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Pilfering passerines? Inter-Class competition: A new direction in foraging ecology

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Pilfering passerines? Inter-Class Competition: A New Direction in Foraging Ecology

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JAMES MADISON UNIVERSITY

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Faculty Committee:
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Dedication Page

I dedicate this thesis to my mentors and peers at James Madison University, as well as my friends and family, without which this would not be possible.

Acknowledgements

I want to thank my advisor, Katrina Gobetz, my committee members, and all the professors at JMU that I've worked with for their help. I also want to thank my family, friends, and coworkers for being there to help me and distract me in equal measure. Lastly, I want to thank my fellow graduate students who were there for me in a way that I will be eternally grateful for.

Table of Contents

Dedication……………………………………………………………………….ii

Acknowledgements………………………………………………………… iii

Table of Contents…………………………………………………………..iv

List of Tables………………………………………………………………vi

List of Figures……………………………………………………………..vii

Abstract…………………………………………………………………...viii

I. Chapter 1 Introduction ………………………………………………..1

- Life below the leaves
- Caching
- The need for improved monitoring techniques

II. Methods ……………………………………………………………....9

- Study Locations
- Quantifying shrew mass and measuring shrew foraging trails
- Analyses

III. Results ……………………………………………………………12

- Caches and foraging trails
- Shrew weight by treatment type
- Shrew weight by season

IV. Discussion ………………………………………………………..14

V. Chapter 2 Introduction ……………………………………………19

- Supplemental food – how are small mammals impacted?
- Caching and pilfering

VI. Methods …………………………………………………………..22

- Measuring cache pilferage behavior and monitoring bird species presence
- Analyses

VII. Results ……………………………………………………………..24

- Overall bird occurrence
- Foraging type

Effects of season

Bird visitation rates and shrew weight

VIII. Discussion …………………………………………………………………….28

X. Literature Cited ..…………………………………………………………………...61

List of Tables

Table 1……………………………………………………………………………32

Table 2……………………………………………………………………………34

Table 3……………………………………………………………………………35

Table 4……………………………………………………………………………36

Table 5……………………………………………………………………………37

Table 6……………………………………………………………………………39

List of Figures

Figure 1 ……………………………………………………………………………..3
Figure 2 ……………………………………………………………………………..7
Figure 3 a,b……………………………………………………………………………8
Figure 4 a,b ……………………………………………………………………….14
Figure 5……………………………………………………………………………23
Figure 6……………………………………………………………………………25
Figure 7……………………………………………………………………………40
Figure 8……………………………………………………………………………41
Figure 9……………………………………………………………………………42
Figure 10………………………………………………………………………...43
Figure 11………………………………………………………………………...44
Figure 12………………………………………………………………………...45
Figure 13………………………………………………………………………...46
Figure 14………………………………………………………………………...47
Figure 15………………………………………………………………………...48
Figure 16………………………………………………………………………...49
Figure 17………………………………………………………………………...50
Figure 18………………………………………………………………………...51
Figure 19………………………………………………………………………...52
Figure 20………………………………………………………………………...53
Figure 21………………………………………………………………………...54
Figure 22………………………………………………………………………...55
Figure 23………………………………………………………………………...56
Figure 24………………………………………………………………………...57
Figure 25………………………………………………………………………...58
Figure 26………………………………………………………………………...59
Figure 27………………………………………………………………………...60

Abstract

Life in the epigeal layer below leaf litterfall often goes unexplored. Shrews (Soricidae, 1910) have foraged in this microhabitat for millions of years, carving out an existence in harsh habitats around the world, ranging from the tropics to subarctic boreal tundra. Two shrew species that inhabit the Shenandoah Valley of Virginia, the least shrew (*Cryptotis parva*) and northern short-tailed shrew (*Blarina brevicauda*), were the focus of this study. Shrews make epigeal foraging trails while they continually forage for food, and caching is a way to save this food for times of low and sporadic food availability. Foraging trails and caches for these species were found, mapped, and marked for both species, and for the first time in the case of the least shrew. A computer-controlled monitoring station, patented at the start of this study, was used to attract shrews and non-invasively obtain weight and morphological data. Also of interest was fate of invertebrate caches that shrews leave along their foraging trails. Some bird and small mammal species are cachers and will in turn pilfer the caches of members of their own taxa. However, inter-Class pilfering behavior between birds and mammals remains unstudied. This possibility may heavily impact the ability of shrews to survive considering their high metabolic rates. This study was conducted in the JMU arboretum and treatment sites included a supplemental feeding platform for birds while controls did not. Cameras were used to observe visiting bird species and whether they foraged in shrew trails or at caches. Treatment shrews of both species weighed less on average than control shrews, although this finding was not significant. Ground-feeding and caching birds were the most prolific visitors ($p = <0.01$), and are the species most often seen near shrew foraging trails ($p = 0.01$) and caches ($p = 0.04$). Treatment sites had significantly more visits by songbirds than control sites ($p = <0.01$). The information presented here

provides a much-needed foundation for future studies focused on foraging interactions across taxa.

Chapter I

Revolutionizing the way small mammals are studied using a non-invasive monitoring device

Introduction

Life below the leaves

Shrews (Soricidae, 1910) are small mammals that inhabit wooded, grassy, and marshy areas, with weights ranging from 2-35g depending on the species and time of year (Churchfield 1990; Nowack 1999; pers. obsv.). Shrews have long snouts and derived ear structures to echolocate their invertebrate prey under leaf litter, which more than makes up for their relatively poor eyesight. They are primarily insectivores, with a specialized neurotoxin secreted from submaxillary glands, which is used to paralyze prey, allowing shrews to store their food for later consumption (Churchfield 1990; Nowack 1999). Shrews are among the most ancient mammals, emerging during the late Eocene or early Oligocene Epoch approximately 38 million years ago and having changed very little since then (Churchfield 1990). They have not survived so long by accident; these small animals are surprisingly adaptable, with populations across the Americas, Africa, Asia, and Europe spanning 26 genera and 385 recognized species (Churchfield 1990; Nowak 1999). Two genera are known to inhabit the Shenandoah Valley of northwestern Virginia: *Cryptotis* (Pomel, 1848) and *Blarina* (Gray, 1838). *Blarina* is fairly widespread, with members of this species ranging over much of the U.S. and Canada, while *Cryptotis* is largely composed of neotropic species, found less commonly across the eastern U.S. (Nowack 1999).

Shrews incur high energy costs because of their high surface area to volume ratios, causing them to lose heat and water (and in turn, energy) rapidly. A study of the common shrew (*Sorex araneus*) found that this species is constantly on the edge of its physiological limits due to these energy costs and small internal fat reserves (Ochocińska and Taylor 2005). Shrews' high basal metabolic rates (BMR) are largely to blame, obligating shrews to eat almost constantly in order to survive. Tiny least shrews (*Cryptotis parva*) weigh ca. 4-10g (Formanowicz et al.1989; Nowack 1999; pers. obsv.) and move continually between burrows and their immediate surroundings to hunt prey. *C. parva* is the smallest shrew found in the Shenandoah Valley, with cinnamon brown fur and obvious countershading (Nowack 1999; pers. obsv.). Individuals of this species operate below leaf litterfall, although they will venture above the epigeal layer to pursue food (pers. obsv.). This species is active year-round, at all hours of the day and is the only species in *Cryptotis* (small-eared shrews) known to occur north of Mexico (Nowack 1999). Not much is known about this species' life history strategies so any data that can be obtained is of utmost importance.

The northern short-tailed shrew (*Blarina brevicauda*) is also of interest to this study, as its range is known to overlap with that of *C. parva*. This shrew is one of three members of *Blarina* (short-tailed shrews) and can be distinguished from *C. parva* by its grayer color, lack of countershading, and larger size, with weights in the range of 15-30g (Gobetz, pers. communication; Nowack 1999; pers. obsv.). Both species live in woodlands, marshes, and open grasslands, making tunnels through grass and under leaves. They create burrow systems under rocks, logs, or other objects using moss, grass, and dried leaves to make nests (Nowack 1999). Shrews live their lives almost exclusively under grass or litterfall, their foraging trails easy to see or feel as small indents through their substrate of choice (Figure 1).

Figure 1: Foraging trails of *B. brevicauda* at a treatment site with a 6 X 4 inch notebook for scale with dashed line superimposed over trail. Edith Carrier Arboretum, Harrisonburg, VA.

Caching

Shrews can store some of their energy reserves internally, usually in the form of thermogenic brown fat (Dew et al. 1998), but they also store food externally as caches. All organisms have limited capacity for internal energy storage, and there are trade-offs to consider when an animal generates a lot of fat, including higher metabolic requirements and an increased risk of predation (Dally et al. 2006; Lucas and Zleliniski 1998; Ydenberg et al. 2007). Caching is a means for animals to stockpile, or hoard, food items for later use. Many taxa engage in this behavior, including small mammals and birds. Caches are an adaptive strategy to protect against a reduction or fluctuation in food availability in an organism's habitat (Dally et al. 2006). Shrews cache invertebrates and seeds (Churchfield 1990; Nowack 1999) and it is well known that many species of shrew cache food, including *B. brevicauda* (Nowack 1999; Robinson and Brodie 1982; Saariko

1989; Smith and Reichman 1984). This species has been observed caching invertebrates in the wild and caching sunflower seeds and other nutmeats in captivity (Nowack 1999). However, caching behavior has never been observed in the least shrew. Understanding how *C. parva* employs this technique is imperative to learning more about possibly diverse foraging strategies and general life history among shrews.

There are two types of food hoarding: scatter and larder. Scatter hoards consist of many locations with only a few food items in each, which are hidden throughout the animal's home range (Smith & Reichman 1984). The concept of scatter hoarding gained traction in the 1940s-1950s and mainly focused on birds, but a study done on a South American forest-dwelling rodent (Morris, 1962) finally coined the term (Brodin 2010). Larder hoards, on the other hand, are central locations where food is collectively stored, generally in or near an animal's burrow or nest. A larder hoard is preferable when the animal stocking it can reliably defend it from pilferage, or exploitation, by other animals (Dally et al. 2006; Smith and Reichman 1984). Shrews are known to partake in both scatter and larder hoarding, caching insects and seeds along their foraging trails as well as within their burrows (Nowack 1999).

In areas with a supplemental food source, mammals such as rodents tend to make high-density caches that cluster around that central source (Vanderwall & Jenkins 2003; White et al. 2012). This is described as the rapid-sequestering hypothesis: animals cache near food sources to maintain a presence at these locations, as opposed to caching food further away and potentially losing the resource to competitors (White et al. 2012). Individuals may use both hoarding techniques depending on pilferage rates. Season is also a factor, with larder hoards being common in winter when the animal is making fewer forays beyond home territory and is therefore centered around its nest or burrow (Brodin 2010, White et al. 2012). Photoperiod (changing amount of daylight with seasons) may influence caching and foraging behavior. In their studies of willow tits (*Poecile montanus*), eastern gray squirrels (*Sciurus carolinensis*), and fox squirrels (*Sciurus niger*), Penner et al. (2013) found that the presence of supplemental food (such as bird feeding stations) increased the likelihood that these animals' caches would be pilfered by approximately 7%. Additionally, provisioned sites often have higher visitation and foraging activity in general by both birds and mammals (Penner et al. 2013). This may lead to sites with supplemental food having higher caching *and* pilferage rates by more individuals.

The caching behaviors of shrews affects the ability of these animals to survive, particularly if those caches are pilfered. Caching helps ensure a stable source of nutrition when food supplies are variable or scarce (Dally et al. 2006; Formanowicz et al. 1989; Smith and Reichman 1984). Caching is therefore imperative for shrews considering their very high BMRs and small internal fat reserves (Ochocińska and Taylor 2005). A cache that contains 20% of an animal's daily energy requirement may increase the probability of that animal's survival by 20-60% (Ydenberg et al. 2007). Shrews are constantly foraging for food; for instance, Saarikko (1989) found that individuals weighing <5g would eat up to 200% of their body weight in 24 h. This implies that if a shrew's cache were pilfered, and particularly if the shrew had employed a larder hoarding technique, that shrew might not survive the night. The caching behavior of shrews has not been investigated as often as that of other small mammals and an analysis of the factors that influence caching and pilferage behavior, including supplemental food and non-provisioned controls, is greatly needed (Brodin 2010; Penner et al. 2013).

The need for improved monitoring techniques

Currently, little is known about foraging behavior and life history of shrews – and the information that is published is often gathered by invasive, and deadly, means. Live trapping has been the primary method to study small mammals for decades, Sherman and Longworth traps being some of the most common. Many of the trap designs were pioneered in the middle of the 20th century and have had very little modification (Flowerdew et al. 2003; Figure 2). Mortality of small mammals, particularly shrews, is pervasive in small mammal studies, despite ethical use and timely monitoring of traps. Mortality rates can range from 40-90% depending on stress, weather, time spent in the trap, and how much food or water the shrew had prior to, and during, trapping (Do et al. 2013). The high metabolic requirements of shrews appear to factor largely in this problem. The masked shrew (*Sorex cinereus*) has been observed foraging up to 19 times in a 24 h period, giving support to the idea that many shrews starve in live traps before researchers can check them. Many shrew species feed every 2-3 hours and if they are unable to do this, they can quickly starve (Churchfield 1990; Do et al. 2013). However, even when traps were checked every hour, a study in Ireland using traditional live trapping methods lead to a 50% mortality rate of the endangered Eurasian pygmy shrew (*Sorex minutus*) (Gobetz, pers. communication).

