influenced by extrinsic factors such as conspecifics, predators, movement among patches, and load times (the amount of time an individual can collect food in its mouth while at a patch).

Central place foragers control their food resources over space and time as an adaptive strategy when deciding which food sources are valuable throughout the year (Wood 1993; Gerber *et al.* 2004). A strategy of storing food is used by some animals that

are dormant during the winter months when food resources are low. However, during the spring, summer, and autumn seasons, food availability generally is sufficient, which allows central place foragers to optimize energy gain for greater fitness.

When examining optimal foraging and central place foraging theory, we need to examine the behaviors of individuals and whether they forage to optimize their level of fitness. Behaviors that are predicted by optimal foraging theory and central place foraging theory typically are studied under laboratory settings. Field studies are sorely needed to better understand how organisms forage under natural conditions (e.g., in an environment in which an individual developed) (Bowers and Adams-Manson, 1993).

Environmental conditions within temperate regions permit animals to cache in an area where food resources are frequently scarce because seasonal differences affect when trees fruit. Because plant reproductive biology influences when certain animals are active, such animals must maximize their resource acquisition when plants are fruiting. Accordingly, these animals are likely to cache seasonally-abundant resources. There are two main types of caches: scatter hoards and larder hoards. Eastern chipmunks (*Tamias striatus*) both larder hoard and scatter hoard their food within their home range or territory (Giraldeau and Kramer, 1982). By choosing between these two hoarding strategies, *T. striatus* essentially chooses how best to optimize its foraging habits, depending on the current conditions of the environment. Environmental conditions influence the timing of plant reproduction and the number of individuals within a population.

To study these optimizing foraging habits, my research examines caching and defensive behaviors of the eastern chipmunk to broaden our knowledge of animal foraging and territorial behaviors and to improve our understanding of the time (and therefore energy) that is allocated to food acquisition. I hypothesize that if *T. striatus* needs to consistently store food to survive year-round, then it will devote more time to food acquisition than to cache defense. This species is an excellent model organism for developing time and energy budgets of foraging and larder defense because it is abundant, widely distributed, and readily observable.

The eastern chipmunk is a small, territorial sciurid (~100 g adult weight) that lives in burrows. Eastern chipmunks range from southern Canada to the southern United States and from the Atlantic coast westward to the Great Plains. They are mainly active from April to November and are dormant from December to mid-March. During its active time, *T. striatus* actively defends its territory while also foraging. This territorial behavior renders it an excellent species to study within the context of optimal foraging and central place foraging theory.

Many factors may influence chipmunk foraging and territorial behaviors. One such factor is reproductive activity. Eastern chipmunks have two breeding seasons: March and July (Elliot 1978; Burke da Salva *et al*. 2002). During these times, above-ground chipmunk activity is typically low, especially during July; however, not all populations may experience a summer lull in above-ground activity (Yahner 1977). After the breeding seasons (late May and early June to September), above-ground

chipmunk activity again increases, with individuals from new litters entering the population (Elliot 1978; Burke da Salva *et al*. 2002). During these times, behaviors of normally solitary chipmunks may be altered, as new burrows are being constructed, and littermates may work cooperatively (Elliot 1978).

Aggressive interactions with conspecifics and predator avoidance behaviors may also influence foraging activities. Giraldeau *et al*. (1994) found that a predator's presence in a given area may affect load and travel times of eastern chipmunks, providing more evidence that central place foraging is critical to a chipmunk's survival. If an area does not contain fruiting trees, an individual may have to seek patches farther from its burrow than if resources were near its central place. During that time spent away from its burrow, the rate of predation increases (Schoener 1971; Orians and Pearson 1979; Bowers 1995; Baack and Switzer 2000; Jackson 2001). However, searching for food farther from the burrow may be critical if resources in the area are depleted, and this increase in foraging distance causes an individual to use more energy.

Because eastern chipmunks are small and consequently have high metabolic rates, they require large amounts of energy (Leqvesque and Tattersall 2010). Such demands necessitate either a large hoard of food or multiple foraging bouts each day (Yahner 1977). Although numerous studies have documented foraging and territorial behaviors of eastern chipmunks, no studies have assessed the relative contributions of those activities to an overall time or energy budget. Indeed, it is unclear if eastern chipmunks spend more time collecting food or defending their caches. Obtaining such information could

aid in future optimal foraging and central place foraging experiments. If we can determine how often *T. striatus* focuses on a particular foraging-related behavior, we could then determine how eastern chipmunks potentially optimize their food acquisition and use.

Foraging by rodents is affected by predators and conspecifics, which disrupt rodents' time spent traveling either within their home range or to a new patch that is outside of their home range (Orians and Pearson 1979; Giraldeau and Kramer 1982; Lair *et al*., 1994; Giraldeau *et al*., 1994 Jackson, 2001; Mcaleer and Giraldeau, 2006; Olsson *et al*., 2008). An individual may actively defend its territory to protect its cached food, or because of risks associated with defending a single cache, may dedicate its time and energy to foraging and partitioning its food among multiple caches. The latter strategy reduces the energy spent in defending caches.

Larder hoarding occurs when an individual caches food in a set location (burrow) and actively defends its area, observed mostly in males (Schoener 1971; Yahner 1977; Smith and Reichman, 1984; Vander Wall 1990; Clarke and Kramer 1994; Chang *et al*. 2010; Penner and Davenport 2011; Zhang *et al*. 2013). Scatter hoarding occurs when an individual caches food in multiple locations around the home range, observed mostly in females (Schoener 1971; Yahner 1977; Smith and Reichman 1984; Vander Wall 1990; Clarke and Kramer 1994; Vander Wall and Jenkins 2003; Moore *et al*. 2007; Chang *et al*. 2010; Penner and Davenport 2011).

