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**THE EFFECTS OF HACKBERRY PSYLLIDS ON REFUELING MIGRATORY
SONGBIRDS AND AUTUMNAL SEED RAIN**

By

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B.S. December 2007, Texas A&M University

A Thesis Submitted the Faculty of
Old Dominion University in Partial Fulfillment of the
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May 2020

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ABSTRACT

THE EFFECTS OF HACKBERRY PSYLLIDS ON REFUELING MIGRATORY SONGBIRDS AND AUTUMNAL SEED RAIN

Chance H. Hines
Old Dominion University, 2020
Director: Dr. Eric L. Walters

Hackberry psyllids (*Pachypsylla sp*) are a galling insect native to North America's hackberry trees (*Celtis sp*). Hackberry leaf-galling psyllids are ephemerally abundant during autumn, a period of time when migratory songbirds are traveling from their breeding areas in temperate North America south to their winter ranges. These migrations are energetically taxing and many songbirds fuel their journey with resources like insects and fruits. I captured birds with mist nets, observed foraging behaviors, and captured avian-dispersed fleshy fruit seeds (hereafter, seed rain) during the autumn of 2016 and 2017 to determine how hackberry psyllids, an ephemerally abundant insect, affect migrating songbird refueling indices estimated from blood samples, foraging activity, and subsequent bird-dispersed seed rain patterns. I used end-point assays to measure bird metabolites to find that hackberry presence and hackberry psyllid were associated with increased protein metabolism and fat accumulation for insectivores and omnivores. I also found that hackberry seeds were most dispersed when hackberry psyllids were present. Allospecific seed rain was greater when eastern baccharis (*Baccharis hamifolia*) shrubs were treated with hackberry leaves and hackberry psyllids, and allospecific seed rain was greater near hackberry trees and when hackberry psyllids were present within mixed-hardwood forests. This study adds to the growing support that insects play a crucial role for refueling migratory songbird stopover sites and that hackberry psyllids can increase the likelihood that hackberry seeds are dispersed away from the host tree and allospecific fruiting seeds are dispersed nearer the host tree.

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My thesis is dedicated to my wife who taught me how to properly use a mist net, handle birds, and subsequently assisted with data collection and labwork. She has shared my passion for the outdoors and I would not have been able to explore the world as I have without her. She has endured through my time in graduate school and supported me in every way possible.

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CHAPTER 1

INTRODUCTION

HACKBERRY PSYLLID LIFE HISTORY

Hackberry psyllids (*Pachypsylla sp*) are a complex of 14 galling, plant-sucking insect taxa (Table 1) that are obligate to the six hackberry (*Celtis sp*) species found in North America (Wheeler et al. 1989). Hackberry psyllids are ubiquitous on hackberry trees, including the two hackberry species that are native to Virginia, northern hackberry (*Celtis occidentalis*) and southern hackberry (*Celtis laevigata*), and most psyllids can be identified by their gall formation (Gagne and Moser 2013). Hackberry psyllids are 2–5 mm long arthropods that mate and lay eggs on hackberry leaves, buds, or twigs in early spring before dying. The eggs hatch and nymphs emerge to feed on phloem within the host tissue, which then grows around the larvae and forms a gall. Hackberry psyllids that use twigs and buds emerge from the gall the following spring, at which point, the adult emerges to complete their life cycle. Adult leaf galls emerge from galls *en masse* during late summer/autumn to seek shelter in bark and leaf litter where they overwinter before completing their life cycle the following spring (Hodkinson 2009; Yang and Mitter 1994).

Table 1: The 14 *Pachypsylla* species with the location that their galls form. *P. tropicala* was only identified as adult and no gall was observed (Hodkinson 1988, Yang et al. 2001, Thomas 2012).

Scientific Name	Common Name	Gall Location
<i>P. celtidisasterisca</i>	star gall psyllid	leaf
<i>P. celtidiscucurbita</i>	glabrous nipple gall psyllid	leaf
<i>P. celtidisgemma</i>	glabrous bud gall psyllid	buds
<i>P. celtidisglobula</i>	glabrous nipple gall psyllid	leaf
<i>P. celtidisinteneris</i>	twig gall psyllid	twigs and base of limbs
<i>P. celtidismamma</i>	hairy nipple gall psyllid	leaf
<i>P. celtidispubescens</i>	hairy nipple gall psyllid	leaf
<i>P. celtidisumbilicus</i>	disc gall psyllid	leaf
<i>P. celtidisvesicula</i>	blister gall psyllid	leaf
<i>P. cohabitans</i>	unnamed	leaf (inquiline)
<i>P. dubia</i>	unnamed	leaf
<i>P. pallida</i>	hairy bud gall psyllid	buds
<i>P. tropicala</i>	unnamed	unknown
<i>P. venusta</i>	petiole gall psyllid	petiole

HACKBERRY PSYLLIDS AND BIRDS

Psyllids and other closely related insects (Homoptera) are nutritious sources of lipid energy relative to other terrestrial arthropod taxa like ants, flies, and spiders (Strong 1963; Rahbé et al. 1994; Lease and Wolf 2011), representing a relatively large proportion of some songbird diets during the breeding season (Sample et al. 1993; Carlisle et al. 2012). Because hackberry psyllids are protected within galls during the summer, they are unavailable to foraging birds during the breeding season. However, when hackberry psyllids are ovipositing on hackberry leaves, they are available for songbird consumption during spring and influence migrating songbird foraging behavior in the mid-western United States (Strode 2009). Hackberry trees are favored for foraging at other locations during spring stopover, though it is not clear whether the disproportionate foraging behavior is due to hackberry psyllid presence or geometrid larvae that are also found on hackberry trees in the midwest (Moore and Yong 1991). The only other time of year that hackberry psyllids are readily available is during autumn when they emerge from galls and move to overwintering habitats. The psyllid irruption often coincides with the peak of autumn songbird migration, when potential avian predators are most abundant (Moser 1965, Suthers et al. 2000; MacMynowski and Root 2007), but it is not known how hackberry psyllids affect migratory songbird foraging behavior or metabolic refueling.

AUTUMN SONGBIRD MIGRATION AND STOPOVER QUALITY

The majority of songbirds that breed in temperate North America migrate south to South America, Central America, or more southern temperate North America (Able 1973). Migratory songbirds travel as far 14,500 km every spring and autumn (Bairlein et al 2012) and though some birds do complete migration in a single flight, most require multiple stops between nocturnal flights to rest and refuel for the next leg of the journey (Able 1973; McWilliams and Karasov 2001). These stops

last one to several days (Mehlman et al. 2005; Buler et al. 2007) and the areas where birds recover and prepare for future flights are known as stopover locations.

Because stopover habitats are critically important to survival (Moore and Gauthreaux 1993; Petit 2000), identifying important stopover locations for conservation are a priority for management agencies (Sheehy et al 2011). To identify important stopover habitat, sampling circulating metabolites like triacylglycerol, B-OH-butyrate, and uric acid (a byproduct from breakdown of proteins that originate from body tissue or the diet) can be used to quantify stopover site quality and guide management decisions. Most autumn migrating songbird refueling studies have found that songbird metabolite profiles are positively influenced by high-fat fruit abundance (Smith et al 2015), but it is not well known how insect abundance affects songbird refueling during autumn migration.

MIGRATORY SONGBIRD METABOLISM

Birds attempt to complete migration using as little time and energy as possible while also minimizing the risk of predation (Alerstam and Lindström 1990) and acquire the necessary fuel at stopover sites to complete migration (Hedenström and Alerstam 1997). The primary fuel for migratory birds is adipose tissue because it approximately contains eight times more energy than sugars and proteins (Blem 1976; Jenni and Jenni-Eiermann 1998). Adipose tissue is composed of triacylglycerol, a compound containing three fatty acids bound to glycerol. Fatty acids can be obtained directly from food sources or synthesized from carbohydrates via fatty acid synthesis (Stevens 2004). Higher concentrations of triacylglycerol are found in the bloodstream of feeding birds (Zajac et al. 2006; Smith et al. 2007) and those that are captured near abundant high-quality resources (Guglielmo et al. 2005; Smith and McWilliams 2010; Smith et al. 2015).

While adipose tissue is the primary fuel for migrating songbirds, other nutrients like carbohydrates and protein are important as well (McWilliams et al. 2004). Some tissues, like the brain and heart, do not utilize fatty acids and are typically glucose-dependent (Robinson 1970). Carbohydrate storage is more energetically expensive because it is eight times heavier than triacylglycerol so birds primarily rely on gluconeogenesis (i.e., generate glucose from fat) to fuel glucose-dependent tissue while in flight (Blem 1976; Langslow 1978).

Protein is also an important nutrient because it provides 5–15% of total migratory in-flight energy (Jenni and Jenni-Eiermann 1998; McWilliams et al. 2004), replenishes spent muscle and gut tissue following long migratory flights (Aamidor et al. 2011), prevents dehydration in flying birds (Gerson and Guglielmo 2011), and facilitates the transport of free fatty acids from adipose tissue to flight muscle mitochondria (Guglielmo 2010). Protein is also heavier than fat so birds will catabolize some muscle tissue and gut tissues prior to and at the beginning of long-distance flights (McWilliams et al. 2004). When birds do utilize gut tissue in this fashion, they must typically replenish their guts by consuming protein after completing their flight (Hume and Biebach 1996; McWilliams et al. 2004). When lipid, carbohydrate, and protein sources have been exhausted during migratory flights, an alternative fuel source, B-OH-butyrate, is synthesized in the liver from the ketone acetoacetate and is used to fuel glucose-dependent tissue (Robinson 1970; Le Maho et al. 1981).

The majority of studies that investigate resources used as a source of fuel for bird migrations have focused on fruit abundance or presence, neglecting the contribution of arthropods. Fats and carbohydrates are readily available in most fleshy fruits that birds consume during autumn migration, but most fruits are relatively protein deficient (Johnson et al 1985). Songbirds prefer to forage on arthropod taxa that are high in fats (Strong 1963; Moermond and Denslow 1985; Rahbé

et al. 1994; Herrera et al. 2006), so it would stand to reason that such arthropods would also be important to migrating birds. However, it is not known how arthropods contribute to migratory songbird refueling metabolism during autumn.

MIGRATING SONGBIRD DIET

Many avian taxa switch from a primarily insectivorous diet during the breeding season to an omnivorous or frugivorous diet during autumn migration at stopover sites when more fruits are available (Bairlein 1996; 1998). High-quality resources for many migrating songbirds typically include fleshy fruits because fruits are aggregated spatially, contain sugars and fats, and are most abundant during the temperate autumn (Thompson and Willson 1979; Johnson et al. 1985, Suthers et al. 2000; Smith et al. 2015). Birds often select fruits that are the richest in their primary fuel, triglycerides, and will also select fruits to meet unique combinations of long and short-chain fatty acids (Herrera 1984; Pierce and McWilliams 2005).

Most songbirds depend upon arthropod prey to fuel their spring migrations to such a degree that arthropod abundance can influence migration phenology (Ashiru 1989; La Sorte et al. 2015; Guil-Guerrero et al. 2018). Insects can have temporary, but large-scale, spikes in abundance that can dramatically alter the density and range of birds during both breeding and wintering periods (Haney 1999; Holmes et al. 2009) but the degree to which arthropods influence refueling songbird foraging behavior during autumn migration is not well understood.

BIRD-PLANT SEED DISPERSAL MUTUALISMS

Interspecific interactions can be characterized by either a positive, negative, or neutral effect (Boucher et al. 1982). When interactions have a positive effect on both organisms involved, the relationship between the two is termed a mutualism (Bronstein 1994). There are many examples of mutualisms in nature including those symbiotic in nature, such as gut biota in vertebrates

(Bäckhed et al. 2005), as well as more diffuse mutualisms between assemblages of mutualist partners, such as those typically observed in pollination and plant-frugivore seed dispersal networks (Jordano 1987).

Seed dispersal is an important process that influences spatial structure of plant communities and several mechanisms of dispersal have evolved in plant taxa that take advantage of animals, wind, and water (Bakker et al 1996; Howe and Smallwood 1982). Individual plants benefit greatly from having their seeds dispersed further away and migratory songbirds are particularly effective at this activity (Nathan et al 2008). Plants that utilize animals as dispersal vectors typically produce fruit with nutritious flesh that can provide energy to animals (Howe and Smallwood 1982).

The ripening of many fleshy fruits in North America occurs during autumn when many songbird species engage in long-distance migrations (Sauer et al. 2013) to escape freezing temperatures and food shortages associated with low plant and arthropod productivity in winter (Hails 1982; Berthold 2001; Boyle et al. 2010). These journeys are energetically taxing (Wikelski et al. 2003; McWilliams et al. 2004; Fristoe 2015) and a strategy many birds use to increase lipid reserves, their primary in-flight fuel, is to consume fruits rapidly that are high in fatty acids and sugars (King and Farner 1965; Bairlein 1998).

Plants capitalize on bird migrations and synchronize fruiting events with periods of higher avian abundance (Stiles 1980; Skeate 1987; Hanya 2005) to facilitate seed dispersal by birds because they are particularly effective seed-dispersal vectors (Willson 1986; Jordano and Schupp 2000; Viana et al. 2016). Many fleshy fruiting plants have developed strategies to increase the likelihood that their fruits are consumed and seeds are subsequently dispersed. Plants can provide unique fatty acids and anti-oxidants that help birds refuel more efficiently at stopover sites (Pierce

et al. 2005; Bolser et al. 2013; Jenni-Eiermann et al. 2014). Plants can also ‘advertise’ their fruits through the color of their leaves (Stiles 1982; Duan and Quan 2013).

The locations to which plant seeds are dispersed are also important, not only to ensure that a seed recruits into an adult plant, but also to determining the composition of future plant communities (Pakeman and Small 2005). Large numbers of dispersed seeds in a limited area often results in a lower likelihood of recruitment (Inouye 1980), but can become an area where a high density of fruiting plants are found (Pakeman and Small 2005).

Locations where frugivorous birds disproportionately spend time such as near fruiting trees, treefall gaps, and favorable perching locations, often receive greater seed rain from defecation (Hoppes 1988; Debussche and Isenmann 1994; Herrera 1984; Smith and McWilliams 2014). Birds refuel more efficiently on a balanced diet than one that relies solely on fruit or arthropods (Bairlein 2002; Bairlein and Gwinner 1994), so even fruit-eating birds must sometimes search for arthropod-rich areas. Migrants may disproportionately spend more time in areas that are rich in arthropods, which could lead to a greater volume of seed rain (Johnson 2000), but no studies that I am aware of have investigated this issue.

STUDY GOALS

I conducted this study at seven migratory songbird stopover sites on the eastern shore of Virginia (USA) from August to November in 2016 and 2017. Foraging birds were observed along foraging transects, blood plasma was collected from captured migratory songbirds and later processed in the lab to obtain plasma, and bird-dispersed seeds were captured in seed traps. In Chapter 2, I classified bird species by diet and use models that determine the best predictors of triacylglycerol, uric acid, and B-OH-butyrate concentrations. In Chapter 3, I tested whether birds disproportionately forage on hackberry trees, quantify psyllid abundance, and use models to

determine the best predictors of seed dispersal patterns. Chapter 4 provides a summary of the findings and sets these findings into the context of previous work on the subject. This study is the first, to my knowledge, to examine the relationships among an insect taxon, migrating songbirds, and seed dispersal patterns during autumn migration.

CHAPTER 2

FRUITS VS INSECTS: ARTHROPODS ARE AN OVERLOOKED BUT IMPORTANT PREY SOURCE FOR MIGRATING SONGBIRDS

INTRODUCTION

Migratory songbirds attempt to complete their biannual journeys using a balance between minimizing energy use and risk of predation (Alerstam and Lindström 1990). Most migrants depend on stopover habitat to rest and refuel following nocturnal migratory flights, but generally lack prior knowledge of stopover site suitability (Hedenström and Alerstam 1997, Schaub and Jenni 2001). Stopover habitats near ecological barriers are particularly important because they represent the last opportunity to acquire lipid reserves required to cross barriers (Rubolini et al. 2002, Buler and Moore 2011). Older birds and those with relatively more fat reserves tend to bypass or spend less time near ecological barriers, while young and lean birds tend to concentrate at these stopover habitats (Alerstam 1978; McCann et al 1993; Hoh et al. 2018), potentially leading to a paucity of food resources as a result of greater competition (Seewagen and Guglielmo 2010). Competition for limited food resources may explain why refueling birds near borders of large water bodies sometimes accumulate lipids at lower rates than birds captured further from barriers (Hoh et al. 2018), though abundant high-quality food resources near barriers can mediate this effect (Smith et al. 2015).

Birds that are better able to locate high-quality stopover habitat are more likely to accumulate primary fuel for migratory flights, adipose tissue, and complete the migration more efficiently and timely (Bayly et al. 2019). Birds rely on three primary nutrients to fuel their flights; the most important nutrient, Triacylglycerol (TAG), is an ideal substrate to fuel migration because it is approximately eight times more energy dense than other nutrients like carbohydrates and proteins (Blem 1976; Jenni and Jenni-Eiermann 1998). Higher concentrations of TAG are found in the

circulatory system of birds while feeding but not when fasting (Zajac et al. 2006; Smith et al. 2007) and often found in individuals captured near abundant high-quality resources (Guglielmo et al. 2005; Smith and McWilliams 2010; Smith et al. 2015). Conversely, circulating concentrations of other nutrients like carbohydrates and proteins tend to be greater in birds captured in areas without high-quality resources (McWilliams and Karasov 2001; Jenni-Eiermann 2011). Migrating birds have digestive mechanisms that increase carbohydrate absorption but this is thought to be an adaptation in response to overnight flight recovery, rather than an energy-storing mechanism for future flights (Tracy et al. 2010). Carbohydrates are also important because some tissues, including the brain, cannot use TAG to meet energetic requirements; rather, these tissues must rely on glucose, or ketones like β -Hydroxybutyrate (BUTY), endogenously produced as a byproduct of lipid metabolism for fuel.

High-quality resources for many migrating songbirds typically include fleshy fruits because fruits are aggregated spatially, contain sugars and fats, and most abundant during the temperate autumn (Thompson and Willson 1979; Johnson et al. 1985; Suthers et al. 2000; Smith et al. 2015). Birds select fruits that offer the greatest metabolic benefit (Herrera 1984) and those with which they are familiar, which are most often native species (Smith et al. 2013). Dogwood (*cornus sp*) and Arrowwood (*viburnum*), species that are distributed over much of the eastern U.S., are examples of native plants that produce energy-rich fruits (Smith and McWilliams 2010; Smith et al. 2015).

Many avian taxa switch from a primarily insectivorous diet during the breeding season to an omnivorous or frugivorous diet during autumn migration at stopover sites when fruits are available (Bairlein 1996; 1998). The sugars and fats, however, found in fruits alone are usually not enough to fuel migrating songbirds, and thus many birds also seek protein sources (McWilliams et al. 2004). Protein provides 5–15% of total migratory in-flight energy (Jenni and Jenni-Eiermann

1998; McWilliams et al. 2004), facilitates the transport of free fatty-acids from adipose tissue to flight muscle mitochondria (Guglielmo 2010), replenishes spent muscle and gut tissue following long migratory flights (Aamidor et al. 2011), and its catabolism mitigates dehydration in flying birds (Gerson and Guglielmo 2011). Because fruits are typically composed of relatively little protein (Johnson et al. 1985), songbirds must usually acquire protein by consuming arthropods (Moermond and Denslow 1985; Herrera et al. 2006). While many songbird species switch from insectivorous to a primarily frugivorous diet during autumn, virtually all migrant birds consume some arthropods during this time (Bairlein 1996; Parrish 1997). In fact, many songbirds depend on lepidopteran larvae, which are high in fatty acids, to fuel their spring migration north (Ashiru 1989; Guil-Guerrero et al. 2018). In fact, arthropod abundance can influence the timing of spring migration by insectivorous birds (La Sorte et al. 2015), but the degree to which arthropods influence refueling songbirds during autumn migration is not well understood.

Arthropods may play a vital role in migrant refueling because, just as fruit availability reaches a peak during autumn (Thompson and Willson 1979), some arthropod taxa also reach peak population size during autumn (Hails 1982). Songbirds are known to disproportionately forage on plant-sucking insects like auchenorrhyncha and sterno-rhyncha (hereafter, Homoptera) throughout North America and such taxa are composed of relatively high concentrations of triacylglycerol (TAG; Strong 1963; Rahbé et al. 1994). Hackberry psyllids (*Pachypsylla* sp) are host-specific Homopteran taxa that affect migratory songbird foraging behavior at spring stopover sites and are an example of arthropod taxa that autumn migrants disproportionately forage upon during autumn migration (Strode 2009).

Hackberry psyllids spend summers within leaf galls and overwinter in nearby shelter, thus, they are only readily abundant to migrant songbirds while ovipositing during spring and when they

emerge from galls during autumn (Hodkinson 2009; Strode 2009; Leatherman 2010). Thus, hackberry psyllids may provide a pulse of a locally abundant source of protein for refueling songbirds, particularly when their emergence coincides with migratory songbird habitat use, a phenomenon that has not been quantified.

Study Goals

The goal of this study was to investigate how food resource abundance affects migratory songbird refueling performance relative to habitat type and proximity to an ecological barrier. I aimed to determine for songbirds during autumn migration whether refueling performance relates to a) arthropod abundance in insectivores, b) fruit availability in frugivores, or c) and abundance of both in omnivores. I predicted that the abundance of Homoptera, such as hackberry psyllids, would have a positive effect on birds that consume insects, and energy-rich native fruits would have a positive effect on birds that consume fruits by increasing fat accumulation and allowing bird to recover from overnight flights. I conducted my study near an ecological barrier, the Chesapeake Bay in Virginia, so that I could also explore whether refueling performance was a function of proximity to an ecological border.

Hypotheses

If Homoptera abundance positively influences migratory songbird refueling performance, I predicted that migratory songbirds would: 1) consume more protein, 2) accumulate more fat, and 3) recover from overnight flights relatively quicker when high-quality arthropods were readily available. Specifically, I predicted that insectivorous songbird refueling performance would be associated with temporal trends in Homoptera abundance and presence of hackberry trees after hackberry psyllids emerge from galls during mid-autumn, a time when other Homoptera are less abundant (Hodkinson 2009; Strode 2009; Thomas 2012).

METHODS

Field work was carried out under the following permits: Old Dominion University Institutional Animal Care Use Committee Protocol (16-025),

Study Site

Field work occurred throughout the southern Delmarva Peninsula, Virginia (fig. 1) from 17 Aug to 29 Nov 2016 and 2017. In autumn, migratory songbirds are more abundant in coastal Virginia than inland and are particularly concentrated nearer the southern tip of the Delmarva Peninsula (hereafter, southern tip) prior to crossing the Chesapeake Bay to the south (McCann et al. 1993). The habitat on the Delmarva Peninsula is a mosaic of agricultural fields, isolated patches of forest, shrub-scrub land cover in the interior, and saltwater-land cover along the coasts. I classified land cover types (hereafter, habitats) as interior forest, upland shrub-scrub (“shrub-scrub”), salt-spray scrub (“salt-scrub”), and edge habitat where scrub habitats and forests meet (Mitchell 2012). On the basis of previous research (Heller et al. 2015), transects (n=16 total [1–3 = per site]) and capture locations (n = 115) were placed representatively at field sites (n = 6; fig. 1) where hackberry and other habitats of interest were found.