Figure 2: A harvest mouse (*Micromys minutus*) inside a Longworth live trap.

Credit: BioOne

High mortality rates aside, these current methods of small mammal research leave much to be desired. Checking traps so frequently, including during the night, can be dangerous and time consuming, and disrupts the natural behavior and physiology of these animals (Do et al. 2013). Traditional live traps are often left over night, for 12 h or more, which only increases the likelihood of mortality among shrews and other species. Alternative strategies to monitor small mammals, and the greatly understudied shrew species of the world, are therefore vital.

The Animal Monitoring Station (AMS) is a newly patented device through James Madison University (U.S. patent no. 10,905,112) that readily solves many of the problems with traditional trapping methods (Figure 3 a,b). This device allows free, uninterrupted movement of the animal, with two small openings on either side letting a shrew, or other small mammal, come and go as it pleases. Coat condition, sex, and even individual identity can be garnered from the data this device provides, without the need for human interference or dangerous trapping mechanisms. I will discuss how I successfully used this device to gather data on *C. parva* and *B. brevicauda* throughout the year in an effort to better understand their foraging strategies. I hypothesize that shrew weight change over time will be directly influenced by levels of observed cache exploitation. I predict that shrew weight may either increase over time as shrews store more energy internally or decrease as their valuable food resources are pilfered.

Figure 3: a) The inside of the AMS marked by shrews (top) and **b)** the AMS covered and placed under leaf litter with tracking powder on the entrance ramp (bottom). Credit: Justin Roth, JMU, Associate Director of Digital Marketing and Event Production.

Methods

Study locations

Seven locations were monitored in the Edith Carrier Arboretum in Harrisonburg, VA, including three treatment sites and four control sites from approximately November 2020 to December 2021. Treatment sites included provisional food for birds in a feeding platform placed about 6cm above ground level while the control sites did not. Provisional food platforms were raised off of the ground slightly to ensure that shrews were not able to access this food source. I consistently used 2/3 c. of sunflower hearts (Kaytee®, Brown's®, and Royal Wing®) as well as 1/3 c. of dried mealworms (Brown's® and Nature's Song®). Enclosures composed of 1 in. x 3ft. x 50 ft. chicken wire and 3ft. tall metal stakes (Everbilt®) surrounded each study site. One game camera (Moultrie M-Series or Moultrie A-900 I series) was positioned at the edge of the enclosure at each location. Cameras were positioned approximately three feet from ground level and were used to continually monitor animal activity at each site.

Before determining study locations, bait was placed beneath leaves or grass near likely shrew habitat, such as in long grass or heavy leaf litter near logs or rocks, to determine if shrews were present. Shrew presence was determined by several factors: absence of bait upon checking back within 24 hrs., presence of foraging trails by sight and/or touch, the obvious scent of shrew musk, and if they were physically seen on site. Once it appeared likely that a shrew was in the area, the AMS was used with a bait source that only shrews could access, both at treatment and control locations. Due to low numbers of AMS devices, and in order to ensure that shrews stayed on site, bait was left under leaf litter in the same location that the AMS is usually placed to condition the animals to return when the AMS wasn't present at a particular site. This study required no capture or handling of shrews, and therefore it was unnecessary to acquire permits or submit IACUC protocols.

Quantifying shrew mass and mapping shrew foraging trails

Shrew presence was established using the AMS. The device has a bait container inside it that attracts the animal. Once an individual enters the device, a weighted scale plate triggers a Raspberry Pi microcomputer attached to the back of the device. This system records weight values of the animal approximately every eight seconds, and once the scale plate is activated, an LED-IR camera/temp-humidity sensor is also triggered. This camera can be set to take .JPG images or 10s mp4 files of the organism as it feeds; the latter format was used for the duration of this study. The scale plate has a 10cm x 10cm grid, allowing for rough body measurements. A set food amount in the AMS was used to continually attract shrews, as described above.

Tracking powder was employed in conjunction with this device to better understand shrews' movements during foraging. Powder-tracking is already known as an efficient, successful means of locating small mammal trails (Lemen and Freeman 1985; Longland and Clements 1995; Nicolas and Colyn 2007). Shrews can be marked with non-toxic, USDA approved, fluorescent powder that is placed at the entrances to the unit. When an individual walks through the powder, the grains adhere to the animal's fur and paws, allowing their path out of the device to be visualized using a UV light (Figure 3 a,b). This is yet another way to ensure that the shrews do not need to be restrained in order to get valuable data on their movements and behavior. In addition to the use of tracking powder, foraging trails were found by sight and by feel, as they are noticeable furrows in the soil underneath leaf cover. Each trail was marked with blue flags (Figure 1). Caches that were found were marked with pink flags while yellow flags were used to mark nests and burrows. Caches were found by removing the leaf litter along the known foraging trails and visually scouring the trail to see if anything was cached. Invertebrates were known to be cached if they were (i) clearly still alive and (ii) appeared to be paralyzed by shrew neurotoxin. This was established by directly handling the invertebrate. If it could still move but was clearly incapacitated, and especially if it had recently been bitten, it was considered to be cached. Developed from the method of Nicolas and Colyn (2007), shrew foraging systems were quantified by measuring the length of each foraging trail segment and measuring the distance of each cache location to the AMS. Segment lengths were summed and averaged to gain further insight into what these species' foraging systems are composed of (Table 4; Table 5).

Analyses

All statistical analyses were done using RStudio v. 1.4.1103 and all data was compiled and viewed in Microsoft Excel 2019 and Canvas. Shrew videos were first analyzed frame by frame to obtain weight values and to determine species and individual. Weight values for each individual were averaged and recorded by species (Table 1) and by season (Table 2; Table 3) before being compiled further. Data was first analyzed to ensure normality and equal variance. Independent t-tests and Pearson's chi-squared tests were used to analyze species, treatment type, season, and photoperiod. For the analysis of shrew weight change by season, a Bonferroni correction was applied to control the familywise error rate. The seasons were defined as follows: Winter (December 21st – March 20th), Spring (March 21st – June 20th), Summer (June 21st – September 20th) and

Fall (September 21st – December 20th). Photoperiod, or minutes of daylight, were used for two scatterplots as another way to visualize shrew weight change over time (Figure 12; Figure 13).

Results

Caches and foraging trails

In total, six caches were found: three at treatment sites and three at control sites (Table 4). These caches consisted of invertebrates (whole organisms and pieces thereof) while no sunflower hearts or dried mealworms were found to be cached. All observed caches were scatter hoards and contained only one (or a piece of one) invertebrate along the shrew's foraging trail. All caches were found relatively close to where the shrews' food source was placed, either in the AMS itself, or under the leaves on the ground when the unit was not present. On average, caches were placed approximately 57.75cm away from the AMS (Table 4).

Foraging trail networks were quantified by measuring each segment of the trail. Segments are defined as straight pieces of the trail before a bend or curve occurred. On average, there were 11.5 segments in each foraging trail network, the smallest trail system including five segments and the largest having 17. On average, foraging trail networks were approximately 237cm long (Table 5).

Shrew weight by treatment type

Shrew weight values for each individual were averaged across the entire study period and average weights of shrews at treatment locations were compared against those taken at control sites. This was done to establish if any significant differences in weight existed between treatment type. Time of year that data were collected was not factored into these analyses. First, an independent t-test was conducted and both species' weight values were included (p = 0.24; Figure 7). Each species was then analyzed independently to determine if either species reacted significantly between treatment types. *C. parva* was examined first, followed by *B. brevicauda,* neither of which were determined to be significant. (p = 0.63; Figure 8 and p = 0.09; Figure 9, respectively). A chi-square test for given probabilities was also conducted using average weight values for both species across all seasons, at both treatment and control sites (p = 0.25; Figure 10).

Shrew weight by season

Weight values were analyzed across the duration of the study to determine if seasonality significantly impacted shrew weight values. The null hypothesis was not able to be rejected, as there was found to be no significant relationship between weight and season (p = 0.75; Figure 11). Each species was also compared across time individually by subsetting my chi-square data. For *C. parva*, it was determined that no significant relationship existed between weight and season (p = 0.67; Figure 11). Additionally, no significant relationship existed between *B. brevicauda* weight and season (p = 0.851; Figure 11). Next, both species were compared to one another to determine if significant differences in weight existed between each species during each season by subsetting the data and running chi-squared tests for given probabilities. First, species were compared during the winter months (p = 0.22; Figure 11). Next, species were compared during the summer (p = 0.46; Figure 11) and during the fall (p = 0.09; Figure 11). Both species' average weight values were also compared against photoperiod or changing minutes of daylight per day throughout the year (Figure 12; Figure 13). While neither relationship was significant, these figures allow a different visualization of how both species' weights changed over time.

Figure 4: Stills captured from videos of **a)** *B. brevicauda* in the AMDS at a treatment site and **b)** *C. parva* in the AMDS at a control site.

Discussion

Caches were composed entirely of paralyzed invertebrate prey. No seeds nor dried mealworms from the AMS were cached, although larder hoards within the shrew's burrow(s) may have contained these items (Dally et al. 2006; Nowack 1999; Smith and Reichman 1984) It has been previously confirmed that wild individuals of *B. brevicauda* will cache invertebrates while only those in captivity have been observed caching seeds (Nowack 1999).

Prior to this study, the foraging and caching behaviors of *C. parva* had never been described. Any site that a shrew was recorded contained instances of both shrews throughout the duration of the study period, meaning that any foraging trails or caches seen could not be definitively attributed to either species, except when visually observed, which occurred twice. *C. parva* was visually observed running from bait, along its foraging trails, to grassy tussocks nearby, before returning to the bait. To my knowledge, this is the first time a direct observation of foraging and caching behavior by this species has been described. Based on results of this study, *C. parva* caches food similarly to what has been described in other shrews (Churchfield 1990; Nowack 1999). It is likely that both species used the same foraging trails with different burrows belonging to each individual, however future studies would benefit from closer examination of interactions between these two species. Many shrews are solitary but may occupy niche microhabitats near one another. *B. brevicauda* is known to eat larger species of invertebrates while smaller shrews, such as the masked shrew (*Sorex cinereus*) or *C. parva* pursues smaller invertebrate prey, allowing larger and smaller shrews to live concurrently by occupying slightly different niches (Getz 1961).

No significant relationship was determined between shrew weight and treatment type. In this study, three caches each were observed at both treatment and control locations. Despite caches not differing between treatment type, foraging activity by birds increased dramatically at provisioned sites and visits to foraging trails and caches are evident, as will be discussed in the next chapter. If caches truly were pilfered, it was hypothesized that shrews significantly lose weight in response to their food resources being taken. Conversely, their weight may increase as they shift their foraging strategies to incorporate more internal energy storage. If shrew caches were directly pilfered, which the data supports that they were, it appears that this activity did not have a demonstrable effect on shrew weight.

The non-significant relationship between shrew weight and treatment type may be partially explained by the low-density caches that were found. All scatter hoards found over the duration of this study were composed of just one invertebrate, or parts of invertebrates, while no sunflower hearts were found to have been cached. This may be because food items that are smaller and decompose quicker are more likely to be eaten while larger, longer lasting organisms (such as paralyzed invertebrates) are more likely to be cached, at least in the wild (Formanowicz et al. 1989; Nowack 1999; Saariko 1989). It may also be that both *C. parva* and *B. brevicauda* utilize larder hoarding techniques inside their burrows and nests, the interior of which were not explored in this study. If these species were experiencing cache pilfering, it follows logically that they would shift to storing food within their nests, as they would be better able to protect their resources from pilfering (Dally et al. 2006; Smith and Reichman 1984). In several instances, shrews appeared to move their nest, or create a nest, very close to where the AMS was placed, helping to support the likelihood of the larder hoarding technique. Optimal foraging theory states that animals are likely to cache food around a central food resource in order to remain present at the resource location and not lose control of that resource to competitors, further supporting why this behavior was observed (Dally et al. 2006). Additionally, this study identified 9 individual shrews throughout the duration of the study so larger sample sizes of both species will aid in elucidating the relationship that may exist between cache pilferage and shrew weight over time.

Changing season was not shown to be significant for any metric that was analyzed. This is likely because there were very few weight values over time that were available to be compared. There was a significant drought in the region throughout much of July and August 2021, leading to shrews largely disappearing from my study locations. Prior to this, six study sites were used. A seventh site (the fourth control site) was added in late August, as it was closer to water. Here, shrews were present throughout the rest of the study. In the future, distance to water resources should be explored as a factor in shrew presence, weight, and survival.