Eastern chipmunks are likely to scatter hoard when food resources are low to reduce pilfering (Smith and Reichman 1984; Moore *et al*. 2007; Zhang *et al*. 2013). This ability to choose between these hoarding styles is an important adaptive strategy that permits flexibility in variable environments (Wood 1993; Gerber *et al*. 2004). Scatter hoarding is therefore successful because lesser quantities of stored food are at risk of being pilfered (Hollander and Vander Wall 2003; Beck and Vander Wall 2010; Vander Wall and Beck 2012).

For scatter hoarding to have evolved, problems with cache pilfering must have occurred, which promoted food storage in multiple locations (Vander Wall and Jenkins 2003). Although pilfering still continued, these animals must have successfully deterred many competitors. From this evolved behavior came the cognitive ability to recall where food was cached throughout space and time (Vander Wall and Jenkins 2003). To limit pilfering from cached locations, individuals must have begun defending their caches. Over time, animals such as the eastern chipmunk began scatter and larder hoarding as two different strategies. Larder hoarding requires an increase in defensive behavior, while scatter hoarding requires less defensive behaviors. However, Wood (1993) found no difference in the numbers of seeds stored in either type of cache.

These two types of caches allow for a difference in eastern chipmunk behaviors that may influence the daily decisions of individuals. Whether an individual larder hoards or scatter hoards could lead to unforeseen factors when creating mathematical models for optimal foraging. If an individual chooses to defend an area, then it may

dedicate less attention to foraging in outlying areas. An individual that scatter hoards will likely dedicate more time foraging in multiple patches and possibly collecting greater amounts of food to cache within its home range.

During late spring, as winter hoards are no longer needed and new resources become available, chipmunks will begin caching food and continue to cache food throughout the summer and into mid-autumn until dormancy resumes (Elliot 1978; Smith and Reichman 1984). During this time, food resources and temperatures may fluctuate, which could lead to a change in an individual's decision whether to forage or defend the larder hoard they already possess (Humphries *et al*. 2002; Moore *et al*. 2007). If food resources are low, an individual may choose to defend the food it already possess until more is available, or if food is abundant, the individual may devote more energy to collecting that food. Temperature may also influence the time of day that individuals may be active or whether being active above ground is necessary.

As caches are being pilfered above ground, an individual may choose to then defend its territory rather than forage; as a consequence, the individual loses time to forage for future resources (Giraldeau and Kramer 1982; Wood 1993; Woodrats Gerber *et al*. 2004; Clarke and Kramer 1994). This decision is made by an individual that larder hoards in a home range or zone of dominance (territory) to reduce pilfering; by defending its territory, it will lose time foraging. However, if an individual chooses to forage more, it is likely to scatter its food throughout a given home range, which may ensure food during times of resource scarcity.

Eastern chipmunks aggressively defend their territories by chasing individuals from their zones of dominance (Elliot 1978; Bowers and Adams-Manson 1993; Vander Wall and Jenkins 2003; Penner and Davenport 2011; Zhang *et al*. 2013). Before a potential chase arises, an individual may discourage conspecifics from entering its zone by emitting a territorial call, signifying it is present and ready to actively defending its territory. There are three distinct territorial or alarm calls: chipping, chucking, and trilling (Baack and Switzer 2000; Burke da Salva *et al*. 2002). Further study is needed to identify the specific meaning of each call; therefore, for my study, all three calls were grouped together as territorial/alarm calling.

By actively defending its territory, *T. striatus* can increase its chances of survival when food resources are scarce. An individual will use the resources that are currently available over the resources that may potentially arrive later, which is known as 'future discounting' (Bowers and Adams-Manson 1993). However, storing for the winter to ensure success for the next spring is important, and chipmunks may spend a majority of their time caching for later consumption (Kuhn and Vander Wall 2009). However, there are no numerical data to support these claims.

There is a dearth of information for several reasons. First, many animals are not amenable to having humans present in their habitat. They avoid potential threats and exploit and manage their food resources when people are not present (Vander Wall *et al*. 2006). Second, many studies are conducted through an experiment, which may not be

the best way to observe true behaviors that would be seen during field observations (Bowers and Adams-Manson 1993).

I observed chipmunks within a single population in central Wisconsin and recorded four common behaviors (territorial or alarm calling, foraging, expelling conspecifics from an area, and scanning for competitors or predators) related to food acquisition and cache defense. Each behavioral tally represented a moment in time during an individuals' above ground presence. When a chipmunk's behavior changed, I tallied a new behavior. These behavioral tallies therefore represented snapshots of an individual's overall activity and in sum served as a proxy for an individual's foraging and defense budget.

Methods

Study area. The study was conducted in Hartman Creek State Park (44˚19'43.0" N, 89˚12'24.0"W), near Waupaca, Wisconsin. The park is geographically located within the Eastern Ridges and Lowlands region and contains dense loam soils and glacially-deposited sand overlying Precambrian granite and metamorphic rock (Vogeler 1986). I used the Munsell soil color chart (1992) and identified a 5YR 2.5/2 dark-reddish-brown color of loam and very fine sand mixture.

First used for agricultural and logging purposes, the area is now reserved strictly for outdoor recreational activities. Adjacent to the Dike Hiking Trail, north of Hartman Lake, I sampled *T. striatus* on one 4-ha plot. The study site was located in a second-

growth forest dominated by sugar maple (*Acer saccharum*), bur oak (*Quercus macrocarpa*), choke cherry (*Prunus virginiana*), and white pine (*Pinus strobus*).

Sampling procedures. I live trapped *T. striatus* during two field seasons from late May through early June in 2013 and 2014. Each season, 20 Sherman live traps (5.08 x 6.35 x 16.51cm) were baited with sunflower seeds and provided with Poly-fil® for insulation and were set along transects throughout the study area. During the 2013 season, traps were set for 200 trap nights, and during the 2014 season, traps were set for 120 trap nights.