Songbird Diet Classification

I observed foraging birds throughout the lower Delmarva Peninsula (fig. 1) along 250-m transects walked during the first 6 hrs of sunlight at a standard pace (approx. 1 km/hr) twice per week. Observers strayed from the central transect line as far as 10 m to collect data on foraging birds. I recorded the diet item (insect, fleshy fruit, or other) associated with the first foraging

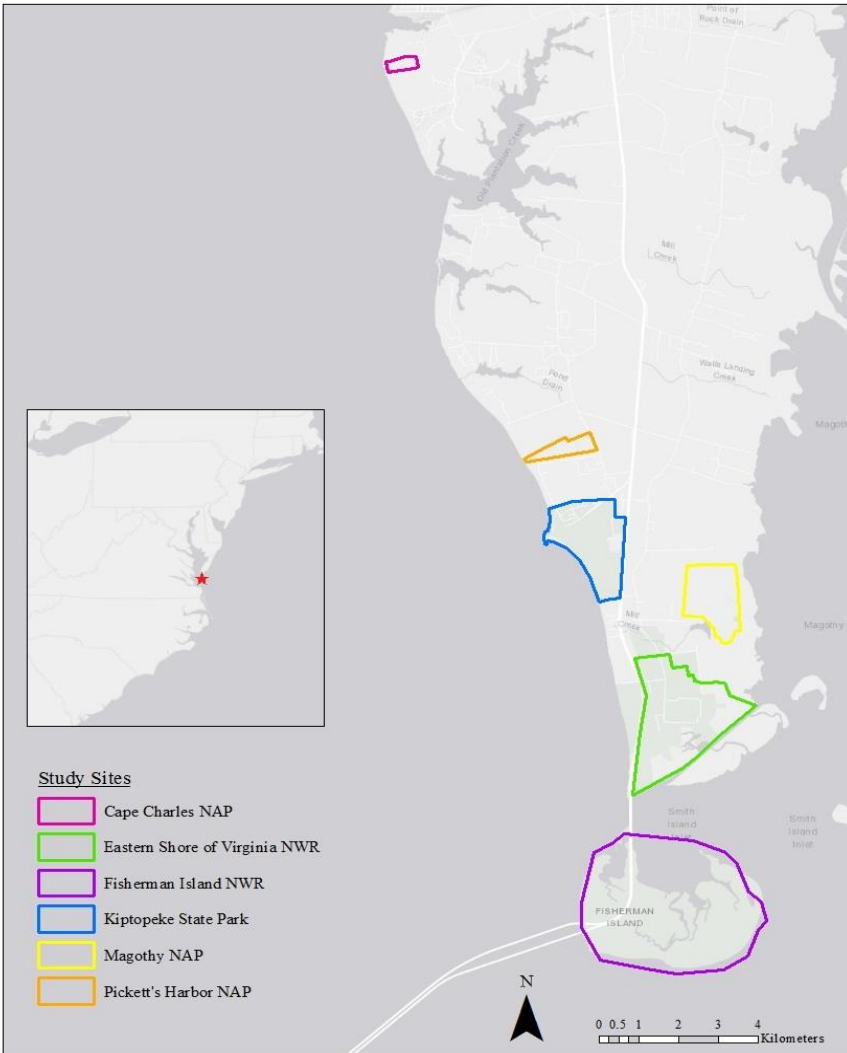


Figure 1: Map of study area study sites on the lower Delmarva Peninsula, Virginia

attempt observed following the methods of Remsen and Robinson (1990). Only individuals that could be identified as a unique individual (i.e., dichromatic species and juvenile/mature birds) were recorded within 100 m of another to avoid double counting (i.e. pseudoreplication; Hurlbert 1984), assuming that birds would not move along the transect for 100 m at the same pace as the observer.

Plasma Metabolite Analyses

Birds feeding on lipid-rich food sources and accumulating body lipids exhibit increased concentrations of TAG; similarly, birds consuming protein-rich meals have elevated plasma uric acid (nitrogenous waste resulting from protein catabolism), and fasting birds have elevated plasma BUTY (β -OH-butyrate) concentration as a result of the oxidation of fatty-acids (needs reference). I quantified migratory refueling indices by measuring blood plasma metabolite concentrations (TAG, uric acid, and BUTY) that were associated with specific dietary nutrients, as described previously (Guglielmo et al. 2005).

I captured birds at 106 locations within the six field sites using mist nets. Birds were sampled throughout the day starting at civil twilight (0606 – 1738, median capture time = 0840). I recorded blood sampling metadata (i.e., covariates) that may influence plasma metabolite concentrations (Schaub and Jenni 2001; Cerasale and Guglielmo 2010; Smith et al. 2015), including bleed time (i.e., the maximum length of time [min] that a bird was captured and held until blood was sampled, to account for changes in metabolite concentrations as a result of not foraging while captured [Guglielmo et al. 2005]), time of day (i.e., the number of minutes that passed between civil twilight and when birds were bled to account for birds that had longer periods of time to recover from overnight flights and accumulate fuel), habitat type, food resources (presence of ripe fleshy fruits within 6 m of the middle of the mist net during every trapping session at every net that birds were captured) and proximity to the southern tip (m).

Migratory passerines were captured with 12 m long x 2.6 m high 38 mm mist nets in forest interiors, edges, upland shrub-scrub, and salt-scrub habitat six days per week from 21 Aug to 21 Nov 2016 and 2017. Nets were monitored every 8–12 min and 10–75 μ L of blood was collected from the brachial vein into a capillary tube. I stored capillary tubes on ice and centrifuged at 9000 rpm for 9 min within 6 h of collection to separate whole blood from blood plasma. The capillary

tube was scored with a file where the red blood cells met the blood plasma and broken to extract the plasma, and subsequently stored in 0.5 mL microcentrifuge tubes in a -20 C freezer for 1–21 days before transporting to a -80 C freezer. Plasma samples were then thawed 2–4 months later in a laboratory and diluted two-fold with a 0.9% NaCl solution. TAG and uric acid were quantified using commercially available endpoint assays (Sigma Aldrich, St. Louis, MI and TECO Diagnostics, Anaheim, CA; T449-10ML and U580-400, respectively); BUTY was quantified using a kinetic assay (Sigma-Aldrich, St. Louis, MI; MAK041-1KT) following protocols by Guglielmo et al. (2005).

Temporal Insect Trend Quantification

During 2016, at sites where hackberry was present, a single branch (with approx. 50 leaves each) was selected randomly (i.e. the nearest branch at a random distance between 1 – 250 m along the transect) each week. On each branch, I counted and identified to species all leaf galls on each leaf and examined the gall for psyllid presence within. Because this sampling approach only informed us of when psyllids emerged from galls rather than when psyllids were abundant, I altered my approach in 2017. During the 2017 field season, I randomly selected 17 branches at trapping locations where hackberry was present and that were at least 50 m apart at the beginning of the season and counted all galls on each branch. I then placed 10 x 13 cm yellow sticky traps (Olson Products Inc, Medina, OH) (Hall et al. 2007) approximately 1.5 – 2.5 m from the ground from 57 hackberry branches 25 m apart (at the branches surveyed for gall abundance and along the remainder of foraging transects where trapping did not occur). While sticky traps can potentially bias estimates of arthropod abundance (Schulze et al. 1997), I chose this method because it allowed us to place traps within the same vertical strata of habitat as birds being captured and because these traps attracted Homopterans, the preferred songbird arthropod prey (Hall et al. 2007). The sticky

traps were checked weekly and insects were counted, and classified as Homoptera, hackberry psyllids, or other insect orders. For subsequent analyses we classified the autumn into two periods, 1. before hackberry psyllids were available, and 2. after hackberry psyllids were available. The available period began after 5% of the total number of galls I observed exhibited exit wounds associated with psyllid emergence in 2016, and after 5% of the total number of hackberry psyllids were captured on sticky traps in 2017.

Statistical Analyses

To partition bird species into collective diet guilds that represented a categorical factor in subsequent modeling analyses, I used an unsupervised k-means cluster analysis (Legendre and Fortin 1989), where observations of each species (n) were partitioned into k clusters that minimized the mean squared distance from each data point to the nearest cluster centroid. I used the percentage of prey items consumed that were insects and fruits, as well as uric acid concentration (table 2) as observations and $k = 3$ for the 3 diet guilds of avian foragers. I analyzed *Catharus* thrushes and *Empidonax* flycatchers as single taxonomic groups because they were difficult to identify to species along foraging transects and they consume similar prey items at other autumn migratory stopover sites on the east coast of the United States (Parrish 1997). I used silhouette width coefficients (s_w) to evaluate how well my observations were clustered; where an s_w near 1 indicated that observations were well clustered, positive s_w near 0 indicated that some observations occurred between two clusters, and negative s_w indicated observations that were placed in the incorrect cluster (Halkidi et al. 2001).

To explore effects related to arthropod and fruit availability, I analyzed the three diet guilds (omnivore, frugivore, insectivore) independently. To identify relationships between each plasma metabolite concentration (TAG, BUTY, and uric acid [n = 284, 279, and 139, respectively])

Table 2: Diet classification (frugivore [F], insectivore [I], omnivore [O]), percentage of prey items that were insects (IP), fruit (FP), and uric acid (UA) concentration for each species.

Species	# Foraging Observations	# Uric Acid Samples	IP (\pm SE)	FP (\pm SE)	UA	Diet
<i>Setophaga ruticilla</i>	116	42	62% (\pm 4.5%)	0% (\pm 0.0%)	2.08 (\pm 0.20)	I
<i>Mniotilta varia</i>	71	11	34% (\pm 5.6%)	0% (\pm 0.0%)	2.01 (\pm 0.56)	I
<i>Geothlypis trichas</i>	46	63	33% (\pm 6.9%)	2% (\pm 2.1%)	1.74 (\pm 0.10)	I
<i>Setophaga discolor</i>	14	5	36% (\pm 12.8%)	0% (\pm 0.0%)	1.70 (\pm 0.19)	I
<i>Empidonax sp</i>	11	8	82% (\pm 11.6%)	0% (\pm 0.0%)	1.38 (\pm 0.26)	I
<i>Parkesia noveboracensis</i>	9	16	44% (\pm 16.5%)	0% (\pm 0.0%)	1.62 (\pm 0.25)	I
<i>Setophaga petechia</i>	9	2	44% (\pm 16.5%)	0% (\pm 0.0%)	2.91 (\pm 1.24)	I
<i>Sayornis phoebe</i>	7	2	83% (\pm 14.2%)	17% (\pm 14.2%)	1.08 (\pm 0.03)	I
<i>Setophaga magnolia</i>	6	5	33% (\pm 19.2%)	0% (\pm 0.0%)	2.12 (\pm 0.54)	I
<i>Helmitheros vermivorum</i>	5	1	60% (\pm 21.9%)	0% (\pm 0.0%)	1.42 (\pm 0.00)	I
<i>Setophaga coronata</i>	215	77	37% (\pm 3.3%)	20% (\pm 2.7%)	0.77 (\pm 0.04)	O
<i>Setophaga americana</i>	40	5	40% (\pm 7.7%)	0% (\pm 0.0%)	0.94 (\pm 0.11)	O
<i>Zonotrichia albicollis</i>	35	47	11% (\pm 5.3%)	29% (\pm 7.7%)	1.23 (\pm 0.08)	O
<i>Vireo olivaceus</i>	33	17	30% (\pm 8.0%)	18% (\pm 6.7%)	1.48 (\pm 0.17)	O
<i>Setophaga palmarum</i>	30	15	30% (\pm 8.4%)	0% (\pm 0.0%)	1.47 (\pm 0.18)	O
<i>Certhia americana</i>	16	1	31% (\pm 11.6%)	0% (\pm 0.0%)	1.16 (\pm 0.00)	O
<i>Catharus sp</i>	13	65	23% (\pm 11.7%)	31% (\pm 12.8%)	0.96 (\pm 0.05)	O
<i>Troglodytes aedon</i>	6	13	33% (\pm 19.2%)	0% (\pm 0.0%)	1.04 (\pm 0.13)	O
<i>Setophaga caerulescens</i>	5	13	20% (\pm 17.9%)	20% (\pm 17.9%)	1.52 (\pm 0.17)	O
<i>Dumetella carolinensis</i>	52	202	4% (\pm 2.7%)	81% (\pm 5.4%)	0.71 (\pm 0.03)	F
<i>Turdus migratorius</i>	37	1	0% (\pm 0.00%)	84% (\pm 6.0%)	0.40 (\pm 0.0)	F
<i>Toxostoma rufum</i>	4	7	0% (\pm 0.00%)	75% (\pm 21.7%)	0.65 (\pm 0.06)	F

and environmental covariates, I used an information theoretic approach (Burnham and Anderson 2002) where the models for the response variables, TAG, BUTY, and uric acid, were constructed using generalized linear mixed models (GLMMs) with a Gamma distribution from the R package MASS (Venables and Ripley 2002) to account for zero-truncated positive skew. Model sets for all bird diets and all metabolites were constructed with the following fixed effects: time of day (min), time since capture (min), distance to the southern tip (m north of the southernmost trapping location on Fisherman's Island), habitat (interior forest, forest edge, shrub-scrub, and salt-scrub), year (2016 and 2017), hackberry presence (within 6 m of the center of the mist net that was used to capture the bird), and psyllid availability (two periods, before and after the period when 5% of hackberry psyllids had emerged from galls or were captured on sticky traps). I also included site as a random intercept to account for potential underlying variance in site-specific bird use. All candidate model sets included a global model, an intercept-only model, models with only each predictor, models with each predictor and time of day (metabolite profiles change throughout the day when refueling [McWilliams et al. 2004, Guglielmo et al. 2005, Cerasale and Guglielmo 2010, Smith et al. 2015]), and a model that included time of day and an interaction between distance to the nearest hackberry tree and psyllid availability. For frugivore and omnivore TAG and BUTY model sets, I also included models with common (as indicated in fig 2) ripe fruit presence (present / not present) within 6 m of the center of the mist net) because fruit availability can influence these metabolites (Smith and McWilliams 2010; Smith 2013; Smith et al 2015). I used Akaike's information criterion for small sample size (AIC_c) and selected the model with the lowest AIC_c score as the best-supported model if no other model was within 2 Δ AIC_c. If two or more models were within 2 Δ AIC_c, I model-averaged those candidate models unless one of the models was a

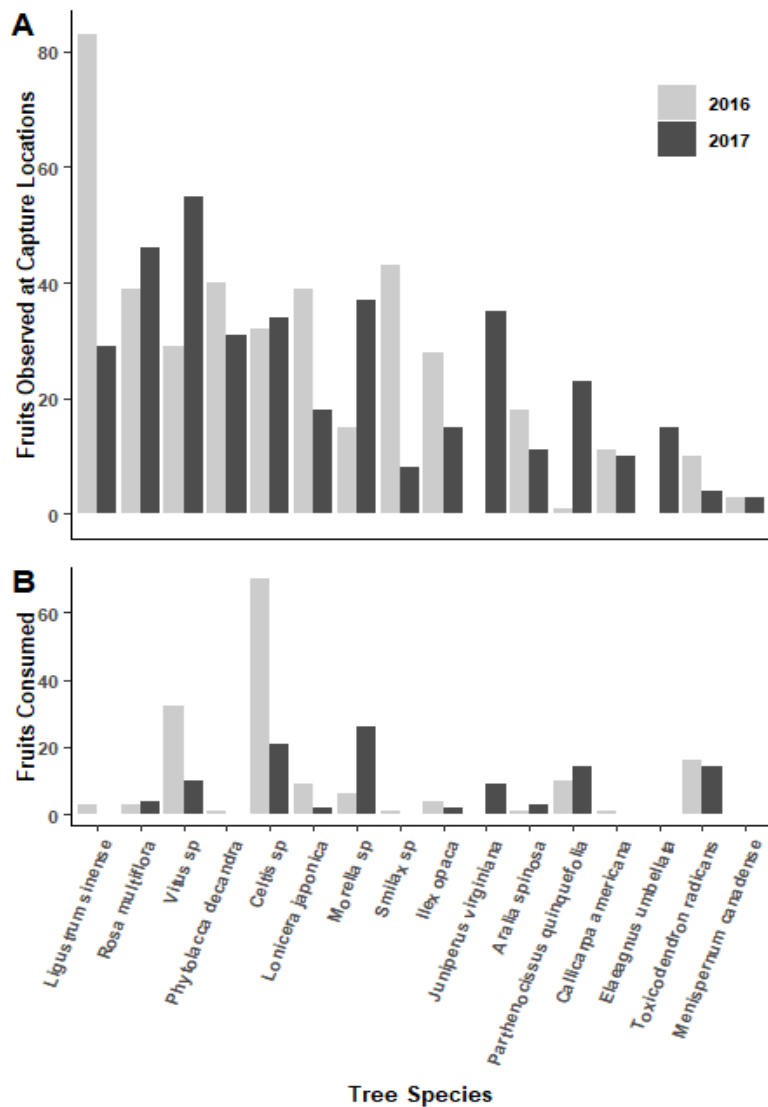


Figure 2: A) total number of capture locations that ripe fruit species were observed and B) total number of fruits observed that were consumed by birds along foraging transects. Differences in fruit availability between 2016 and 2017 likely due to environmental variation between years while interannual variation in migratory songbird community composition may also contribute to differences in fruit consumption between 2016 and 2017.

null model (Burnham and Anderson 2002; Symonds and Moussalli 2011). All statistical analyses were performed with R 3.6 (R Core Team 2019).

RESULTS

Diet: I recorded a total of 1,107 migratory songbird foraging attempts during the autumn of 2016 (n = 538) and 2017 (n = 569). Most diet items were unknown (563), followed by arthropods (351), fruits (155), and other plant parts (38) (table 3). Arthropod consumption was widespread among songbirds (41 of 65 bird species), while fruit consumption was restricted to relatively fewer taxa (18 species, table 2). Only 22 taxa were recorded foraging on four or more prey items and I classified these species as insectivores (n=11), frugivores (n=3), and omnivores (n=8), based on a cluster analysis (fig. 3).

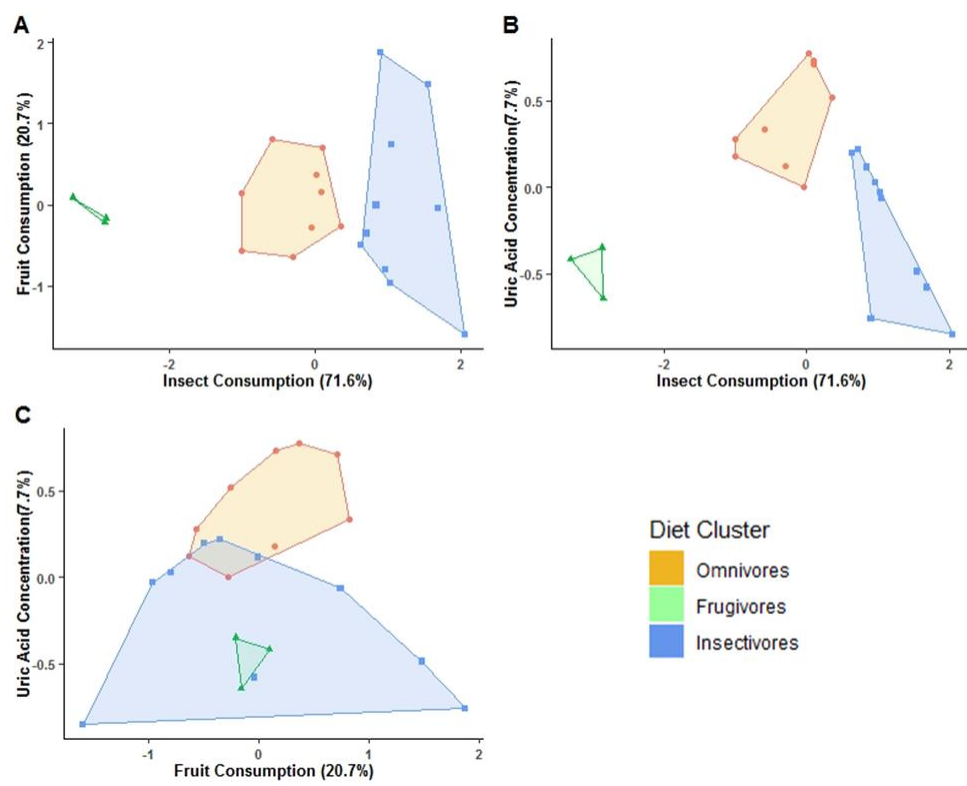


Figure 3: K-means cluster plot showing three clusters of diet groups. Dimensions represent the three explanatory variables, percentage of insects in diet, percentage of fruits in diet, and uric acid concentrations.

No observations were incorrectly clustered, though some species classified as insectivores may have occurred between clusters ($s_w = 0.17, 0.84, 0.44$ for insectivores, omnivores, and frugivores, respectively).

Homoptera Abundance

Galls were ubiquitous on hackberry trees during both seasons and three hackberry psyllid species were identified by gall morphology (*Pachypsylla celtidisasterisca*, *P. celtidisglobulus*, and *P. celtidisumbilicus*). There was a mean of 0.26 galls \pm 0.05 SE per leaf during 2016 when the first galls to open were observed 2 Oct and 0.41 \pm 0.12 SE during 2017 when adult psyllids were first captured on sticky traps on 10 Sep (fig 4).

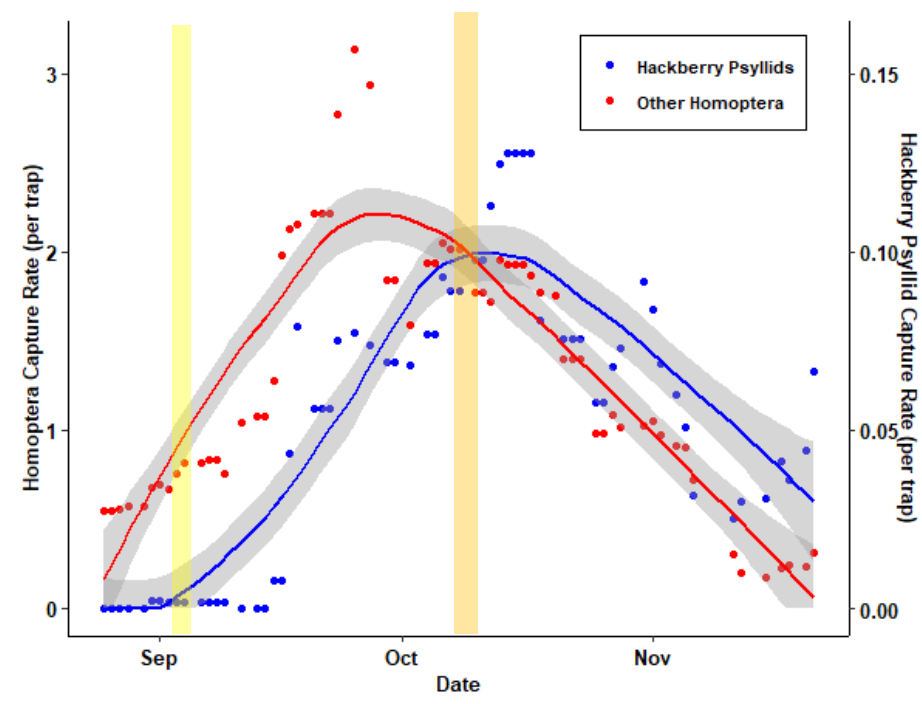


Figure 4: Temporal trends of Homoptera and hackberry psyllids during the 2017 field season. Hackberry psyllids and other Homoptera are plotted on different scales. The light gray lines represent a loess smoothing parameter (Jacoby 2000). The light yellow shaded rectangle represents the period of time that Hermine (2 – 4 Sep) affected the study area during 2016. The light orange shaded rectangle represents the period of time that Matthew (7 – 10 Oct) affected the study area during 2016.