Photoperiod was analyzed for one metric of this study which was how each species' weight changes as minutes of daylight changes. Neither relationship was significant, however it is interesting to note that *B. brevicauda* weighed the most around spring and fall while *C. parva* weighed the most during the summer, on average. Further exploration into shrew weight data using photoperiod as a metric would be beneficial in future studies.

Interestingly, weight values of *C. parva* often exceeded the weights explained previously in the literature, with their weight range recorded as 4-7g prior to this study (Churchfield 1990; Formanowicz et al.1989; Nowack 1999). On average, *C. parva* weighted 8.73g across all seasons and treatment types in this study (Table 3). I hypothesize that this may be because of live trapping techniques. If a shrew is starving, or if a dead shrew is weighed (as often happens), it is likely that the average weight values currently described are not fully accurate. Conversely, weight values for *B. brevicauda* were often on the lower end of their known weight values discussed by Nowack (1999). On average, *B. brevicauda* weighed 14.62g in this study (Table 3), while previous literature indicates they weigh between 15-30g. Previous lab tests indicate that the weight values given by the AMS, when properly calibrated and tared, are not significantly different from other calibrated lab scales, supporting that these weight values obtained were accurate (Gobetz, pers. communication). Based on this wide weight range, and results gathered in this study, further research into shrew weight, and what may impact those values, is needed.

This novel study will provide a base map for future inter-Class foraging interaction studies. More data taken across the entire year will help to clarify what was seen here. Goals of future studies should (i) further explore how supplemental feeding impacts shrew weight through cache pilfering, (ii) gather more data on more individuals across all seasons of the year, and (iii) utilize a burrow camera or similar device to examine the interior of these nests and burrows to get a broader understanding of these shrew species' caching techniques.

Chapter II

The effect of supplemental feeding on bird exploitation of shrews' sub-litterfall food caches

Introduction

Supplementary food – how are small mammals impacted?

Provisioning wildlife, particularly songbirds, is a global, multi-million dollar industry, with approximately 43% of U.S. households regularly feeding birds (Dayer et al. 2019; Plummer et al. 2019; Robb et al. 2008a,b). This large influx of resources to the avian community has far reaching implications and there is evidence to support the idea that this anthropogenic food source may influence natural selection (Robb et al. 2008a,b). Food availability may be the primary factor in population size and distribution of animal populations. Many studies address the myriad contradictory effects of anthropogenic food on songbird survival, fecundity, and overall health (Brown and Sherry 2006; Dayer et al. 2019; Fischer and Miller 2015; Murray et al. 2016; Nagy et al. 2007; Plummer et al. 2019; Robb et al. 2008a,b; Studds and Marra 2011; Tryjanowski et al. 2018). The wide range of literature available on this topic is in stark contrast to shrew foraging ecology publications; highlighting the need for further study on shrews in general, as well as how supplemental food designed for birds has cascading effects throughout the birds' community.

Competition over food resources between members of a community is a biological certainty. Food availability is the main facilitator of inter- and intra-specific interactions, particularly during the non-breeding season (Plummer et al. 2019; Robb et al. 2008a,b). Shrews and other small mammals often use the same resources that songbirds seek at ground level, particularly birds who are ground forager specialists.

Therefore, it is likely that birds and shrews compete when foraging and quantifying how this occurs is necessary to form a more holistic model of feeding behaviors. Reliable, artificial food sources naturally attract animals, such as birds and small mammals. How these animals interact, directly or indirectly, while foraging is largely unknown. Experimentally adding a food source for songbirds near known shrew habitat will aid in addressing landscape-level impacts of supplemental feeding.

Caching and Pilfering

Many songbirds cache food, including Virginia residents such as Carolina chickadees (*Poecile carolinensis*), tufted titmice (*Baeolophus bicolor*), and white-breasted nuthatches (*Sitta carolinensis*) (Lucas and Zlelinski 1998; Smith and Reichman 1984; pers. obsv.). In addition to resident species, many others migrant to, and through, the Shenandoah Valley from spring-fall, and this change in species composition may be reflected at feeding stations. The most likely species to pilfer another's cache are often cachers themselves (Dally et al. 2006) and many ground feeding birds pry up leaf litter to methodically search for prey, including sparrows, thrushes, and wrens (Holmes and Robinson 1988).

As cachers are often also pilferers, this results in a positive feedback loop of these behaviors occurring between members of the same taxa and exploring if this occurs between members of differing taxa is crucial. Among mammals, flying squirrels, chipmunks, and other sciurids readily exploit bird caches (Smith and Reichman 1984). However, evidence for the reciprocal case is rare, with one mention of an American crow (*Corvus brachyrhynchos*) pilfering an Eastern gray squirrel (*Sciurus carolinensis*) cache described in the literature (Steele et al. 2014). Thus, caching and pilferage at the intersection of avian and mammal ecology is mostly unknown (Dittel et al. 2017). Yet these relationships are important considering the high energy investment of foraging and caching, combined with ever-changing food availability that can make pilfering disastrous to the cacher. Understanding the impacts of these behaviors on small mammals is imperative, shrews particularly, as they are an understudied mammal with a high metabolic rate. Animals cache around a central food resource, as per optimal foraging theory (Dally et al. 2006), so shrew caches may center around where the AMS is located at each site. Birds and mammals are known to increase foraging activity at provisioned sites, including searching around that provided source for further resources (Penner et al. 2013). The provisional food platform provided to birds may lead to increased bird foraging activity, and increased cache exploitation, at sites with supplemental food platforms. Determining the effects of inter-Class interactions on species' ability to secure food resources will fill gaps in our knowledge of this critical survival technique.

Caching may be an evolutionarily stable strategy (ESS) if a cacher has increased fitness compared to non-cachers in the population, after taking pilferage of the cache(s) into account (Brodin 2010). Pilferage levels may be as high as 30% in areas where a supplemental food source is present, whereas the levels may be much lower (around 10%) in non-provisioned areas (Penner et al. 2013). However, other studies have reported percentages of cache pilferage varying greatly from 2-60% per day (Dally et al. 2006; Vanderwall and Jenkins 2003), indicating that further study into this topic is necessary to clarify pilferage rates. The presence of supplemental food can impact the behavior of birds, including their motivation for and success in cache pilferage of conspecifics

(Penner et al. 2013). Discovering if this pattern holds true for cache pilferage of heterospecifics as well, such as shrews, is the next frontier for foraging ecology.

I hypothesize that (i) songbirds, specifically ground foragers and cachers, will pilfer small mammal caches; (ii) changing season will coincide with variance in predictable bird species assemblages seen at each study location; and (iii) cache exploitation by passerines will directly influence shrew weight. I predict that (i) cachers and ground feeders will be most prevalent at locations with a supplemental bird feeding platform and that birds with these foraging strategies will be the ones primarily seen at caches; (ii) during spring and fall, more birds, both by species and by raw number, pilfer small mammal caches; and (iii) shrew weight will shift with cache exploitation, either by weight decreasing as the shrews' resources are stolen, or by increasing as shrews switch to storing their food differently to avoid pilferage.

Methods

Measuring cache pilferage behavior and monitoring bird species presence

Six sites were used to conduct this study in the Edith Carrier Arboretum in Harrisonburg, VA, three of which were treatment locations and three of which were control. They were monitored from approximately February 2021 to December 2021. Game cameras (Moultrie M-Series and Moultrie A-900 i Series) attached to the edge of enclosures were used to capture bird activity, including the number and type of species observed within the enclosure, as well as if they are at or near foraging trails and caches. Each enclosure had one camera attached to the top of a 3 ft. tall metal stake that is positioned to survey as much of the area as possible (Figure 5). All enclosures are made of 1ft. x 3 ft. x 50ft. chicken wire wrapped around metal stakes (Everbilt®). At treatment sites, feeding platforms with a set food amount to attract birds was filled with 2/3 cup of sunflower hearts (Kaytee®, Brown's®, and Royal Wing®) and 1/3 cup of dried mealworms (Brown's® and Nature's Song®) while being placed ~6cm above the ground to deter shrew visitation. At control sites, no supplemental feeding platform was added.

Figure 5: View from a game camera pointing in the direction of a study site. Field of view contains AMS, supplemental feeding platform, and flags indicating shrew foraging trails, caches, and burrows/nests.

Rate of visitation was determined by the length of time that passed between seeing a species in frame. If only one minute or less had passed before seeing a given species again, that was determined to be one visit. If longer than one minute passed between seeing that species in frame, it was counted as multiple visits. Foraging trail visits were counted as a bird standing directly in the trail, or within approximately 10cm of the trail. This was done in order to account for the bird not being captured exactly in the trail at the time the game camera was activated, due to a delay of a few seconds between bird landing and camera detection. Similarly, if a bird was seen standing or foraging directly at a known cache or seen standing or foraging within approximately 10cm of a known cache, this was counted as pilfering behavior by that individual (Figure 6).

Analyses

All statistical analyses were performed using RStudio v. 1.4.1103 and all data was compiled and viewed using Microsoft Excel 2019 and Microsoft Powerpoint 2019. Bird images were viewed and date, time, study site, species, and location of individual in frame were recorded. All data was combined with emphasis on what species were seen at what time of year, and how many of those individuals were seen at or near foraging trails and at or near known cache locations. Analyses were done on foraging type, treatment type, and season. The seasons were defined as follows: Winter (December 21st – March 20th), Spring (March 21st – June 20th), Summer (June 21st – September 20th) and Fall (September 21st – December 20th). Analyses were conducted using Welch's t-tests, Pearson's chi-squared tests and logistic regressions. Welch's t-tests were used due to unequal sample sizes. For some chi-squared tests, p-values were simulated due to there being less than five samples in a group. For chi-squared tests that were comparing more than two groups, a Bonferroni correction was applied to control the familywise error rate.

Results

Overall bird occurrence

There were 4,269 recorded visits by birds to six study locations and 4,162 of those visits were to treatment sites that included the supplemental bird feeding platform, while 107 were recorded at control sites. In total, 23 species were recorded: 14 ground feeders, five cachers, and five that use a different foraging strategy (Table 6). The blue jay

(*Cyanocitta cristata*) is both a ground feeder and a cacher, so this species was included in both groups for analyses. Using a Welch's t-test, occurrence rates were found to be significant between treatment and control sites by total visitation, visits to foraging trails, and visits to shrew caches (Figure 14; Figure 15). Birds were observed within or close to (within ~10cm) of a foraging trail a total of 347 times, 324 of those occurring at treatment sites and 23 occurring at control sites. The differences observed in foraging trail visitation were found to be significant by treatment type. Birds visited or appeared close to (within ~ 10cm) of a cache 22 times, 18 of which were observed at treatment sites and 4 of which occurred at control sites (Figure 15).

Figure 6: Carolina chickadee (*Poecile canadensis*), circled, foraging at a known shrew cache at a treatment site. Supplemental feeding platform at left of frame.

Foraging Type

Species were analyzed by their foraging type by designating species as cachers, ground feeders, or other and observing any significant differences observed therein. This information was obtained by following the foraging strategies described for each species on the All About Birds webpage which is run by the Cornell Lab of Ornithology. All birds observed cleanly fit into a category except for the blue jay, as there is evidence that they are both a cacher and ground feeder. Whenever foraging type was analyzed by splitting these two groups apart, the number of blue jays recorded was added into both categories to account for this.

A Pearson's chi-squared test was used to analyze the relationships between foraging type and treatment type. The number of ground feeders and cacher visits were significantly more frequent at both treatment and control sites than those species with other foraging types (p = <0.01, Figure 16). In addition, the frequency at which cachers and ground foragers were seen within or near both foraging trails and caches were both significantly more frequent, at both treatment and control sites, than birds that had neither foraging strategy (p = <0.01; Figure 17; p = <0.01; Figure 18). A Pearson's chi-squared test was also used to analyze any significant differences that existed within the frequency of visits of cachers and ground feeders, those birds with other foraging strategies excluded. Significantly more cachers visited treatment locations, while significantly more ground feeders visited control locations (p = <0.01; Figure 19). Interestingly, ground feeders were seen at or near foraging trails significantly more often than cachers, while cachers and ground feeders occurred equally at caches (p = <0.01; Figure 20).

Effects of season

Foraging type and treatment type were compared against season to analyze how the changing daylight duration impacts bird visitation rates. Pearson's chi-squared tests were used for all of these comparisons and p-values were simulated when sample sizes were less than five. Predictably, birds visited treatment locations significantly more often than control sites in all seasons of the year, both when combining seasons and when analyzing each season separately. A Bonferroni correction was applied, making a significant p-value for this data 0.007 ($p = <0.007$; Figure 21).