From June through October, temperatures during field observations ranged from approximately -1.1˚C to 26.6˚C. In the northern part of its geographical distribution, *T. striatus* is active above ground from April to early November when food is available (Elliot 1978). I therefore began sampling chipmunks at the end of May when nightly temperatures did not fall below 0°C, and juveniles from the March breeding season were emerging (Elliot 1978; Vander Wall 1990; Burke da Silva *et al*. 2002). I ended observations in October due to low chipmunk activity.

All captured *T. striatus* were uniquely marked with hair dye (Hart 1971; Yahner, 1977; Elliot 1978), weighed, and sexed (Burke da Silva *et al*. 2002). I used Clairol Natural Instincts©, 36 Black and 23R Medium Auburn (cf. Baack and Switzer 2000) to mark each individual with a unique color combination for observations during the behavioral study. Weight was measured using a 300-g Pesola scale. Individuals were immediately released at their capture site after data collection and marking. Recaptured

individuals in the same sampling season were released without further data collection. My goal with the live trapping was to provide a sample of uniquely-marked individuals for focal behavioral observations. For every new day of observations, my minimum goal was to record 50 different behavioral activities from as many different individuals as possible. I anticipated observing the uniquely-marked individuals during every observational session.

Behavioral procedures. I observed *T. striatus* using 8x40 Orion waterproof binoculars during daylight hours, 2-3 hours/day, 3 days/week for approximately 20 weeks. Behavioral observations began when I encountered the first eastern chipmunk for that sampling day. During observations, I stood in approximately 15 locations throughout the 4-ha plot, relocating to a different location >10 m distant approximately every 20 minutes. When moving to a new location, I would not stop until I encountered a new individual. Occasionally, I would not have to relocate because new individuals would move into the area in which I was conducting observations.

I recorded four behaviors including territorial/alarm calling, foraging, expelling conspecifics from a territory, and scanning for competitors or predators. Each time an observed chipmunk changed its behavior, I recorded the new behavior as a tally under one of the four columns that represented a behavior. I observed an individual until it returned to its burrow or was no longer within view; observations of an individual would range from 1-15 minutes. Every new tally was based on a specific behavior that an individual performed. Activities for each behavior are as follows. Territorial/alarm calls

were recorded when an individual made a chipping, chucking, or trilling sound (Burke da

Salva *et al*. 2002). The chipping sound was high pitched and the chipmunk was in an

alert posture (motionless body, with tail flicking up and down). Chucking was a lower

barking sound; however, the same alert posture and tail flick occurred. The trill was a

quick, high-pitched sound of 1-3 seconds duration and was followed most of the time by

a chase (a chase was when an individual ran after and sometimes attacked another

individual until the initiated trilling chipmunk stopped pursuit). The foraging behavior

occurred when an individual was searching for (e.g., sniffing), consuming, or caching

food on the ground. Expelling occurred when an individual chased another individual

from its territory. Scanning was recorded when an individual assumed a motionless

position or exhibited active head movements or an alert posture (Baack and Switzer

2000). Scanning was performed near the burrow and allowed the individual to maintain

an active presence within its territory (Bowers 1995). Individuals were observed by their

unique marking or recorded as an unmarked individual. I observed chipmunks between

0800 and 1200 hours (CST) because those are typically the hours of greatest above-

ground activity (Yahner 1977; Elliot 1978).

    Data analysis. To search for differences in the distributions of behaviors, I used

linear analysis of categorical data. I first analyzed the data of all individuals (both

marked and unmarked) by constructing a full model that included month and year as

main effects and the month*year interaction. I then analyzed only marked individuals

from 2014 by constructing a full model that included sex and month as main effects and

the sex*month interaction (no marked females were observed during 2013). All data

analysis was conducted using SAS Version 9.2 (SAS Institute Inc. 1990).

Results

During the 2013 field season, I captured and marked 10 *T. striatus* individuals

during 200 trapnights. I recorded 1,330 behavioral observations that were tallied among

all marked and unmarked individuals (Table 1). I then took the total number of tallies

from each behavior and converted them into a proportion and plotted them on a line

graph across months (Figure 2). All uniquely marked and sexed individuals were

documented separately during observations (Table 2). I then converted the total number

of tallies from all marked individuals to a proportion and plotted them on a bar graph

based on sex and monthly distributions of behaviors (Figure 3).

For the 2014 field season, I captured and marked 25 different *T. striatus* during

120 trapnights. The 3,658 observed behaviors of all marked and unmarked individuals

were tallied and recorded (Table 3). I constructed a line graph to portray the proportions

of observations in each behavior across months (Figure 4). All uniquely marked

individuals were documented separately during observations (Table 4). The bar graph

represents the proportions of each behavior from all marked individuals by sex across

months (Figure 5).

Including all individuals (marked and unmarked) from both years of the study,

linear analysis of categorical data revealed a difference in the distributions of behaviors

across months ($x^2 = 52.50$, P = <.0001) and between years ($x^2 = 21.12$, P = <.0001). The

month*year interaction was also significant ($x^2 = 74.67$, P = <.0001). Thus, individuals

changed their behavioral activities across months and between years, but the monthly

changes were not consistent between years. Although there were changes in behavior,

foraging remained the predominant single behavior across months and between years.

Using the marked male and female data from the 2014 field season, I looked at

the difference in distribution between behaviors for sex and month. Linear analysis of

marked individuals from 2014 revealed that there were no differences between sexes (x^2

= 0.17, P = .9827), but distributions of behaviors across months varied ($x^2 = 25.99$, P =

.0020). There was no month*sex interaction ($x^2 = 6.33$, P = .7061). I could not include

corresponding data from 2013 because I made no observations of marked females.