A total of 6,481 Homoptera were collected from sticky traps during the 2017 autumn migration, including 244 hackberry psyllids. Overall, Homoptera abundance peaked approximately 20 days prior to hackberry psyllid peak abundance during 2017

Fruit Availability

Twenty species of ripe fruits were recorded at capture locations throughout the 2016 and 2017 autumn migrations. The most common species found at net locations included Chinese Privet, multiflora rose (*Rosa multiflora*), and grape (*Vitis sp*), though fruits found at capture locations between 2016 and 2017 differed to some degree (fig. 2).

Plasma Metabolites

TAG: Mean TAG concentrations were greatest in frugivores (1.50 ± 0.11), followed by omnivores ($\pm 1.29, 0.07$), and insectivores ($1.20, \pm 0.06$) (fig. 5). Results of TAG model selection analyses are presented in tables 4–6. Time of day was an important predictor for all diets and TAG concentrations increased throughout the day (table 7). Hackberry presence, psyllid availability, and the interaction between the two predictors were all important within the top insectivore model set. Insectivore TAG concentrations were greater when captured near hackberry trees and when hackberry psyllids were available (fig 5). Hackberry presence was also important within the omnivore model set; omnivore TAG concentrations were greater when captured near hackberry trees (fig 5). Year was the only other predictor with support within the top frugivore model; frugivore TAG concentrations were greater in 2016 than in 2017 (fig 5).

Uric acid: Mean uric acid concentrations were greatest in insectivores ($1.77, SE = \pm 0.08$), followed by omnivores ($\pm 1.03, 0.04$), and frugivores ($0.71, \pm 0.03$). Results of uric acid model

Table 3: All migratory songbirds observed foraging on transects and the total number of each food item that each consumed.

Bird Species	Scientific Name	Number of Food Items Consumed			
		Fruits	Insects	Other	Unknown
American Goldfinch	<i>Spinus tristis</i>	0	0	1	9
American Redstart	<i>Setophaga ruticilla</i>	0	71	0	45
American Robin	<i>Turdus migratorius</i>	31	0	0	6
Baltimore Oriole	<i>Icterus galbula</i>	1	1	2	6
Black-and-white Warbler	<i>Mniotilta varia</i>	0	24	0	47
Blackpoll Warbler	<i>Setophaga striata</i>	0	2	0	1
Black-throated Blue Warbler	<i>Setophaga caerulescens</i>	1	1	0	3
Black-throated Green Warbler	<i>Setophaga virens</i>	0	0	0	2
Blue Jay	<i>Cyanocitta cristata</i>	2	0	5	2
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	0	16	0	14
Blue-headed Vireo	<i>Vireo solitarius</i>	0	0	0	1
Blue-winged Warbler	<i>Vermivora cyanoptera</i>	0	1	0	1
Brown Creeper	<i>Certhia americana</i>	0	5	0	11
Brown Thrasher	<i>Toxostoma rufum</i>	3	0	0	1
Brown-headed Nuthatch	<i>Sitta pusilla</i>	0	0	0	1
Catharus Thrushes	<i>Catharus sp</i>	4	3	0	6
Cedar Waxwing	<i>Bombycilla cedrorum</i>	2	0	0	0
Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>	0	1	0	2
Chipping Sparrow	<i>Spizella passerina</i>	0	0	0	3
Common Grackle	<i>Quiscalus quiscula</i>	0	0	0	1
Common Yellowthroat	<i>Geothlypis trichas</i>	1	15	0	30
Dark-eyed Junco	<i>Junco hyemalis</i>	0	0	4	1
Eastern Kingbird	<i>Tyrannus tyrannus</i>	0	2	0	1

Table 3. Continued

Bird Species	Scientific Name	Number of Food Items Consumed			
		Fruits	Insects	Other	Unknown
Eastern Phoebe	<i>Sayornis phoebe</i>	1	5	0	1
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	0	0	0	3
<i>Empidonax</i> flycatchers	<i>Empidonax sp</i>	0	9	0	2
Field Sparrow	<i>Spizella pusilla</i>	0	0	3	4
Fox Sparrow	<i>Passerella iliaca</i>	0	0	0	2
Golden-crowned Kinglet	<i>Regulus satrapa</i>	1	13	0	23
Gray Catbird	<i>Dumetella carolinensis</i>	43	2	0	8
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	0	4	0	3
House Finch	<i>Carpodacus mexicanus</i>	0	0	0	1
House Wren	<i>Troglodytes aedon</i>	0	2	0	4
Indigo Bunting	<i>Passerina cyanea</i>	0	1	0	4
Magnolia Warbler	<i>Setophaga magnolia</i>	0	2	0	4
Marsh Wren	<i>Cistothorus palustris</i>	0	0	1	0
Northern Parula	<i>Setophaga americana</i>	0	16	0	24
Northern Waterthrush	<i>Parkesia noveboracensis</i>	0	4	0	5
Olive-sided Flycatcher	<i>Contopus borealis</i>	0	1	0	0
Ovenbird	<i>Seiurus aurocapillus</i>	0	2	0	1
Palm Warbler	<i>Setophaga palmarum</i>	0	9	0	21
Philadelphia Vireo	<i>Vireo philadelphicus</i>	0	1	0	0
Pine Warbler	<i>Setophaga pinus</i>	0	0	0	8
Prairie Warbler	<i>Setophaga discolor</i>	0	5	0	9
Purple Finch	<i>Carpodacus purpureus</i>	0	1	0	2
Red-breasted Nuthatch	<i>Sitta canadensis</i>	0	1	0	15
Red-eyed Vireo	<i>Vireo olivaceus</i>	6	10	0	17
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	0	0	0	2

Table 3. Continued

Bird Species	Scientific Name	Number of Food Items Consumed			
		Fruits	Insects	Other	Unknown
Ruby-crowned Kinglet	<i>Regulus calendula</i>	2	18	0	42
Savannah Sparrow	<i>Passerculus sandwichensis</i>	0	0	0	2
Scarlet Tanager	<i>Piranga olivacea</i>	0	0	0	1
Song Sparrow	<i>Melospiza melodia</i>	3	1	9	11
Summer Tanager	<i>Piranga rubra</i>	1	3	0	3
Swamp Sparrow	<i>Melospiza georgiana</i>	0	2	10	15
Tennessee Warbler	<i>Leiothlypis peregrina</i>	0	0	0	2
Tree Swallow	<i>Tachycineta bicolor</i>	1	0	0	0
White-eyed Vireo	<i>Vireo griseus</i>	0	1	0	3
White-throated Sparrow	<i>Zonotrichia albicollis</i>	10	4	1	20
Winter Wren	<i>Troglodytes troglodytes</i>	0	1	0	2
Worm-eating Warbler	<i>Helmitheros vermivorum</i>	0	3	0	2
Yellow Warbler	<i>Setophaga petechia</i>	0	4	0	5
Yellow-billed cuckoo	<i>Coccyzus americanus</i>	0	5	0	3
Yellow-rumped Warbler	<i>Setophaga coronata</i>	42	79	2	92
Yellow-throated Warbler	<i>Setophaga dominica</i>	0	0	0	1
Yellow-throated Vireo	<i>Vireo flavifrons</i>	0	0	0	2

Table 4: Results from model comparison for insectivore TAG concentrations. Models with $\Delta AIC < 2.0$ are bolded. Fixed effects within the model set include time of day (Bleed), handling time (Time), distance to the southern tip of the Delmarva Peninsula, year (2016 and 2017), habitat (Shrub, Forest Interior, Forest Edge), hackberry presence, hackberry psyllid capture rate (Psyllid Abundance), and the interaction between hackberry presence and hackberry psyllid capture rate (HP X PA).

Model Predictors	K	AICc	Delta_AICc	AICcWt	LL
Bleed + Hackberry Presence	5	435.36	0.00	0.46	-212.53
Bleed + Hackberry Presence + Psyllid Abundance + HP X PA	7	436.30	0.94	0.29	-210.87
Global Model	12	438.00	2.64	0.12	-206.20
Bleed	5	438.50	3.14	0.09	-214.10
Bleed	4	442.69	7.34	0.01	-217.25
Bleed + Psyllid Availability	5	443.17	7.81	0.01	-216.44
Bleed + Time	5	443.21	7.85	0.01	-216.46
Bleed + Distance	5	444.16	8.81	0.01	-216.93
Bleed + Habitat	7	444.98	9.63	0.00	-215.21
Bleed + Time + Distance + Habitat	9	448.10	12.74	0.00	-214.59
Year	4	448.75	13.39	0.00	-220.27
Time	4	450.16	14.81	0.00	-220.98
Intercept	3	451.82	16.46	0.00	-222.85
Hackberry Presence + Psyllid Abundance + HP X PA	6	451.93	16.58	0.00	-219.76
Distance	4	453.43	18.07	0.00	-222.61
Habitat	6	456.21	20.85	0.00	-221.89

Table 5: Results from model comparison for frugivore TAG concentrations. Models with $\Delta AIC_c < 2.0$ are bolded. Fixed effects within the model set include time of day (Bleed), handling time (Time), distance to the southern tip of the Delmarva Peninsula, year (2016 and 2017), habitat (Shrub, Forest Interior, Forest Edge), hackberry presence, hackberry psyllid capture rate (Psyllid Abundance), the interaction between hackberry presence and hackberry psyllid capture rate (HP X PA), and fruit presence at the capture location (*sp* fruit).

Model Predictors	K	AIC _c	ΔAIC_c	AIC _c Wt	-2LogLik (deviance)
Bleed + Year	5.00	567.39	0.00	0.71	-278.54
Bleed + <i>Vitis</i> sp fruit	5.00	571.49	4.10	0.09	-280.59
Bleed + <i>Celtis</i> sp fruit	5.00	573.41	6.02	0.04	-281.55
Bleed + <i>Ilex opaca</i> fruit	5.00	573.55	6.17	0.03	-281.62
Bleed + <i>Lonicera japonica</i> fruit	5.00	574.68	7.29	0.02	-282.19
Bleed	4.00	575.20	7.81	0.01	-283.50
Bleed + <i>Rosa multiflora</i> fruit	5.00	575.25	7.86	0.01	-282.47
Bleed + Psyllid Availability	5.00	575.30	7.92	0.01	-282.50
Bleed + <i>Parthenocissus quincifolia</i> fruit	5.00	576.04	8.66	0.01	-282.87
Bleed + <i>Ligustrum sinense</i> fruit	5.00	576.59	9.20	0.01	-283.14
Bleed + <i>Juniperus virginiana</i> fruit	5.00	576.94	9.55	0.01	-283.32
Bleed + Hackberry Presence	5.00	577.06	9.68	0.01	-283.38
Bleed + Distance	5.00	577.08	9.70	0.01	-283.39
Bleed + <i>Phytolacca americana</i> fruit	5.00	577.27	9.89	0.01	-283.48
Bleed + <i>Morella</i> sp fruit	5.00	577.29	9.90	0.01	-283.49
Bleed + <i>Toxicodendron radicans</i> fruit	5.00	577.29	9.91	0.01	-283.49
Bleed + Time	5.00	577.30	9.91	0.01	-283.50
Year	4.00	577.37	9.98	0.00	-284.58
Bleed + Hackberry Presence + Psyllid Abundance + HP X PA	7.00	577.75	10.36	0.00	-281.59
Intercept	3.00	579.61	12.23	0.00	-286.75
Distance	4.00	580.79	13.40	0.00	-286.29
Bleed + Habitat	7.00	581.45	14.07	0.00	-283.44
Time	4.00	581.69	14.30	0.00	-286.74
Hackberry Presence + Psyllid Abundance + HP X PA	6.00	584.22	16.83	0.00	-285.90
Habitat	6.00	585.01	17.62	0.00	-286.29
Bleed + Time + Distance + Habitat	9.00	585.39	18.00	0.00	-283.23
Global Model	12.00	587.33	19.94	0.00	-280.84

Table 6: Results from model comparison for omnivore TAG concentrations. Models with $\Delta AIC < 2.0$ are bolded. Fixed effects within the model set include time of day (Bleed), handling time (Time), distance to the southern tip of the Delmarva Peninsula, year (2016 and 2017), habitat (Shrub, Forest Interior, Forest Edge), hackberry presence, hackberry psyllid capture rate (Psyllid Abundance), the interaction between hackberry presence and hackberry psyllid capture rate (HP X PA), and fruit presence at the capture location (*sp* fruit).

Model Predictors	K	AIC _c	ΔAIC_c	AIC _c Wt	-2LogLik (deviance)
Bleed + Hackberry Presence	5	603.62	0.00	0.43	-296.69
Bleed + <i>Juniperus virginiana</i> fruit	5	605.67	2.05	0.15	-297.71
Bleed + Hackberry Presence + Psyllid Abundance + HP X PA	7	607.10	3.48	0.08	-296.32
Bleed + <i>Ligustrum sinense</i> fruit	5	607.17	3.55	0.07	-298.46
Bleed + Year	5	608.26	4.64	0.04	-299.01
Bleed + <i>Ilex opaca</i> fruit	5	609.22	5.60	0.03	-299.49
Bleed + Distance	5	609.33	5.71	0.02	-299.54
Bleed + <i>Vitus sp</i> fruit	5	609.38	5.76	0.02	-299.57
Bleed	4	609.73	6.11	0.02	-300.78
Bleed + <i>Lonicera japonica</i> fruit	5	610.32	6.70	0.02	-300.04
Global Model	12	610.38	6.76	0.01	-292.53
Bleed + Time	5	610.77	7.15	0.01	-300.26
Hackberry Presence + Psyllid Abundance + HP X PA	6	610.78	7.16	0.01	-299.21
Year	4	610.95	7.33	0.01	-301.39
Bleed + <i>Rosa multiflora</i> fruit	5	611.19	7.57	0.01	-300.47
Bleed + Psyllid Availability	5	611.44	7.82	0.01	-300.60
Distance	4	611.54	7.92	0.01	-301.69
Bleed + <i>Phytolacca americana</i> fruit	5	611.55	7.93	0.01	-300.65
Bleed + <i>Celtis sp</i> fruit	5	611.59	7.97	0.01	-300.67
Bleed + <i>Morella sp</i> fruit	5	611.69	8.07	0.01	-300.72
Bleed + <i>Parthenocissus quincifolia</i> fruit	5	611.81	8.19	0.01	-300.78
Intercept	3	613.04	9.41	0.00	-303.47
Time	4	613.75	10.13	0.00	-302.79
Bleed + Habitat	7	614.23	10.61	0.00	-299.88
Bleed + Time + Distance + Habitat	9	615.67	12.05	0.00	-298.46
Habitat	6	617.42	13.80	0.00	-302.54

Table 7: Parameters, parameter estimates, and 95% confidence intervals (CI) included in top triacylglycerol (TAG) metabolite models. 95% CI that do not overlap zero are bolded. Parameters include handling time, time of day, distance to the southern tip of the Delmarva Peninsula, year (2016 and 2017), habitat (Shrub, Forest Interior, Forest Edge), hackberry availability, hackberry psyllid capture rate (Psyllid Abundance), and the interaction between hackberry presence and hackberry psyllid capture rate (HP X PA)

TAG (mM)		Parameter		
		Estimate	2.5%	97.5%
Insectivores	Time of Day	0.15	0.07	0.23
	Hackberry Presence (Present)	0.27	0.04	0.50
	Hackberry Psyllid Availability (Available)	-0.04	-0.36	0.28
	HP (presence) X PA (Available)	0.34	-0.12	0.80
Frugivores	Time of Day	0.18	0.07	0.30
	Year (2017)	-0.42	-0.69	-0.16
Omnivores	Time of Day	0.15	0.02	0.28
	Hackberry Presence (Present)	0.35	0.11	0.57

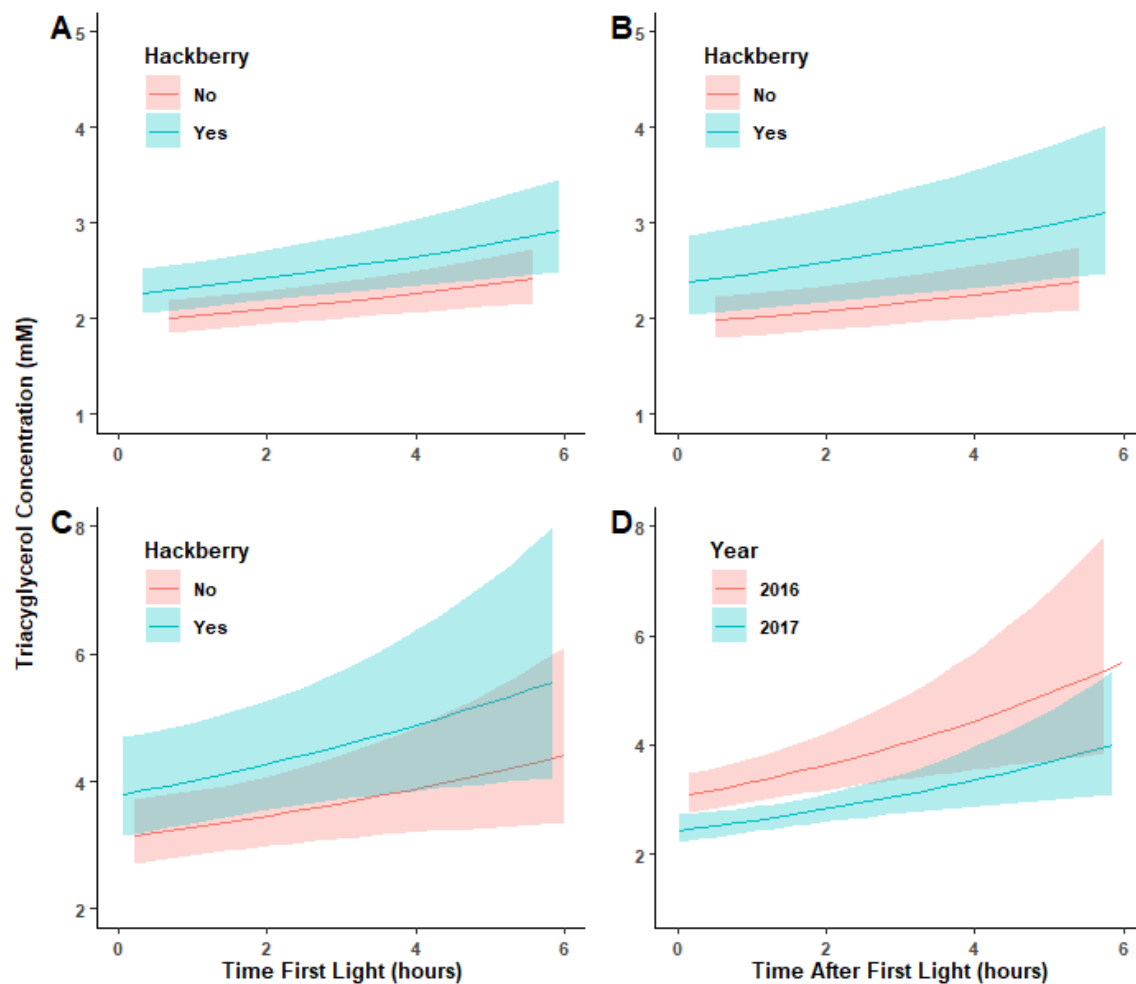


Figure 5: Predicted values of TAG concentrations as time after first light increased for A.) insectivores captured in areas where hackberry was present (blue) and where hackberry was absent (red) when hackberry psyllids were unavailable, B.) insectivores captured in areas where hackberry was present (blue) and where hackberry was absent (red) when hackberry psyllids were available, C.) omnivores captured in areas where hackberry was present (blue) and where hackberry was absent (red), and D.) frugivores during 2016 and 2017. The shaded areas represent 95% confidence intervals.

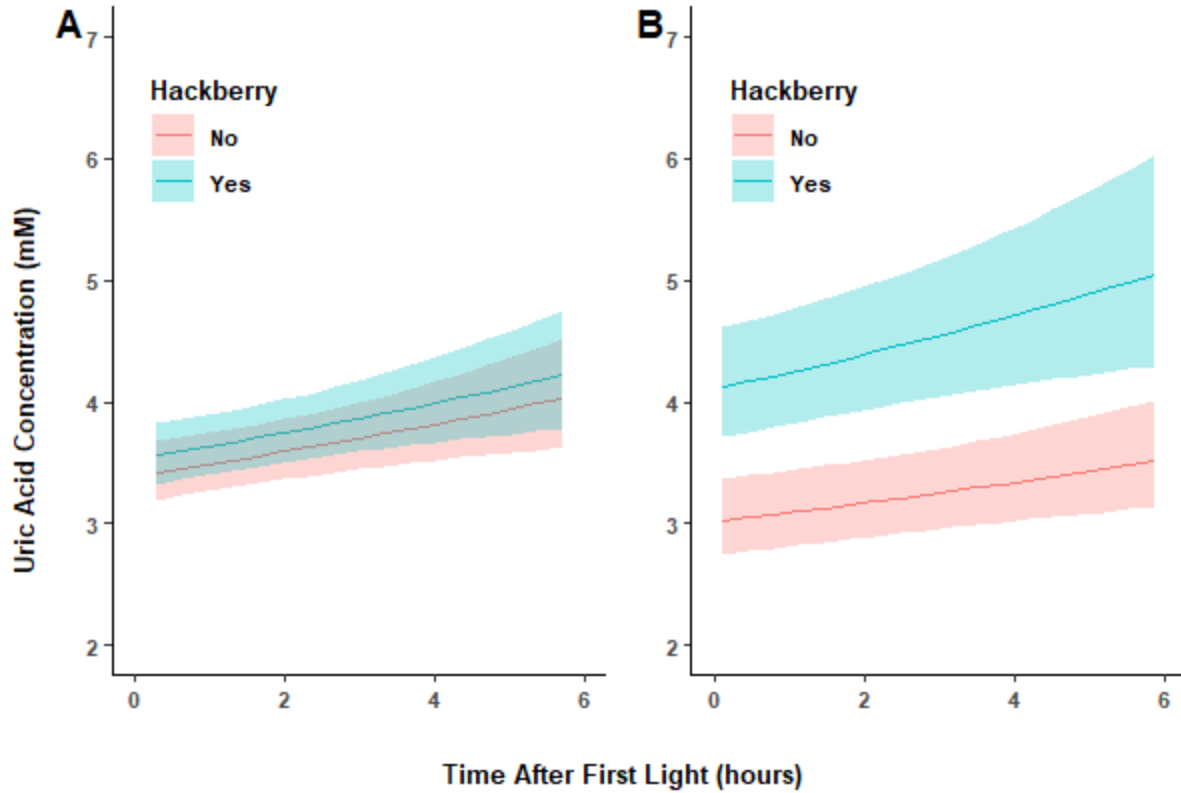


Figure 6: Predicted values of uric acid concentrations as time after first light increased for A.) insectivores captured in areas where hackberry was present (blue) and where hackberry was absent (red) before hackberry psyllids were available and B.) when hackberry psyllids were available. The shaded areas represent 95% confidence intervals.

selection analyses are presented in tables 8–10. Time of day, hackberry presence, area-wide psyllid abundance, and the interaction between these two predictors were all included in the top model for insectivore uric acid concentrations. The interaction between hackberry tree presence and hackberry psyllid availability indicated that uric acid concentrations were greater after psyllids were available and near hackberry trees for insectivores (fig 6). Time of day and handling time were both included within the top candidate models for omnivore uric acid concentrations, but time of day was an uninformative parameter and was not used for any further analyses (Arnold 2010; Leroux 2019). Omnivore uric acid concentrations decreased with increasing time since first light (table 11). Time after first light and year were both included in top frugivore uric acid models. Greater frugivore uric acid concentrations were found in birds captured in 2016 and, unlike insectivores, uric acid concentrations decreased throughout the day.