Significant differences existed between foraging type and season where cachers and ground feeders visited treatment sites significantly more often than control sites when analyzing each season separately using a Bonferroni correction p-value of 0.007($p = <0.007$; Figure 22). Interestingly, when looking at foraging type across all seasons combined, the results were not significant. Yet, when the prevalence of cachers and ground feeders compared against all seasons combined was analyzed, and when other foraging types were compared against all seasons combined, there were significant differences ($p = <0.007$; Figure 22).

The effects of season on foraging type and prevalence of bird visitation to shrew foraging trails and caches was also analyzed. Here, when comparing foraging trail and cache visitation rates across all seasons combined, results were not found to be significant. However, when analyzing the differences between foraging type and each season separately, all results were found to be significant even when a Bonferroni correction was applied to the p-value ($p = <0.007$; Figure 22). Cachers and ground feeders were significantly more prevalent in, and near, foraging trails and caches than birds with other foraging strategies. Here, a Bonferroni correction of 0.007 was applied to the p-value for foraging trail analysis while the p-value for caches did not need to be corrected ($p = <0.007$; Figure 23; $p = 0.02$ and $p = <0.01$; Figure 24). Foraging trail data was obtainable across all four seasons, however visitation rates at caches could only be compared during the summer and fall as those are the only seasons when caches were located.

Birds with foraging strategies other than caching or ground feeding were removed from analyses and differences amongst these two groups alone were compared. Interestingly, ground feeders were significantly more prevalent at all sites in the spring, while cachers were significantly more present in both the summer and fall when a Bonferroni correction of 0.007 was applied ($p = <0.007$; Figure 25). When comparing occurrence of cachers and ground feeders in both trails and caches, ground feeders were significantly more prevalent. A Bonferroni correction of 0.007 was applied to the p-value for occurrence in foraging trails. This led to significant differences in the spring, summer, and fall but differences in winter ($p =0.11$) and overall ($p =0.01$) were not ($p = <0.007$; Figure 26). This is due to the high number of ground feeders seen within or near foraging trails. The p-value for occurrence at caches was not corrected ($p = <0.01$; Figure 27). The same number of ground feeders and cachers were seen at or near caches.

Bird visitation rates and shrew weight

Two logistic regressions were performed to determine if the frequency of pilfering activity by birds significantly affected the mass of shrews over time. One was used to compare *C. parva* weight values to pilfering rates, while the other was used to analyze the same type of relationship of pilfering rates to *B. brevicauda* weight change over time. Based on the data that I had, pilfering frequency was not found to significantly predict shrew weight change over time in either species ($p = 0.9$, for both species). Due to the lack of relationship found, figures of this data were not included.

Discussion

As predicted, more birds visited treatment sites in general, and more birds visited both foraging trails and caches at treatment sites than at control sites. Birds are attracted to the supplemental feeding platform at these locations, and it has been established in previous studies that provisioned sites experience significantly more pilfering than non-provisioned sites (Penner et al. 2013). In addition, provisioned sites are more likely to experience increased foraging activity in and around the central food source, as well as increased pilfering activity, by both mammals and birds alike. Knowing this and knowing that caches are often made close to a central food source per the rapid-sequestering hypothesis, allows a better understanding of the rates of cache exploitation experienced at treatment locations in this study (Penner et al. 2013; White et al. 2012).

Ground feeders were one of the most common foraging strategies seen which is as predicted; feeding platforms placed on the ground, and caches hidden under leaf litter that these birds already forage in, is certain to attract birds with this foraging strategy. Cachers were also very prevalent, and in fact were the most common overall at treatment sites, especially during the summer and fall months. Animals begin storing food at times when food is readily available and before the animal begins needing those stores (Smith & Reichman 1984). Therefore, hoarding food in the summer and fall months in order to prepare for winter is as expected, and what was reflected in this study. Why ground feeders were seen significantly more often at control sites than cachers, and why cachers were seen significantly more often at treatment sites than ground feeders, is not fully understood. This could be explained by cachers naturally gravitating towards supplemental food sites while ground feeders are more likely to feed in the leaf litter at any location, regardless of whether or not supplemental food is present.

Ground feeders were far more prevalent in and near foraging trails than caching birds. However, both cachers and ground feeders were found in and near caches the same number of times. Ground feeders are always searching under the leaf litter for their food, so seeing them along or near a foraging trail more often than birds without that foraging strategy is predictable. However, cachers being just as prevalent as ground feeders at cache locations may indicate that these birds have an ability to detect specifically where a cache is, and only choose to forage on the ground when this is known. Exactly how this may occur needs to be explored further, as historically, studies have indicated that songbirds have poor olfactory capabilities, thus lowering the probability of this mechanism as a means of cache detection (Corfield et al. 2015). Although, recent studies have begun challenging this claim, so further research into songbird olfaction will aid in exploring this avenue (Molina-Morales et al. 2020).

Birds that have neither caching nor ground feeding as their foraging strategy were the least prevalent across all treatment types and seasons. They were also the least prevalent near shrew foraging trails and caches. Birds that are foliage gleaners, such as many warbler species, would not be expected to be searching for food resources at ground level as they often flit through the trees many feet above the ground in search of non-flying invertebrate prey (Hutto 1981). Throughout the duration of this study, I had only one species of warbler, the worm-eating warbler (*Helmitheros vermivorum*), visit two of my treatment sites, likely for the reason stated above (Table 6). Perhaps this species was utilizing the dried mealworms provided in the supplemental platforms. A red-shouldered hawk (*Buteo lineatus*) was also recorded at a treatment location (Table 6). The foraging strategy of this hawk is aerial diving for prey. It is likely that this bird was attracted to the location because of the prevalence of small birds and mammals that were clustering around that food source.

Finally, bird visitation rates were compared against shrew weight change over time to determine whether or not pilfering by songbirds had a significant effect on shrew weight. I analyzed this by shrew species to ascertain that differing weights between those species did not impact the results. Additionally, I further looked at how each individual's weight changed over time, based on season. Neither species was significantly impacted by observed pilfering behaviors. This may be for several reasons. First, the shrews that were weighed were often not weighed enough times, for a long enough period, to see definitive trends and differences in these individual's weights. Additionally, caches were only found during the summer and fall months, limiting how many of the weight values of the shrews could be directly compared to those caches being pilfered.

This study began setting the stage for the exploration of inter-Class foraging relationships and further elucidated the relationship between caching and pilfering behavior. Future research should focus on (i) collecting more data taken at all seasons of the year; (ii) exploring how and why caching bird species are found as often at shrew caches as ground feeding species despite ground feeders being far more prevalent in shrew foraging trials; and (iii) exploring how this cache exploitation behavior truly impacts shrew foraging and survival. Further studies well aid in fully explaining the relationships between different classes of animals while foraging that have just begun to be explored here.

Table 1: Individual shrew weight per night observed

Location (Treatment or Control)	Species	Individual	Weight (g)
Greenhouse (T)	*C. parva*	1	5.32
Greenhouse (T)	*B. brevicauda*	2	13.4
Greenhouse (T)	*C. parva*	3	13.35
Red-Green Tree (T)	*C. parva*	4	1.76
Red-Green Tree (T)	*C. parva*	4	11.97
Red-Green Tree (T)	*B. brevicauda*	5	12.44
Red-Green Tree (T)	*B. brevicauda*	5	11.81
Red-Green Tree (T)	*B. brevicauda*	5	15.2
Red-Green Tree (T)	*B. brevicauda*	5	11.48
Bear Statue (T)	*B. brevicauda*	6	11.01
Log City (C)	*B. brevicauda*	7	14.91
Log City (C)	*B. brevicauda*	7	16.42
Log City (C)	*C. parva*	8	10.63
Log City (C)	*C. parva*	8	8.88
Log City (C)	*C. parva*	8	9.09
Log City (C)	*C. parva*	8	10.21
Log City (C)	*C. parva*	8	11.17
Log City (C)	*C. parva*	8	9.18
Log City (C)	*C. parva*	8	8.68
Log City (C)	*B. brevicauda*	9	15.8
Log City (C)	*B. brevicauda*	9	22.31
Marsh Spot (C)	*B. brevicauda*	7	13.43
Marsh Spot (C)	*B. brevicauda*	7	10.57
Marsh Spot (C)	*B. brevicauda*	7	11.5
Marsh Spot (C)	*B. brevicauda*	7	13.3

Marsh Spot (C)	*B. brevicauda*	7	12.06
Marsh Spot (C)	*B. brevicauda*	7	14.76
Marsh Spot (C)	*B. brevicauda*	7	15.55
Marsh Spot (C)	*B. brevicauda*	7	15.15
Marsh Spot (C)	*C. parva*	10	10.76

Table 2: Average shrew weight by treatment type per season

Treatment	Species	Weight (g)	Season
	B. brevicauda	12.2	Winter
	B. brevicauda	11.87	Summer
	C. parva	7.56	Winter
	C. parva	11.97	Summer
	C. parva	5.32	Fall
Treatment average across study period	*B. brevicauda*	12.03	
	C. parva	8.58	
Control	*B. brevicauda*	14.91	Winter
	B. brevicauda	16.42	Summer
	B. brevicauda	16.18	Fall
	C. parva	9.76	Summer
	C. parva	10.22	Fall
Control average across study period	*B. brevicauda*	15.84	
	C. parva	9.99	

Table 3: Average shrew weight by season and species

Season	Species	Weight	Species	Weight
Winter	*B. brevicauda*	13.11	*C. parva*	7.56
Summer	*B. brevicauda*	14.58	*C. parva*	10.87
Fall	*B. brevicauda*	16.18	*C. parva*	7.77
Average across all seasons	*B. brevicauda*	14.62	*C. parva*	8.73

Table 4: Cache locations with distance from cache to AMS.

Location	Cache Number	Distance of Cache to AMS(cm)
Rock Table (control)	1	38.1
Rock Table (control)	2	151.9
Log City (control)	3	33
Bear Statue (treatment)	4	33
Red-Green Tree (treatment)	5	27.5
Red-Green Tree (treatment)	6	63
Avg. distance		57.75

Table 5: Shrew foraging trail segment lengths.

Location	Segment Length (cm)	Avg. Segment Length by Location (cm)	Location Segment Total (cm)
Rock Table (Control)	12.7	23.10	300.36
	76.2		
	15.24		
	34.29		
	12.7		
	30.48		
	16.51		
	10.8		
	33.02		
	17.78		
	13.97		
	13.97		
	12.7		
Log City (Control)	23.5	11.38	91
	13		
	8		
	10		
	10.5		
	6.5		
	12		
	7.5		
Red-Green Tree (Treatment)	25.5	27.95	139.75
	23.5		
	28		
	32.75		
	30		
Bear Statue (Treatment)	12.5	19.19	307
	14		
	9.5		
	12		

	23		
	18		
	15		
	15		
	42		
	28		
	20		
	17		
	13.5		
	9.5		
	11		
	47		
Greenhouse (Treatment)	13.5	23.13	347
	24.5		
	13		
	7.5		
	25		
	7		
	13.5		
	45.5		
	26.5		
	54		
	16		
	15.5		
	30		
	16.5		
	39		
Total Average Segment Length (cm)	86.26		
Total Sum of all Segment Lengths (cm)	1185.11		

Table 6: Visitation numbers of all bird species seen, listed by foraging strategy.

