THE FORAGING ECOLOGY AND THE AVAILABILITY OF FOOD RESOURCES FOR TWO FOREST-ASSOCIATED BIRD INHABITING COFFEE AGROECOYSTEMS IN CHIAPAS, MEXICO

by

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Abstract

Shade-grown coffee has received much attention for providing bird habitat in tropical regions. Within shade coffee production, canopy management can vary greatly, and this variation may produce changes in the availability of food resources for forest-associated birds. To evaluate food availability and habitat quality in two farms with different shade management styles, bird foraging behavior was analyzed in terms of prey attack rates and foraging substrates utilized. These behaviors were examined in two species, the Yellow-green Vireo (*Vireo flavoviridis*) and the White-winged Tanager (*Spermagra leucoptera*). Measurements of individual body condition, including fat reserves, mass, and blood hematocrit levels were compared to provide an additional index of habitat quality.

Significant differences were encountered between farm types both in the variety of shade trees used as foraging substrates and the rate of prey attack, indicating a decreased availability of food resources for birds foraging in the low shade coffee farm. A confounding factor in comparing these farms is that in addition to differences in the amount of shade cover, there is a vast difference in the diversity of trees present. To control for this, foraging behaviors were also compared within common shade tree genera between farms, which led to similar results as those found in the aggregate data. These results suggest that the shade management style--both shade tree diversity and amount of shade cover--affects the availability of food for forest-associated birds, and this likely contributes to the high avian diversity observed in high shade coffee farms.

Table of Contents

Chapter 1

Introduction: The Foraging Ecology and Availability of Food Resources of Two Forest-Associated Breeding Birds Inhabiting the Coffee Agroecosystem in Chiapas, Mexico

It has frequently been observed that the regions of the tropics harbor more than 90% of global biodiversity, and also are undergoing a large and rapid loss of forest habitat (Groombridge and Jenkins 2000, Curran et al. 2004, DeFries et al. 2005). Birds present a particularly well studied taxa in this realm, and it has been estimated that half of all threatened bird species and approximately one third of the global bird population that is considered at risk of extinction due to habitat loss reside in tropical forests (Birdlife-International 2000, Gaston et al. 2003). Perhaps not surprisingly, forest-dwlling species have been described as the most threatened in the tropics (Stotz et al. 1996), with forest-dwelling insectivores in particular being highly vulnerable to habitat loss or degradation (Sekercioglu et al. 2002, Gray et al. 2007). Insectivores tend to be more sensitive to small changes in habitat structure due to specialization in prey selection and microhabitat use (Sekercioglu et al. 2002). Food availability has been noted to be central to the success of songbirds generally speaking (Martin 1987), and has been indicated as a possible explanation for declines in forest insectivore species richness and abundance (Burke and Nol 1998, Zanette et al. 2000, Ford et al. 2001).

Traditional approaches to biodiversity conservation focus on the preservation of relatively pristine habitats with large numbers of endemic and total species (Myers 1988, Stattersfield et al. 1998, Myers et al. 2000). However, only a small amount of the remaining habitat can be expected to be effectively preserved (Petit and Petit 2003). Currently, roughly 11.5% of the land area in the world is classified as protected (Rodrigues et al. 2004), while approximately 40% of the land area is under agricultural management (FAO 2007). As a result, increased attention is being paid to the potential conservation value for biodiversity of those lands found outside of preserves and parks (Vandermeer and Perfecto 2007, Harvey et al. 2008). It has been observed by many that although there may not be a suitable "replacement" for pristine habitats (Cohen and Lindell 2004), a gradient of habitat degradation and biodiversity loss does exist for many taxa, including birds (Canaday 1996, Daily et al. 2001, Hughes et al. 2002, Perfecto et al. 2003, Petit and Petit 2003, Donald 2004, Mas and Dietsch 2004). Some land-use types, such as traditional agroforests, might be expected to have a reduced impact on local biodiversity compared to that of highly intensive uses such as industrial agricultural production (Perfecto and Vandermeer 2008).

One land-use type of particular importance in tropical regions is coffee production, which spans most of the tropics. Coffee is the second most important commodity in legal trade after petroleum (O'Brien and Kinnaird 2003). Annually, its production has a value of approximately $100 billion, making it an important source of foreign capital for many tropical countries (Donald 2004). Globally, about 7 million tons are produced from 11.5 million hectares each year (Donald 2004). Most of the world's higher quality Arabica coffee is produced in Latin America, where production is dominated by smallholders—98% of coffee farms in Mexico and 90% in Central America are enterprises under 10ha (Rice and Ward 1996). Coffee production is also largely focused in those areas identified as biodiversity hotspots (Myers et al. 2000), and thus can impact biodiversity disproportionately to the relatively small global land area that it occupies (Donald 2004). World coffee prices has been found to be correlated to deforestation in producing countries and some argue that it can contribute to deforestation (O'Brien and Kinnaird 2003), however, it has long been noted that shaded coffee farms can serve as habitat for a large number of organisms, particularly birds (Griscom 1932).

These varying outcomes can be traced to the wide intensity gradient that exists in coffee production (Moguel and Toledo 1999). This gradient ranges from heavily shaded "rustic" management, which involves leaving the native forest canopy intact and planting coffee underneath, to intensely managed open-sun monocultures with high levels of agrochemical use and mechanization. In between, with increasing intensification and decreasing amounts of shade cover and canopy diversity, coffee farms can be classified as traditional polycultures/coffee gardens, commercial polycultures, and shaded monocultures (Moguel and Toledo 1999). The use of shade trees can positively affect pest management (Staver et al. 2001) and bean quality, size, and taste (Muschler 2001).

In some cases, shade cover up to 50% can increase coffee yields (Soto-Pinto et al. 2000). Open-sun production is increasingly common due to its short-term increases yield/unit area under favorable soil and climatic conditions (Perfecto et al. 1996, Donald 2004). However, the transition to this intensive-style production has in some cases led to increased pest problems and secondary pests (Staver et al. 2001) and threatens the long-term sustainability of production due to increased water and soil runoff (Rice 1990).

Patterns of diversity vary by taxa, but the general pattern is that as vegetative and structural diversity increases, the ability of a coffee system to provide habitat for a diversity of organisms increases (Perfecto et al. 1996, Moguel and Toledo 1999, Perfecto et al. 2003, Carlo et al. 2004, Donald 2004). This is especially true for birds, whose relationship with the coffee agroecosystem has been well-studied (Wunderle and Latta 1996, Greenberg et al. 1997a, Greenberg et al. 1997b, Petit et al. 1999, Dietsch 2003, Perfecto et al. 2003, Petit and Petit 2003, Pomara et al. 2003, Tejeda-Cruz and Sutherland 2004, Johnson et al. 2006). Although even the more structurally complex coffee systems differ in species composition from intact forest (Greenberg et al. 1997a, Greenberg et al. 1997b), shaded coffee systems have been observed to provide habitat for a large diversity and abundance of bird species, including many forest species (Wunderle and Latta 1996, Greenberg et al. 1997a, Greenberg et al. 1997b, Dietsch 2003, Petit and Petit 2003).

As a result of these biodiversity patterns, and the threat of increasing intensification in the production of coffee, several "biodiversity-friendly" certification systems have been developed by organizations such as the Smithsonian Migratory Bird Center (SMBC), Conservation International, and the Rainforest Alliance; all with varying goals and certification criteria (Perfecto and Armbrecht 2003, Mas and Dietsch 2004). These were spurred in part by concern about habitat loss for declining North American migratory birds in Latin America (Robbins et al. 1989, Messer et al. 2000). Although these programs have remained small compared to the total coffee market (Messer et al. 2000), they have had some success in identifying farms with significant conservation value and providing incentives for the maintenance of biodiversity (Mas and Dietsch 2004, Philpott et al. 2007).

The "Bird-Friendly" certification developed by the SMBC is the most stringent certification program, and is focused on encouraging conservation of existing shade-coffee habitat for North American migratory birds (Rice and McLean 1999). Its certification criteria are based on those drawn up by the First Sustainable Coffee Congress (organized by SMBC) in 1996, and are entirely focused on shade management, although organic production is a prerequisite for certification (Mas and Dietsch 2004).