BUTY: Mean BUTY concentrations were greatest in insectivores (1.11, SE = ± 0.15), followed by omnivores (± 1.05 , 0.11), and frugivores (0.77, ± 0.07). Results of BUTY model selection analyses are presented in tables 12–14. Year, distance to the tip, hackberry presence, area-wide psyllid abundance, and the interaction between these two predictors were all included within the top model set for insect BUTY concentrations. The intercept-only model was also included in the top insectivore BUTY model set but 95% confidence intervals for all model-averaged parameter estimates overlapped zero (table 15). For omnivores, time of day, hackberry presence, psyllid availability, handling time, and seven ripe fruiting species were included within the top model set. However, all predictors except for time of day and ripe bayberry (*Morella sp*) fruit presence were removed from subsequent analyses because they were uninformative parameters (Leroux 2019). BUTY concentrations were lower for omnivores captured later in the

Table 8: Results from model comparison for insectivore uric acid concentrations. Fixed effects within the model set include time of day (Bleed), handling time (Time), distance to the southern tip of the Delmarva Peninsula, year (2016 and 2017), habitat (Shrub, Forest Interior, Forest Edge), hackberry presence, hackberry psyllid capture rate (Psyllid Abundance), and the interaction between hackberry presence and hackberry psyllid capture rate (HP X PA).

Model Predictors	K	AIC _c	ΔAIC _c	AIC _c Wt	-2LogLik (deviance)
Distance	4	245.08	0	0.11	-118.36
<i>Intercept</i>	3	245.53	0.44	0.08	-117.49
Bleed + Hackberry Presence	5	245.53	0.45	0.02	-117.49
Hackberry Presence + Distance	5	245.93	0.85	0.07	-117.69
Bleed	4	246.02	0.94	0.06	-117.74
Year	4	246.77	1.69	0.04	-115.87
Time	4	246.81	1.73	0.04	-118.13
Habitat	6	246.82	1.74	0.04	-118.13
Bleed + Year	5	246.94	1.86	0.04	-118.19
Bleed + Habitat + Hackberry Presence + Psyllid Abundance + HP X PA	7	246.95	1.87	0.04	-118.20
Bleed + Time	5	246.96	1.88	0.04	-118.21
Bleed + Psyllid Abundance	5	247.0	1.94	0.04	-118.24
Hackberry Presence + Psyllid Abundance + HP X PA	6	247.06	1.98	0.04	-118.26
Bleed + Hackberry Presence + Psyllid Abundance + HP X PA	7	247.12	2.04	0.03	-118.29
Bleed + Time + Distance + Habitat	9	247.17	2.09	0.03	-118.31
Global Model	12	247.26	2.18	0.03	-118.35

Table 9: Results from model comparison for frugivore uric acid concentrations. Fixed effects within the model set include time of day (Bleed), handling time (Time), distance to the southern tip of the Delmarva Peninsula, year (2016 and 2017), habitat (Shrub, Forest Interior, Forest Edge), hackberry presence, hackberry psyllid capture rate (Psyllid Abundance), and the interaction between hackberry presence and hackberry psyllid capture rate (HP X PA).

Model Predictors	K	AIC _c	ΔAIC _c	AIC _c Wt	-2LogLik (deviance)
Bleed + Year	5	115.50	0	0.35	-52.61
Bleed	4	116.94	1.43	0.17	-54.37
Bleed + Distance	5	118.33	2.83	0.08	-54.02
Bleed + Habitat	7	118.49	2.99	0.08	-51.97
Bleed + Psyllid Availability	5	118.55	3.05	0.08	-54.13
Bleed + Hackberry Presence	5	118.62	3.11	0.07	-54.16
Year	4	118.84	3.33	0.07	-55.32
Bleed + Time	5	118.99	3.49	0.06	-54.35
Bleed + Hackberry Presence + Psyllid Abundance + HP X PA	7	122.18	6.68	0.01	-53.82
Intercept	3	122.34	6.83	0.01	-58.11
Bleed + Time + Distance + Habitat	9	122.70	7.2	0.01	-51.91
Habitat	6	123.78	8.28	0.01	-55.69
Distance	4	124.12	8.61	0.00	-57.96
Time	4	124.37	8.86	0.00	-58.09
Hackberry Presence + Psyllid Abundance + HP X PA	6	126.95	11.44	0.00	-57.27
Global Model	12	129.2	13.69	0.00	-51.82

Table 10: Results from model comparison for omnivore uric acid concentrations. Fixed effects within the model set include time of day (Bleed), handling time (Time), distance to the southern tip of the Delmarva Peninsula, year (2016 and 2017), habitat (Shrub, Forest Interior, Forest Edge), hackberry presence, hackberry psyllid capture rate (Psyllid Abundance), and the interaction between hackberry presence and hackberry psyllid capture rate (HP X PA).

Model Predictors	K	AIC _c	ΔAIC _c	AIC _c Wt	-2LogLik (deviance)
Time	4	304.94	0.00	0.38	-148.38
Bleed + Time	5	305.75	0.80	0.25	-147.73
Bleed + Time + Distance + Habitat	9	308.01	3.07	0.08	-144.57
Global Model	12	308.59	3.64	0.06	-141.53
Hackberry Presence + Psyllid Abundance + HP X PA	6	310.03	5.08	0.03	-148.81
Bleed	5	310.04	5.10	0.03	-149.88
Year	4	310.20	5.26	0.03	-151.01
Distance	4	310.24	5.30	0.03	-151.03
Bleed + Hackberry Presence	5	310.53	5.59	0.02	-150.12
Bleed + Distance	5	310.60	5.66	0.02	-150.16
Bleed + Psyllid Availability	5	310.62	5.68	0.02	-150.17
Intercept	3	311.18	6.23	0.02	-152.53
Bleed + Hackberry Presence + P. Abundance + HP X PA	7	311.23	6.28	0.02	-148.35
Bleed	4	312.01	7.07	0.01	-151.91
Habitat	6	313.65	8.71	0.00	-150.63
Bleed + Habitat	7	314.45	9.50	0.00	-149.96

Table 11: Parameters, parameter estimates, and 95% confidence intervals (CI) included in top uric acid metabolite models. 95% CI that do not overlap zero are bolded. Parameters include handling time, time of day, distance to the southern tip of the Delmarva Peninsula, year (2016 and 2017), habitat (Shrub, Forest Interior, Forest Edge), hackberry availability, hackberry psyllid capture rate (Psyllid Abundance), and the interaction between hackberry presence and hackberry psyllid capture rate (HP X PA).

Uric Acid (mM)		Parameter Estimate	2.5%	97.5%
Insectivores	Time of Day	0.10	0.03	0.16
	Hackberry Presence (Present)	0.08	-0.094	0.25
	Hackberry Psyllid Availability (Available)	-0.27	-0.52	0.01
	HP (presence) X PA (Available)	0.54	0.22	0.88
Frugivores	Handling Time	-0.08	-0.13	-0.02
	Year (2017)	-0.13	-0.26	0.01
Omnivores	Handling Time	-0.06	-0.57	0.46

Table 12: Results from model comparison for insectivore BUTY concentrations. Models with $\Delta AIC_c < 2.0$ are bolded. Fixed effects within the model set include handling time (Bleed), time of day (Time), distance to the southern tip of the Delmarva Peninsula, year (2016 and 2017), habitat (Shrub, Forest Interior, Forest Edge), hackberry presence, hackberry psyllid capture rate (Psyllid Abundance), the interaction between hackberry presence and hackberry psyllid capture rate (HP X PA), and fruit presence at the capture location (*sp* fruit).

Model Predictors	K	AIC _c	ΔAIC_c	AIC _c Wt	-2LogLik (deviance)
Bleed	4	245.08	0.00	0.11	-118.36
Bleed + <i>Morella sp</i> fruit	5	245.53	0.45	0.09	-117.49
Bleed + <i>Vitis sp</i> fruit	5	245.54	0.46	0.09	-117.50
Bleed + <i>Juniperus virginiana</i> fruit	5	245.93	0.85	0.07	-117.69
Bleed + Hackberry Presence	5	246.03	0.95	0.07	-117.74
Bleed + Habitat	7	246.78	1.70	0.05	-115.87
Bleed + Psyllid Availability	5	246.81	1.73	0.05	-118.13
Bleed + Year	5	246.82	1.74	0.05	-118.14
Bleed + Time	5	246.94	1.86	0.04	-118.20
Bleed + <i>Parthenocissus quincifolia</i> fruit	5	246.95	1.87	0.04	-118.20
Bleed + <i>Ilex opaca</i> fruit	5	246.97	1.89	0.04	-118.21
Bleed + <i>Ligustrum sinense</i> fruit	5	247.03	1.95	0.04	-118.24
Bleed + <i>Lonicera japonica</i> fruit	5	247.07	1.99	0.04	-118.26
Bleed + <i>Celtis sp</i> fruit	5	247.13	2.05	0.04	-118.29
Bleed + <i>Rosa multiflora</i> fruit	5	247.18	2.10	0.04	-118.32
Bleed + <i>Phytolacca americana</i> fruit	5	247.26	2.18	0.04	-118.36
Bleed + Distance	5	247.26	2.18	0.04	-118.36
Bleed + Hackberry Presence + Psyllid Abundance + HP X PA	7	248.91	3.83	0.02	-116.94
Intercept	3	249.46	4.38	0.01	-121.62
Habitat	6	249.61	4.53	0.01	-118.42
Distance	4	250.69	5.61	0.01	-121.17
Bleed + Time + Distance + Habitat	9	250.85	5.77	0.01	-115.58
Time	4	251.22	6.14	0.01	-121.43
Year	4	251.50	6.42	0.00	-121.57
Hackberry Presence + Psyllid Abundance + HP X PA	6	254.57	9.49	0.00	-120.90
Global Model	12	256.51	11.43	0.00	-114.74

Table 13: Results from model comparison for frugivore BUTY concentrations. Models with $\Delta AIC < 2.0$ are bolded. Fixed effects within the model set include handling time (Bleed), time of day (Time), distance to the southern tip of the Delmarva Peninsula, year (2016 and 2017), habitat (Shrub, Forest Interior, Forest Edge), hackberry presence, hackberry psyllid capture rate (Psyllid Abundance), the interaction between hackberry presence and hackberry psyllid capture rate (HP X PA), and fruit presence at the capture location (*sp* fruit).

Model Predictors	K	AIC _c	ΔAIC_c	AIC _c Wt	-2LogLik (deviance)
Bleed + Time	5	196.11	0.00	0.25	-92.86
Bleed + <i>Ilex opaca</i> fruit	5	197.71	1.60	0.11	-93.66
Bleed + <i>Toxicodendron radicans</i> fruit	5	197.93	1.82	0.10	-93.77
Bleed + <i>Phytolacca americana</i> fruit	5	198.36	2.25	0.08	-93.98
Bleed + <i>Vitis sp</i> fruit	5	198.78	2.67	0.07	-94.19
Bleed	4	199.03	2.92	0.06	-95.38
Bleed + <i>Ligustrum sinense</i> fruit	5	199.78	3.67	0.04	-94.69
Bleed + <i>Celtis sp</i> fruit	5	200.02	3.91	0.04	-94.81
Bleed + <i>Rosa multiflora</i> fruit	5	200.11	4.00	0.03	-94.86
Bleed + Distance	5	200.26	4.15	0.03	-94.93
Bleed + <i>Juniperus virginiana</i> fruit	5	200.43	4.32	0.03	-95.02
Bleed + <i>Morella sp</i> fruit	5	200.76	4.66	0.02	-95.18
Bleed + Psyllid Availability	5	200.79	4.68	0.02	-95.20
Bleed + Hackberry Presence	5	201.10	4.99	0.02	-95.35
Bleed + Year	5	201.14	5.03	0.02	-95.37
Bleed + <i>Lonicera japonica</i> fruit	5	201.14	5.03	0.02	-95.37
Bleed + <i>Parthenocissus quincifolia</i> fruit	5	201.16	5.05	0.02	-95.38
Bleed + Hackberry Presence + Psyllid Abundance + HP X PA	7	203.05	6.94	0.01	-94.15
Bleed + Time + Distance + Habitat	9	203.65	7.54	0.01	-92.21
Bleed + Habitat	7	204.41	8.30	0.00	-94.83
Global Model	12	208.46	12.35	0.00	-91.15
Time	4	229.00	32.89	0.00	-110.37
Intercept	3	231.00	34.89	0.00	-112.42
Year	4	232.36	36.26	0.00	-112.05
Distance	4	232.95	36.84	0.00	-112.34
Hackberry Presence + Psyllid Abundance + HP X PA	6	233.94	37.83	0.00	-110.69
Habitat	6	237.19	41.08	0.00	-112.32

Table 14: Results from model comparison for omnivore BUTY concentrations. Models with $\Delta AIC < 2.0$ are bolded. Fixed effects within the model set include handling time (Bleed), time of day (Time), distance to the southern tip of the Delmarva Peninsula, year (2016 and 2017), habitat (Shrub, Forest Interior, Forest Edge), hackberry presence, hackberry psyllid capture rate (Psyllid Abundance), the interaction between hackberry presence and hackberry psyllid capture rate (HP X PA), and fruit presence at the capture location (*sp* fruit).

Model names	K	AIC _c	ΔAIC_c	AIC _c Wt	-2LogLik (deviance)
Bleed	4	245.08	0	0.11	-118.36
Bleed + <i>Morella sp</i> fruit	5	245.53	0.45	0.09	-117.49
Bleed + <i>Vitis sp</i> fruit	5	245.54	0.46	0.09	-117.5
Bleed + <i>Juniperus virginiana</i> fruit	5	245.93	0.85	0.07	-117.69
Bleed + Hackberry Presence	5	246.03	0.95	0.07	-117.74
Bleed + Habitat	7	246.78	1.7	0.05	-115.87
Bleed + Psyllid Availability	5	246.81	1.73	0.05	-118.13
Bleed + Year	5	246.82	1.74	0.05	-118.14
Bleed + Time	5	246.94	1.86	0.04	-118.2
Bleed + <i>Parthenocissus quincifolia</i> fruit	5	246.95	1.87	0.04	-118.2
Bleed + <i>Ilex opaca</i> fruit	5	246.97	1.89	0.04	-118.21
Bleed + <i>Ligustrum sinense</i> fruit	5	247.03	1.95	0.04	-118.24
Bleed + <i>Lonicera japonica</i> fruit	5	247.07	1.99	0.04	-118.26
Bleed + <i>Celtis sp</i> fruit	5	247.13	2.05	0.04	-118.29
Bleed + <i>Rosa multiflora</i> fruit	5	247.18	2.1	0.04	-118.32
Bleed + <i>Phytolacca americana</i> fruit	5	247.26	2.18	0.04	-118.36
Bleed + Distance	5	247.26	2.18	0.04	-118.36
Bleed + Hackberry Presence + Psyllid Abundance + HP X PA	7	248.91	3.83	0.02	-116.94
Intercept	3	249.46	4.38	0.01	-121.62
Habitat	6	249.61	4.53	0.01	-118.42
Distance	4	250.69	5.61	0.01	-121.17
Bleed + Time + Distance + Habitat	9	250.85	5.77	0.01	-115.58
Time	4	251.22	6.14	0.01	-121.43
Year	4	251.5	6.42	0.00	-121.57
Hackberry Presence + Psyllid Abundance + HP X PA	6	254.57	9.49	0.00	-120.9
Global Model	12	256.51	11.43	0.00	-114.74

Table 15: Parameters, parameter estimates, and 95% confidence intervals (CI) included in top B-OH-butyrate (BUTY) metabolite models. 95% CI that do not overlap zero are bolded. Parameters include handling time, time of day, distance to the southern tip of the Delmarva Peninsula, year (2016 and 2017), habitat (Shrub, Forest Interior, Forest Edge), hackberry availability, hackberry psyllid capture rate (Psyllid Abundance), and the interaction between hackberry presence and hackberry psyllid capture rate (HP X PA).

	BUTY (mM)	Parameter		
		Estimate	2.5%	97.5%
Insectivores	Distance	-0.25	-0.54	0.04
	Year (2017)	0.31	-0.29	0.91
	Time of Day	-0.24	-0.65	0.17
	Hackberry Presence	-0.54	-1.13	0.06
Frugivores	Time of Day	-0.50	-0.64	-0.37
	Handling Time	-1.50	-2.83	-0.18
	Poison Ivy presence	-1.77	-3.26	-0.27
	American Holly Presence	-0.63	-1.25	-0.02
Omnivores	Time of Day	-0.26	-0.45	-0.08
	Bayberry Fruit Presence	-0.46	-1.11	0.18

day and near-ripe bayberry fruits (table 15). Time of day, handling time, and two ripe fruiting species were important parameters within the top BUTY model set for frugivores. BUTY concentrations were lower later in the day, after a greater handling time, near ripe poison ivy (*Toxicodendron radicans*), and near-ripe American holly (*Ilex opaca*) (table 9).

DISCUSSION

I found that Homopteran abundance influenced migratory insectivorous songbird refueling performance at an autumn stopover location (fig. 5, 6). I identified a tree species, hackberry, that provided a protein source for migrating songbirds—the hackberry psyllid, a host-specific Homopteran that was associated with greater protein metabolism for birds that consumed insects (fig. 6). Other plasma metabolite studies have identified important fruits for autumn migratory

songbirds, but insectivorous birds are a group that have largely been neglected in North American studies (Seewagen et al. 2011; Smith and McWilliams 2010; Smith 2013; Smith et al. 2015; Hoh et al. 2018). Establishing the link between important arthropod taxa and physiological condition highlights the importance of conservation initiatives that promote insect abundance in avian stopover sites. Identifying high-quality insect prey such as hackberry psyllids, is particularly promising for restoration projects because hackberry psyllids are plant taxon-specific so host plants can be established to increase insect abundance.

Increasing hackberry psyllid abundance would be particularly beneficial for birds migrating later in the season because psyllids are available after other Homopteran populations have decreased (fig 3), although temporal availability was not consistent between years at my study site. Interestingly, hackberry psyllids were available approximately one month earlier in 2017 than in 2016. The methods used to quantify availability differed between years, but I believe tropical storms Hermine (2 – 4 Sep) and Matthew (7 – 10 Oct) (fig 4) may have limited insect availability during 2016. I observed hackberry psyllids often emerging from galls on leaves that were yellowing prior to leaf senescence and these leaves were not as firmly attached to the branch as greener leaves and likely blew onto the ground during the 2016 storms. While psyllids can emerge from leaves after leaf senescence, rainfall increases gall mortality for gall-forming psyllids (Semeão et al. 2012) and the excessive rainfall associated with the storms may have increased hackberry psyllid and other arthropod mortality during 2016, resulting in significantly lower uric acid concentrations. Similar patterns have been observed at a coastal stopover following Hurricane Rita in Louisiana, USA; fewer Homoptera were observed on dead branch clippings following the storm (Dobbs et al 2009). These observations highlight the stochastic nature of migration along the east coast of North America during autumn and adds further explanation for why older migrants

choose to migrate via more inland routes and some coastal bird populations migrate earlier in years when tropical storm potential is greater (Hecksher 2018; Clipp et al. 2020).

In addition to tropical storms, birds that migrate along the coast must also face ecological barriers associated with variation in coastal geography (i.e., large water bodies). Bird density will often be greatest in proximity to these barriers and the greatest concentration of birds in the study area examined here are thought to be in the southernmost 5 km of the Delmarva Peninsula nearest the mouth of the Chesapeake Bay (McCann et al. 1993). I observed concentrations of north-bound birds flying at canopy height, typically just after sunrise, on most mornings at sites that were within 5 km of the southern tip and the “morning flight” (Wiedner et al. 1992) did seem to be greater nearer the tip of the peninsula. This pattern is consistent with other coastal areas where birds are abundant near ecological barriers and often participate in diurnal morning flights (Wiedner et al. 1992). Morning flights are often thought to be a response to increased competition (Lindström and Alerstam 1986; Chernetzov 2006), and I expected that proximity to the barrier at my study area would be included in the best supported models if birds encountered greater competition near the mouth of the Chesapeake Bay as a result. However, proximity to the barrier did not appear in any of the top-ranked model sets, which supports more recent evidence that points to correction for nocturnal wind drift as a potential mechanism (Van Doren et al. 2014; 2016).

Time since first light was an important predictor of metabolite concentrations (figs 5–7), suggesting that birds that begin foraging earlier can accumulate fuel and recover from overnight fasting more readily. Birds that arrive at new stopover sites often lack knowledge of spatial patterns of food resources, yet can recognize food sources that they have previously encountered (Telleria and Pérez-tris 2007). Because many plants experience fruit ripening and leaf senescence (e.g. when most hackberry psyllids emerge from leaf galls) earlier at higher latitudes, birds may encounter

hackberry psyllids at sequential stopover sites along their southward migration and choose to forage in areas where hackberry is present based on their prior experience (Schafer et al. 2008). I suggest that plants like hackberry, that are widely available throughout North America, provide a source of insects for birds are more likely to attract migrating songbirds. This hypothesis is supported by a parallel study examining foraging tree preference at the study area (Hines et al unpublished) and because both insectivores and omnivores exhibited greater protein consumption and lipid accumulation when captured near hackberry trees. Hackberry trees do produce ripe fruits during autumn but frugivore refueling indices were not affected by hackberry presence in these areas, supporting my contention that the psyllids are responsible for elevated insectivore and omnivore refueling performance.

The autumnal fruiting plant assemblage at my site is different than other stopover sites to the north and inland, where many of the birds I captured likely originated (Parrish 1997, Smith et al. 2013). Two fruiting plant taxa (*Cornus* sp and *Viburnum* sp) that typically provide abundant, high-quality nutrition at other eastern United States stopover habitats were practically nonexistent at my sampling locations, which may have affected foraging behavior. Migratory songbirds display a high degree of diet plasticity during migration and, in lieu of abundant high-quality fruits, may focus more on arthropods or less nutritious fruits and insects along the Delmarva Peninsula. I did observe a greater number of bird species forage primarily on insects at my study site than in other stopover locations along the east coast (Parrish 1997), and my observations of several species consuming bayberries, which contain saturated fatty acids, seem to support this contention because they are reportedly indigestible for all birds except yellow-rumped warblers (*Setophaga coronata*) and tree swallows (*Tachycineta bicolor*) (Place and Stiles 1992). Despite the paucity of high-quality fruits, I observed few birds consuming non-native fruits and I had zero non-native fruits

included in any top models for frugivores or omnivores. Chinese privet, for example, is one of the least consumed fruits (Hines unpub), despite being widely available (fig. 2) and nutritious (Greenberg and Walter 2010). Many nonnative fruits were eaten less often than would be expected given their availability (fig. 2), likely because they lack a coevolutionary history with North American songbirds.

My results suggest habitat with mostly non-native fruiting plants represents relatively poor-quality refueling habitat and support the contention that removal of these non-native fruits will not harm refueling songbirds if they are replaced by native species (Smith et al. 2013). Removal of non-native fruiting species would likely also benefit insectivores because greater insect-biomass is found on native plants than non-native plants because they lack a coevolutionary history with native insects (Zuefle et al. 2008). Homoptera are strictly phytophagous and typically restricted to a narrow range of native host plants (Frost 1954; Jaenike 1990), so they would likely increase in abundance if non-native plants were to be replaced by native taxa.