Species	Foraging Strategy	Resident (R) or Migrant (M)	Number of Total Visits
Turdus migratorius	Ground Feeder	R	49
Dumetella carolinensis	Ground Feeder	M	55
Thryothorus ludovicianus	Ground Feeder	R	239
Hylocichla mustelina	Ground Feeder	M	3
Cardinalis cardinalis	Ground Feeder	R	726
Pipilo erythrophthalmus	Ground Feeder	M	1
Seiurus aurocapilla	Ground Feeder	M	5
Quiscalus quiscula	Ground Feeder	R	2
Zonotrichia albicollis	Ground Feeder	M	277
Toxostoma rufum	Ground Feeder	M	1
Melospiza melodia	Ground Feeder	R	118
Junco hyemalis	Ground Feeder	M	46
Haemorhous mexicanus	Ground Feeder	R	5
Cyanocitta cristata	Ground Feeder/Cacher	R	142
Poecile carolinensis	Cacher	R	884
Baeolophus bicolor	Cacher	R	1,260
Sitta carolinensis	Cacher	R	111
Melanerpes carolinus	Cacher	R	60
Dryobates villosus	Other	R	10
Dryobates pubescens	Other	R	72
Spinus tristis	Other	R	27
Buteo lineatus	Other	R	1
Helmitheros vermivorum	Other	M	2

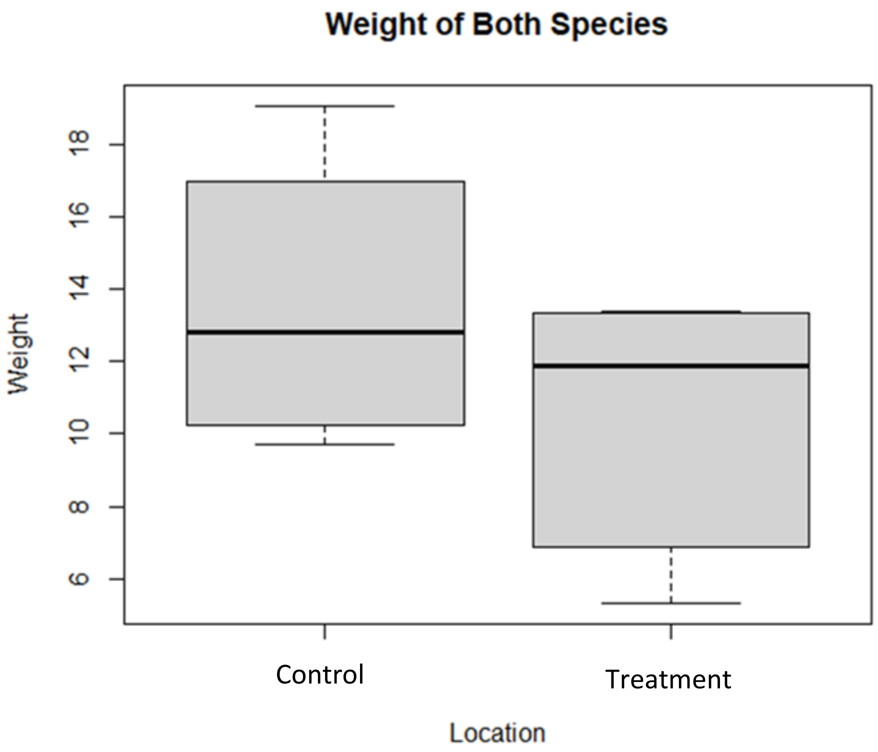

Figure 7: Average weights of both shrew species combined at control and treatment sites; p = 0.24

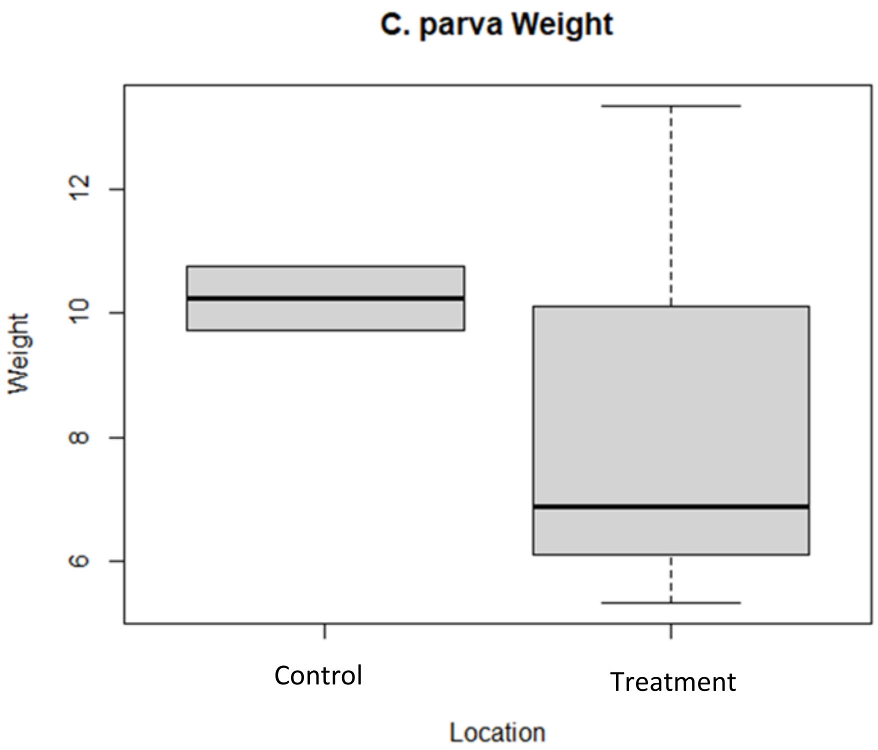

Figure 8: Average weights of *Cryptotis parva* at control and treatment sites; p = 0.63

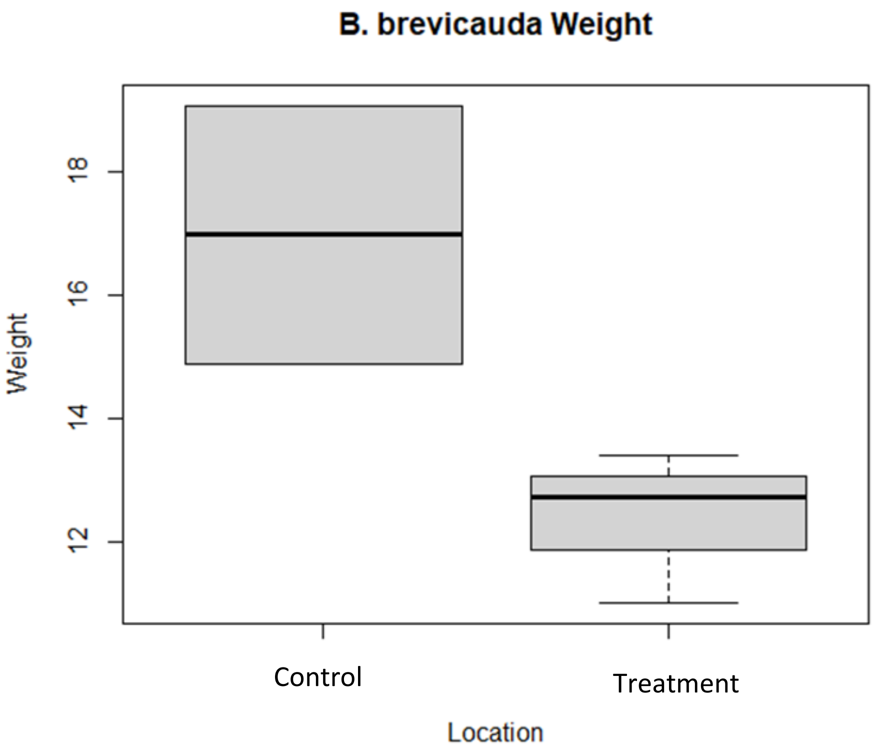

Figure 9: Average weights of *Blarina brevicauda* at control and treatment sites; $p = 0.09$

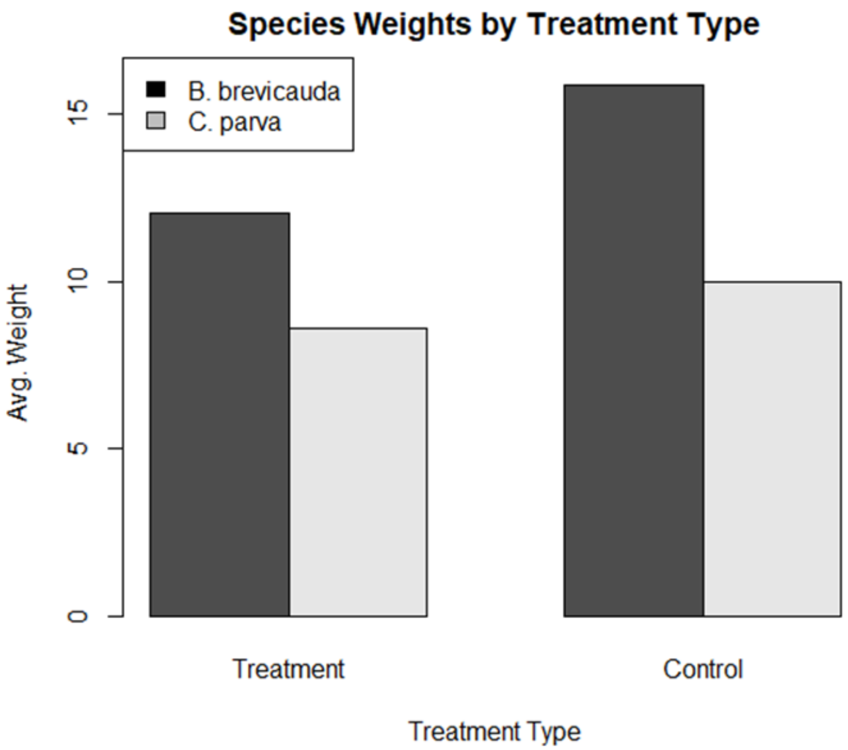

Figure 10: Average weights of both species, grouped by treatment type; p = 0.25

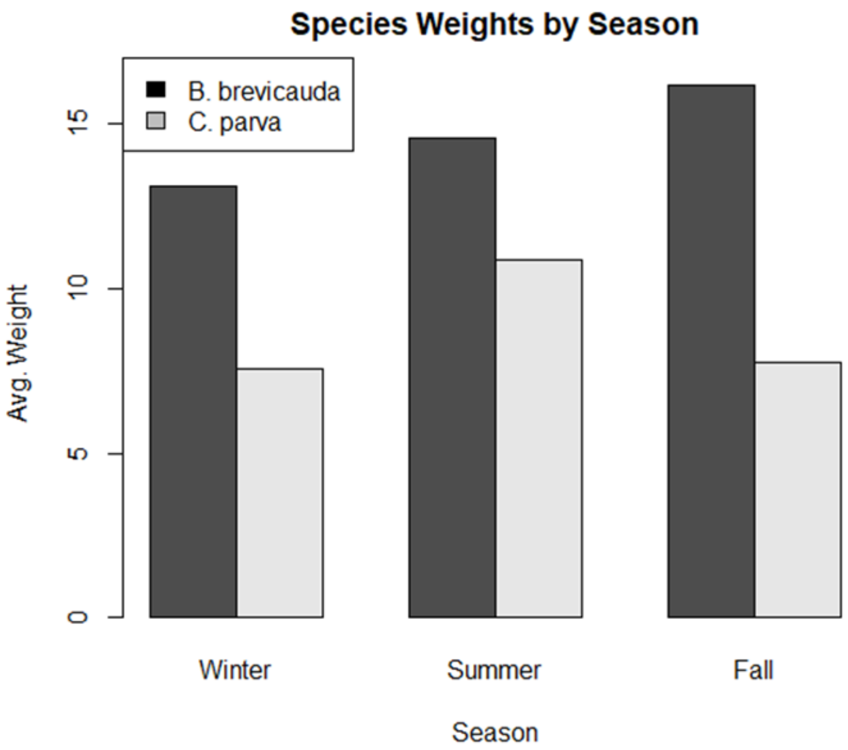

Figure 11: Average weights of both species across seasons. Difference in both species' weights across all seasons (p = 0.75), Difference in each species weights across seasons (*C. parva* p = 0.67, B. *brevicauda* p = 0.85), and species comparisons by season (winter p = 0.22, summer p = 0.46, fall = 0.09).

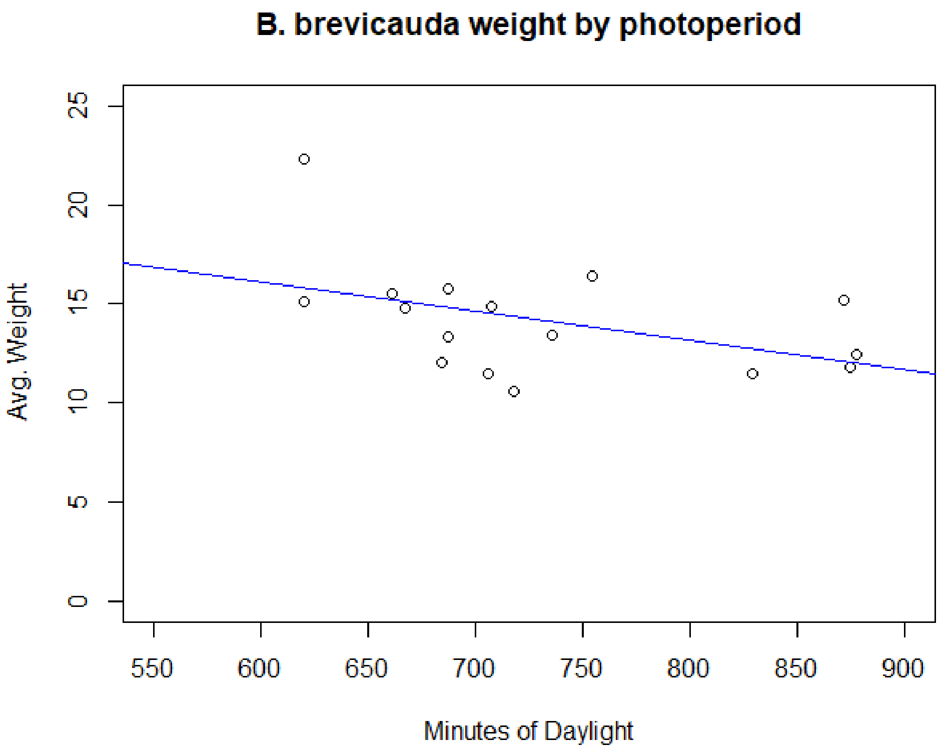

Figure 12: Scatterplot of average weight for *B. brevicauda* compared against minutes of daylight for each value