Much of the marketing and impetus for developing "Bird-Friendly" coffee has been based on the value for North American birds wintering in coffee-producing regions. Neotropical resident and breeding species also face declines and habitat loss across much of their range, and also can be found utilizing shaded coffee farms for habitat (Wunderle 1996, Greenberg et al. 1997c, Hughes et al. 2002, Petit and Petit 2003). However, these resident species are more likely to have specialized foraging and breeding requirements compared to their generalist migrant counterparts, and seem to be more sensitive to the intensification process in coffee production (Bierregaard et al. 1992, Petit et al. 1999, Perfecto and Armbrecht 2003, Tejeda-Cruz and Sutherland 2004). In coffee-producing areas whose forests are either gone or highly fragmented, though, shaded coffee farms may represent a refuge for many resident species by acting either as habitat or a high-quality matrix to supplement limited forest resources (Perfecto and Armbrecht 2003). Indeed, many studies have found indications of resident forest species utilizing shaded coffee farms for foraging and breeding resources (Wunderle and Latta 1996, Greenberg et al. 1997a, Greenberg et al. 1997b, Dietsch 2003, Petit and Petit 2003). However, more studies are necessary to understand the dynamics of resident and breeding birds in these systems and the value shade coffee for their conservation.

As previously described, there is a great diversity of management styles involved even in so-called "shade coffee." Coffee agroecosystems represent a potentially crucial refuge habitat for the conservation of forest-associated resident birds. It has been noted that resident and breeding species in coffee-producing regions are more sensitive to habitat perturbations than migrants, perhaps due to more specialized foraging and breeding requirements (Perfecto and Armbrecht 2003, Tejeda-Cruz and Sutherland 2004). Therefore, in order to understand how valuable shaded coffee farms are for the conservation of these birds, it is important to understand what influences their use of the coffee agroecosystem, and how that use is impacted by intensification in shade management.

The intent of this research is to explore what aspects of shade management in the coffee agroecosystems affect the foraging resources available to forest birds during the breeding season, a time of highly elevated energetic demand for most songbirds, and whether high shade coffee farms represent a higher quality habitat in terms of foraging resources. Data was collected in two farms to compare the habitat quality and available foraging resources in a high shade commercial polyculture versus a low shade shaded monoculture in southern Chiapas, Mexico. Two forest-associated species that breed in the area, the Yellow-green Vireo (*Vireo flavoviridis*) and the White-winged Tanager (*Spermagra leucoptera*), were selected for analysis. These are not strict forest specialists, but are traditionally associated with forested habitats and are commonly found on coffee farms in the area of study. They are commonly found in both of the farms studied here, but are found with considerably higher abundance in the higher shade farm (Dietsch 2003, Mas and Dietsch 2004). These species were selected to exemplify forest-associated species that *can* and do exist in a more intensified system, but are clearly affected by that intensification (as indicated by their lower abundance in the low shade farm). Examining how the availability of food resources varies and is affected by the intensification of shade management for these relatively common species may provide an indication as to how and why diversity is structured the way it is for the broader group of forest birds in the region.

In this research I have used foraging behavior indices as a proxy for food availability. There are specific aspects of foraging behavior that have been observed to have a predictable relationship with prey abundance and food availability (Thiollay 1988, Hutto 1990, Lovette and Holmes 1995, Lyons 2005). As a result, these behaviors can be used as an indicator of food availability in place of traditional prey sampling methods, and may be more effective (Hutto 1990).

Direct prey sampling has many associated problems which are avoided in studies using foraging behavior. Particularly for insectivore species, issues of spatial and temporal scale in sampling makes it difficult to determine if your sample accurately reflects prey availability as the birds see it (Smith and Rotenberry 1990). In addition, the perspective of a bird researcher is not identical to that of a foraging bird, and direct prey samples may not properly assess food availability due to foraging limitations and preferences (i.e. which prey items are distasteful, difficult to handle, easiest to catch, etc.) (Hutto 1990). Thus such samples, when taken, need to be analyzed with the understanding of these and other limitations (see Hutto 1990 for a more complete listing).

Instead, foraging variables derived from optimal foraging theory may provide a more realistic assessment of food availability, since they take a bird's perspective of its prey directly into account. Two common behavioral variables used in this regard are attack rate and foraging speed (Hutto 1990, Lyons 2005). Attack rate during active foraging provides a measure of prey-encounter rate, and is therefore indicative of prey density and abundance (Hutto 1990). Foraging speed, which is less commonly assessed, derives from the assumption that in areas of high prey density, a foraging individual will move more slowly because a successful attack is more likely and thus worth the time investment. In areas of lower prey density, a foraging individual would be expected to move more quickly in order to find a prey-rich area without wasting too much time in the prey-poor area (Zach and Falls 1976, Zach and Falls 1979, Pienkowski 1983).

In the second chapter of this thesis, I use these indices (attack rate and foraging speed) to assess food availability as a general indicator of habitat quality between high and low shade coffee farms. The availability of food is thought to be a commonly limiting resource for many bird populations (Martin 1987, Martin 1992). This is especially true for tropical insectivores faced with habitat loss (Canaday 1996, Tejeda-Cruz and Sutherland 2004). Therefore, differences in the availability of food resources may speak heavily toward the overall quality of a given habitat (Lyons 2005). In addition, data describing body condition of individuals (furcular fat scores, mass, blood hematocrit levels) was collected in an attempt to correlate multiple indices of habitat quality.

Two of the most important and noticeable variables associated with various shade management systems are shade tree diversity and the intensity of shade management. In chapter three, I examine more closely how these two variables are affecting the results found in chapter two. While descriptive as to the comparative habitat quality presented by these two farm types, my initial results are inherently complicated by the variation in shade tree diversity found between the two farms and the differing foraging resources presented by different shade tree types. Given the differences in foraging behavior and food availability that were found between high and low shade coffee farms, what part of those differences was caused by differences in the shade trees available in the different farms? Within the same shade tree species, what effect does shade management have on foraging resources for forest birds? I attempt to answer these questions in chapter four, and conclude by suggesting how my results may be used to improve standards and recommendations used in biodiversity-friendly certification programs for coffee production.

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Chapter 2

Foraging Behavior of Two Forest-associated Birds in a Coffee Agroecosystem in Mexico: An Indication of Habitat Quality?

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Abstract

Widespread attention has been focused on the role of shade-grown coffee farms in providing habitat and aiding in the conservation of Neotropical forest-associated birds. In coffee-producing regions, there exists a spectrum of management practices that vary in intensity and shade cover, with implications for the quality of habitat available for Neotropical birds, particularly resident species. The availability of foraging resources for these birds represents one habitat feature that is likely to be strongly affected by the intensification of agricultural management. We studied the availability of food resources for two species of resident forest-associated birds, the Yellow-green Vireo (*Vireo flavoviridis*) and the White-winged Tanager (*Spermagra leucoptera*), which are commonly encountered in the coffee farms of the Soconusco region of Chiapas, Mexico. We used indices of foraging behavior (attack rates and foraging speeds) as an indication of food availability between two types of coffee agroecosystems of differing management intensity, and then used to measures of individual body condition to assess whether potential variation in food availability was affecting the physical health of foraging birds. Significant differences were found in the attack rates of both species, indicating a higher prey encounter rate and increased food availability in the lower intensity, high shade site. Analysis of foraging speeds did not yield significant differences between farms for either species, contributing to a debate of the ambiguity of this measure an index of food availability. No strong patterns were determined from analysis of body condition data, although small sample sizes and conflicting factors such as parasite loads may be

affecting these results. Considered together, data from body condition and foraging behavior suggest that agricultural intensification in coffee farms adversely affects the availability of food resources for some species of forest-associated resident birds.

Introduction

Shade-grown coffee has received much attention in the conservation literature in past years, particularly for its documented benefit of providing habitat for Neotropical migratory birds (Perfecto et al. 1996, Greenberg et al. 1997a, Greenberg et al. 1997b, Sherry 2000, Dietsch 2003). Neotropical resident species have also been observed to benefit from shade coffee, particularly in the face of increasing forest loss within much of their range (Wunderle and Latta 1996, Greenberg et al. 1997b, Hughes et al. 2002, Petit and Petit 2003). Of particular interest is the use of shade-grown coffee farms by bird species that are generally considered forest dwellers or forest specialists. Studies have pointed out that shade coffee systems provide habitat for forest species in the tropics, and have observed similar levels of species diversity between the two systems (Perfecto et al. 1996, Donald 2004).

As a result of these findings, a certification program for Bird-Friendly© coffee was developed by the Smithsonian Migratory Bird Center (Mas and Dietsch 2004). This program entails specific criteria for what constitutes appropriate conservation properties, and provides a higher price for the farmer producing the coffee and a politically-based consumer option for those concerned about wildlife conservation. Multiple other biodiversity-friendly certification programs have followed (Giovannucci 2003, Perfecto and Armbrecht 2003).