Conclusion

The study of insects as an important nutritional resource for migrating songbirds has been neglected. This study demonstrates that insectivorous songbirds accumulate more fuel when preferred arthropod prey are more available and near sources of host-specific arthropods. This is especially important in areas where migratory songbirds concentrate and high-quality fruiting species are scarce, so birds must rely on novel or less-nutritional food. In this study, I found that native fruits were more likely to benefit frugivorous. Many of these native plants provide additional benefits to other species; hackberry trees, for example, provide fruit to many vertebrate taxa (Koprowski 1991; Juan et al. 2006), but the plant tissue is also the exclusive larval food for six Lepidopteran (Brock and Kaufman 2003), 12 psyllidae (Thomas 2012), and 23 midge (Order:

Diptera) taxa (Gagne and Moser 2013). Species that have a disproportionately large effect on their surrounding communities and interact with other organisms across trophic levels, such as hackberry, are of high conservation value (Power et al. 1996; Dattilo et al. 2016) and would be candidate plant species for stopover habitat restoration projects. Hackberry is also native to eastern North America (Krajicek and Williams 1990) and occupies a wide range of habitat, further qualifying it as a viable tree choice for restoration projects because birds would be more likely to recognize it as a source of fruit and/or insect prey because they had encountered it before. Stopover locations with more abundant food resources that songbirds recognize may be more likely to attract migrating birds. Therefore, native plants that provide greater sources of energy are likely recognized by bird to facilitate more accurate migratory decisions.

CHAPTER 3

HOST-DEPENDENT INSECTS MODULATE SEED DISPERSAL PATTERNS AND PLANT COMMUNITY ASSEMBLAGE

INTRODUCTION

Plant-animal mutualism interactions are ubiquitous in nature and have played a key role in plant species diversification for over 100 million years (Bascompte and Jordano 2007; Bascompte 2019). Seed dispersal mutualisms are widespread and involve primarily vertebrates (Van der Pijl 1982; Nuismer et al. 2013; Valido and Olesen 2019), while insect-mediated seed dispersal is limited to ants, hornets, and camel crickets (Chen et al. 2017; Penn and Crist 2018; Suetsugu 2018). Of course, not all plant-animal interactions are mutualistic. Many animals depend on plants for food, including many taxa of host-specific insects that are generally considered to be parasites because they glean nutrition from the host plant while providing no obvious benefit in return (Hodkinson 2009; Yang and Mitter 1994). However, parasitism is favored to evolve into mutualism if the survival of the parasite depends upon the host's survival (Ewald 1987), such that these insects may confer an unobserved benefit to the host. These cryptic interactions may be indirect and not readily apparent and often discovered accidentally (Wootton 1994). Seed dispersal mutualisms offer a potential conduit for insect parasites to benefit host plants that produce fleshy fruits with seeds that are often dispersed by birds that also consume insects (Parrish 1997).

Avian Seed Dispersal

Avian taxa most commonly disperse seeds in North America during autumn when many songbird species engage in long-distance migrations (Sauer et al. 2013) to escape freezing temperatures and food shortages associated with low plant and arthropod productivity in winter (Hails 1982; Berthold 2001; Boyle et al. 2010). These journeys are energetically taxing (Wikelski

et al. 2003; McWilliams et al. 2004; Fristoe 2015) and a strategy many birds use to increase lipid reserves, their primary in-flight fuel, is to consume fruits rapidly that are high in fatty acids and sugars (King and Farner 1965; Bairlein 1998). Plants capitalize on bird migrations and synchronize fruiting events with periods of higher avian abundance (Stiles 1980; Skeate 1987; Hanya 2005) to facilitate seed dispersal by birds because they are particularly effective seed-dispersal vectors (Willson 1986; Jordano and Schupp 2000; Viana et al. 2016). Some autumn-fruiting plants have developed strategies to attract birds, though such strategies may come at a cost for the plant (Snow and Whigham 1989). For example, increasing fruit pulp, which is generally a good indicator of nutritional quality (Johnson et al. 1985), may decrease overall fruit production and vice versa (Snow and Whigham 1989). Other strategies plants use to attract birds include the use of contrasting colored leaves and fruits to facilitate discovery (Stiles 1982; Duan and Quan 2013), as well as producing secondary compounds within their fruits that counter oxidative stress when consumed by avian migrants (Bolser et al. 2013) brought on by long distance flights (Jenni-Eiermann et al. 2014). Such strategies represent attempts by plants to co-opt the mutualism between birds and other autumn-fruiting plants.

More generally, almost all plant taxa support symbionts and these symbionts can affect growth and survival of host plants through a variety of mechanisms (Ruehle and Marx 1979). Most recognized among plant symbionts are microbes and underground fungi, but many galling and mining insects depend on a single plant host and, thus, are also symbionts (Giron et al. 2016; Klepzig et al 2009). Because symbionts are capable of affecting their hosts in a variety of ways, such relationships may also affect mutualistic relationships between host plants and other organisms. In the case of autumn-fruiting plants, a symbiont may be able to co-opt and otherwise

manipulate the likelihood of fruit consumption and subsequent seed dispersal, mediated through the host plant.

Fruits are integral to the diet of many migratory birds, but most fruits do not meet metabolic protein needs (Witmer 1998; Smith et al. 2007), so most birds must seek another source of protein (Izhaki and Safriel 1989). Protein is critical as it replenishes spent muscle and gut tissue following long migratory flights (Aamidor et al. 2011), is a metabolic source of water (Gerson and Guglielmo 2011), and facilitates the transport of free fatty acids from adipose tissue to flight muscle mitochondria (Guglielmo 2010). Birds refuel more efficiently on a balanced diet than one that relies solely on fruit or arthropods (Bairlein 2002; Bairlein and Gwinner 1994), so birds must sometimes search for arthropod-rich areas. If an area is particularly rich in arthropods, migrants may disproportionately spend more time in that area (Johnson 2000). Other locations where frugivorous birds disproportionately spend time such as tree-fall gaps, favorable perching locations, and near other fruiting trees, often receive greater seed rain from defecation (Hoppes 1988; Debussche and Isenmann 1994; Herrera et al. 1994; Smith and McWilliams 2014) so arthropod-rich areas may also induce secondary seed deposition.

Songbirds are known to disproportionately forage on plant-sucking insects like Auchenorrhyncha and Sternorrhyncha (hereafter, Homoptera) throughout North America, likely because such taxa are composed of relatively high concentrations of triacylglycerol (Strong 1963; Rahbé et al. 1994). Phytophagous insects like Homoptera are more likely to be host-specific (i.e., symbionts) than other arthropod taxa (Jaenike 1990). These Homoptera that foraging birds prefer may act as a mechanism to facilitate fruiting plant community development if they attract songbirds and, subsequently, seeds from allospecific plants. These insects would likely also affect seed dispersal patterns of their host plant if the host also produced fleshy fruit.

One potentially important plant that seems to fit within this theme of offering both fruits and insects to autumn migrants in eastern North America is the hackberry tree (*Celtis spp*). The fruit is consumed throughout the autumn and winter seasons by resident, migrating, and wintering birds (Everitt and Alaniz 1981; Thompson and Willson 1979) despite relatively low nutritional content and with no apparent fruit-related mechanism to attract avian dispersers (Stiles and White 1982; Johnson et al. 1985). Hackberry trees can be found throughout North America (Gagne and Moser 2013) where they serve as the obligate host for hackberry psyllids (*Pachypsylla spp.*), an ephemerally abundant, phytophagous arthropod (Thomas 2012). The 2–5 mm long psyllids overwinter in cracks and crevices of trees or in leaf litter, and then, mate and lay eggs on hackberry leaf buds in early spring, after which the adults die. The eggs hatch and nymphs emerge to feed on phloem within the host leaf, which then grows around the larvae to form a gall. The larvae mature within the galls before emerging as adults *en masse* in late summer/autumn (Hodkinson 2009).

The psyllid irruption often coincides with the peak of autumn songbird migration, when avian predators are most abundant (Moser 1965; MacMynowski and Root 2007; Thomas 2012). Hackberry psyllids attract migratory songbirds during the early spring when they are ovipositing on leaves (Strode 2009) and possibly also during autumn migration. Therefore, if birds are foraging preferentially on hackberry psyllids, they may be more likely to consume hackberry fruits, and subsequently disperse them. Additionally, fruit seeds from other plants may already be in the bird's gut (Wenny 2000) and be disproportionately dispersed in the local habitat when psyllids are most abundant. However, no research that I am aware has tested whether psyllids, or any other arthropod taxa, affect bird-plant seed dispersal mutualisms by enhancing host plant mutualisms or by interfering with the relationship between birds and other plants.

Hypotheses

I tested whether the emergence of hackberry psyllids 1) attracts birds to the host tree; 2) facilitates dispersal of hackberry seeds away from the mother plant, and 3) facilitates the dispersal of other autumn-fruiting plant seeds to the host tree and surrounding habitat, resulting in an increase in fruiting plant richness near the host tree.

METHODS

Study Site

The study was conducted in 2016 and 2017 on the southern Delmarva Peninsula, Virginia; an important autumn migratory stopover area (McCann et al. 1993) where hackberry is patchily available. The habitat on the southern Delmarva Peninsula consists primarily of agricultural fields and isolated patches of forest and shrub-scrub on the interior and salt-water influenced habitats along the coasts. Sites included: Eastern Shore of Virginia National Wildlife Refuge (NWR), Fisherman's Island NWR, Kiptopeke State Park, Cape Charles Natural Area Preserve (NAP), Pickett's Harbor NAP, and Savage Neck Dunes NAP (fig 7).

Foraging Bird Surveys

To determine if birds foraged disproportionately in hackberry trees relative to other trees, 250 m transects were walked through forested habitat where hackberry was present for the first six hours post-sunrise at a standard pace (approx. 1 km hr⁻¹) twice per week. Observers were allowed to stray from the central transect line as far as 10 m to facilitate observation of foraging birds to record the following: date, time, site, species and sex of bird, species of tree, bird substrate, prey substrate, foraging maneuver (following Remsen and Robinson 1990), and prey

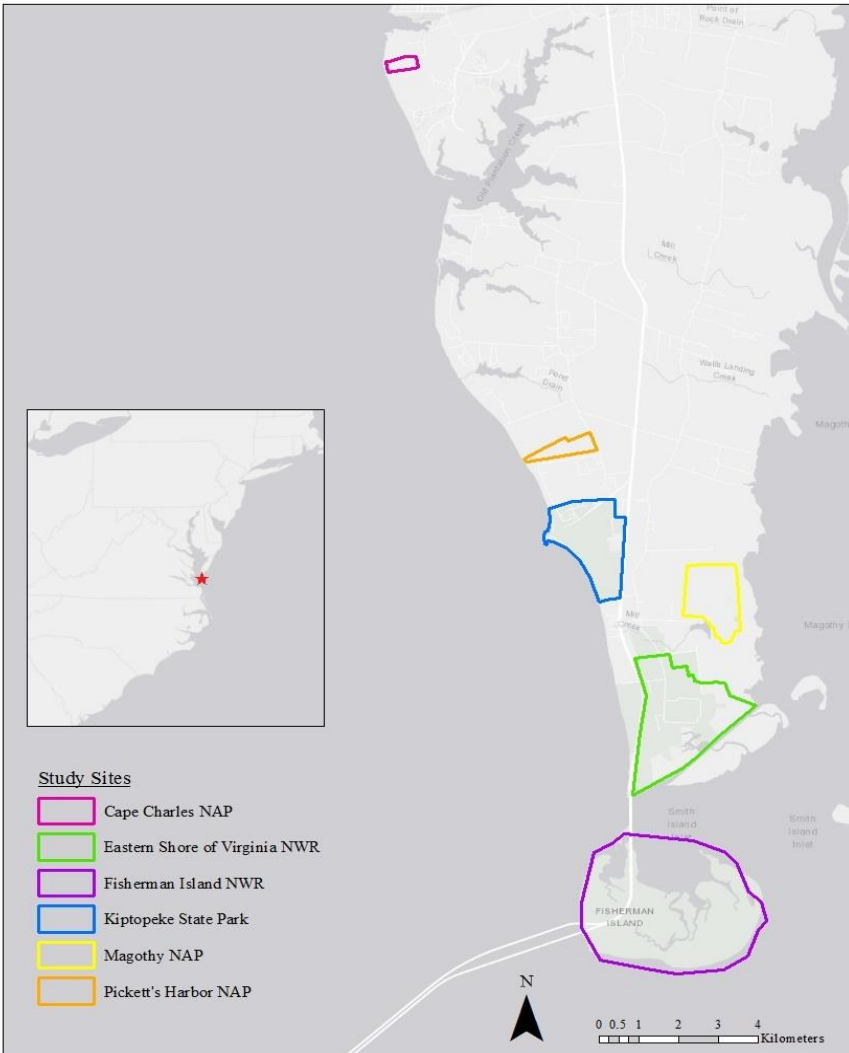


Figure 7: Map of study area study sites on the lower Delmarva Peninsula, Virginia

identity (when possible). Only individuals that could be positively identified as a unique bird (i.e., dichromatic species and juvenile/mature birds) were recorded within 100 m of another to avoid pseudoreplication (Hurlbert et al. 1984). An angle order-method (using third nearest individual tree to avoid potential bias associated with clumping) was used to quantify tree species availability (Engemann et al. 1994) at 25 random points along each transect (as far as 10 m from the central transect line). Diameter at breast height (dbh, approximately 140 cm from the ground) was used to calculate basal area for trees >4 cm because basal area can be used to indicate relative proportion of foraging substrate available to foraging birds (Jose and Gillespie 1997).

Hackberry Psyllid Abundance

To determine the phenology of emergence of adult hackberry psyllids, yellow sticky traps (Hall et al. 2007) were hung approximately 2 m high from ten hackberry branches (spaced 25 m apart) along foraging transects and four yellow sticky traps were hung at isolated hackberry trees at Pickett's Harbor NAP from 24 Aug – 21 Nov 2017. The sticky traps were checked weekly and arthropods were identified as hackberry psyllids or to order, counted, and the sticky trap was replaced.

Hackberry Seed Dispersal

To determine if hackberry psyllid abundance was associated with temporal hackberry seed dispersal patterns, seed rain was recorded from an area surrounding four isolated hackberry trees located along the eastern portion of Pickett's Harbor NAP. The surrounding habitat is a former agricultural field that was planted with shrubs and mixed hardwoods in the autumn of 2013; resulting in a 2–3 m high shrub-scrub habitat with emergent 4–6 m tall hardwoods at the time of the study. Emergent hardwoods, such as these, represent suitable locations for birds to perch and thus, likely locations to capture the local seed rain dynamics (McDonnell and Stiles 1983;

Debussche and Isenman 1994). Thus, seed traps (30 x 23 x 6 cm aluminum trays covered by 1 x 1 cm wire screen to exclude mammalian seed predators) were placed beneath six willow oaks (*Quercus phellos*) that represented suitable perching locations to quantify how many seeds were being dispersed away from the hackberry trees. All seeds were collected, counted, and identified weekly.

Experimental Seed Dispersal

To isolate the effects of hackberry psyllids, hackberry and black cherry leaves (*Prunus serotina*) were collected by hand from branches at the Eastern Shore of Virginia NWR and stored in separate mesh bags (agrifabric with < 1 mm holes sewn together with fishing line) from 25 Sep – 01 Nov 2017; black cherry leaves were chosen as a control because they were common throughout my field sites, their leaf morphology is similar to hackberry (oblong with a relatively short petiole), and no galling Homoptera are known to live on them (Marquis 1990). No efforts were made to count the number of galls on leaves collected, but galls were ubiquitous on branches where leaves were collected. Each mesh bag contained approximately 150 g of leaves, was sealed with cable ties, and stored in a dry location exposed to regular light patterns (sunrise/sunsets). The bags were monitored for the presence of adult psyllid irruption (adult psyllids were typically observed climbing the interior sides of the mesh bag after 2–3 weeks) and then transported to Fisherman’s Island NWR once per week, from 15 Oct – 15 Nov, when yellow-rumped warblers (*Setophaga coronata*), the most abundant omnivorous migratory songbird in the area, were present. One bag of hackberry leaves/psyllids was emptied at the base of an eastern baccharis (*Baccharis hamifolia*) shrub and a bag of black cherry leaves (to serve as a control) was emptied at the base of another baccharis shrub approximately 10 m away. Baccharis shrubs were chosen because they do not produce a fleshy fruit that would also potentially attract a bird. One day per week from 15 Oct to

15 Nov, a seed trap (30 x 23 x 6 cm aluminum trays covered by 1 x 1 cm wire screen to exclude mammalian seed predators) was placed adjacent to the main trunk of each experimental (n = 4) and control (n = 4) shrub immediately after the mesh bags containing leaves were emptied. The paired shrubs were located at least 100 m away from each other and the same shrubs were used throughout the field season. Each shrub pairing was observed for one hour after treatment leaves were placed and the number of foraging attempts and time spent in shrub was recorded for birds that entered the shrubs. If birds entered the two shrubs simultaneously, the shrub that had least recently been observed was chosen and birds that entered shrubs while another bird was already under observation were ignored. The seed traps were collected after approx. 24 hrs and all seeds were counted and identified. Control and experimental shrubs were alternated every week and distance to the nearest fruiting bayberry (*Morella spp*) was recorded because the number of seeds dispersed decreases with increasing distance from the seed source (Debussche et al. 1982).

Local Fruit Dispersal and Recruitment

Seed traps and young ground layer fruiting vine (vine stems that were free-standing with dbh < 1 cm²) surveys were also used to determine if hackberry presence influenced seed rain and the resulting plant recruitment patterns within forests at Cape Charles NAP and Savage Neck Dunes NAP. These sites were chosen for the presence of hackberry trees within interior forest habitat. Ten seed traps were placed on the ground along seven 250-m transects at each site; at both sites, hackberry was most abundant along the middle transect and parallel transects were located 25, 50, and 100 m from the central transect. Seeds were collected, counted, and identified once per week (± 2 days). At each trap; distance to nearest hackberry tree (dbh > 4 cm), canopy closure (four densiometer measurements), cumulative dbh of the nearest trees in four quadrats (to account for biases associated with greater seed dispersal occurring beneath larger, more mature trees [Leicht-

Young et al., 2010]), and the total number and species of all vines climbing the nearest tree (dbh > 4 cm) in each quadrat were recorded. To determine if a potential effect of hackberry on seed dispersal resulted in fruiting vine recruitment, ground-layer fruiting vine seedling abundance was quantified using a 1 m² plot immediately north of each seed trap and all woody vines / stems that were not climbing trees were counted.

Statistical Analyses

Foraging observations along transects for all songbird species were pooled and differences between observed and expected (calculated by multiplying total foraging observations by the relative basal area of each tree species) frequencies of observations within different tree species were evaluated using a Chi-square goodness of fit test. Preference values were calculated by finding the difference between the percent of individuals observed foraging in each tree species and the percent basal area.

Zero-inflated Poisson (ZIP) and zero-inflated negative binomial distributions (ZINB) were employed to determine if hackberry psyllids influenced seed rain patterns (table 16). These models were chosen because they account for overdispersion of data caused by excessive zeroes (Zuur et al. 2009). For each analysis, I used an information-theoretic approach to select among candidate models of distribution. I initially compared intercept-only models with ZIP and ZINB probability distributions and chose the distribution with the lowest Akaike's Information Criterion corrected for small sample size (AIC_c) score for subsequent modeling (Burnham and Anderson 2002). For the subsequent modeling procedures, I compared AIC_c scores of my model set, and, I selected the model with the lowest AIC_c score as the best-supported model if

Table 16: AIC scores of intercept-only models with the four distributions tested. The lowest AIC score for each analysis is bolded.

		Fisherman's Island	Pickett's Harbor	Interior Forest Seeds	Interior Forest Stems
Zero-Inflated	Negative binomial	87.48	176.85	860.61	568.61
	Poisson	89.33	201.16	870.43	637.24

no other model was within $\Delta 2$ AIC_c. If two or more models were within $\Delta 2$ AIC_c, I model-averaged those candidate models (Burnham and Anderson 2002, Symonds and Moussalli 2011). I restricted the model set to the global model, models containing only individual predictors, and models with interactions that I thought would be biologically meaningful.

To quantify the effect of hackberry psyllids on songbird foraging behavior at the experimental baccharis shrubs, a Mann-Whitney-Wilcoxon test was used to test for differences between shrubs in total foraging attempts and total time spent in shrubs during the hour immediately following the treatments. Seeds collected beneath the baccharis shrubs were used as a response variable within a candidate model set that included ZINB generalized mixed-effects models (GLMM) with the following fixed effects: distance to the nearest bayberry shrub, treatment type, and an interaction between distance to nearest bayberry shrub and treatment type (table 17). I also included shrub ID as a random effect because I repeatedly sampled the same shrubs every week.

Seeds collected at Pickett's Harbor NAP were treated as a response variable within a candidate model set that included ZINB GLMMs with the following fixed effects: distance to the nearest hackberry tree, area-wide psyllid capture rate, and an interaction between distance to nearest

hackberry tree and area-wide psyllid capture. I also included seed trap ID as a random effect because I repeatedly sampled the same seed traps every week.

Table 17: Results from model comparison procedure for models explaining hackberry seed rain at Pickett's Harbor NAP. Predictors include the distance to the nearest hackberry tree (Hackberry Distance), hackberry psyllid rate (Psyllid Rate), and the interaction between distance to the nearest hackberry tree and hackberry psyllid rate (D X R).

Model Predictors	K	-2LogLik (deviance)	AIC _c	ΔAIC _c	Model Weight
Psyllid Rate	4	-82.36	176.6	0	0.595
Distance + Psyllid Rate + D X P	6	-81.06	177.7	2.17	0.2012
<i>Intercept only</i>	3	-84.96	178.5	2.91	0.139
Distance	4	-84.585	180.0	4.45	0.064

The total combined grape (*Vitus spp*), poison ivy (*Toxicodendron radicans*), and Virginia creeper (*Parthenocissus quincuefolia*) seeds collected each week within forest interiors were treated as a response variable within a candidate model set that included ZINB GLMMs with the following fixed effects: canopy closure, total DBH of the four nearest trees, total number of conspecific vines on the four nearest trees, distance to the nearest hackberry tree, area-wide rate of psyllid availability, an interaction between distance to the nearest hackberry tree and area-wide rate of psyllid emergence. I also included seed trap ID and site as random intercepts because I repeatedly sampled the same seed traps every week and to account for potential biases associated with site-specific bird assemblages.

To determine if increased local seed rain resulted in greater recruitment of fruiting vines, total combined grape, poison ivy, and Virginia creeper stems counted within each plot were used as a response variable within a ZINB GLMM that included the following explanatory variables: distance to the nearest hackberry tree, canopy closure, total DBH of the four nearest trees, and total

number of conspecific vines on the four nearest trees. I also included site as random intercepts because to account for potential biases associated with site-specific growing conditions. All statistical analyses were performed with R 3.6.2 (R Core Team 2019) in the packages glmmTMB (Brooks et al. 2017) and MuMIn (Barton 2019).