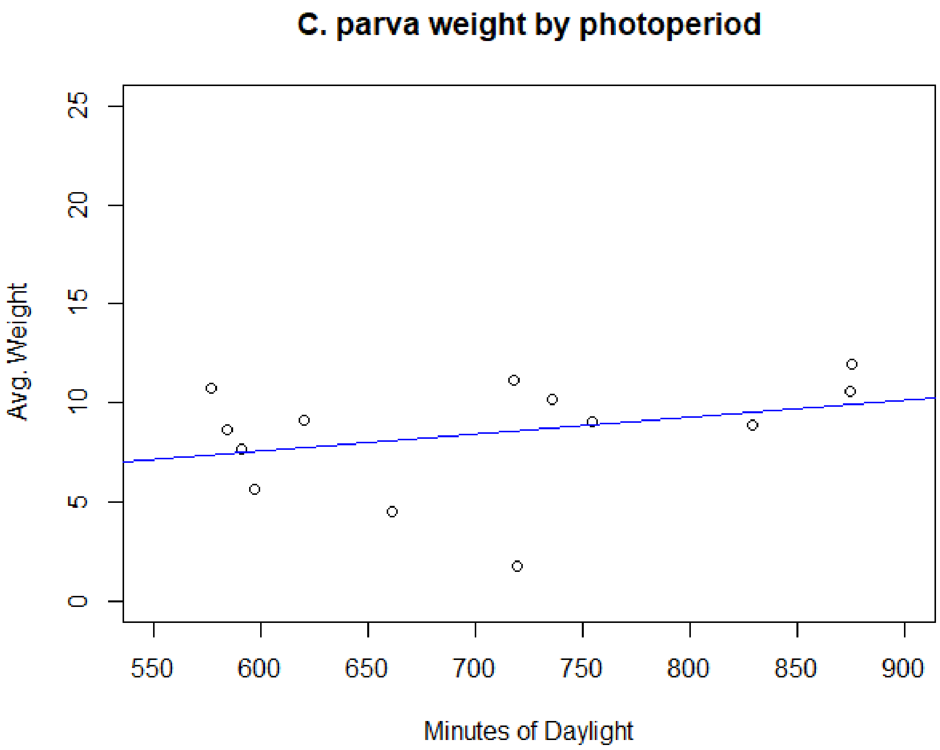

Figure 13: Scatterplot of average weight for *C. parva* compared against minutes of daylight for each value

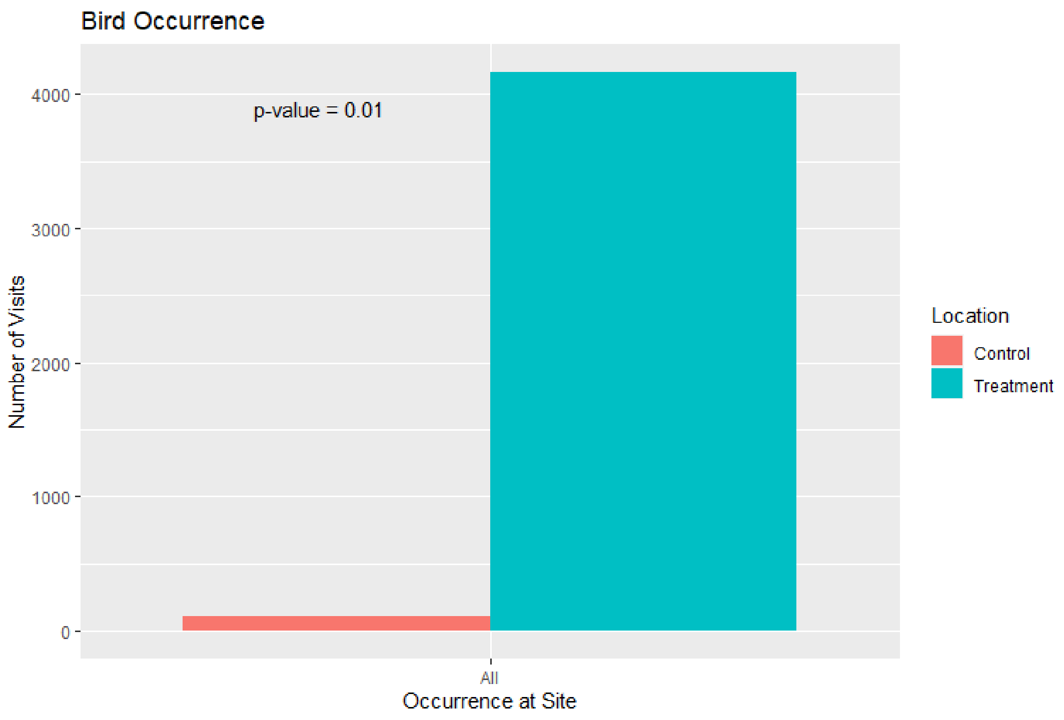

Figure 14: Bird occurrence sorted by treatment type. Total visitation (p = 0.01) to both treatment and control sites is shown.

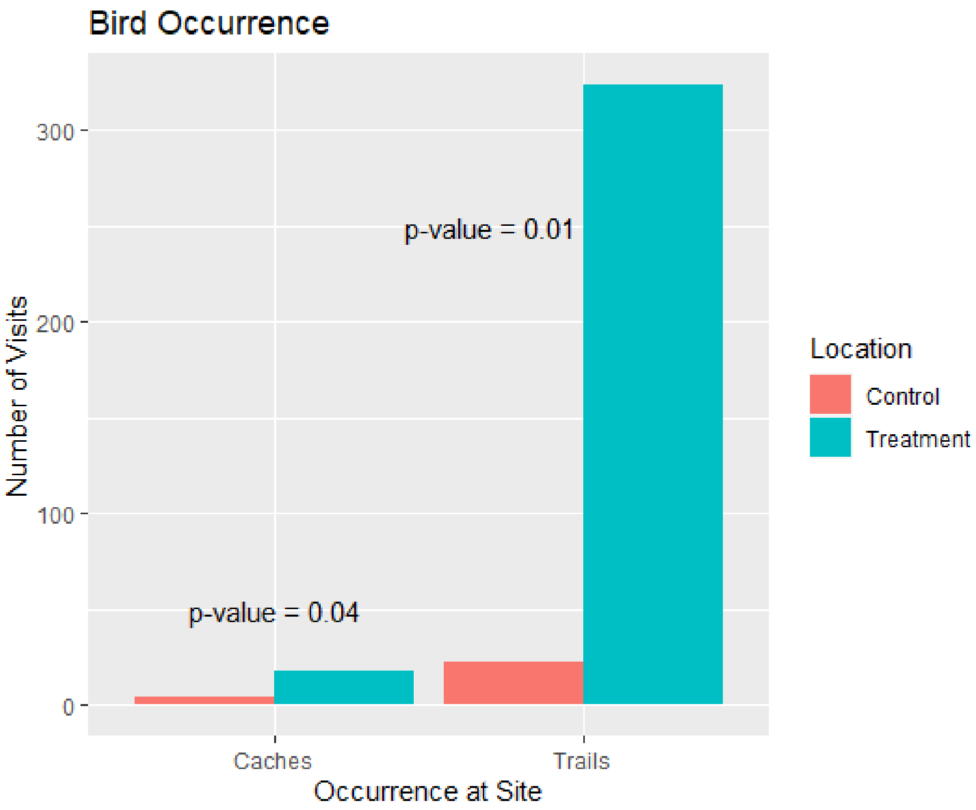

Figure 15: Bird occurrence sorted by treatment type with total visitation rates removed. Visitation to trails (p = 0.01) and caches (p = 0.04) is shown.

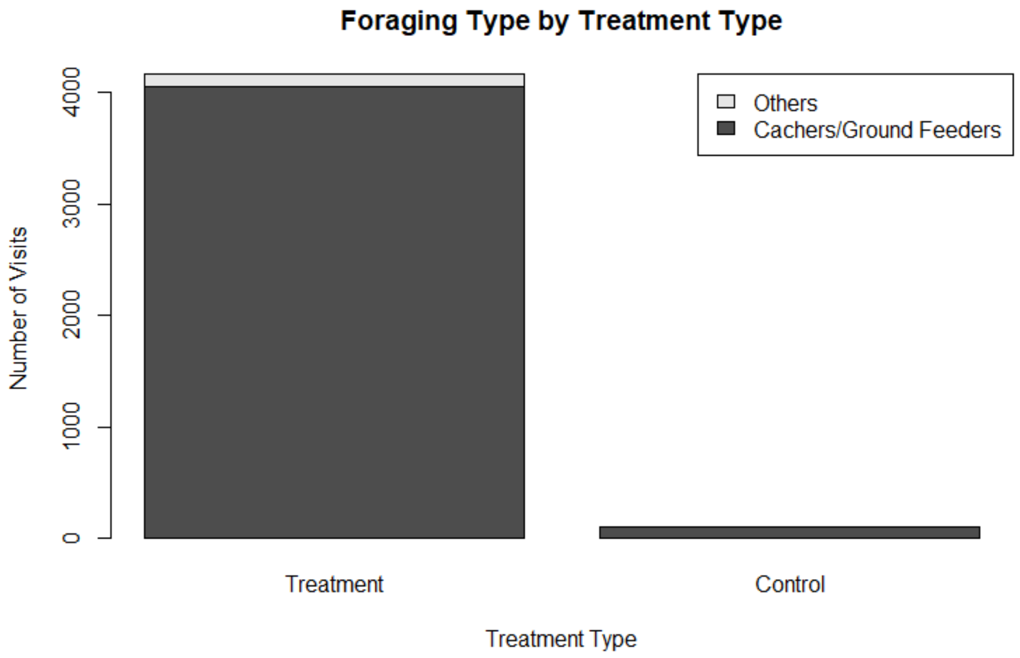

Figure 16: Bird occurrence sorted by treatment type and split by foraging strategy. Cachers/Ground Feeder difference by treatment (p = <0.01); other strategies by treatment (p = < 0.01)

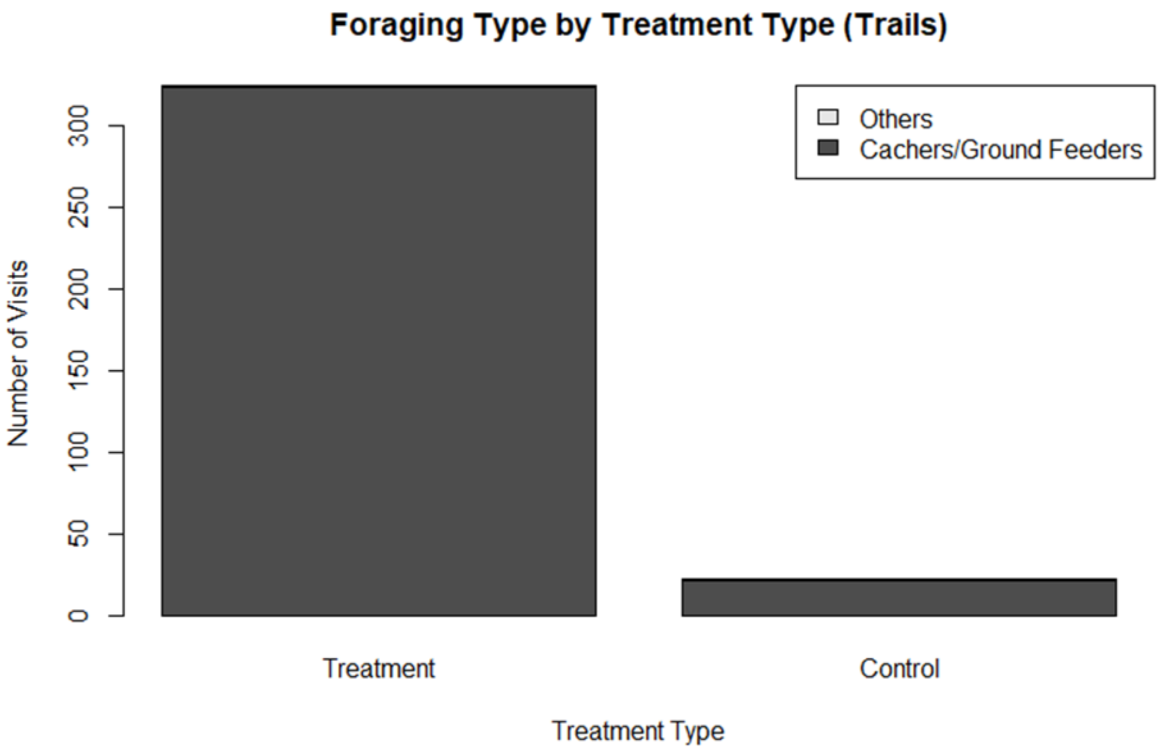

Figure 17: Bird occurrence sorted by treatment type at foraging trails and split by foraging strategy. Cachers/Ground Feeder difference by treatment ($p = <0.01$); other strategies by treatment ($p = < 0.01$)