By looking at the difference in distribution of behaviors we can see whether

individuals within a population are similar. Finding a population that is similar we can

say individuals within a population are behaving in a way that benefits them dependent

on the environment. If individuals behave based on environmental conditions, then

optimal foraging and central place foraging theory models cannot accurately predict how

an individual may behave because behaviors are not uniform. A difference in distribution

of behaviors is dependent on the time of month throughout the year.

Discussion

My prediction that food acquisition would be a more common behavior than any

behavior associated with cache defense was largely supported. Overall, nearly 50% of all

recorded behaviors were foraging. Although behaviors changed from June to October

and from 2013 to 2014, foraging was nonetheless the pre-dominant behavior. Although

the other three behaviors are at least partly related to cache defense, scanning also is an

anti-predator behavior. My results corroborate the results from previous studies on

eastern chipmunks that suggested that chipmunks spend a greater amount of their time on

foraging for food than on any other activity (Kuhn and Vander Wall 2009). Foraging

therefore appears to be an overall pre-dominant behavior (Hart 1971) that outweighs

defensive behaviors throughout an entire year of above-ground activity. Although

foraging can lead to dangerous encounters with conspecifics or predators, this necessary

activity is performed by chipmunks to acquire food not only for immediate consumption

but also for storage and later consumption (Hart 1971; Baack and Switzer 2000).

I suggest that the reason for foraging being the predominant behavior is due to the

amount of food resources that are available in the study area during the spring, summer,

and autumn seasons. There are data that suggest that a chipmunk's survival is largely

based on the interannual variation of food resources and its winter hoards during low and

high mast years (Humphries *et al*. 2002; Moore *et al*. 2007). Food within my study site

was abundant; I observed large numbers of acorns that were available for collection.

These observations suggest that both 2013 and 2014 were adequate mast years, thereby

allowing chipmunks to spend considerable time acquiring excess food for storage.

There was no difference in behaviors between males and females, contrary to my

prediction. Earlier studies suggested that males tended to be more active and aggressive,

while females spent more time foraging (Schoener 1971; Yahner 1977; Smith and Reichman 1984; Clarke and Kramer 1994; Vander Wall and Jenkins 2003; Moore *et al*. 2007; Chang *et al*. 2010; Penner and Davenport 2011; Zhang *et al*. 2013). Smith and Reichman (1984) suggested that females cached more frequently than males as a form of parental care. I found no such differences. However, because I found differences between years, I suggest that chipmunks adjust their activities in response to environmental conditions. Studies of short duration are sampling only a snapshot of a chipmunk's lifetime activities. Conclusions derived from one study therefore may differ dramatically from those of another study, depending upon environmental conditions. One environmental condition that is no doubt of paramount importance is the mast crop, which largely determines the amount of food that individuals can cache (Humphries *et al*. 2002).

My study supports the idea that male and female eastern chipmunk behaviors related to food acquisition and defense are similar and do not diverge from each other according to season. Thus, there was no interaction between sex and month, showing that behaviors of males and females change throughout a year but do not differ from each other.

I did not see evidence of a summer lull, as Yahner (1977) and Elliot (1978) have suggested. I recommend that more studies be implemented to determine conditions that might cause such a lull. It may even be possible that not all eastern chipmunk populations show a summer lull.

Studying food acquisition and cache defense is critical to developing optimal foraging and central place foraging theory. Eastern chipmunks can change their behaviors according to environmental conditions, and this plasticity no doubt allows them to survive in changing environments. However, because chipmunks live in variable environments and adjust their behaviors, it is currently difficult to place chipmunks within this theoretical framework. Therefore, additonal studies on caching behaviors need to be conducted because of the crucial role that caching plays in the lives of chipmunks (Vander Wall and Jenkins 2003). For instance, Skorka *et al*. (2009) proposed that metapopulation theory can be used as a catalyst for studies on foraging behaviors and can be a vital addition to optimal foraging and central place foraging theory.

Acknowledgements

Conclusion

The focus of my study was whether foraging would be the predominant behavior over cache defense (territorial/alarm calling, expelling competition from home range, and scanning). By knowing which behaviors are more common will support future central place foraging theory models as these models will better predict the outcome of eastern chipmunks and other central place foragers. These data aid in our understanding of how environmental conditions such as food production from plants affect how central place foragers like the eastern chipmunk survive. I found that foraging is the predominant behavior among eastern chipmunks than cache defense. These data show eastern chipmunks are dedicating more of their time and energy to searching, collecting, and caching food for later consumption. The decision to forage suggests *T. striatus* are unable to predict food availability in the future and therefore cache as much food in the present.

I also showed that male and female *T. striatus* devote similar times to foraging and defensive behaviors. However, the time devoted to specific behaviors changes over the course of a single year and between years. These data show behavioral differences between genders are consistent with one another supporting the idea that gender does not play a role to which behaviors are predominant to the other. The environment shapes the behaviors of eastern chipmunks which are supported by my hypothesis that *T. striatus* need to consistently store food to survive year-round.

My study was the first to examine behavioral differences of *T. striatus* in the field over the course of an entire year of above-ground activity. Including all individuals (marked and unmarked) from both years of the study, linear analysis of categorical data revealed a difference in the distributions of behaviors across months and between years. Supporting the idea that eastern chipmunks are changing their activities based on the environment i.e. food availability and surrounding conspecifics. The month*year interaction was also significant indicating the behavioral activities are changing throughout each seasonal and each year. Although there are changes in behavior, foraging remained the predominant behavior across months and between years.

Using the marked male and female data from the 2014 field season, I looked at the difference in distribution between behaviors for sex and month. Linear analysis of marked individuals from 2014 revealed that there were no differences between gender but distributions of behaviors across months varied. There was no month*sex interaction.