One issue involved with certification programs to protect biodiversity is the high variability of management systems, even within those that might be called “shade-grown” (Moguel and Toledo 1999). Specifically, coffee that is “shade-grown” can be broken down further into groups such as Rustic, Traditional Polyculture, Commercial Polyculture, and Shaded Monoculture (see Moguel and Toledo 1999 for further descriptions of these groupings). Most studies of birds in coffee have focused on bird diversity and the existence of forest-dwelling birds (Greenberg et al. 1997a, Greenberg et al. 1997b, Dietsch 2003, Perfecto et al. 2003) in coffee plantations. There is a growing literature however, that describes the ecological responses and functions of avian diversity in coffee plantations (Pomara et al. 2003, Tejeda-Cruz and Sutherland 2004, Cruz-Angon and Greenberg 2005, Philpott et al. 2005, Jedlicka et al. 2006, Dietsch et al. 2007). Some studies have suggested that certain shade coffee habitats may provide adequate foraging resources for insectivorous birds relative to undisturbed forest, and that no additional foraging effort is necessary (Wunderle and Latta 2000, Johnson and Sherry 2001, Pomara et al. 2003).

The availability of foraging resources is one possible measure of habitat quality. While an evaluation of food resources should be a fitting measure of habitat quality, such an endeavor is filled with substantial difficulties. These can largely be attributed to issues of study-scale and differences in perception of resources between a researcher and the organism being studied, particularly for insectivorous species (Hutto 1990, Smith and Rotenberry 1990). In an effort to address such issues, many researchers have turned instead to studies of foraging behavior that can serve as a proxy for resource abundance (Robinson and Holmes 1982, Robinson and Holmes 1984, Lyons 2005, Lebbin 2007).

It has been suggested that measurements of certain behaviors on the part of the foraging individual are a more effective measurement of resource availability for some purposes than a direct measurement of the resources involved (Hutto 1990) . In particular, measures of prey attack rates (as an indication of prey-encounter rate) appear to provide a relevant estimate of actual prey abundance and availability, since it measures directly how the foraging bird perceives its resources (Delestrade 1999, Sheperd and Boates 1999, Lyons 2005). Foraging speed has also been cited as an indicator of resource availability and abundance, although it has been used less frequently in the literature, and with mixed results (Zach and Falls 1976, Zach and Falls 1979, Pienkowski 1983, Lyons 2005).

Measures of body condition are another method of analyzing habitat quality. Methods such as furcular fat scoring and mass/morphological size measurements tell us about habitat conditions of birds insofar as habitat conditions constrict the ability of individuals to grow in size and physiological energy reserves (Johnson 1985, Conway 1994, Strong and Sherry 2001). Lipids in particular are the major form of energy storage for birds, and are the first to be utilized in times of hardship (Griminger 1986, Blem

1990). As a result, lipids are thought to be a limiting physiological requirement during annual avian cycles (Johnson 1985).

As a measure of habitat quality, I compared the variables of foraging behavior, attack rate and foraging speed, along with indicators of body condition, for two forest-associated species, the Yellow-green Vireo (*Vireo flavoviridis*) and the White-winged Tanager (*S. leucoptera*), in two shaded coffee farms of varying management intensity. The diet of the Yellow-green Vireo is largely composed of insects, particularly in the summer (Howell and Webb 2005). The White-winged Tanager has a more variable diet, feeding on insects, fruit, and seeds (Howell and Webb 2005). During this study, it was observed to eat mostly insects. I selected these two species for study because they are associated with forest habitats and are commonly found in both high and low shade coffee. Comparing foraging resources of those forest-associated species that are able to persist in and use multiple coffee habitats may provide additional insight to understanding how intensification of coffee systems impacts such species in terms of food resources.

I focused my attention on a comparison between two types of coffee management to determine relative availability of prey in these habitats, which differ in vegetation, habitat structure, and species diversity. Foraging observations and body condition measurements were taken during the breeding season (May-July) in order to assess foraging resources in a time of intensive resource needs, when nesting birds must feed themselves and nestlings (Martin 1987, Martin 1992).

Methods

This study was carried out within two shaded coffee farms in the Soconusco region of the Sierra Madre Mountains in Chiapas, Mexico. Finca Irlanda (15°10' N, 92°20'W) is a highly diverse shaded organic farm, with up to 200 shade tree species. Finca Hamburgo (15°10' N, 92°19' W) is managed in a more intensive fashion, has a lower amount of shade cover, and is dominated almost entirely by *Inga* species. There are some synthetic fertilizers used in Finca Hamburgo, but on an infrequent basis. These two farms are separated by an unmanaged forest fragment. Table 1 lists additional properties of these two farms.

Foraging data was collected between late May and late July, 2006, with most observations taken between 0600 and 1200 Eastern Standard Time (EST). We used existing roads and trails throughout both farms for transects, as these were already dispersed at regular intervals throughout the farms, generally followed elevational terraces, and allowed increased visual ability and bird observation than straight transects through 2-3 meter tall coffee.

Foraging observations were made along 500 meter transects, stopping every 50 meters for a 10 minute observation period. During that period, if a foraging individual was detected, it was followed for as long as it remained in sight up to five minutes, and its behavior and all movements were dictated into a portable voice recorder. Observations were also recorded opportunistically if focal species were found foraging between established observation periods and transects. Observations were conducted only 2-3 times on each transect over the study period to avoid multiple observations of the same individuals. The recorded data on movements, foraging activity, and other behaviors was transcribed from the tapes each evening, using a stopwatch to determine the timing of each behavioral sequence.

Prey attack maneuvers included gleans, sally-hovers, sally-strikes, and sallies (after Remsen and Robinson 1990, Lovette and Holmes 1995, Lyons 2005). Gleans refer to any attack from a stationary position on a stationary prey item. Sally-hovers include attacks from a hovering position on stationary prey, and sally-strikes were similar but lacking the hovering motion. Sallies, or aerial attacks from a perch on flying prey, were only rarely observed in this study, while the other three maneuvers were quite common.

Foraging movements involved hops, short flights (<1m), or long flights (>1m) (Robinson and Holmes 1982, Robinson and Holmes 1984, Lyons 2005, Lebbin 2007). Time, foliage density (0-5, see Remsen and Robinson 1990), and tree species (if foraging in the shade canopy) were also noted by the observer. If the focal individual went out of sight and was quickly resighted, this was noted into the recorder, and the unobserved time was subtracted for the total time accumulation for the foraging bout. Prey attack maneuvers and movements were tallied, and they and all associated information (time, location, observer, etc) were entered into a database for analysis.

Body condition information was also collected from individuals captured in order to compare multiple methods of habitat quality analysis. Mist-nets were operated from late May through late July 2006, generally two or three 10-12 meter nets at each site for three consecutive days and then rotated through different habitat types (high and low shade coffee, forest).

Furcular fat scores are a relatively accurate index of body condition that is easily measurable in the field (Conway 1994), and were collected on a scale of 0-5 based on MAPS protocol (2006). Mass and wing chord measurements were also collected as an indicator of mass corrected for structural size (Conway 1994, Strong and Sherry 2001 , Latta and Faaborg 2002, Johnson 2006) to provide an additional indicator of individual body condition. Body conditional indicators were additionally analyzed across all species captured, as well as by general groups based on broad foraging guilds (frugivores/granivores/nectivores, insectivores, and omnivores) and habitat associations (forest/woodland or open/disturbed habitats).

Additionally, blood samples were taken to provide hematocrit data, another indicator of individual health and resource availability within each habitat. Hematocrit levels have often been used to assess nutritional states in the past (Amand 1986), and may indicate a variety of health issues for an individual bird, including anemia or other mineral deficiency, and bacterial and parasite infections (Carpenter 1975). In a lower quality habitat, one would expect that foraging birds faced with substandard nutritional resources would have lower hematocrit values than birds foraging in a higher quality habitat (Owen et al. 2005). Hematocrit levels were measured from blood samples taken in 14 individuals in the high shade coffee farm and 16 individuals in the low shade farm.

Attack rates and foraging speed were computed by tallying the number of attack maneuvers or movements and then dividing by the amount of time spent foraging in each observation, and then compared between low shade and high shade habitats using ANOVA and linear regression analysis (SPSS v. 13.0). Attack rates and foraging speed were square root-transformed in order to fulfill assumptions of normality. Attack maneuvers and movements were also analyzed to determine if the varying habitat structures between the coffee farms was having additional effects for the types of behavior that focal species displayed while foraging. Hematocrit levels were compared across all species between the high and low shade farms using ANOVA.