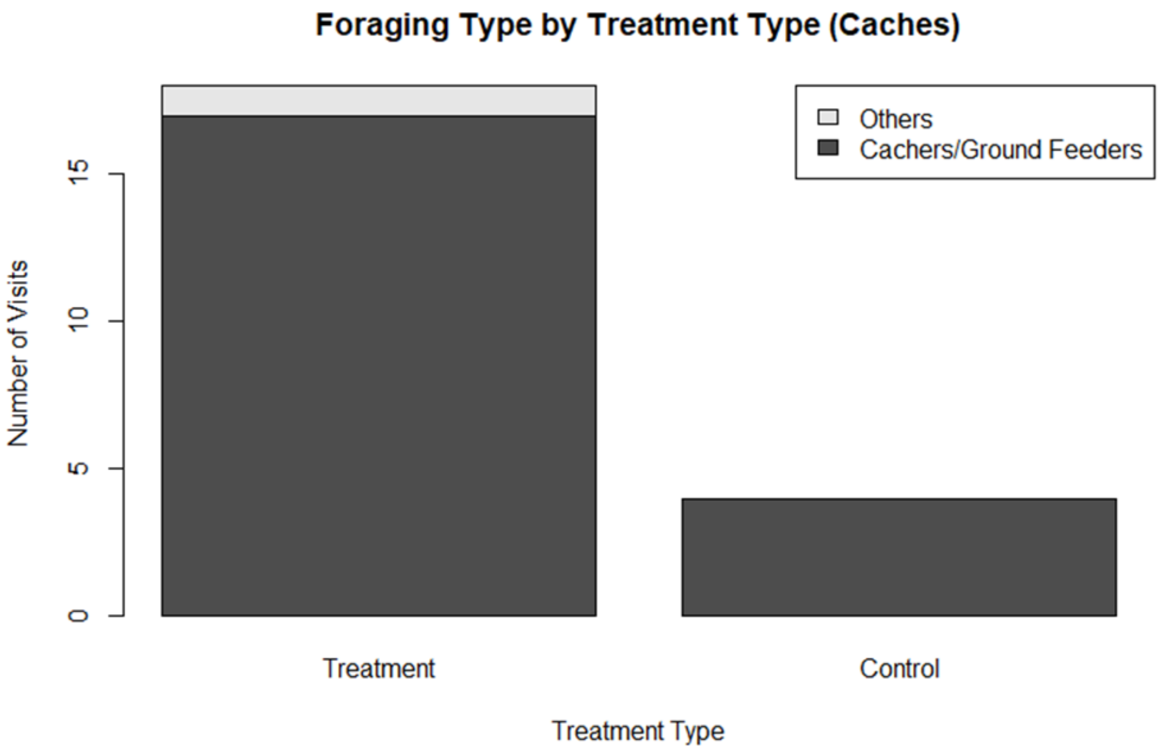

Figure 18: Bird occurrence sorted by treatment type at shrew caches and split by foraging strategy. Cachers/Ground Feeder difference by treatment (p = <0.01); other strategies by treatment (p = < 0.01)

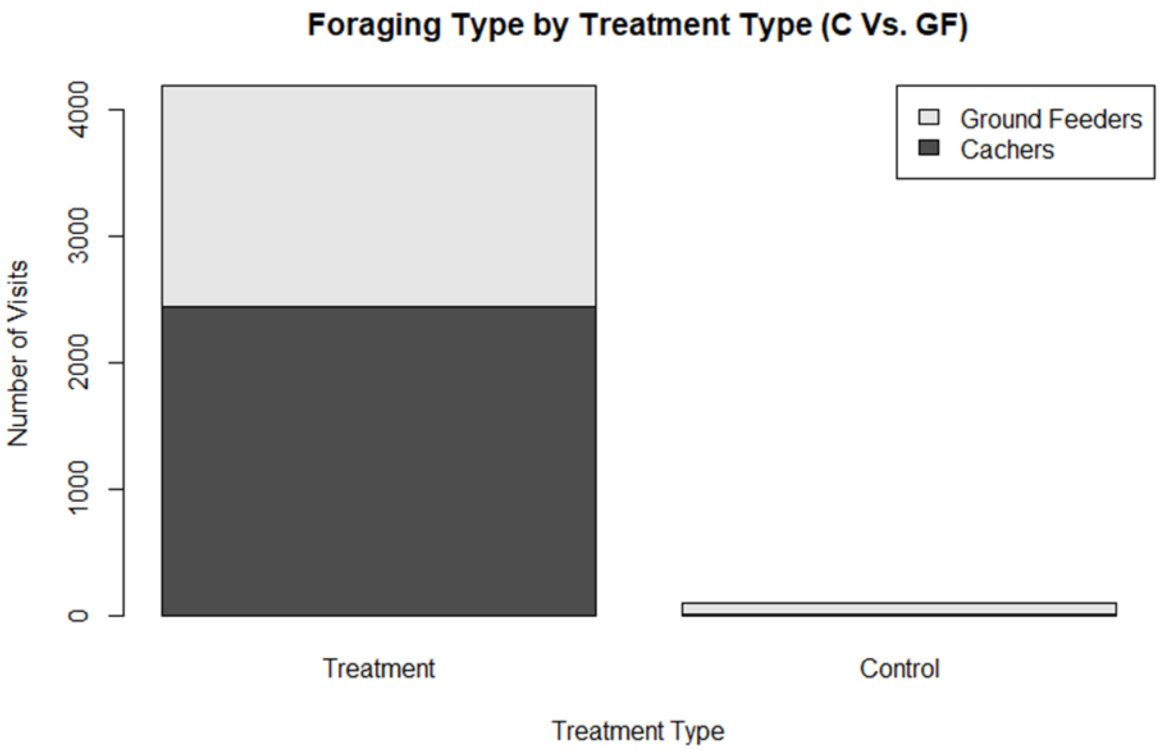

Figure 19: Total bird occurrence sorted by treatment type with other foraging strategies removed. Total (p = <0.01), cacher occurrence by treatment (p = <0.01); ground feeder occurrence by treatment (p = < 0.01)

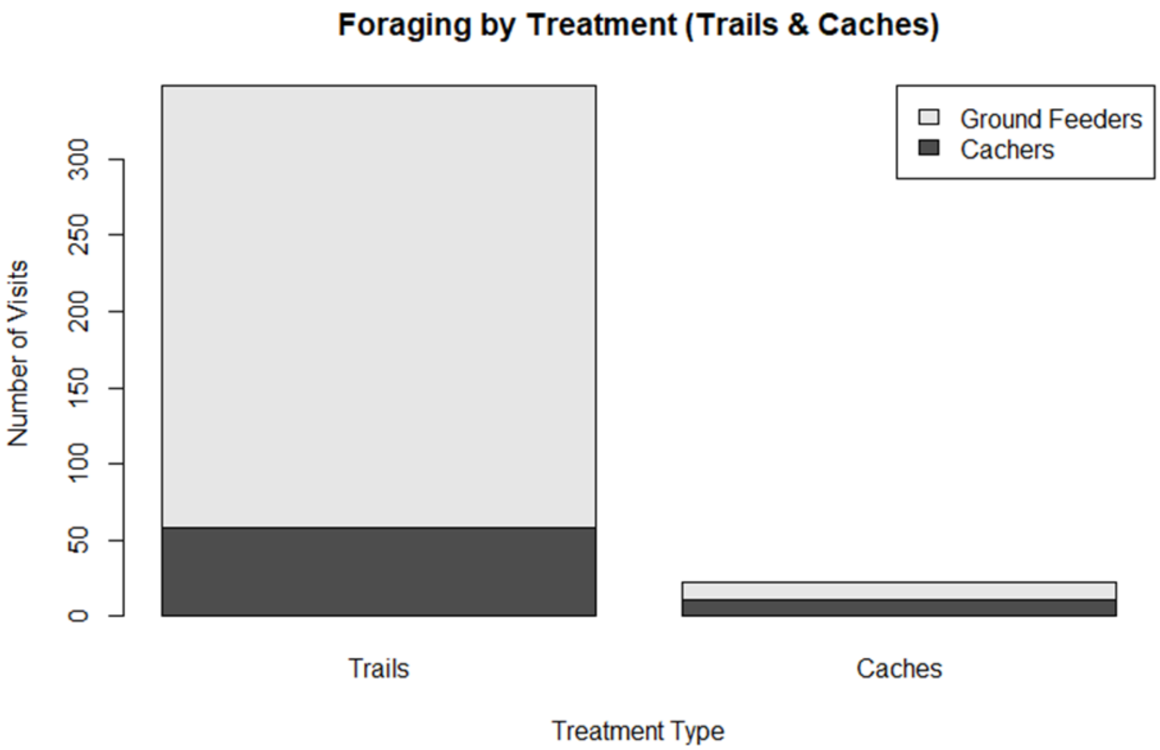

Figure 20: Bird occurrence at foraging trails and caches, sorted by treatment type with other foraging strategies removed. Total (p = <0.01), occurrence at trails (p = <0.01); occurrence at caches (p = 1; even number of both foraging type seen at caches).

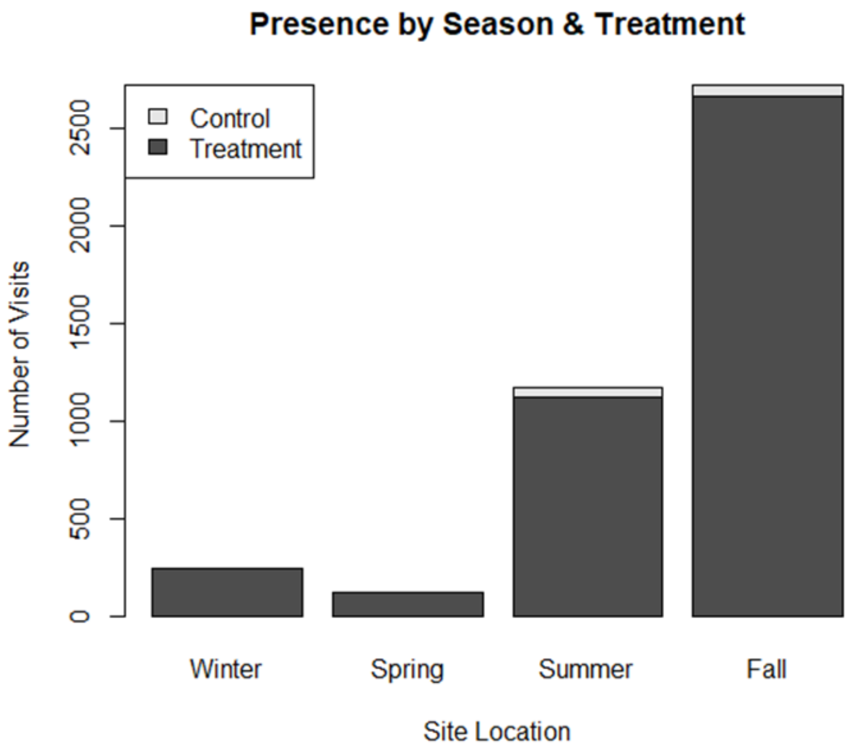

Figure 21: Bird occurrence split by treatment type in all seasons of the year. All combined (p = <0.007), treatment sites over time (p = <0.01), control sites over time (p = <0.007), treatment type by each season individually (all p = <0.007).

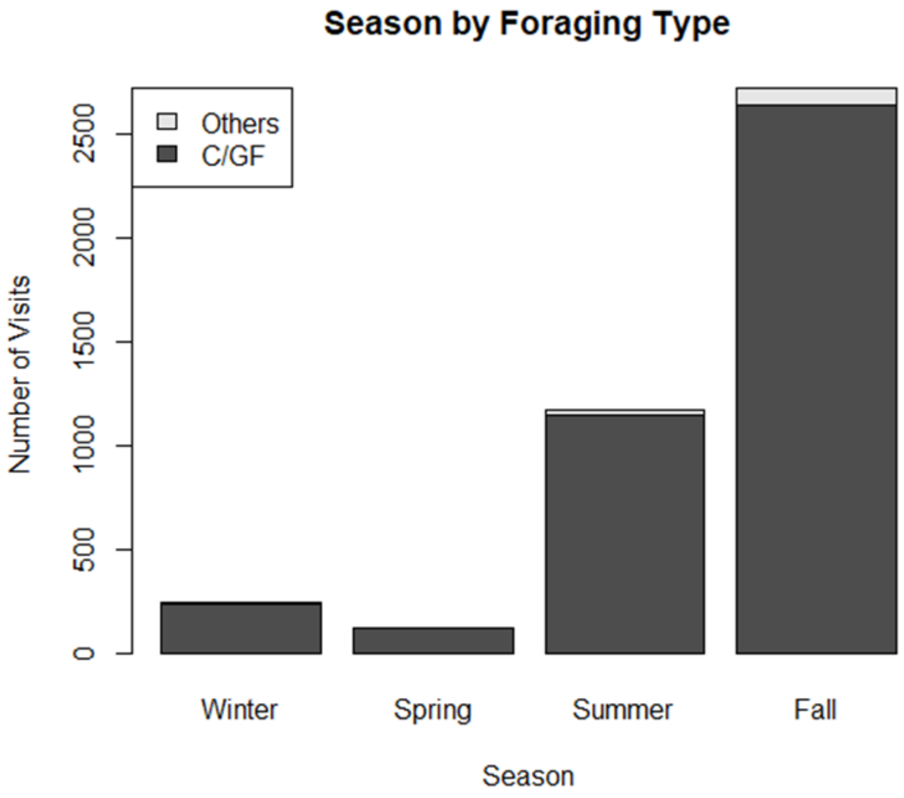

Figure 22: Bird occurrence split by foraging type in all seasons of the year. All combined (p = 0.30), cachers and ground feeders over time (p = <0.007) other foraging strategies over time (p = <0.007), foraging type by each season individually (all p = <0.007).