Observing individuals within a single population over two field seasons may be inadequate to give us a thorough understanding of eastern chipmunk behaviors of across a full range of environmental conditions. However, my study did indeed advance our understanding of chipmunk foraging and defensive behaviors by showing most individuals choose the predominant behavior of foraging over different types of cache defending. Furthermore, my study suggests avenues for further behavioral studies on *T. striatus*. In particular, I suggest studying the three different calls to determine their functions. Observations could also be conducted later in the day, despite the reduced

activity levels. It is possible that chipmunks may engage in somewhat different behaviors when their activity is suppressed. It is clear that chipmunks exhibit considerable behavioral plasticity, which no doubt allows them to exploit changing environmental conditions. Thus, studies conducted over multiple years may give insight into the environmental conditions that influence behaviors and cause inter-annual behavioral differences.

The environment is shaping the behaviors of eastern chipmunks based on fruiting of vegetation and the number of conspecifics in the area. The predictability of food in uncertain and therefore individuals are likely to dedicate their time foraging for food. By searching and caching food in the present ensures food for the future which individuals are unable to predict whether food will be available. This type of 'food discounting' is supported by Bowers and Adams-Manson (1993). The environment also affects individuals within a population as they compete for food resources with conspecifics and other competition. If individuals are unable to retain enough food resources they will not survive. Therefore, by dedicating more attention to caching food, an individual has a greater chance of surviving.

Table 1. Total behavioral tallies for marked and unmarked males and females from the

2013 field season.

2013

Sample Size	Territorial /Alarm Calling	Foraging	Expelling conspecifics from a territory	Scanning for conspecifics /predators	Total number of tallies
Male-Marked	25	85	64	83	**257**
Female-Marked	0	0	0	0	**0**
Unmarked	271	441	125	236	**1073**
Total	**296**	**526**	**189**	**319**	**1330**

Table 2. Total behavioral tallies of marked individuals from June-October 2013.

Marked Individuals	Sex	Territorial /Alarm Calling	Foraging	Expelling conspecifics from a territory	Scanning
Black Center Hind	Male	0	0	0	0
Black Left Hind	Male	0	0	0	0
Black Left Shoulder	Male	3	9	0	1
Black Right Hind	Male	0	1	0	0
Black Right Shoulder	Male	1	0	0	1
Red Center Hind	Male	6	23	4	24
Red Center Hind	Male	0	1	4	1
Red Left Shoulder	Male	0	7	33	14
Red Left-Right Hind	Male	15	42	23	41
Red Right Hind	Male	0	2	0	1
	Total	**25**	**85**	**64**	**83**

Table 3. Total behavioral tallies for marked and unmarked males and females from the

2014 field season.

2014

Sample Size	Territorial /Alarm Calling	Foraging	Expelling conspecifics from a territory	Scanning for conspecifics /predators	Total number of tallies
Male-Marked	17	124	8	92	**241**
Female-Marked	33	127	15	66	**241**
Unmarked	1001	1424	97	654	**3176**
Total	**1051**	**1675**	**120**	**812**	**3658**

Table 4. Total behavioral tallies of marked individuals from June-October 2014.

Marked Individuals	Sex	Territorial /Alarm Calling	Foraging	Expelling conspecifics from a territory	Scanning
Black Center Hind	Male	0	0	0	0
Black Center Hind/Black Left Shoulder	Male	0	0	0	0
Black Center Hind/Red Left-Right Hind	Male	0	3	0	3
Black Center hind/Red Left-Right Shoulder	Male	0	7	0	5
Black Left Hind	Female	9	24	3	11
Black Left Shoulder/ Black Left Hind	Male	0	0	0	0
Black Left Shoulder/Red Right Hind	Female	6	44	3	30
Black Right Hind	Female	3	7	0	0
Black Right Shoulder	Male	0	0	0	0
Black Right Shoulder/Black Right Hind	Female	5	18	1	12
Black Right-Left Hind	Male	0	0	0	0
Red Center hind	Male	9	27	1	27
Red Center Hind/Black Left-Right Hind	Male	3	42	1	28

Table 4. (Continued)