Results

Foraging observations were collected from 376 total individuals during the study period. Foraging observations of 92 Yellow-green Vireos (80.7 minutes of active foraging) and 39 White-winged Tanagers (40.3 minutes of active foraging) were collected in Finca Irlanda, the high shade farm. On the low shade farm, Finca Hamburgo, 54 Yellow-green Vireo observations (77.9 minutes) and 44 White-winged Tanager observations (62.6 minutes) were collected. Samples were concentrated in the hours between 0600 and 1200 EST.

Regression analysis found no evidence that of date, time, or transect location within a site influenced attack rate or movement rate results for either species ($p>0.10$ for all variables). Sex, which could only be determined in White-winged Tanager data, also did not significantly influence results ($p>0.10$).

Attack rates were significantly higher in both Yellow-green Vireo ($F=2.549$, $df=4$, $p=0.02$) and White-winged Tanager ($F=2.635$, $df=4$, $p=0.028$) in the high shade farm than the low shade farm (Fig. 1). Mean attack rate of Yellow-green Vireo in the high shade farm was doubled that in the low shade farm, with 2.61 (±0.24) attacks/minute in the high shade farm and 1.30 (±0.11) attacks/minute in the low shade farm. Mean attack rate for the White-winged Tanager in the high shade farm was more than doubled that in the low shade farm, with 2.57 (±0.49) attacks/minute in high shade 1.16 (±0.13) attacks/minute in the low shade farm. Attack rates were not affected by foliage density (i.e. the density of foliage immediately surrounding the foraging individual) in either habitat ($p>0.10$).

Foraging speed did not differ significantly between farms for either species (Yellow-green Vireo: $F=1.745$, $df=4$, $p=0.575$; White-winged Tanager: $F=0.408$, $df=4$, $p=0.264$). Yellow-green Vireos moved 12.48 (±0.70) times per minute on average in the high shade farm, and 11.38 (±0.64) times per minute in the low shade farm. White-winged Tanagers moved on average 12.12 (±0.97) times per minute in the high shade farm and 13.09 (±0.65) times per minute in the low shade farm. Movement distance (i.e., the relative proportions of hops, short flights and long flights) did not vary significantly between high and low shade farms for the Yellow-green Vireo (χ^2=1.082, df=2, p>0.05), but was significant for the White-winged Tanager (χ^2=6.357, df=2, p<0.05). In the high shade farm, White-winged Tanagers used more hops and less short flights while foraging than tanagers foraging in the low shade farm, and vice versa for foraging patterns in the low shade farm (Fig. 4). Foliage density around foraging individuals did not significantly affect patterns of foraging speed (p>0.10).

Slight differences were observed for both species in terms of frequency of attack maneuvers used between habitats (Fig. 2). Both species used gleans to attack prey an increased percentage of the time when foraging in the high shade farm, and used aerial attack types a larger percentage of the time when foraging in the low shade farm. Although there is a visible difference in attack maneuver use by habitat (especially when broken down to gleaning vs. aerial maneuvers, Figure 3) these patterns are not statistically significant for the Yellow-green Vireo (χ^2=4.815, df=2, p>0.05) or White-winged Tanager (χ^2=4.762, df=2, p>0.05). These patterns remain statistically insignificant even when lumped into broader "gleaning" versus "aerial" categories (p>0.05).

Approximately 8073 cumulative net-hours yielded 111 individual birds caught. The high shade farm yielded 0.0140 birds/net hour (67 birds from 4789.5 total net hours), and the low shade farm yielded 0.0134 birds/net hour (44 birds from 3283.5 total net hours) Fourteen Yellow-green Vireos were caught in the high shade farm, and four in the low shade farm. No White-winged Tanagers were caught in the high shade farm, and only two were caught in the low shade farm, preventing analysis of body condition in that species. Body condition data is presented for the Yellow-green Vireo, and was also compared at broader scopes including all individuals of various species caught and measured and based on broadly defined foraging guilds and habitat associations.

Initial analysis indicated significantly higher fat scores on Yellow-green Vireos on the high shade farm (Fig. 5; Mann-Whitney U-test p=0.043). No significant differences were found for Yellow-green Vireo individuals in mass/wing chord measurements (Fig. 6). Across all species, furcular fat scores were not significantly different (Fig. 7, Mann-Whitney U-test p= 0.667). Transformed mass/wing chord measurements were also statistically insignificant (Fig. 8; F=1.99, df=1, p=0.161).

No groupings or combinations based on habitat or foraging guild showed any significant effect of habitat type on fat scores or mass/wing chord ratios. Date of measurement was significant in the fat scores of forest-associated species (p=0.024) and mass/wing chord ratios in omnivores (F=1.211, df=4, p=0.044). Age and sex of the birds sampled was not a significant factor in this model (p>0.05 for both), nor was date of measurement except for that noted above (p>0.05).

Analysis of blood hematocrit levels did not indicate any significant differences for birds foraging in the high versus low shade coffee farms (F=2.020, df=1, p=0.166). In the high shade farm, mean hematocrit levels were 46.57 ± (3.59 SE, N=14) compared to 51.63 (± 1.11 SE, N=16) in the low shade farm.

Discussion

Many forest birds can be found in shaded coffee plantations, and some exist in farms with even minimal shade cover, but a disparity in diversity and abundance has been shown between farms of varying management intensity (Dietsch 2003). The hypothesis of this study was that these differences could be due to variation in food resource availability, especially in light of many studies documenting differences in arthropod diversity and abundance along an intensification gradient in coffee cultivation (Perfecto and Vandermeer 1994, Perfecto et al. 1996, Perfecto et al. 1997), and along structural complexity gradients in other habitats (Bunnell and Huggard 1999, Hijii et al. 2001, Ishii et al. 2004, Maleque et al. 2006).

Significant differences in attack rate appear to support this hypothesis, as both Yellow-green Vireos and White-winged Tanagers attacked prey more frequently in the high shade farm compared to individuals in the low shade farm. This suggests that there is a higher availability of food resources in the high shade farm and may account for some of the differences observed in forest bird diversity and abundance among various management styles. These results are consistent with other studies that have compared aspects of foraging behavior with other indices of food resource abundance (Hutto 1990, Johnson 2000).

Although not significant, differences were also found in the relative proportions of attack maneuver use by birds within each farm. Foraging individuals of both species used gleaning attacks a higher percentage of the time in the high shade farm than in the low shade farm. In addition, aerial attacks were used more often in the low shade farm for both species. This could be indicative of differences in habitat structure and prey items affecting foraging behavior between two otherwise similar landscapes. Vegetation structure and prey availability has been shown to affect tactics used while foraging as well as foraging success, although this varies among bird species (Holmes et al. 1978, Robinson and Holmes 1984, Broadman 1997). In general, it has been suggested that foraging birds will use gleans for larger, higher quality prey items and aerial attacks for smaller flying insects (Remsen and Robinson 1990, Lovette and Holmes 1995, Lyons 2005).

Some studies have shown that foraging individuals move predictably just enough to take them into a new foraging area beyond their original field of vision, and will use various attack maneuvers based on visual ability (Fitzpatrick 1981, Robinson and Holmes 1982). Thus, changes in habitat structure may affect the maneuvers used by altering the extent of the foraging bird's field of vision. Whelan (2001) experimentally demonstrated this pattern in several insectivorous warblers, and found that changes in foliage structure often require different attack maneuvers or constrain those maneuvers which are used most efficiently by the foraging individual. Gleaning may be more efficient in areas with a higher density structure, while aerial attacks (including sally-strikes) may be of increased utility in more open habitats where field of view is less inhibited (Robinson and Holmes 1984). It has also been suggested that birds may alter their prey attack methods depending on the abundance of different groups of insects, as in the case of several species that use more aerial attack maneuvers as flying insects increase in abundance (Robinson and Holmes 1984, Hutto 1990). Either of these concepts may explain the difference in proportional use of gleans versus sally-strikes in Yellow-green Vireos and White-winged Tanagers foraging in high and low shade coffee plantations. These results were not significant, but perhaps patterns would become clearer with increasing sample sizes. In addition, in conditions of varying predation risk, foraging birds may modify their use of certain attack maneuvers to minimize visual exposure to predators, thus affecting other potential foraging patterns based on prey type and availability, vegetation structure, etc.