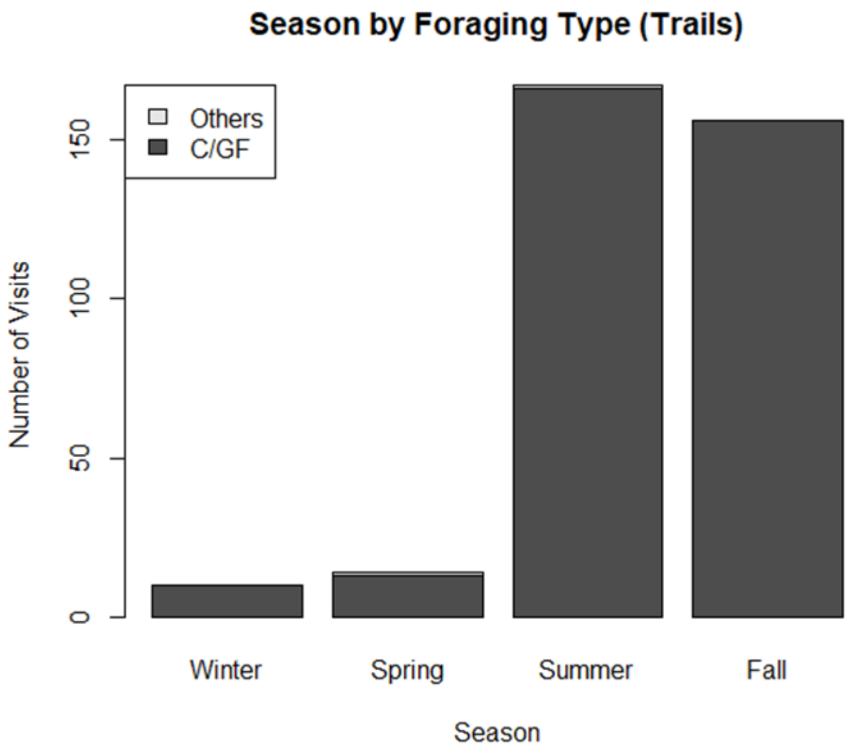

Figure 23: Bird occurrence at shrew foraging trails split by foraging type in all seasons of the year. All combined (p = 0.15), foraging type by each season individually (all p = <0.007).

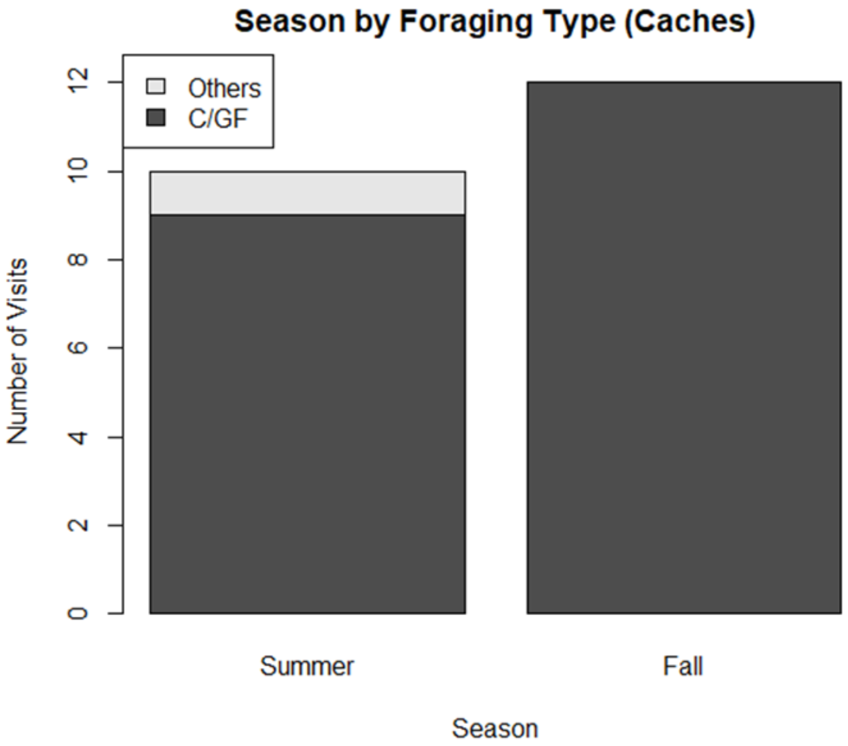

Figure 24: Bird occurrence at shrew caches split by foraging type in all seasons of the year. Both combined (p = 0.5), summer (p = 0.02), fall (p = <0.01).

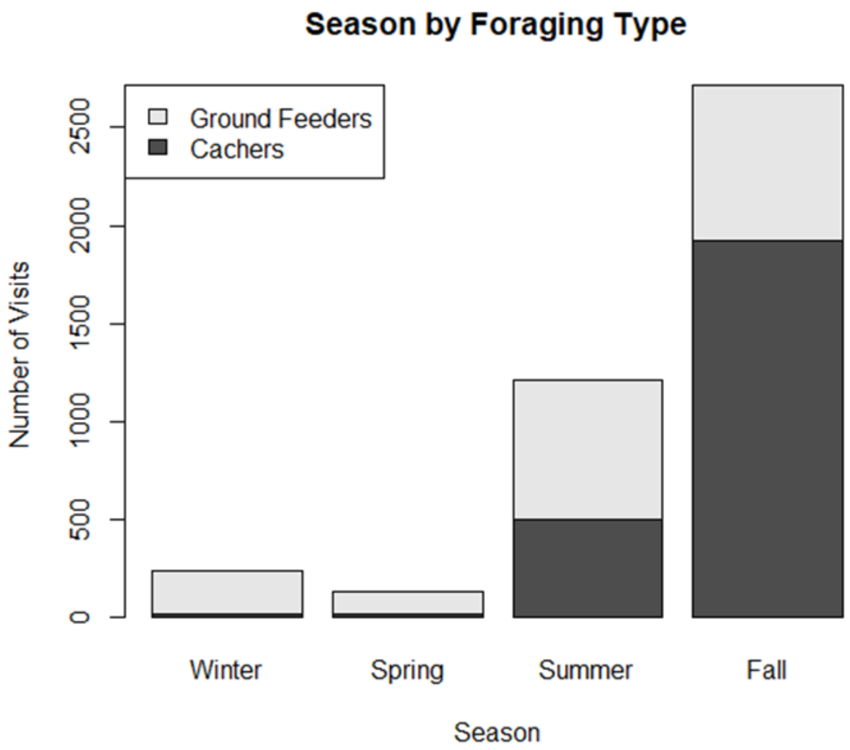

Figure 25: Bird occurrence split by foraging type in all seasons of the year with other foraging strategies removed. All combined (p = <0.007), treatment type by each season individually (all p = <0.007).

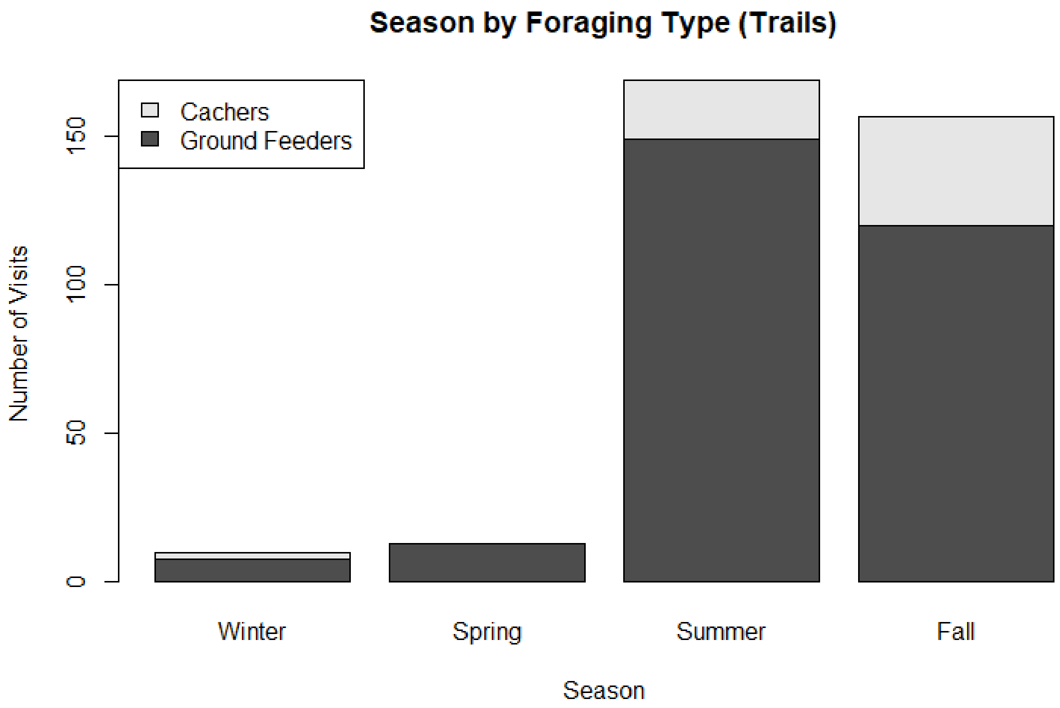

Figure 26: Bird occurrence in foraging trails split by foraging type in all seasons of the year with other foraging strategies removed. All combined (p = 0.01), winter (p = 0.11), spring (p = <0.007), summer (p = <0.007), and fall (p = <0.007).

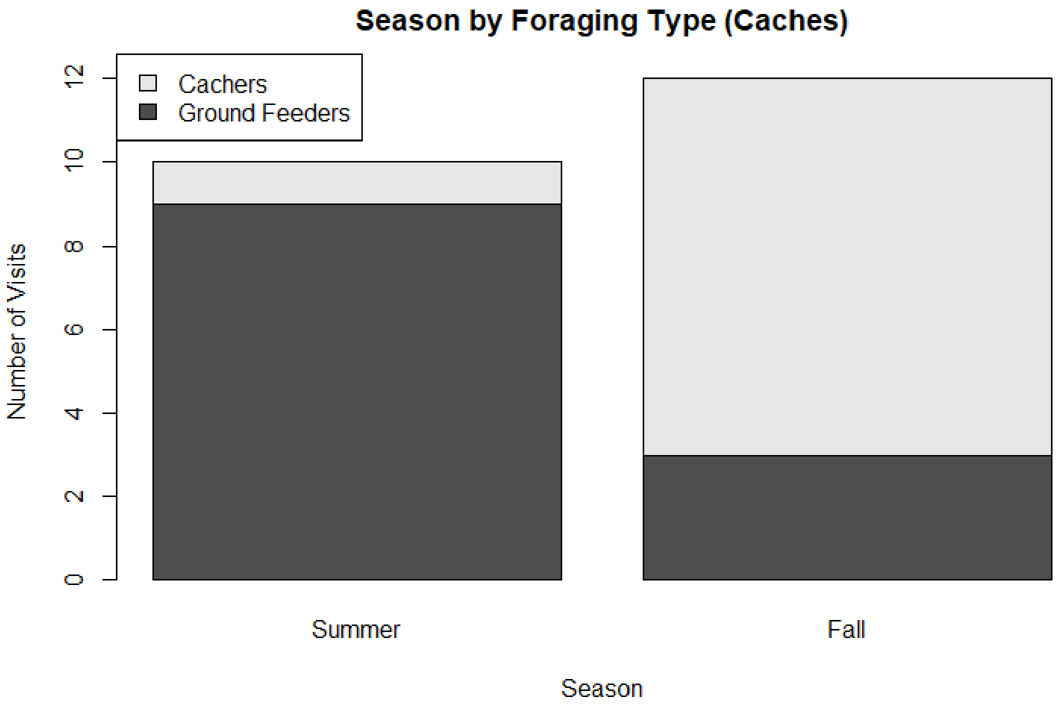

Figure 27: Bird occurrence at shrew caches split by foraging type in summer and fall with other foraging strategies removed. All combined (p = <0.01), summer (p = 0.02), and fall (p = 0.14).

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