| Marked Individuals	Sex	Territorial /Alarm Calling	Foraging	Expelling conspecifics from a territory	Scanning
Red Center Hind/Black Left-Right Shoulder	Male	0	0	0	0
Red Left Hind	Female	2	15	5	4
Red Left Shoulder	Male	0	26	4	17
Red Left Shoulder/Black Right Hind	Male	1	4	0	2
Red Left-Right hind	Female	4	9	1	4
Red Right Hind	Female	4	8	1	4
Red Right Hind/Black Left Hind	Male	0	5	0	3
Red Right Shoulder	Male	1	5	2	4
Red Right Shoulder/Black Left Hind	Male	3	5	0	3
Red Right Shoulder/Red Right Hind	Female	0	2	1	1
Red Right Shoulder/Red Right Hind	Female	0	0	0	0
	Total	50	251	23	158
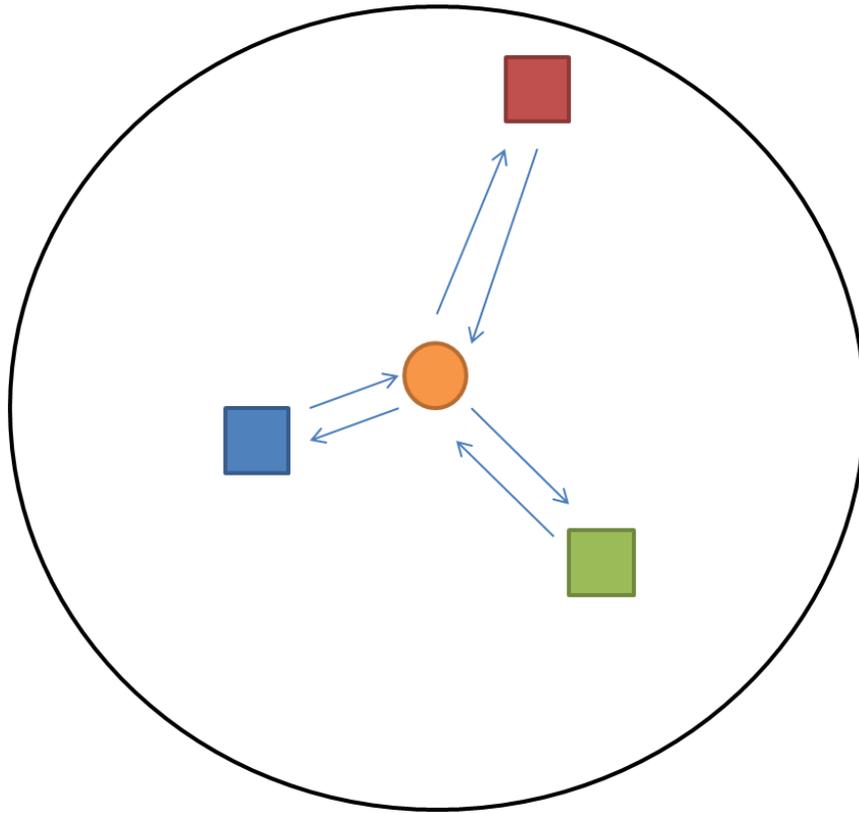