Foraging speed did not differ significantly between farms for either species. Lyons (2005) had similar results with foraging speed, and suggested that birds may not have increased foraging speed in low-food habitats due to physiological or energetic limitations, while others have suggested that foraging speed decreases as predation risk increases to avoid detection in more open habitats (Pomara et al. 2003). If increasing foraging speed also increases the energetic costs of foraging, then it seems reasonable that birds in low-food habitats would not do so, as otherwise they may decrease the efficiency of their foraging efforts (Lyons 2005). There was a significant effect of habitat on the types of foraging movement used for the White-winged Tanagers ($p<0.05$), although this effect was absent for Yellow-green Vireos. This was anticipated, as one would expect that there would be a higher use of longer distance movements (long flights) in areas of lower structural complexity (and likely less food availability) than in areas of high habitat complexity. This may be related to previous discussion regarding attack maneuvers and habitat structure. If an individual is foraging in a highly structurally complex habitat, its field of vision is much more locally constrained, making it more difficult to evaluate prey presence. This may cause the individual to forage more slowly and carefully so as not to miss potential food items, especially given that arthropod abundance appears to increase with habitat complexity (Bunnell and Huggard 1999, Hijii et al. 2001, Ishii et al. 2004, Maleque et al. 2006), tying in also with analysis of foraging speed. However, this was not observed in the Yellow-green Vireos, so further study would be necessary to address this dynamic.

The limited fat score data collected from Yellow-green Vireos suggests that individuals in the high shade coffee have larger furcular fat reserves, suggesting better body condition and higher quality habitat. Mass/wing chord analysis did not reveal differences between low shade and high shade habitat. Since samples sizes were small however, it is difficult to derive strong conclusions based only on this species.

Very few of groupings based on foraging guild or habitat association resulted in a significant pattern of body condition based on habitat type. The forest and woodland-associated species, with a significance value of $p=0.065$, is the only group to display a possible relationship between body condition (in this case, fat scores) and habitat type. It is possible that this indicates a particular sensitivity on the part of these species to differences with high and low shade coffee habitats. This is supported by past conclusions that forest-specialists and forest-associates are the hardest hit by the intensification of coffee production (Greenberg et al. 1997b, Lindell et al. 2004, Tejeda-Cruz and Sutherland 2004). These results contribute to the conclusion that food resources may be a leading factor in the diversity patterns that have been observed along gradients of coffee management. Further study is necessary to determine what effects these patterns may have on particular forest species and bird communities of conservation interest. In addition, these results may also be conflicted by multiple habitat factors, such as breeding resources and activity and bacterial or parasite infection (Goodall 2008).

Analysis of blood hematocrit levels did not indicate a significant difference between birds captured in the low versus high shade farms (Fig. 9), although these results should be viewed cautiously due to variations across species sampled and aforementioned possible confounding factors influencing hematocrit levels, including breeding condition and infection by bacteria or parasites.

Conclusion

When body condition results are put into the context of increased attack rates and more generalized trends of canopy arthropod abundance, it appears that the availability of foraging resources is an important factor in determining the structure and diversity of forest bird communities that utilize shade coffee farms. Analysis of foraging mode (i.e., attack maneuvers) also suggests that variations in habitat structure may be having an affect on foraging behavior patterns of these birds, aswell as on the prey quality. Although such affects may not indicate changes in absolute food abundance (i.e., there may be an equal abundance but of different arthropod types) they may still be of interest in terms of food availability for particular species. Since habitat structure determines how accessible food is for individuals (different arthropod communities, making prey more/less visible, size of field of view, etc.), it affects the availability of food resources for a foraging bird as well. Therefore, effects of habitat structure on foraging behavior do not necessarily take away from the conclusion that a higher availability of food resources exists in high shade coffee farms compared to low shade farms, but may instead be an additional contributing factor (c.f. Lyons 2005). Variation in the availability of food resources may help to explain why some forest bird species manage to persist in farms with very low shade cover while others do not. Additional analysis of resource use by forest birds in diversely managed shade coffee plantations may provide for management suggestions and guidelines on how to increase availability of higher quality habitat for forest birds in coffee producing regions, as well as encouraging an increased understanding of how birds utilize habitat resources.

Figures

Table 1. Features of sites Finca Irlanda and Finca Hamburgo, adapted from Mas and Dietsch (2003)

	Finca Irlanda (High Shade)	**Finca Hamburgo (Low Shade)**
Management Type	Commercial Polyculture	Shaded Monoculture
Tree Species Richness	3.8	2.0
Tree Abundance	8.8	4.3
Trees with Epiphytes (%)	17%	6.3%
Average Tree Height (m)	9.0	7.9
Average Tree DBH (cm)	11.4	8.8
Canopy Cover (%)	58.8%	14.5%
Altitude (m)	1004	1018
Slope (%)	28.3	41.8
Aspect (°)	142.3	272.0
Management Index (scored out of total of 7)	4.5	5.71

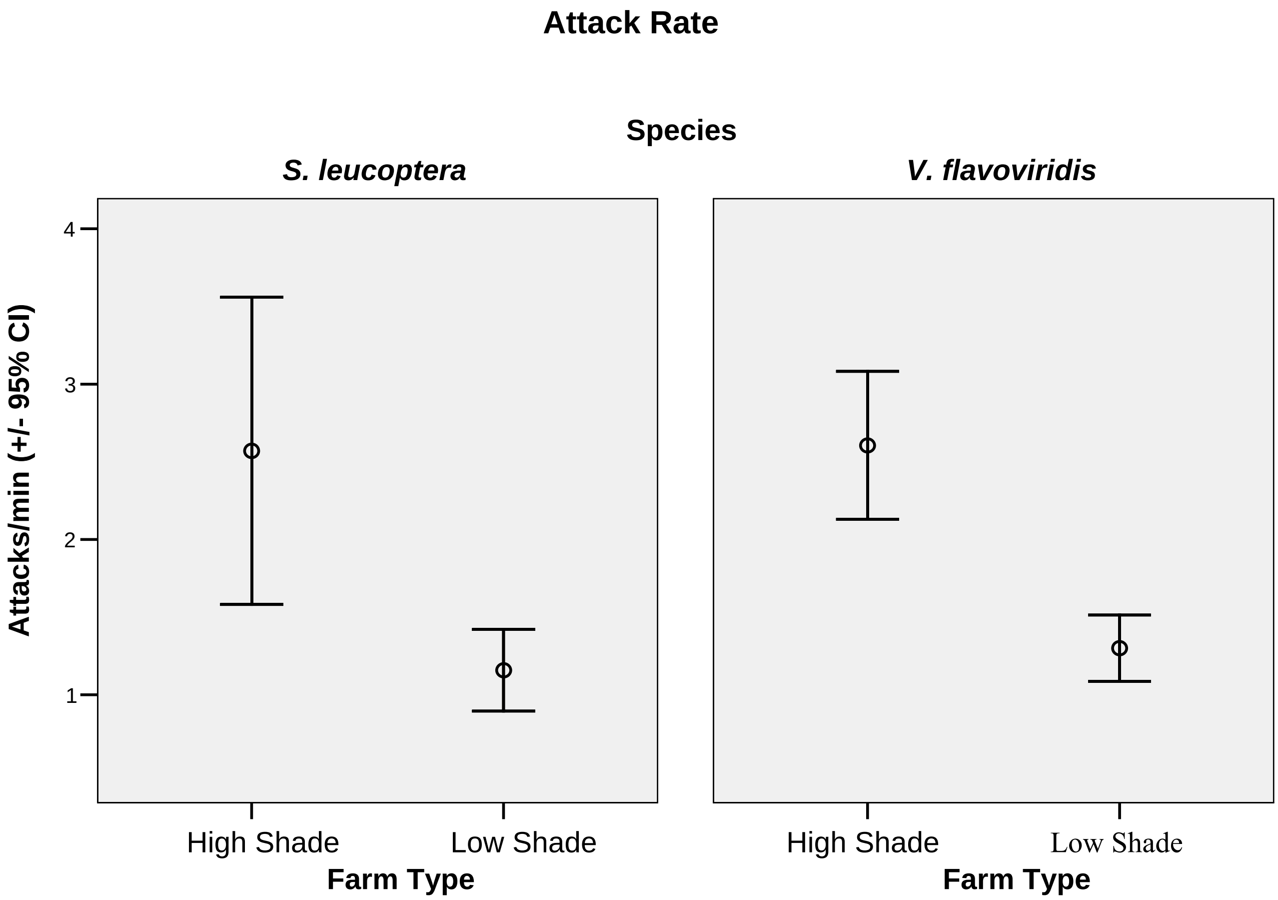


Figure 1. Attack rates of White-winged Tanagers (*S. leucoptera*) and Yellow-green Vireos (*V. flavoviridis*) in high and low shade coffee farms.