RESULTS

Foraging Bird Surveys

I recorded foraging observations during the 2016 (n = 344) and 2017 (n = 353) autumn migrations along forested transects. The trees along the transects consisted of 29 species; sweetgum (*Liquidambar styraciflua*), black cherry, and hackberry represented the greatest proportion of basal area (20.1% 19.6%, and 14.3%, respectively [total basal area = 5,548 m²]). Songbirds did not forage in trees according to availability ($X^2=500.32$, df_{14} , $p<.001$). Trees that were used in greater proportion than their availability (fig 1) included hackberry (27% more often than expected), southern red oak (*Quercus falcata*, 4% more often), and black walnut (*Juglans nigra*, 1% more often).

Psyllid Abundance

Hackberry psyllids were captured from 10 Sep to 21 Nov and psyllid abundance peaked 21–24 Oct (fig 9).

Hackberry Seed Dispersal

The first hackberry seeds were collected at Pickett's Harbor NAP on 9 Sep and the greatest number of seeds were collected on 14 Oct (fig 10), approximately one week before the peak of psyllid abundance (fig 9). The top model within my candidate set included psyllid capture rate

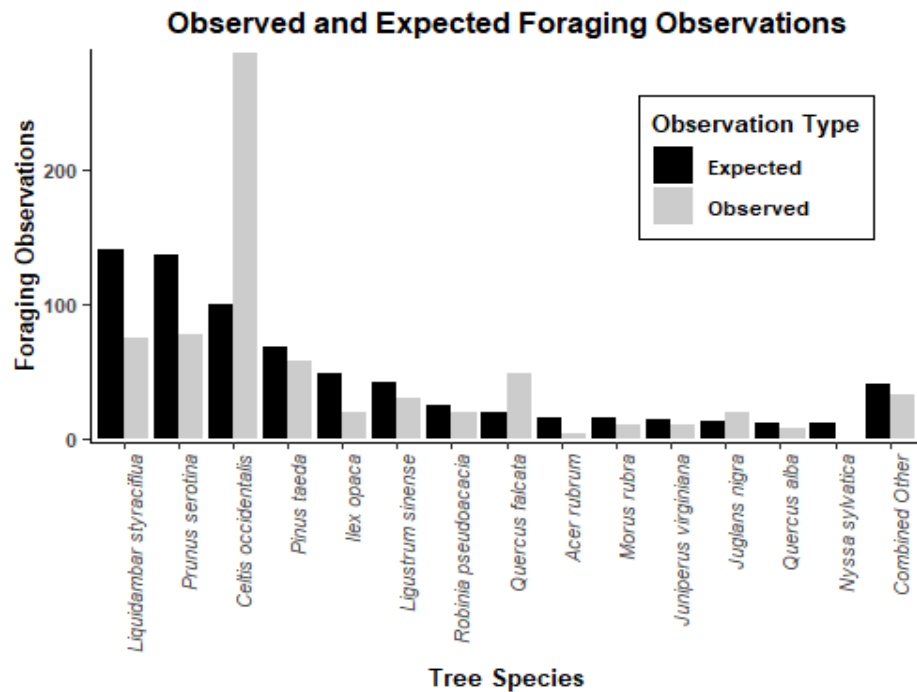


Figure 8: Expected and observed foraging maneuvers of songbirds on tree species found along transects. Tree species that represented $>2\%$ of the total basal area along transects are shown, while the right most column (Combined Other) represents 14 other tree species that collectively represented 6% of the total basal area.

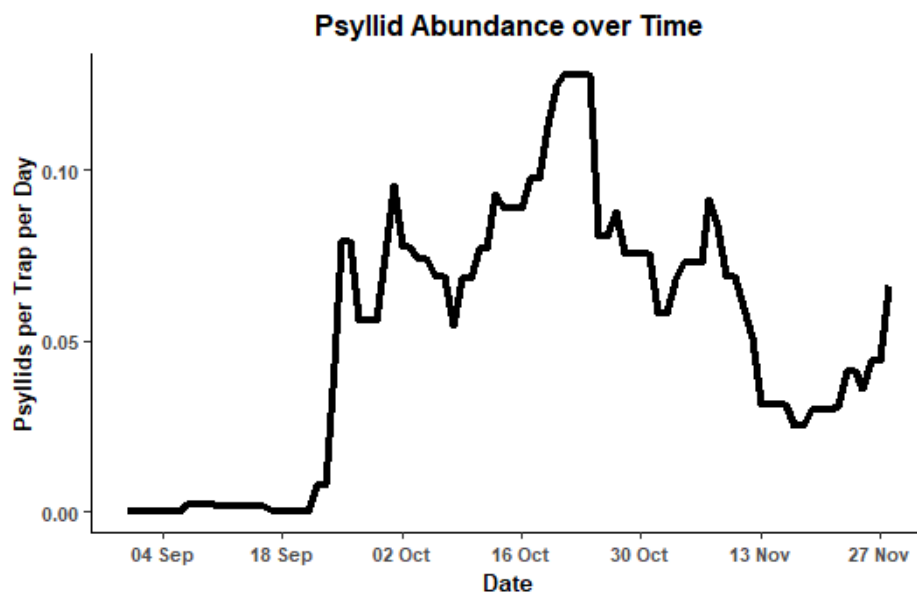


Figure 9: Hackberry psyllid abundance during 2017 autumn migration.

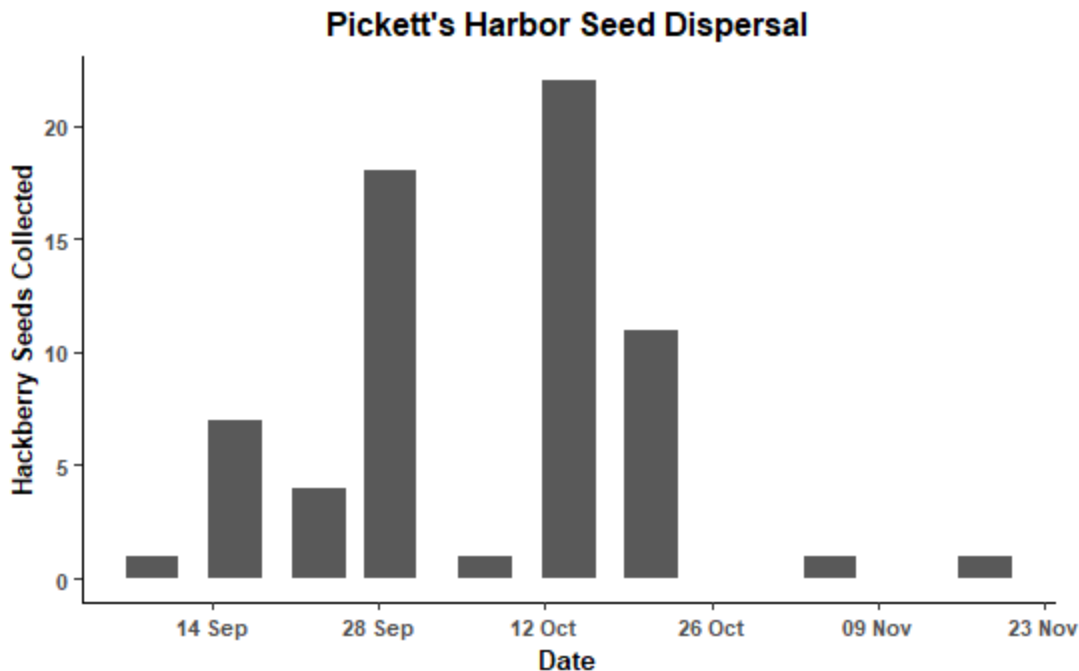


Figure 10: Hackberry seeds collected at Pickett's Harbor NAP during 2017 autumn migration.

(table 18) and a greater number of seeds were dispersed when hackberry psyllids were more abundant (fig 11 and table 3).

Experimental Shrubs

There was no significant difference in foraging attempts or total time spent foraging between baccharis shrubs treated with hackberry psyllids and controls ($W = 130$, $p=0.954$ and $W = 116.5$, $p = 0.678$, respectively), but a greater number of seeds were collected beneath shrubs treated with hackberry psyllids (25) than controls (6). The top model predicting wax myrtle seed rain included hackberry psyllid treatment, though the null model was within 2 Δ AIC points of the top model (table 19). The top model predicted the number of bayberry seeds collected in seed traps increased when shrubs were treated with hackberry psyllids (fig 12).

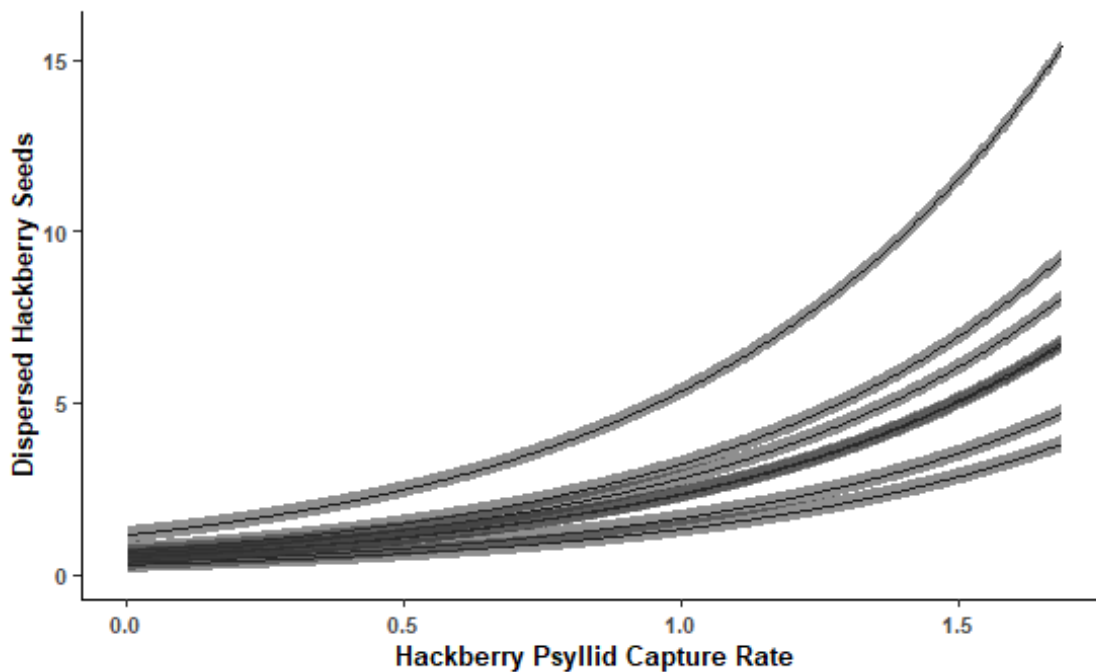


Figure 11: Predicted mean daily capture rate for hackberry seeds surrounding isolated hackberry trees at Picket's Harbor NAP. Each line represents predicted values from individual seed traps. Each line represents predicted values from individual seed traps and the gray shaded areas represent the standard error for the hackberry psyllid rate parameter.

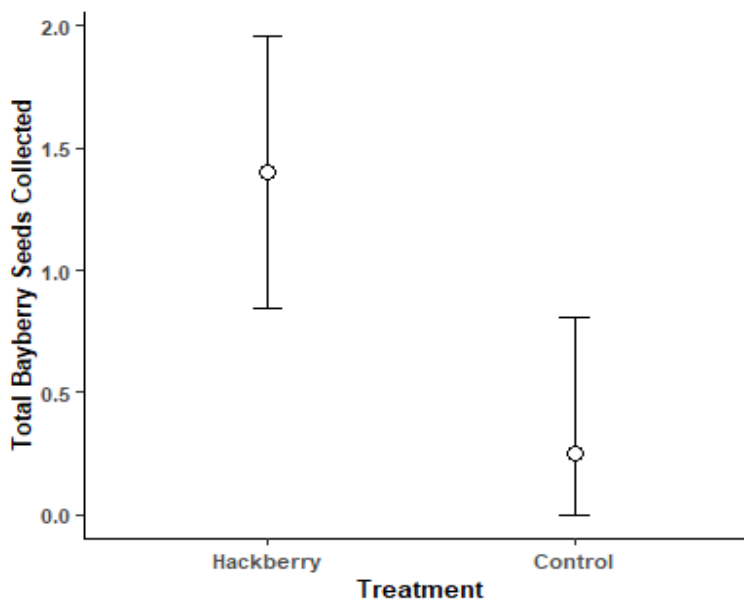


Figure 12: Predicted bayberry seeds captured at shrubs treated with hackberry leaves and psyllids versus control shrub treated with black cherry leaves on Fisherman's Island NWR. The error bars represent 95% confidence intervals.

Table 18: Parameter estimates and 95% confidence intervals for parameters included within the A. Pickett’s Harbor Hackberry top model, B. Fisherman’s Island top model, C. Cape Charles and Savage Neck Dunes NAPs allospecific seed dispersal model, D. Cape Charles and Savage Neck Dunes NAPs allospecific fruiting stem model. Confidence intervals that do not overlap zero are bolded.

Model	Factor	Parameter Estimate	Lower 95% CI	Upper 95% CI
A.	Psyllid Availability	0.62	0.15	1.10
Intercept	Conditional	0.19	-1.04	1.42
Intercept	Zero Inflation	0.06	-1.38	1.51
B.	Hackberry Treatment	1.37	0.07	2.67
Intercept	Conditional	-0.20	-1.38	1.47
Intercept	Zero Inflation	0.06	-1.38	1.51
C.	Hackberry Distance	-0.53	-0.98	-0.09
	Psyllid Availability	0.94	0.66	1.22
	D X P	0.11	-0.22	0.45
Intercept	Conditional	-2.99	-4.61	-1.38
Intercept	Zero Inflation	0.60	-0.18	1.38
D.	Conspecific Vines	0.32	00.09	0.55
Intercept	Conditional	0.95	0.62	1.27
Intercept	Zero Inflation	-1.75	-3.49	0

Local Seed Recruitment

Three species of fruiting plants, grape, poison ivy, and Virginia creeper, represented 70% of non-hackberry fruit consumption events along foraging transects (n = 66) and 64% of non-hackberry seeds collected in seed traps (n= 205). So, analyses were restricted to grape, poison ivy, and

Virginia creeper, all of which are hard-bodied seeds that readily pass through bird digestive tracts (Schupp 1993; Traveset 1998). Seeds were collected within forest interiors from 31 Aug – 21 Nov

Table 19: Results from model comparison procedure for models wax myrtle seed rain at Fisherman’s Island NWR. Predictors include the distance to the nearest bayberry shrub (Bayberry Distance), hackberry psyllid treatment (Treatment), and the interaction between distance to the nearest bayberry shrub and hackberry psyllid treatment (D X T).

Model Predictors	K	-2LogLik (deviance)	AIC _c	ΔAIC _c	Model Weight
Treatment	5	-38.55	89.40	0	0.59
Intercept Only	4	-40.74	91.0	1.54	0.27
Bayberry Distance	5	-40.64	93.6	4.18	0.07
Bayberry Distance + Treatment + D X T	7	-37.52	93.7	4.28	0.07

(fig 13). More seeds were collected at Cape Charles (88%, n = 132) than Savage Neck (fig 14). Seed deposition was greatest from 11 Oct to 20 Oct, 1 – 1.5 weeks prior to the peak of psyllid abundance (fig 9). The top model within my candidate set included distance to the nearest hackberry tree, hackberry psyllid capture rate, and the interaction between hackberry distance and capture rate (table 20). Seed dispersal was greater nearer hackberry trees and when hackberry psyllids were most abundant (fig 14). In contrast to seed dispersal patterns, fruiting stems were more abundant at Savage Neck NAP (n = 2136) than at Cape Charles (n = 1887). The top model predicting stem density within interior forests within the candidate set included the count of nearby conspecific vines (table 21) and more stems were found when near more vines (table 18).

DISCUSSION

Galling arthropods, such as hackberry psyllids, are generally thought to be parasites of their host plants (Jensen 1957; Stireman and Cipollini 2008; Tooker et al. 2008). However, parasitic relationships can vary along a spectrum that includes both commensalism and mutualism

(Neuhauser and Fargione 2004). The evolution toward mutualism is particularly likely when the parasite benefits from greater host survival as is the case with galling insects (Ewald 1987). In

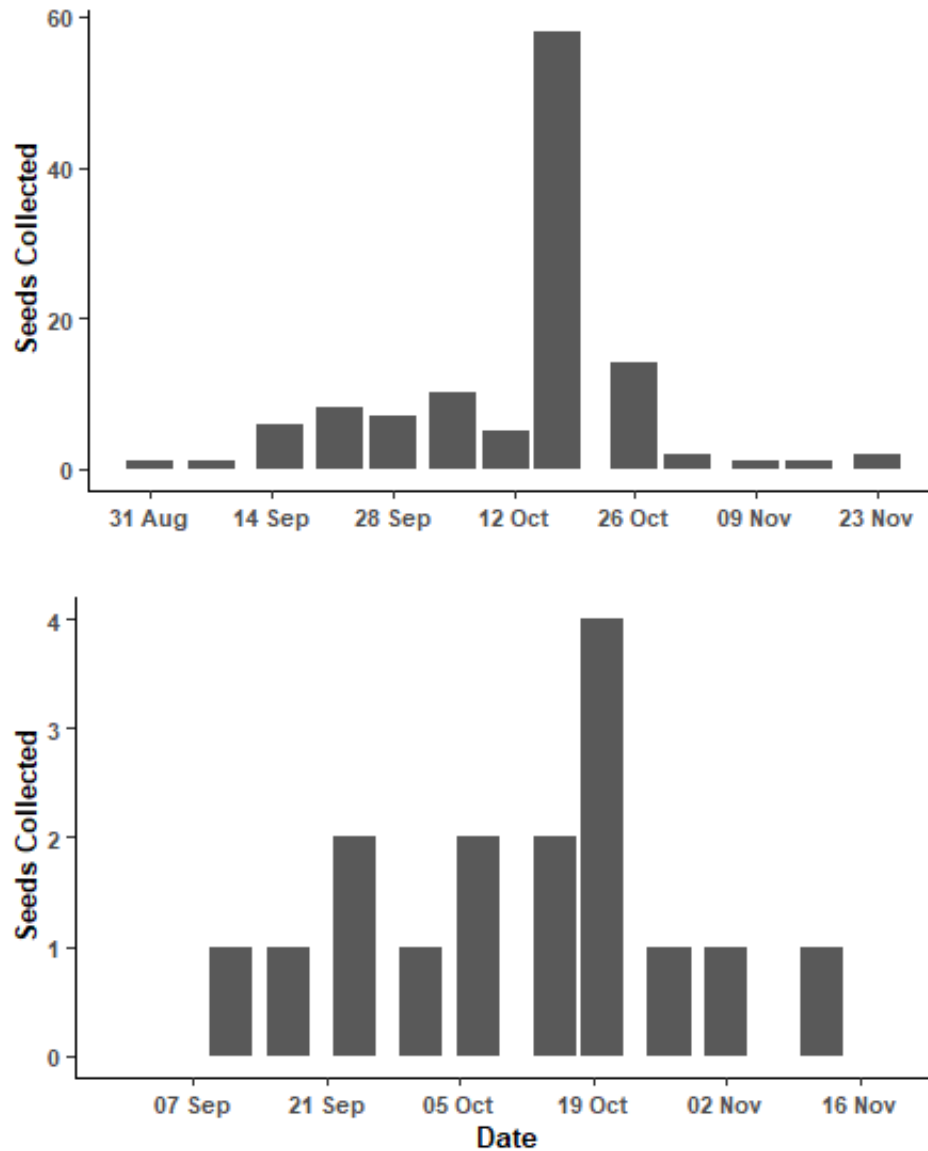


Figure 13: Allospecific seeds collected within interior forests during 2017 autumn migration. The top plot represents seed collected at Cape Charles NAP and the bottom plot represents seeds collected at Savage Neck Dunes NAP.

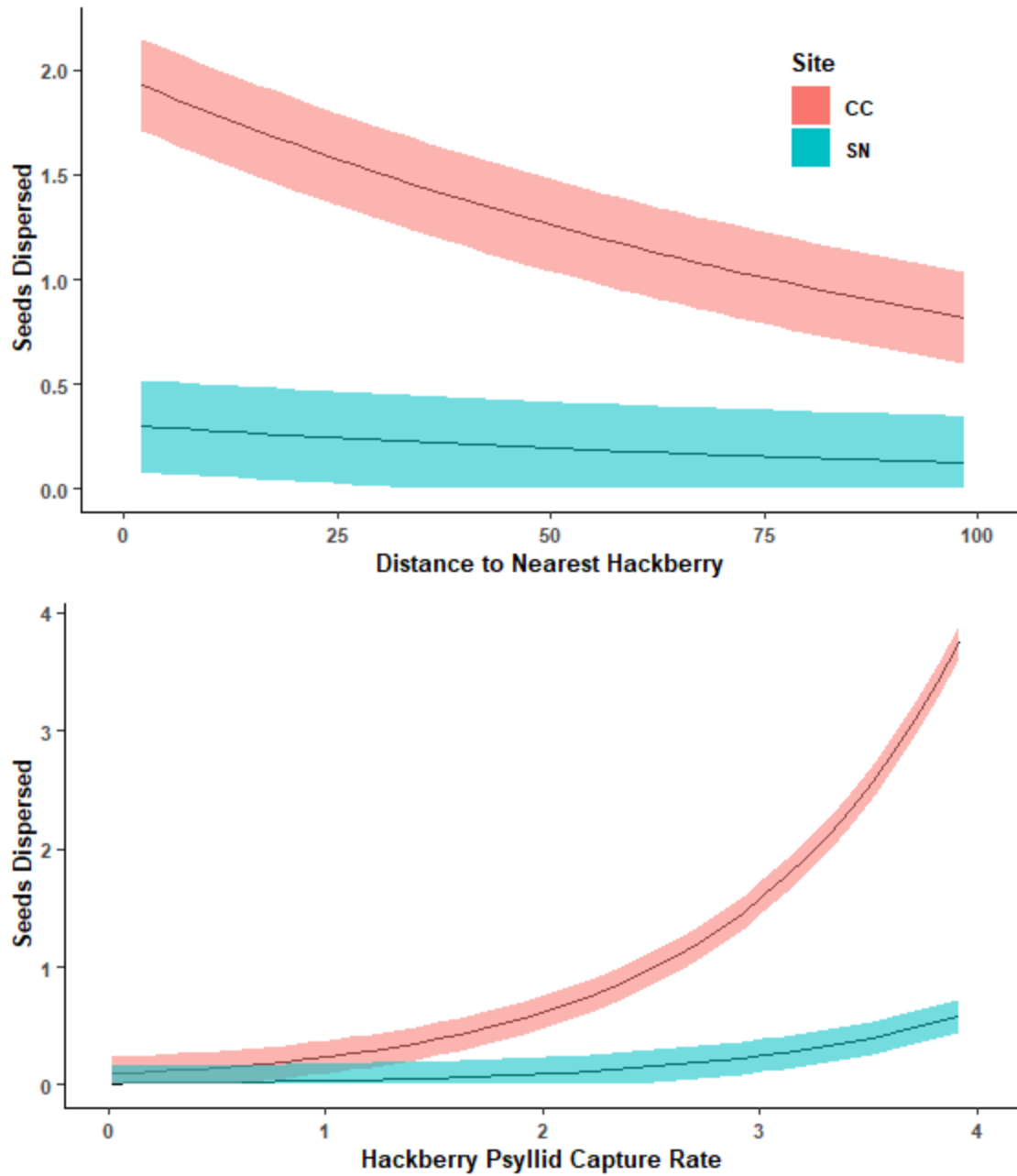


Figure 14: Predicted seed rain as distance to the nearest hackberry tree increases and hackberry psyllid abundance increases

Table 20: Results from model comparison procedure for models explaining seed rain within interior forests. Predictors include the number of nearby conspecific vines (Conspecific Vines), distance to the nearest hackberry tree (Hackberry Distance), hackberry psyllid rate (Psyllid Rate), canopy cover, site, and the interaction between distance to the nearest hackberry tree and hackberry psyllid rate (D X R).