Figure 1. The orange circle represents an organism's central place where food items are consumed. The red, blue, and green squares represent different food patches. The arrows show how an organism may travel to a food patch, collect food item(s) and then return to its central place for immediate or later consumption.
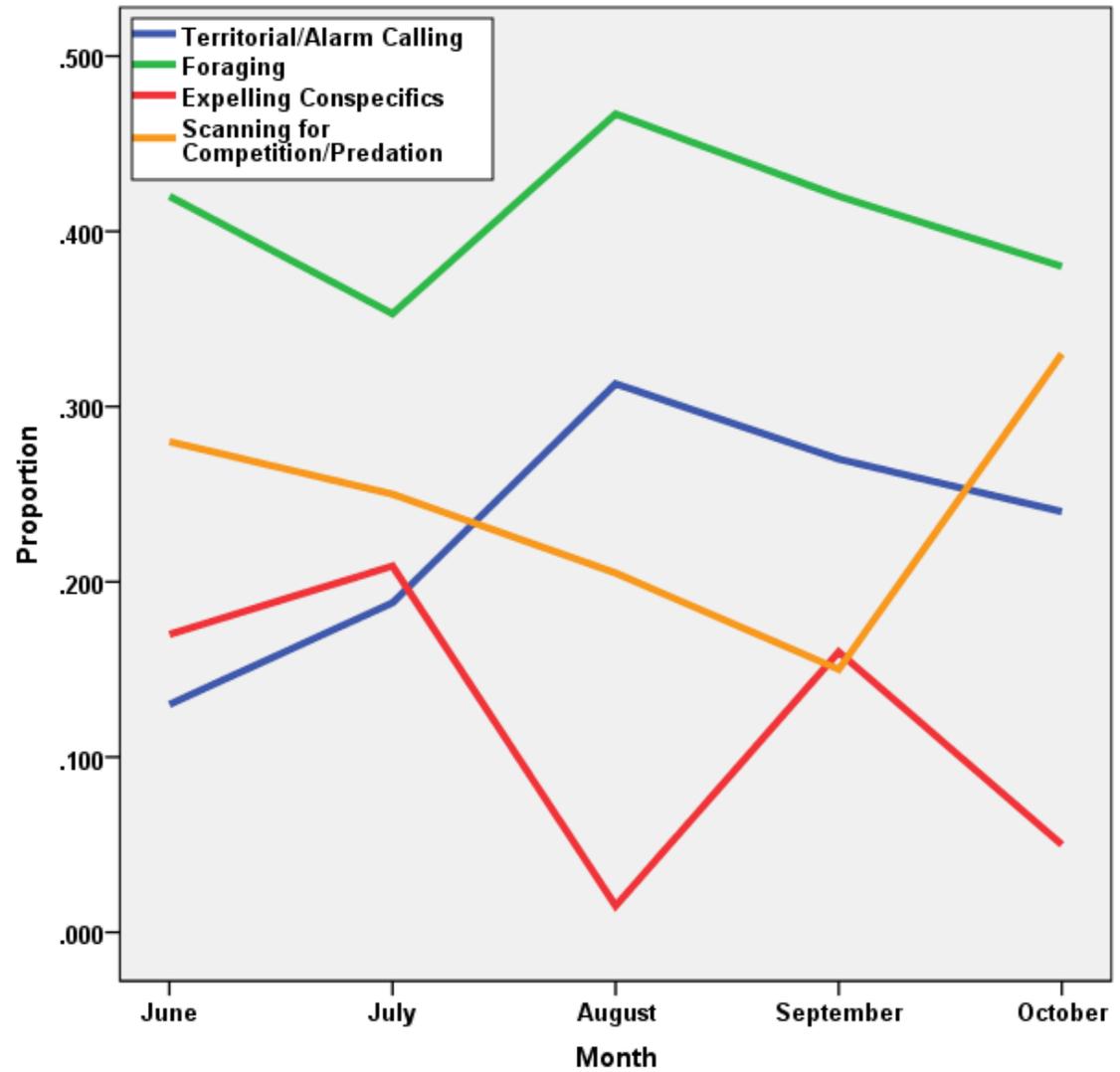
Figure 2. Proportions of behaviors based on all marked and unmarked individuals from June-October 2013.
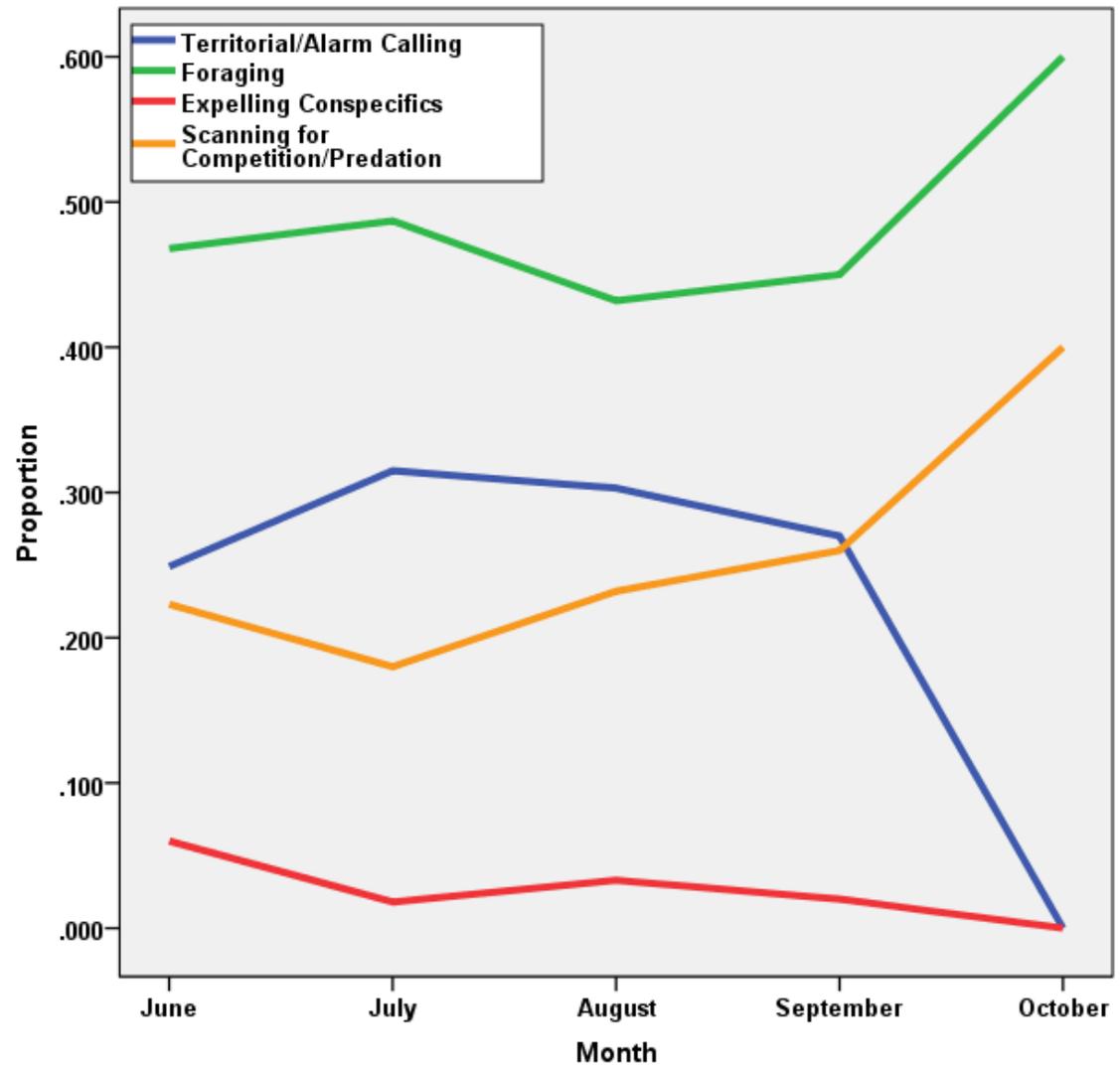
Figure 3. Proportions of behaviors based on all marked and unmarked individuals from June-October 2014.
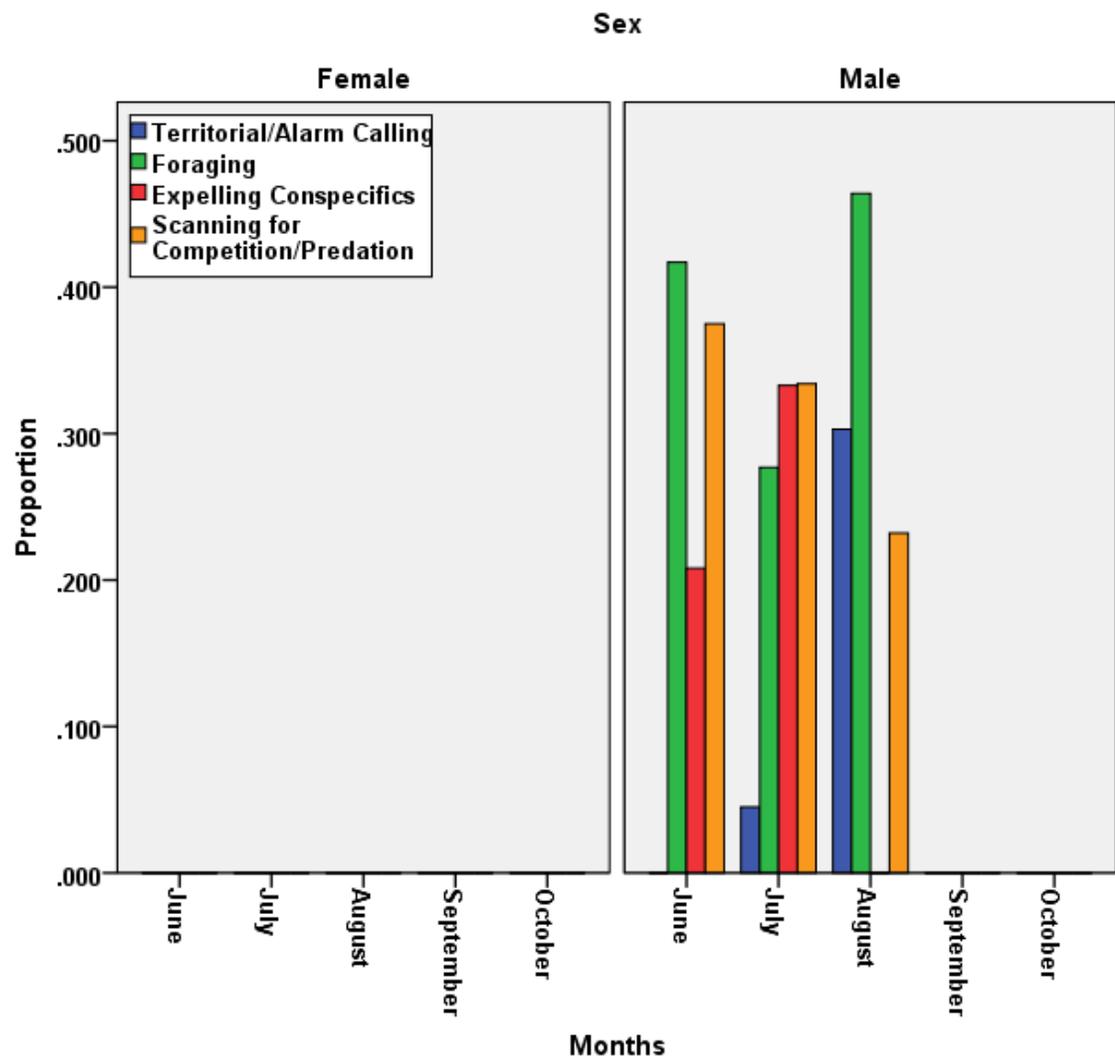
Figure 4. Proportions of behaviors based on marked males from June-October 2013.