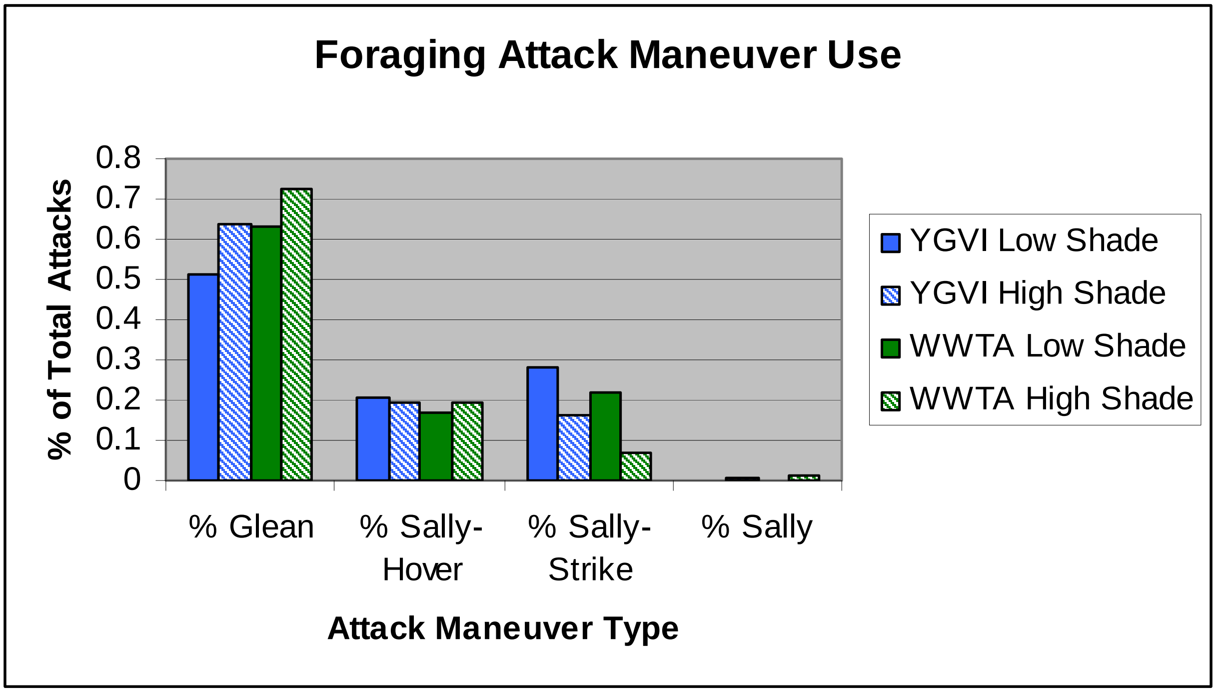


Figure 2. Percentage of attack maneuver use by Yellow-green Vireos (YGVI) and White-winged Tanagers (WWTA) in high and low shade coffee farms.

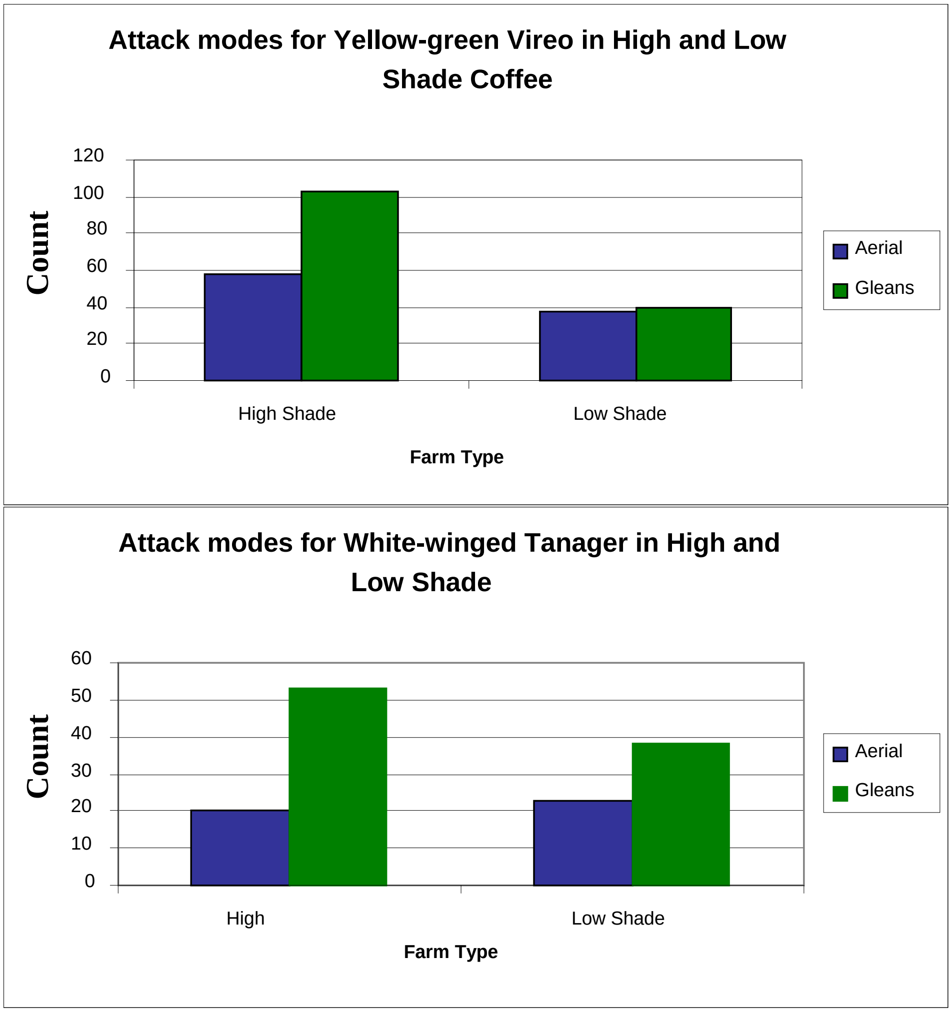


Figure 3. Attack modes used by Yellow-green Vireos and White-winged Tanagers in high and low shade coffee.

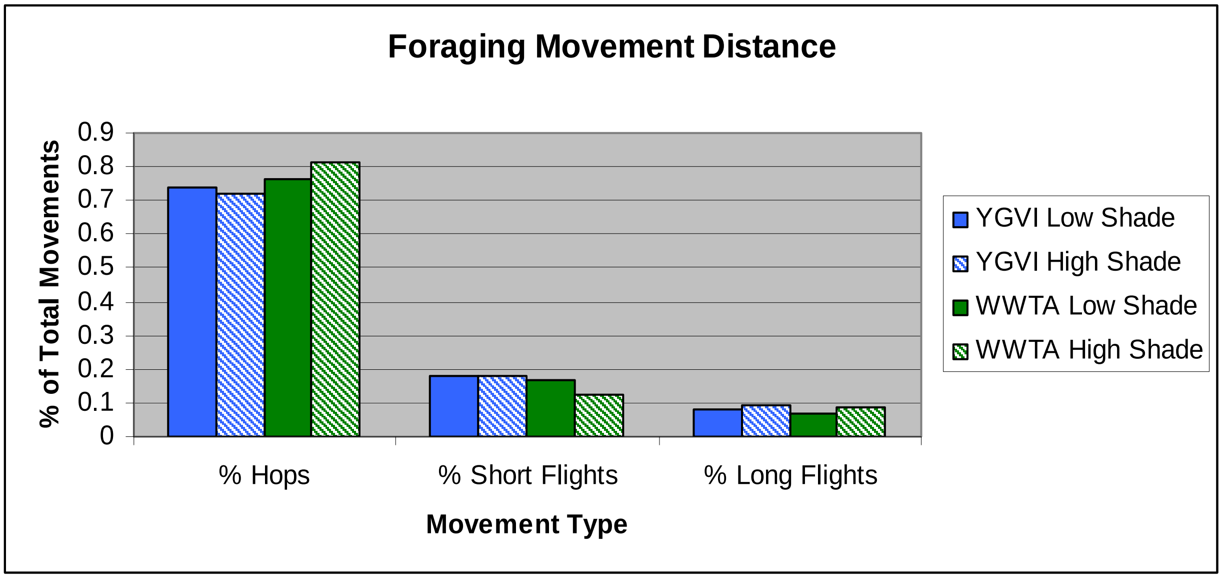


Figure 4. Percentage of movement use by Yellow-green Vireos and White-winged Tanagers in high and low shade coffee farms.