Model Parameters	-2LogLik (deviance)	AIC _c	ΔAIC _c	Model Weight
hackberry distance + psy. capt. rate + interaction	-374.73	765.54	0.00	0.75
psyllid capture rate	-378.18	768.42	2.88	0.18
global model	-374.02	770.20	4.65	0.07
hackberry distance	-398.21	808.46	42.92	0.00
<i>intercept only</i>	-401.48	812.99	47.44	0.00
canopy closure	-400.75	813.54	48.00	0.00
conspecific vines	-401.47	814.98	49.44	0.00
tree DBH	-401.48	815.00	49.46	0.00

Table 21: Results from model comparison procedure for models explaining stem density within interior forests. Predictors include the number of nearby conspecific vines (Conspecific Vines), distance to the nearest hackberry tree (Hackberry Distance), cumulative diameter at breast height of nearby trees (DBH), canopy cover, and site.

Model Parameters	-2LogLik (deviance)	AIC _c	ΔAIC _c	Model Weight
conspecific vines	-277.05	564.5	0.00	0.80
global model	-275.67	568.4	3.89	0.11
hackberry distance	-281.31	570.9	6.36	0.03
<i>intercept only</i>	-280.27	571.0	6.44	0.03
canopy closure	-281.13	572.7	8.15	0.01
DBH	-281.31	573.1	8.51	0.01

this case; hackberry psyllids provide a benefit to their host plant by strengthening songbird foraging intensity. The greater number of foraging songbirds in hackberry trees benefits the host plant through greater seed dispersal opportunities (Schupp 1993) because more seeds are likely to recruit by escaping density- and distance-dependent effects associated with differential survival of

seeds (Comita et al. 2014). Psyllids attract foraging songbirds and subsequently secondary allospecific seed dispersal is greater nearer hackberry trees, but the only predictor associated with greater stem abundance was the abundance of established conspecific vines and more stems were found when a greater number of conspecifics were nearby (table 17). Greater stem abundance may not have been associated with hackberry proximity, perhaps due to the relatively strong allelopathic properties of hackberry (Lodhi 1975), which may be a response to greater allospecific seed rain. Without strong allelopathic properties, the benefit associated with increased seed dispersal opportunities for the hackberry tree associated with hackberry psyllids (fig 4) may be offset to some degree (Whittaker 1972; Whittaker et al. 2001) as allospecific saplings would compete for many of the same nutrients as hackberry (Clarkson and Hanson 1980) and damage the host tree that they climb in a variety of ways (Putz 1984; Schnitzer 2018).

However, hackberry trees in early successional habitats may encourage the recruitment of allospecific fruiting species if seeds are dispersed near hackberry trees, but outside of the hackberry leaf litter zone where the allelopathic effect would be diminished (del Morel and Muller 1970). As early-successional habitats surrounding hackberry trees reach an older seral age, the long-term aggregation of fruiting plants enhances the value of habitat nearby to hackberry for frugivorous birds by providing nutritious fruits, thus benefitting migrating birds even if they do not forage directly on hackberry psyllids or energy-deficient hackberry fruits. In this way, insects also indirectly modulate autumn stopover habitat quality, the mutualism between migratory songbirds and hackberry trees, and provide an opportunity for birds to complete migration more efficiently (Suthers et al. 2000, Carlo et al. 2004, Schaub et al. 2008). Identifying plant species that disproportionately benefit migratory songbirds at stopover habitat can be particularly useful in

restoration projects where stopover habitat is fragmented (Greco and Airola 2018; McCann et al. 1993), as it is at the study site reported here.

This is the first study that I am aware that provides a mechanism by which an insect modulates local seed dispersal, resulting in spatially aggregated plant recruitment. Though insects are known to participate in mutualisms with plants, particularly through diffuse mutualisms (such as pollinators, Jordano 1987), and ants (hymenoptera: formicidae) are generally the only insect taxon regarded as facilitators of plant communities through seed dispersal (Howe and Smallwood 1982; Handel and Beattie 1990). However, hackberry psyllids mediate the dispersal of their host plant and other common autumn-fruiting plants and, thus, demonstrate that galling insects can play a role in spatial aggregations of plant communities through their relationships with their host plants.

The loss of taxa such as hackberry psyllids that directly and indirectly interact across trophic levels can have a disproportionately large effect on community dynamics (Mills et al. 1993; Harrison 2000). Hackberry psyllids are vulnerable to climatic extremes (Beck 1953) and a bottom-up trophic cascade could result in the event of hackberry psyllid extinction (Pace et al. 1999; Kagata and Ohgushi 2006). Individual hackberry tree health may increase after its release from the phloem-feeding psyllids, but vertebrates that prey upon the psyllids would find fewer foraging opportunities and the long-term survival of hackberry trees could potentially suffer as fewer birds would choose to forage on hackberry fruits and subsequently disperse seeds. The future spatial aggregation of other autumn- fruiting plants could be altered, and in turn, autumn migrating songbirds may refuel less efficiently in areas where hackberry is present than they would otherwise.

I found that hackberry is a preferred tree for foraging, an observation previously reported during the spring season (Strode 2009), but the resulting effects on seed dispersal patterns and

subsequently, altering plant community organization are a novel finding. The effects that hackberry psyllids exert on the surrounding plant and animal community may not be unique. If similar relationships are common in nature, one would expect other autumn-fruiting plants to be more likely to host arthropods that would attract foraging songbirds when fruits are ripe and potential seed dispersers are most abundant. Further investigation into songbird foraging preferences could reveal such plant taxa that maintain complex relationships with insects, a relationship with obvious application to restoration efforts in fragmented areas that also support large numbers of autumn migratory songbirds.

CHAPTER 4

IV. CONCLUSIONS

Galling insects rely upon their hosts for shelter and food resources for a significant portion of their life cycle (Fernandes 1994). In the absence of any obvious benefit to their hosts, they would be considered parasites because they are stealing energy/resources from the host plant (Silva et al. 1996). However, parasitic relationships can evolve toward mutualistic relationships and this evolution toward mutualism is particularly likely when the parasite benefits from greater host survival (Ewald 1987; Neuhauser and Fargione 2004). Hackberry trees provide songbirds a fruit that is relatively deficient in energy (Johnson et al. 1985), but also provide an insect that is ephemerally abundant during autumn migration (Hodkinson 2009). Hackberry psyllids are galling insects, but because they enhance the mutualism between songbirds and hackberry trees, appears to also engage in a mutualism with their host. Hackberry psyllids increase the likelihood that songbirds disperse hackberry seeds away from the host tree while hackberry trees provide the insect shelter and food through the growing season.

In Chapter 2, I examined prey choices of foraging birds by observing their behavior along transects. After assigning different species to foraging guilds (i.e, insectivore, omnivore, and frugivore), I explored how temporal trends in hackberry psyllid availability and hackberry tree availability influenced lipid accumulation, protein consumption, and recovery from overnight flights. I found that insectivores and omnivores refueling profiles were both influenced by these variables. Insectivore lipid accumulation and protein consumption were both greater near hackberry trees and the interaction between hackberry tree presence and hackberry psyllid availability indicated that both metabolites were greater near hackberry trees when psyllids were

available. Omnivores also displayed greater lipid accumulation when captured near hackberry trees.

Other environmental factors that affected refueling songbird metabolites included time of day, handling time, year, and fruit presence. As time of day increased, all birds accumulated greater amounts of lipids, insectivores and omnivores were consistent with greater protein metabolism, and omnivores and frugivores both recovered from overnight flights. Frugivore lipid concentrations and protein metabolism were negatively influenced by handling time and both metabolites were also greater in frugivores captured during 2016

In Chapter 3, I quantified temporal hackberry psyllid trends, examined which tree species foraging songbirds disproportionately chose for foraging, and explored how those choices influenced seed rain patterns. I also experimentally manipulated shrubs to isolate the influence of hackberry psyllids on seed rain.

I found that foraging songbirds disproportionately used trees within the forest. Songbirds preferred hackberry more so than all other tree species, but also preferred foraging on southern red oak (*Quercus falcata*). Hackberry psyllids peaked in mid-autumn and hackberry seeds were most dispersed when hackberry psyllids were more available. Hackberry proximity, hackberry psyllid availability, and the interaction between these variables were the model that best predicted allospecific seed rain and greater allospecific seed rain also occurred when hackberry psyllids were more available. When isolated hackberry psyllids were supplemented to eastern Baccharis (*Baccharis hamifolia*) shrub, bayberry (*Morella sp*) seed rain was greater than controls.

During migration, birds forage on fruits and insects that offer the greatest metabolic reward in order to fuel their flights to more suitable climates (Herrera 1984). Many fleshy fruits are rich in

lipids and carbohydrates so many birds take advantage of nutritious fruits by switching to a more frugivorous diet during autumn (Bairlein 1996; 1998). Many fleshy fruit-producing plants synchronize their fruiting periods with autumn migration to take advantage of the greater number of birds migrating through temperate North America (Stiles 1980; Skeate 1987). However, migrating birds do require some protein and, because most fruits are protein-deficient, birds must also consume insects to meet their protein demands (McWilliams et al. 2004). Migrating songbird metabolite studies typically explore the effects associated with fruit abundance or presence. I found that insectivorous and omnivorous bird metabolite profiles were affected by hackberry trees and the associated hackberry psyllids. The nutritional benefit that hackberry psyllids provide songbirds appears to increase the likelihood that migrating birds will forage on hackberry trees, consume energy-deficient hackberry fruits, and subsequently disperse the hackberry seeds to the surrounding landscape. In this way, hackberry psyllids facilitate the diffuse mutualism between hackberry trees and migrating songbirds. The only other insects that I am aware that participate in seed dispersal mutualisms are ants, which physically move seeds away from fruiting plants.

Of course, most ecological studies do have weaknesses. For example, galls are most abundant higher in hackberry tree canopies (Lill 1998) so I likely would have gathered more accurate estimates of psyllid availability and gall density by sampling tree canopies than at eye level. Weather may have also influenced psyllid capture rate because the psyllid traps seemed to be stickier on warmer days. Additionally, songbirds may have depredated arthropods that I had captured on sticky traps.

There are also limitations associated with collecting blood plasma samples. Daily songbird abundance could have been an important predictor of metabolite concentrations if competition exists at stopover sites. My mist netting effort was not consistent day to day so I could not quantify

songbird density through capture rate. Strong winds and precipitation both affect songbird capture efficacy, though songbirds sometimes were abundant in such conditions. I also chose to limit capture rate by closing nets when birds were abundant to minimize the likelihood that birds were injured in mist nets and because extracting additional birds from mist nets occupies time that could be spent collecting blood plasma. I did not quantify songbird density along foraging transects because I was not counting the total number of birds along transects, but more focused on quantifying the behavior of foraging birds.

Overall, this study showed that host-specific insects can provide benefits to their host plant via interactions with other trophic levels. Gall-forming insects can be found on a wide variety of plant species (Gonçalves-Alvim and Fernandes 2001) and other gall-forming insects may impart benefits to their host plants that are not immediately apparent. I have demonstrated how studies of songbird foraging behavior could expose what seems to be a simple parasite as an indirect mutualistic partner.

BIBLIOGRAPHY

- Aamidor, S. E., U. Bauchinger, O. Mizrahy, S. R. McWilliams, and B. Pinshow. 2011. During stopover, migrating blackcaps adjust behavior and intake of food depending on the content of protein in their diets. *Integrative and Comparative Biology* 51:385–393.
- Able, K. P., 1973. The role of weather variables and flight direction in determining the magnitude of nocturnal bird migration. *Ecology* 54:1031–1041.
- Alerstam, T., 1978. Reoriented bird migration in coastal areas: dispersal to suitable resting grounds?. *Oikos* 30:405–408.
- Alerstam, T. and A. Lindström. 1990. Optimal bird migration: the relative importance of time, energy, and safety. Pages 331–351 in Gwinner, E. eds, *Bird Migration*. Springer Verlag, Berlin.
- Arnold, T. W., 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74:1175–1178.
- Ashiru, M. O., 1989. The food value of the larvae of *Anaphe venata* Butler (Lepidoptera: Notodontidae). *Ecology of food and nutrition* 22:313–320.
- Bäckhed, F., R. E. Ley, J. L. Sonnenburg, D. A. Peterson, and J. I. Gordon. 2005. Host-bacterial mutualism in the human intestine. *Science* 307:1915–1920.
- Bairlein, F., 1996. Fruit-eating in birds and its nutritional consequences. *Comparative Biochemistry and Physiology Part A: Physiology* 113:215–224.
- Bairlein, F., 1998. The effect of diet composition on migratory fueling in garden warblers *Sylvia borin*. *Journal of Avian Biology* 29:546–551.

- Bairlein, F., 2002. How to get fat: nutritional mechanisms of seasonal fat accumulation in migratory songbirds. *Naturwissenschaften* 89:1–10.
- Bairlein, F. and E. Gwinner. 1994. Nutritional mechanisms and temporal control of migratory energy accumulation in birds. *Annual Review of Nutrition* 14:187–215.
- Bairlein, F., Norris, D.R., Nagel, R., Bulte, M., Voigt, C.C., Fox, J.W., Hussell, D.J. and Schmaljohann, H., 2012. Cross-hemisphere migration of a 25 g songbird. *Biology Letters* 8:505–507.
- Bakker, J. P., P. Poschlod, R. J. Strykstra,, R. M. Bekker. and K. Thompson. 1996. Seed banks and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica* 45:461–490.
- Barton, K., 2019. MuMIn: multi-model inference. R package version 1.43.15.
<https://CRAN.R-project.org/package=MuMIn>
- Bascompte, J., 2019. Mutualism and biodiversity. *Current Biology* 29:467–470.
- Bascompte, J. and P. Jordano. 2007. Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology and Systematics* 38:567–593.
- Bayly, N. J., K. V. Rosenberg, C. Gómez, and K. A. Hobson. 2019. Habitat choice shapes the spring stopover behaviour of a Nearctic-Neotropical migratory songbird. *Journal of Ornithology* 160:1–12.
- Beck, E. G., 1953. Near extinction of the *Celtis* petiole gall insect in North Georgia. *Ecology* 34:207–207.
- Berthold, P., 2001. Bird migration: a general survey. Oxford University Press, Oxford.

- Blem, C. R., 1976. Patterns of lipid storage and utilization in birds. *American Zoologist* 16:671–684.
- Bolser, J. A., R. R. Alan, A. D. Smith, L. Li, N. P. Seeram, and S. R. McWilliams. 2013. Birds select fruits with more anthocyanins and phenolic compounds during autumn migration. *Wilson Journal of Ornithology* 125:97–108.
- Boucher, D. H., S. James, and K. H. Keeler. 1982. The ecology of mutualism. *Annual Review of Ecology and Systematics* 13:315–347.
- Boyle, W. A., D. R. Norris, and C. G. Guglielmo. 2010. Storms drive altitudinal migration in a tropical bird. *Proceedings of the Royal Society of London Biological Sciences* 277:2511–2519.
- Brock, J. P. and K. Kaufman. 2003. *Kaufman Field Guide to Butterflies of North America*. Houghton Mifflin Harcourt Publishing Company, New York.
- Bronstein, J. L., 1994. Our current understanding of mutualism. *Quarterly Review of Biology* 69:31–51.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Bolker. 2017. Modeling zero-inflated count data with glmmTMB. *bioRxiv* 1–14. preprint [bioRxiv:132753](https://doi.org/10.1101/132753).
- Buler, J.J. and F. R. Moore. 2011. Migrant–habitat relationships during stopover along an ecological barrier: extrinsic constraints and conservation implications. *Journal of Ornithology* 152:101–112.
- Buler, J.J., F. R. Moore, and S. Woltmann. 2007. A multi-scale examination of stopover habitat use by birds. *Ecology* 88:1789–1802.

- Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd ed. Springer Verlag New York.
- Carlisle, J. D., K. L. Olmstead, C. H. Richart, and D. L. Swanson. 2012. Food availability, foraging behavior, and diet of autumn migrant landbirds in the Boise foothills of southwestern Idaho. *Condor* 114:449–461.
- Carlo, T. A., J. A. Collazo, and M. J. Groom. 2004. Influences of fruit diversity and abundance on bird use of two shaded coffee plantations. *Biotropica* 36:602–614.
- Cerasale, D. J. and C. G. Guglielmo. 2010. An integrative assessment of the effects of tamarisk on stopover ecology of a long-distance migrant along the San Pedro River, Arizona. *Auk* 127:636–646.
- Chen, G., Z. W. Wang, Y. Qin, and W. B. Sun. 2017. Seed dispersal by hornets: An unusual insect-plant mutualism. *Journal of integrative plant biology* 59:792–796.
- Chernetsov, N., 2006. Habitat selection by nocturnal passerine migrants en route: mechanisms and results. *Journal of Ornithology* 147:185–191.
- Clarkson, D. T. and J. B. Hanson. 1980. The mineral nutrition of higher plants. *Annual Review of Plant Physiology* 31:239–298.
- Clipp, H. L., E. B. Cohen, J. A. Smolinsky, K. G. Horton, A. Farnsworth, and J. J. Buler. 2020. Broad-scale weather patterns encountered during flight influence landbird stopover distributions. *Remote Sensing* 12:565.
- Comita, L. S., S. A. Queenborough, S. J. Murphy, J. L. Eck, K. Xu, M. Krishnadas, N. Beckman, and Y. Zhu. 2014. Testing predictions of the Janzen–Connell hypothesis: a

meta-analysis of experimental evidence for distance-and density-dependent seed and seedling survival. *Journal of Ecology* 102:845–856.

Dáttilo, W., N. Lara-Rodríguez, P. Jordano, P. R. Guimarães, J. N. Thompson, R. J. Marquis, L. P. Medeiros, R. Ortiz-Pulido, M. A. Marcos-García, and V. Rico-Gray. 2016, November. Unravelling Darwin's entangled bank: architecture and robustness of mutualistic networks with multiple interaction types. *Proceedings of the Royal Society B* 283:20161564.

Debussche, M., J. Escarré, and J. Lepart. 1982. Ornithochory and plant succession in Mediterranean abandoned orchards. *Vegetatio* 48:255–266.

Debussche, M. and P. Isenmann. 1994. Bird-dispersed seed rain and seedling establishment in patchy Mediterranean vegetation. *Oikos* 69:414–426.

del Moral, R. and C. H. Muller. 1970. The allelopathic effects of *Eucalyptus camaldulensis*. *American Midland Naturalist* 83:254–282.

Dobbs, R. C., W. Barrow, C. W. Jeske, J. DiMiceli, T. C. Michot. and J. W. Beck. 2009. Short-term effects of hurricane disturbance on food availability for migrant songbirds during autumn stopover. *Wetlands* 29:123–134.

Duan, Q. and R. C. Quan. 2013. The effect of color on fruit selection in six tropical Asian birds. *Condor* 115:623–629.

Engemann, R. M., R. T. Sugihara, L.F. Pank, and W. E. Dusenburry. 1994. A comparison of plotless density estimators using Monte Carlo simulation. *Ecology* 75:1749–1779.

Everitt, J. H. and M. A. Alaniz. 1981. Nutrient content of cactus and woody plant fruits eaten by birds and mammals in south Texas. *Southwestern Naturalist* 26:301–305.

- Ewald, P. W., 1987. Transmission modes and evolution of the parasitism-mutualism continuum. *Annals of the New York Academy of Sciences* 503:295–306.
- Fernandes, G. W., A. C. F. Lara, and P. W. Price. 1994. The geography of galling insects and the mechanisms that result in patterns. Pages 42–28 *in* Price, P.W., Lewinsohn, T.M., Fernandes, G.W. and Benson, W.W. eds, *The ecology and evolution of gall-forming insects*. United States Department of Agriculture, St. Paul.
- Fristoe, T. S., 2015. Energy use by migrants and residents in North American breeding bird communities. *Global Ecology and Biogeography* 24:406–415.
- Frost, S. W., 1954. The numerical relationships between phytophagous insects and their hosts. *Scientific Monthly* 79:10–12.
- Gagne, R. and J. Moser. 2013. The North American gall midges (Diptera: Cecidomyiidae) of hackberries (Cannabaceae: *Celtis* spp.). *Memoirs of the American Entomological Society* 49:1–103.
- Gerson, A. R. and C. G. Guglielmo. 2011. Flight at low ambient humidity increases protein catabolism in migratory birds. *Science* 333:1434–1436.
- Giron, D., E. Huguet, G. N. Stone, and M. Body. 2016. Insect-induced effects on plants and possible effectors used by galling and leaf-mining insects to manipulate their host-plant. *Journal of Insect Physiology* 84:70–89.
- Gonçalves-Alvim, S. J. and G. W. Fernandes. 2001. Biodiversity of galling insects: historical, community and habitat effects in four neotropical savannas. *Biodiversity & Conservation* 10:79–98.

- Greco, S. E. and D. A. Airola., 2018. The importance of native valley oaks (*Quercus lobata*) as stopover habitat for migratory songbirds in urban Sacramento, California, USA. *Urban Forestry & Urban Greening* 29:303–311.
- Greenberg, C. H. and S. T. Walter. 2010. Fleshy fruit removal and nutritional composition of winter-fruited plants: a comparison of non-native invasive and native species. *Natural Areas Journal* 30:312–322.
- Guglielmo, C. G., 2010. Move that fatty acid: fuel selection and transport in migratory birds and bats. *Integrative and Comparative Biology* 50:336–345.
- Guglielmo, C. G., D.J. Cerasale, and C. Eldermire, 2005. A field validation of plasma metabolite profiling to assess refueling performance of migratory birds. *Physiological and Biochemical Zoology* 78:116–125.
- Guil-Guerrero, J. L., R. P. Ramos-Bueno, M. J. González-Fernández, D. Fabrikov, M. J. Sánchez-Muros, and F. G. Barroso. 2018. Insects as food: fatty acid profiles, lipid classes, and sn-2 fatty acid distribution of lepidoptera larvae. *European Journal of Lipid Science and Technology* 120:1700391.
- Hails, C. J., 1982. A comparison of tropical and temperate aerial insect abundance. *Biotropica*,14:310–313.
- Halkidi, M., Y. Batistakis and M. Vazirgiannis. 2001. On clustering validation techniques. *Journal of intelligent information systems* 17:107-145.
- Hall, D. G., M. G. Hentz, and M. A. Ciomperlik. 2007. A comparison of traps and stem tap sampling for adult Asian citrus psyllid (Hemiptera: Psyllidae) in citrus. *Florida Entomologist* 90:327–334.

- Handel, S. N. and A. J. Beattie. 1990. Seed dispersal by ants. *Scientific American* 263:76–83.
- Haney, J. C. 1999. Numerical response of birds to an irruption of elm spanworm (*Ennomos subsignarius* [Hbn.]; Geometridae: Lepidoptera) in old-growth forest of the Appalachian Plateau, USA. *Forest Ecology and Management* 120:203–217.
- Hanya, G. 2005. Comparisons of dispersal success between the species fruiting prior to and those at the peak of migrant frugivore abundance. *Plant Ecology* 181:167–177.
- Harrison, R. D. 2000. Repercussions of El Nino: drought causes extinction and the breakdown of mutualism in Borneo. *Proceedings of the Royal Society of London B: Biological Sciences* 267:911–915.
- Heckscher, C. M., 2018. A Nearctic-Neotropical migratory songbird's nesting phenology and clutch size are predictors of Accumulated Cyclone Energy. *Scientific Reports* 8:1–6.
- Hedenström, A. and T. Alerstam. 1997. Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. *Journal of Theoretical Biology* 189:227–234.
- Heller, E. L., J. A. Arnold. And E. L. Walters. 2015. Migrant bird research at Old Dominion University. *Virginia Birds* 11:4–5.
- Herrera, C. M., 1984. A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. *Ecological monographs* 54:1–23.
- Herrera, C. M., P. Jordano, L. Lopez-Soria, and J. A. Amat. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecological Monographs* 64:315–344.