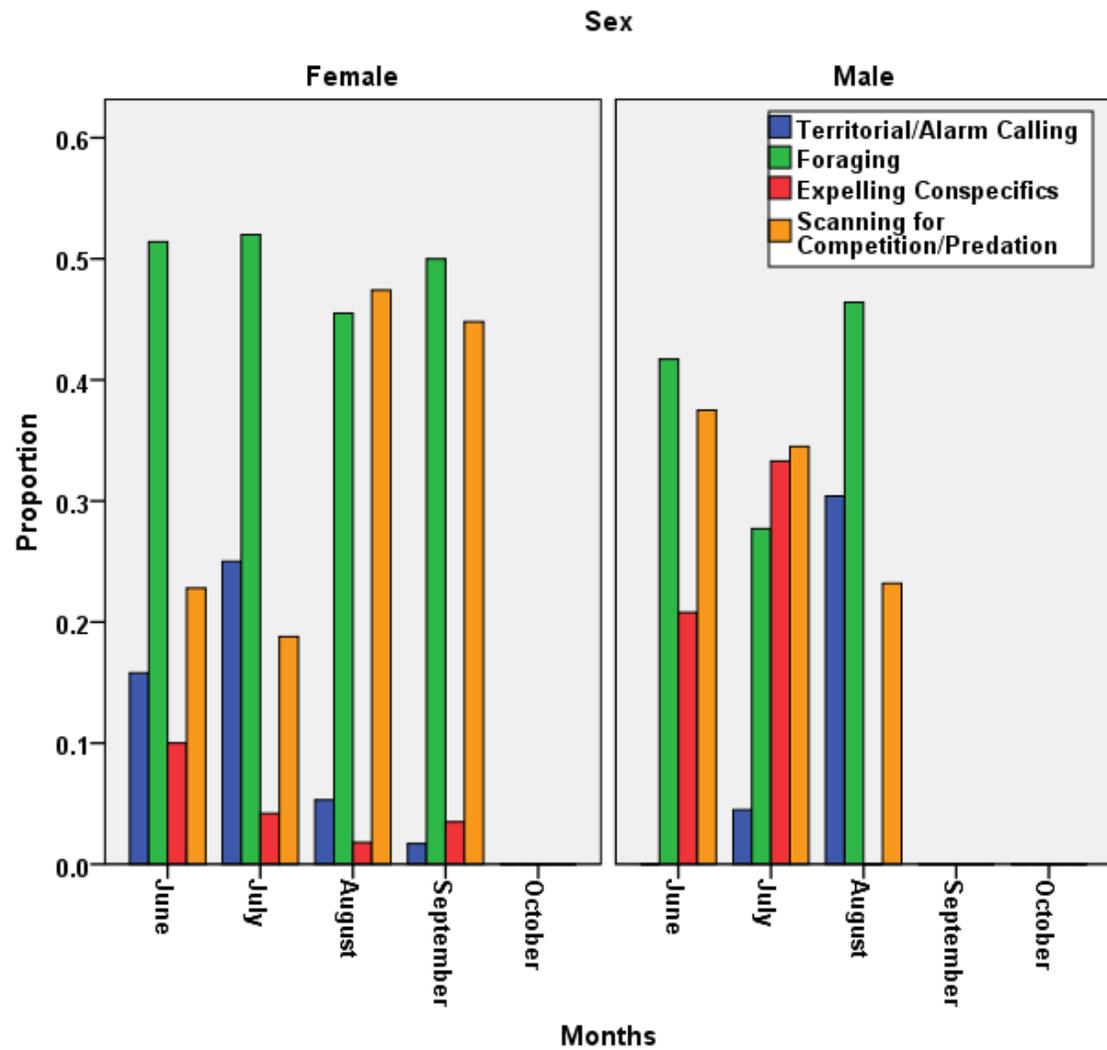Marked females were not observed during the 2013 season.

Figure 5. Proportions of behaviors based on marked females and males from June-

October 2014.

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