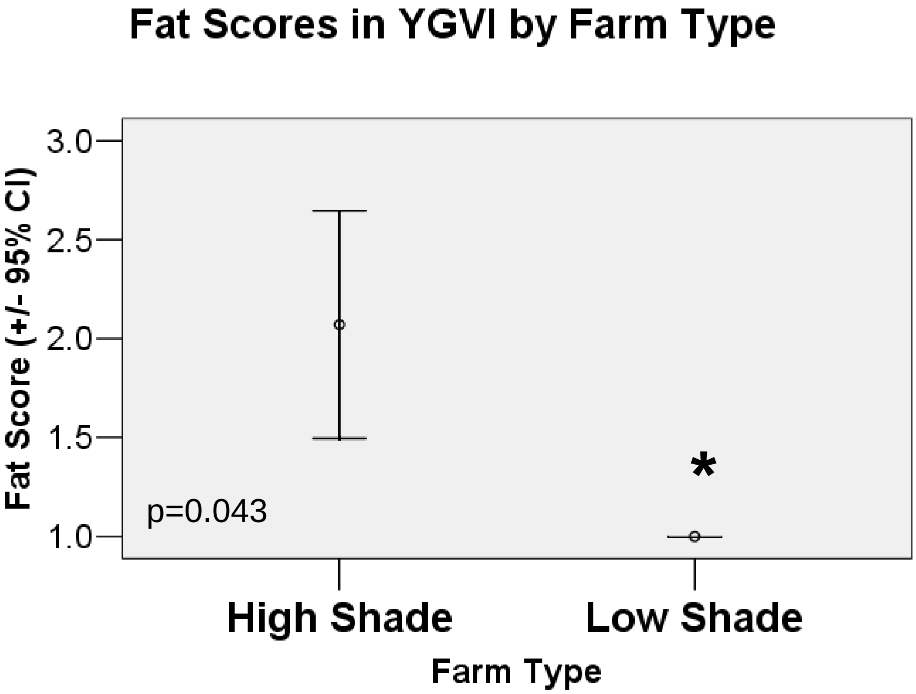


Figure 5. Furcular fat scores of captured Yellow-green Vireos. N(L)=4, N(H)=14.

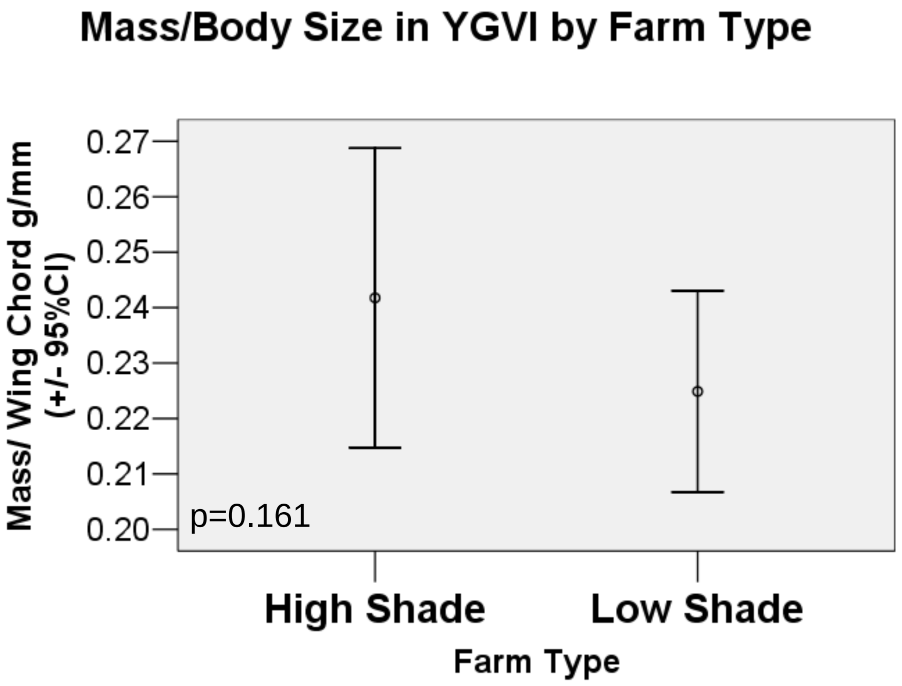


Figure 6. Mass/Wing Chord measurements of Yellow-green Vireos (N1=4, N2=14).

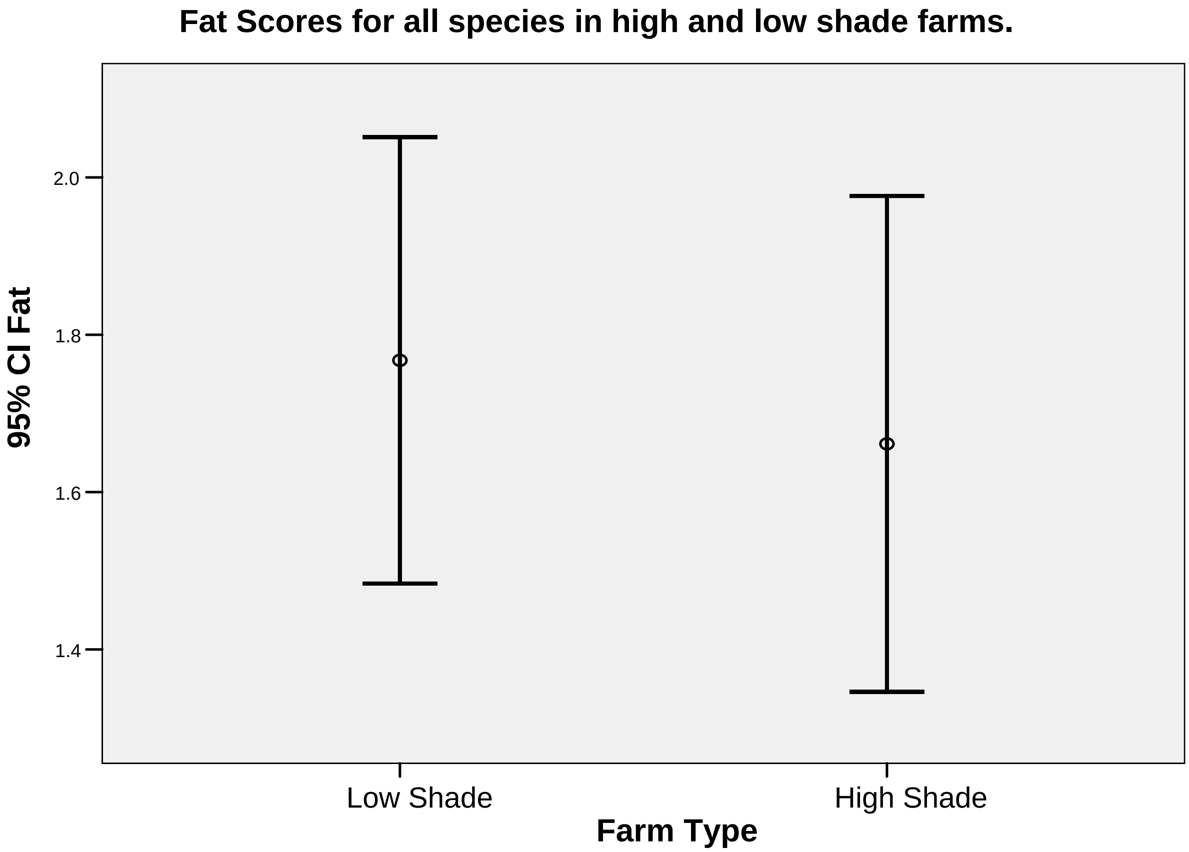


Figure 7. Furcular fat scores for all species in high and low shade coffee farms.