- Herrera M, L. G. Hobson, K. A. Martínez, and C. G. Méndez. 2006. Tracing the origin of dietary protein in tropical dry forest birds 1. *Biotropica* 38:735–742.
- Hodkinson, I. D., 1988. The nearctic Psylloidea (Insecta: Homoptera): an annotated check list. *Journal of Natural History* 22:1179–1243.
- Hodkinson, I. D. 2009. Life cycle variation and adaptation in jumping plant lice (Arthropoda: Hemiptera: Psylloidea): a global synthesis. *Journal of Natural History* 43:65–179.
- Hoh, C. M., S. S. Pagano, and C. J. Norment. 2018. Spatial variation in White-throated Sparrow (*Zonotrichia albicollis*) refueling rate near a migratory barrier. *Wilson Journal of Ornithology* 130:891–901.
- Holmes, S. B., C. J. Sanders, D. Fillman, and D. A. Welsh. 2009. Changes in a forest bird community during an outbreak cycle of the spruce budworm in northwestern Ontario. *Bird Populations* 9:13–28.
- Hoppes, W. G., 1988. Seedfall pattern of several species of bird-dispersed plants in an Illinois woodland. *Ecology* 69:320–329.
- Howe, H. F. and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13:201–228.
- Hume, I. D. and H. Biebach. 1996. Digestive tract function in the long-distance migratory garden warbler, *Sylvia borin*. *Journal of Comparative Physiology Biology* 166:388–395.
- Hurlbert, S. H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- Inouye, R. S., 1980. Density-dependent germination response by seeds of desert annuals. *Oecologia* 46:235–238.

- Izhaki, I. and U. N. Safriel. 1989. Why are there so few exclusively frugivorous birds? Experiments on fruit digestibility. *Oikos* 54:23–32.
- Jaenike, J. 1990. Host specialization in phytophagous insects. *Annual Review of Ecology and Systematics* 21:243–273.
- Jenni, L. and S. Jenni-Eiermann. 1998. Fuel supply and metabolic constraints in migrating birds. *Journal of Avian Biology* 29:521–528.
- Jenni-Eiermann, S., B. Almasi, I. Maggini, V. Salewski, B. Bruderer, F. Liechti. and L. Jenni. 2011. Numbers, foraging and refuelling of passerine migrants at a stopover site in the western Sahara: diverse strategies to cross a desert. *Journal of Ornithology* 152:113–128.
- Jenni-Eiermann, S., L. Jenni, S. Smith, and D. Costantini. 2014. Oxidative stress in endurance flight: an unconsidered factor in bird migration. *PLoS One* 9:p.e97650.
- Jensen, D., 1957. Parasites of the Psyllidae. *Hilgardia* 27:71–99.
- Johnson, M. D., 2000. Effects of shade-tree species and crop structure on the winter arthropod and bird communities in a Jamaican shade coffee plantation
1. *Biotropica* 32:133–145.
- Johnson, R. A., M. F. Willson, J. N. Thompson and R. I. Bertin. 1985. Nutritional values of wild fruits and consumption by migrant frugivorous birds. *Ecology*, 66:819–827.
- Jordano, P., 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *American Naturalist* 129:657–677.

- Jordano, P. and E. W. Schupp. 2000. Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs* 70:591–615.
- Jose, S. and A. R. Gillespie. 1997. Leaf Area productivity relationships among mixed-species hardwood forest communities of central hardwood region. *Forest Science* 43:56–64.
- Juan, T., A. Sagrario, H. Jesús, and C. M. Cristina. 2006. Red fox (*Vulpes vulpes* L.) favour seed dispersal, germination and seedling survival of Mediterranean Hackberry (*Celtis australis* L.). *Acta Oecologica* 30:39–45.
- Kagata, H. and T. Ohgushi., 2006. Bottom-up trophic cascades and material transfer in terrestrial food webs. *Ecological Research* 21:26–34.
- King, J. R. and D. S. Farner. 1965. Studies of fat deposition in migratory birds. *Annals of the New York Academy of Sciences* 131:422–440.
- Klepzig, K. D., A. S. Adams, J. Handelsman and K. F. Raffa. 2009. Symbioses: a key driver of insect physiological processes, ecological interactions, evolutionary diversification, and impacts on humans. *Environmental Entomology* 38:67–77.
- Koprowski, J. L., 1991. Response of fox squirrels and gray squirrels to a late spring-early summer food shortage. *Journal of Mammalogy* 72:367–372.
- Krajicek, J. E. and R. D. Williams. 1990. *Celtis occidentalis* L. Hackberry. *Silvics of North America* 2:262.
- La Sorte, F. A., W. M. Hochachka, A. Farnsworth, D. Sheldon, D. Fink, J. Geevarghese, K. Winner, B. M. Van Doren, and S. Kelling. 2015. Migration timing and its determinants for nocturnal migratory birds during autumn migration. *Journal of Animal Ecology* 84:1202–1212.

- Langslow, D. R., 1978. Gluconeogenesis in birds. *Biochemical society Transactions* 6:1148–1154.
- Le Maho, Y., H. Vu Van Kha, H. Koubi, G. Dewasmes, J. Girard, P. Ferre, and M. Cagnard. 1981. Body composition, energy expenditure, and plasma metabolites in long-term fasting geese. *American Journal of Physiology* 241: E342–E354
- Lease, H. M. and B. O. Wolf. 2011. Lipid content of terrestrial arthropods in relation to body size, phylogeny, ontogeny and sex. *Physiological Entomology* 36:29–38.
- Leatherman, D., 2010. Hackberry Psyllids. *Colorado Birds* 44:185–189.
- Legendre, P. and M. J. Fortin. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80:107–138.
- Leicht-Young, S.A., N. B. Pavlovic, K. J. Frohnapple, and R. Grundel. 2010. Liana habitat and host preferences in northern temperate forests. *Forest Ecology and Management* 260:1467–1477.
- Leroux, S. J., 2019. On the prevalence of uninformative parameters in statistical models applying model selection in applied ecology. *PloS one* 14:e0206711.
- Lill, J. T., 1998. Density-dependent parasitism of the hackberry nipplegall maker (Homoptera: Psyllidae): a multi-scale analysis. *Environmental Entomology* 27:657–661.
- Lindström, Å. and T. Alerstam. 1986. The adaptive significance of reoriented migration of chaffinches *Fringilla coelebs* and bramblings *F. montifringilla* during autumn in southern Sweden. *Behavioral Ecology and Sociobiology* 19:417–424.
- Lodhi, M. A. K., 1975. Allelopathic effects of hackberry in a bottomland forest community. *Journal of Chemical Ecology* 1:171–182.

- MacMynowski, D. P. and T. L. Root. 2007. Climate and the complexity of migratory phenology: sexes, migratory distance, and arrival distributions. *International Journal of Biometeorology* 51:361–373.
- Marquis, D. A., 1990. *Prunus serotina* Ehrh. Black cherry. *Silvics of North America* 2:594–604.
- McCann, J. M., S. E. Mabey, L. J. Niles, C. Bartlett, and P. Kerlinger. 1993 A regional study of coastal migratory stopover habitat for Neotropical migrant songbirds: land management implications. *Transactions of the North American Wildlife and Natural Resources Conference* 58:398–407.
- McDonnell, M. J. and E. W. Stiles., 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* 56:109–116.
- McWilliams, S. R., C. Guglielmo, B. Pierce, and M. Klaassen. 2004. Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. *Journal of Avian Biology* 35:377–393.
- McWilliams, S. R. and W. H. Karasov, 2001. Phenotypic flexibility in digestive system structure and function in migratory birds and its ecological significance. *Comparative Biochemistry and Physiology* 128:577–591.
- Mehlman, D. W., S. E. Mabey, D. N. Ewert, C. Duncan, B. Abel, D. Cimprich, R. D. Sutter, and M. Woodrey. 2005. Conserving stopover sites for forest-dwelling migratory landbirds. *Auk* 122:1281–1290.
- Mills, L. S., M. E. Soulé, and D. F. Doak, D.F., 1993. The keystone-species concept in ecology and conservation. *BioScience* 43:219–224.

- Mitchell, J. C., 2012. Amphibians and reptiles of the Eastern Shore of Virginia National Wildlife Refuge and Fisherman Island National Wildlife Refuge. *Banisteria* 39:21–33.
- Moermond, T. C. and J. S. Denslow. 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. *Ornithological Monographs* 36:865–897.
- Moore, F. R., S. A. Gauthreaux Jr., P. Kerlinger, and T. R. Simons. 1993. Stopover habitat: management implications and guidelines. Pages 58–69 *in* D. M. Finch and P. W. Stangel, eds. Status and management of Neotropical migratory birds. General Technical Report RM-229, U.S. Department of Agriculture, Forest Service, Fort Collins.
- Moore, F. R. and W. Yong. 1991. Evidence of food-based competition among passerine migrants during stopover. *Behavioral Ecology and Sociobiology* 28:85–90.
- Moser, J. C., 1965. The interrelationships of three gall makers and their natural enemies, on hackberry (*Celtis occidentalis* L.). *New York State Museum and Science Service* 402:1–95
- Nathan, R., F. M. Schurr, O. Spiegel, O. Steinitz, A. Trakhtenbrot, and A. Tsoar., 2008. Mechanisms of long-distance seed dispersal. *Trends in Ecology & Evolution* 23:638–647.
- Neuhauser, C. and J. E. Fargione. 2004. A mutualism–parasitism continuum model and its application to plant–mycorrhizae interactions. *Ecological Modelling* 177:337–352.
- Nuismer, S.L., P. Jordano, and J. Bascompte. 2013. Coevolution and the architecture of mutualistic networks. *Evolution: International Journal of Organic Evolution* 67:338–354.
- Pace, M.L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution* 14:483–488.

- Pakeman, R. J. and J. L. Small., 2005. The role of the seed bank, seed rain and the timing of disturbance in gap regeneration. *Journal of Vegetation Science* 16:121–130.
- Parrish, J. D., 1997. Patterns of frugivory and energetic condition in Nearctic landbirds during autumn migration. *Condor* 99:681–697.
- Penn, H. J. and T. O. Crist. 2018. From dispersal to predation: A global synthesis of ant–seed interactions. *Ecology and Evolution* 8:9122–9138.
- Petit, D. R., 2000. Habitat use by landbirds along Nearctic-Neotropical migration routes: implications for conservation of stopover habitats. *Studies in Avian biology* 20:15–33.
- Pierce, B. J., S. R. McWilliams, T. P. O'Connor, A. R. Place, and C. G. Guglielmo. 2005. Effect of dietary fatty acid composition on depot fat and exercise performance in a migrating songbird, the red-eyed vireo. *Journal of Experimental Biology* 208:1277–1285.
- Place, A. R. and E. W. Stiles. 1992. Living off the wax of the land: bayberries and yellow-rumped warblers. *Auk* 109:334–345.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. *BioScience* 46:609–620.
- Putz, F. E., 1984. How trees avoid and shed lianas. *Biotropica* 16:19–23.
- R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Rahbé, Y., Delobel, B., Febvay, G. and Chantegrel, B., 1994. Aphid-specific triglycerides in symbiotic and aposymbiotic *Acyrtosiphon pisum*. *Insect Biochemistry and Molecular Biology* 24:95–101.

- Remsen, J. V. and S. K. Robinson. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. *Studies in Avian Biology* 13:144–160.
- Robinson, D. S. 1970. The function of plasma triglyceride in fatty acid transport. *Comprehensive biochemistry* 18:51–116.
- Rubolini, D., A. Gardiazabal Pastor, A. Pilastro, and F. Spina. 2002. Ecological barriers shaping fuel stores in barn swallows *Hirundo rustica* following the central and western Mediterranean flyways. *Journal of Avian Biology* 33:15–22.
- Ruehle, J. L. and D. H. Marx. 1979. Fiber, food, fuel, and fungal symbionts. *Science*, 206:419–422.
- Sample, B. E., R. J. Cooper, and R. C. Whitmore. 1993. Dietary shifts among songbirds from a diflubenzuron-treated forest. *Condor* 95:616–624.
- Sauer, J. R., W. A. Link, J. E. Fallon, K. L. Pardieck, and D. J. Ziolkowski Jr. 2013. The North American breeding bird survey 1966–2011: summary analysis and species accounts. *North American Fauna* 79:1–32.
- Schaefer, H. M., K. Spitzer, and F. Bairlein. 2008. Long-term effects of previous experience determine nutrient discrimination abilities in birds. *Frontiers in Zoology* 5:4.
- Schaub, M. and L. Jenni. 2001. Variation of fuelling rates among sites, days and individuals in migrating passerine birds. *Functional Ecology*, 15:584–594. Schaub, M., Jenni, L. and Bairlein, F., 2008. Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. *Behavioral Ecology* 19:657–666.
- Schnitzer, S. A., 2018. Testing ecological theory with lianas. *New Phytologist* 220:366–380.

- Schulze, T. L., R. A. Jordan, and R. W. Hung. 1997. Biases associated with several sampling methods used to estimate abundance of *Ixodes scapularis* and *Amblyomma americanum* (Acari: Ixodidae). *Journal of Medical Entomology* 34:615–623.
- Schupp, E. W., 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Plant Ecology* 107:15–29.
- Seewagen C. L, and C. G. Guglielmo. 2010. Effects of fat and lean body mass on migratory landbird stopover ecology. *Wilson Journal of Ornithology* 122:82–87.
- Seewagen, C. L., C. D. Sheppard, E. J. Slayton, and C. G. Guglielmo. 2011. Plasma metabolites and mass changes of migratory landbirds indicate adequate stopover refueling in a heavily urbanized landscape. *Condor* 113:284–297.
- Semeão, A. A., J. C. Martins, M. C. Picanço, M. Chediak, E. M. Da Silva, and G. A. Silva. 2012. Seasonal variation of natural mortality factors of the guava psyllid *Triozoida limbata*. *Bulletin of Entomological Research* 102:719–729.
- Sheehy, J., C. M. Taylor, and D. R. Norris. 2011. The importance of stopover habitat for developing effective conservation strategies for migratory animals. *Journal of Ornithology* 152:161–168.
- Silva, I. M., G. I. Andrade, G. W. Fernandes, and J. P. L. Filho. 1996. Parasitic relationships between a gall-forming insect *Tomoplagia rudolphi* (Diptera: Tephritidae) and its host plant (*Vernonia polyanthes*, Asteraceae). *Annals of Botany* 78:45–48.
- Skeate, S. T., 1987. Interactions between birds and fruits in a northern Florida hammock community. *Ecology* 68:297–309.

- Smith, S. B and S. R. McWilliams. 2014. Fruit removal rate depends on neighborhood fruit density, frugivore abundance, and spatial context. *Oecologia* 174:931–942.
- Smith, S. B., 2013. A physiological assessment of seasonal differences in spring and autumn migration stopover at Braddock Bay, Lake Ontario. *Condor* 115:273–279.
- Smith, S. B., S. A. DeSando, and T. Pagano. 2013. The value of native and invasive fruit-bearing shrubs for migrating songbirds. *Northeastern Naturalist* 20:171–185.
- Smith, S. B., K. H. McPherson, J. M. Backer, B. J. Pierce, D. W. Podlesak, and S. R. McWilliams. 2007. Fruit quality and consumption by songbirds during autumn migration. *Wilson Journal of Ornithology* 119:419–428.
- Smith, S. B., A. C. Miller, C. R. Merchant, and A. F. Sankoh. 2015. Local site variation in stopover physiology of migrating songbirds near the south shore of Lake Ontario is linked to fruit availability and quality. *Conservation Physiology* 3:1–14.
- Smith, S. B. and S. R. McWilliams. 2010. Patterns of fuel use and storage in migrating passerines in relation to fruit resources at autumn stopover sites. *Auk* 127:108–118.
- Snow, A. A. and D. F. Whigham. 1989. Costs of flower and fruit production in *Tipularia discolor* (Orchidaceae). *Ecology* 70:1286–1293.
- Stevens L., 2004. Avian biochemistry and molecular biology. Cambridge University Press, Cambridge.
- Stiles, E. W., 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. *American Naturalist* 116:670–688.
- Stiles, E. W., 1982. Fruit flags: two hypotheses. *American Naturalist* 120:500–509.

- Stiles, E. W. and D. W. White. 1982. Additional information on temperate bird-disseminated fruits: response to Herrera's comments. *American Naturalist* 120:823–827.
- Stireman III, J.O. and D. Cipollini. 2008. Stealth tactics of galling parasites and their potential indirect effects. *New Phytologist* 178:462–465.
- Strode, P. K. 2009., Spring tree species use by migrating Yellow-rumped Warblers in relation to phenology and food availability. *Wilson Journal of Ornithology*, 121:457–468.
- Strong, F., 1963. Studies on lipids in some homopterous insects. *Hilgardia* 34:43–61.
- Suetsugu, K., 2018. Seed dispersal in the mycoheterotrophic orchid *Yoania japonica*: Further evidence for endozoochory by camel crickets. *Plant Biology* 20:707–712.
- Suthers, H. B., J. M. Bickal, and P. G. Rodewald. 2000. Use of successional habitat and fruit resources by songbirds during autumn migration in central New Jersey. *Wilson Bulletin* 112:249–260.
- Symonds, M. R. and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology* 65:13–21.
- Telleria, J. L. and J. Pérez-Tris. 2007. Habitat effects on resource tracking ability: do wintering blackcaps *Sylvia atricapilla* track fruit availability?. *Ibis* 149:18–25.
- Thomas, D. B., 2012. The Authority and types for the hackberry gall psyllid genus *Pachypsylla* (Riley)(Hemiptera: Psyllidae). *Entomological News* 122:279–287.
- Thompson, J. N. and M. F. Willson. 1979. Evolution of temperate fruit/bird interactions: phenological strategies. *Evolution* 33:973–982.

- Tooker, J. F., J. R. Rohr, W. G. Abrahamson, and C. M. De Moraes. 2008. Gall insects can avoid and alter indirect plant defenses. *New Phytologist* 178:657–671.
- Tracy, C. R., T. J. McWhorter, M. S. Wojciechowski, B. Pinshow, and W. H. Karasov. 2010. Carbohydrate absorption by blackcap warblers (*Sylvia atricapilla*) changes during migratory refuelling stopovers. *Experimental Biology* 213:380–385.
- Traveset, A., 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives in Plant Ecology, Evolution and Systematics* 1:151–190.
- Valido, A. and J. M. Olesen. 2019. Frugivory and seed dispersal by lizards: a global review. *Frontiers in Ecology and Evolution* 7:1–8.
- Van der Pijl, L. 1982. Principles of seed dispersal in higher plants. Springer, Berlin.
- Van Doren, B. M., D. Sheldon, J. Geevarghese, W. M. Hochachka and A. Farnsworth. 2014. Autumn morning flights of migrant songbirds in the northeastern United States are linked to nocturnal migration and winds aloft. *Auk: Ornithological Advances* 132:105–118.
- Van Doren, B. M., K. G. Horton, P. M. Stepanian, D. S. Mizrahi and A. Farnsworth. 2016. Wind drift explains the reoriented morning flights of songbirds. *Behavioral Ecology* 27:1122–1131.
- Venables, W. N. and B. D. Ripley. 2002. Modern applied statistics with S. Fourth Edition. Springer, New York. <http://www.stats.ox.ac.uk/pub/MASS4>
- Viana, D. S., L. Gangoso, W. Bouten, and J. Figuerola. 2016. Overseas seed dispersal by migratory birds. *Proceedings of the Royal Society of London Biological Sciences* 283:20152406.

- Wenny, D. G., 2000. Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecological Monographs* 70:331–351.
- Wheeler, E. A., C. A. LaPasha. And R. B. Miller. 1989. Wood anatomy of elm (*Ulmus*) and hackberry (*Celtis*) species native to the United States. *IAWA Journal* 10:5–26.
- Whittaker, R. H., 1972. Evolution and measurement of species diversity. *Taxon* 21:213–251.
- Whittaker, R. J., K. J. Willis, and R. Field. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography* 28:453–470.
- Wiedner, D. S., P. Kerlinger, D. A. Sibley, P. Holt, J. Hough, and R. Crossley. 1992. Visible morning flight of Neotropical landbird migrants at Cape May, New Jersey. *Auk* 109:500–510.
- Wikelski, M., E. M. Tarlow, A. Raim, R. H. Diehl, R. P. Larkin, and G. H. Visser. 2003. Avian metabolism: costs of migration in free-flying songbirds. *Nature* 423:704–704.
- Willson, M. F., 1986. Avian frugivory and seed dispersal in eastern North America. *Current Ornithology* 3: 223–279.
- Witmer, M. C., 1998. Ecological and evolutionary implications of energy and protein requirements of avian frugivores eating sugary diets. *Physiological Zoology* 71:599–610.
- Wootton, J. T., 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* 25:443–466.
- Yang, M. M. and C. Mitter. 1994. Biosystematics of hackberry psyllids (*Pachypsylla*) and the evolution of gall and lerp formation in psyllids (Homoptera: Psylloidea): a preliminary report. Pages 172–185 in P. W. Price, W. J. Mattson and Y. N. Baranchikov, eds. In *The ecology and evolution of gall-forming insects*. US Department of Agriculture, St Paul

- Yang, M. M., C. Mitter, and D. R. Miller. 2001. First incidence of inquilinism in gall-forming psyllids, with a description of the new inquiline species (Insecta, Hemiptera, Psylloidea, Psyllidae, Spondylaspidinae). *Zoologica Scripta*, 30:97–113.
- Zajac, R., J. Cerasale, and C. Guglielmo. 2006. The rapid response of plasma metabolites to changes in feeding rate in a small passerine *Wilsonia pusilla*. *Journal of Avian Biology* 37:405–408.
- Zuefle, M. E., W. P. Brown, and D. W. Tallamy. 2008. Effects of non-native plants on the native insect community of Delaware. *Biological Invasions* 10:1159–1165.
- Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer. New York.

VITA

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EDUCATION

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SELECTED EXPERIENCE

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William and Mary, Williamsburg, VA

Field Assistant – Breeding Bird Atlas (May 2018 – July 2018)

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SELECTED AWARDS

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Virginia Society of Ornithologists (VSO) Small Research Grant (2016). Selected as recipient of \$500 to fund field work.

Virginia Academy of Science (VAS) Small Research Grant (2017) Selected as a recipient of \$1250 to fund field work

SELECTED PRESENTATIONS

Hines, C.H., and Walters, E. L., 2019. The Effects of Migratory Songbird Foraging Behavior. At Virginia Society of Ornithologist meeting, Harrisonburg VA

Hines, C. H., and Walters, E. L., 2019. Poster: An indirect mutualism between host-specific insects and Hackberry trees (*Celtis* spp), mediated by migratory songbirds. At National American Ornithology Society Meeting, Tucson, AZ

Hines, C. H., and Walters, E. L., 2019. Songbird Stopover Habitat Amid a Rising Tide. At BGSO Graduate Symposium, Norfolk, VA