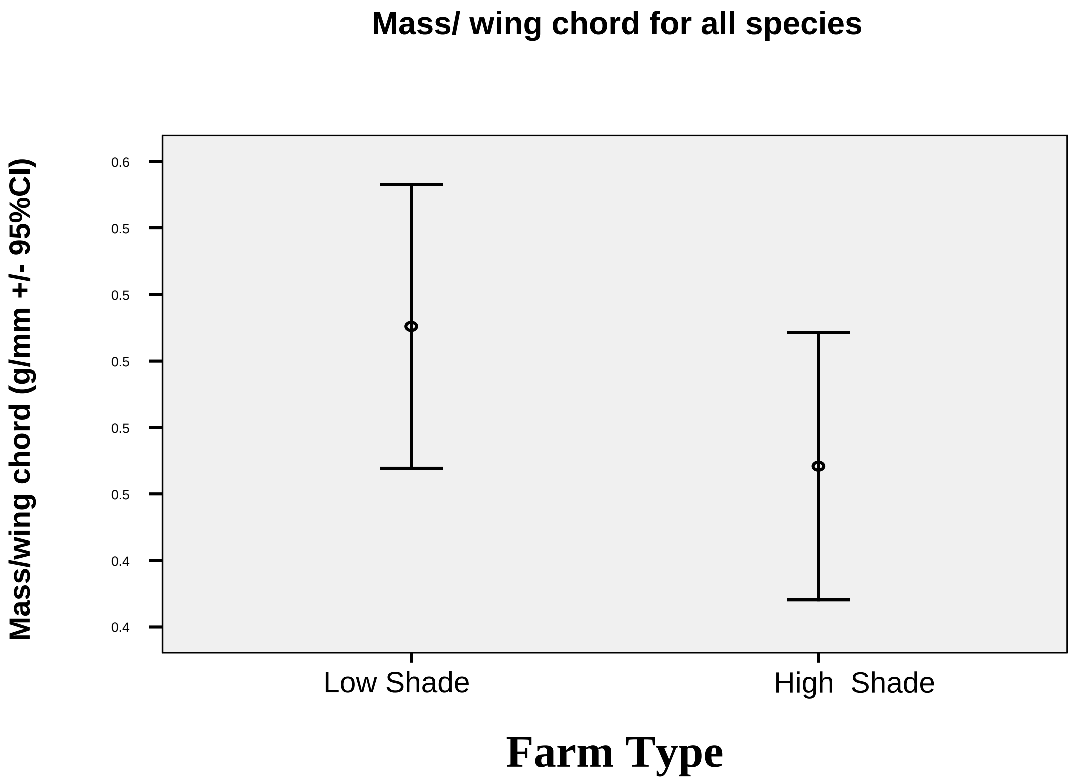
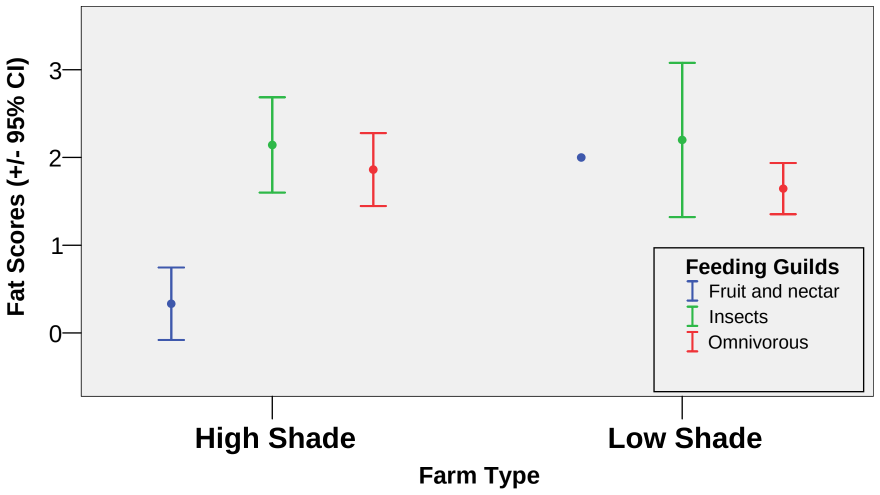
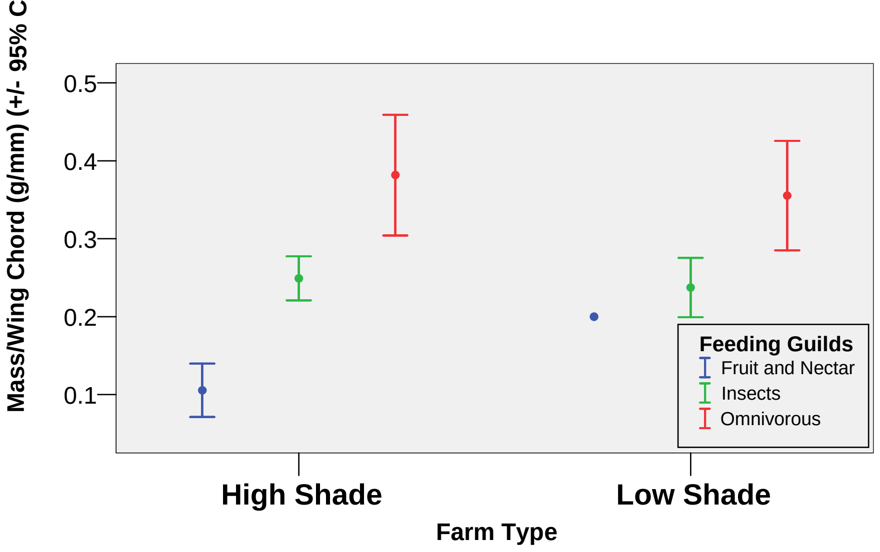


Figure 8. Mass/wing chord measurements for all species in high and low shade coffee farms.



A) Fat Scores in Feeding Guilds by Farm Type



B) Mass/Wing Chord in Feeding Guilds by Farm Type

Figure 9. Fat Scores and Mass/Wing Chord for all species broken down into three broad feeding guilds.

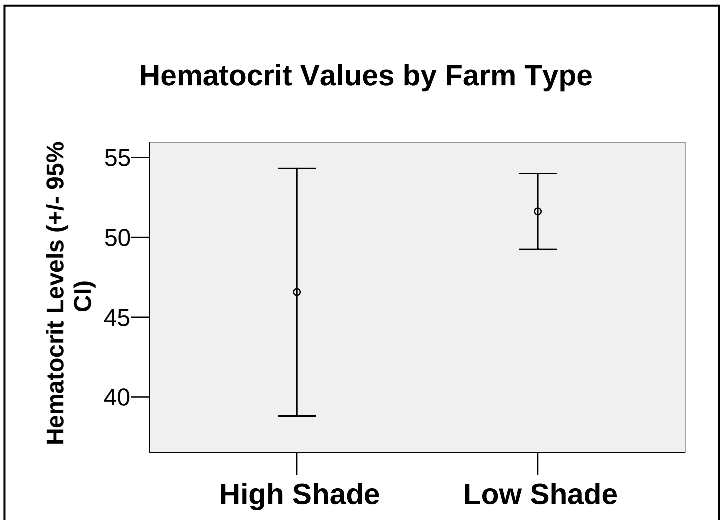


Figure 10. Blood hematocrit values for all birds in high and low shade coffee farms.

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Chapter 3

The effects of shade tree diversity and canopy management intensity on the availability of food resources for two forest birds in coffee agroecosystems

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Abstract

Certain types of shade-grown coffee can represent a high-quality refuge habitat for many forest-associated Neotropical bird species. In addition, the wide gradient of coffee production practices also makes the coffee agroecosystem a good model system to assess the impacts of agricultural intensification on the habitat needs of biodiversity. For instance, foraging resources may become a limiting resource. We studied the effects that two management variables--shade tree diversity and canopy cover management--have on the availability of foraging resources for two resident forest-associated birds, the Yellow-green Vireo (*Vireo flavoviridis*) and the White-winged Tanager (*Spermagra leucoptera*), that are commonly found in two coffee farms of differing management in the Soconusco region of Chiapas, Mexico. We compared the shade trees used as foraging sites by these two birds with the proportional availability of trees, and found that in the high shade farm, with its increased shade tree diversity, that foraging birds sought out more rare trees present on the farm at the expense of foraging in more common shade trees such as *Inga* sp. The rate of use in these rarer trees was greater than the proportional availability of tree presence, suggesting that foraging birds were making use of the diversity of trees when available. In the low shade farm, this did not occur, and both species selected foraging sites that was more in line with the proportional availability of trees in the less diverse, low shade farm, rather than selecting certain trees as preferred foraging sites.

We studied the effects of pruning and canopy management by selecting the two most common shade trees used for foraging (*Inga* sp. and *Trema* sp.), and comparing the foraging behavior indices to assess food availability between canopy management strategies. For both species, foraging attack rates were significantly higher in the high shade farm for individuals foraging in *Inga* sp, suggesting increased prey availability in the high shade farm over the low shade farm, even within the same shade tree types. The same pattern was found for Yellow-green Vireos foraging in *Trema* sp, also suggesting that within this shade tree there is also an increase in prey availability in the high shade farm. These results suggest that both shade tree diversity and canopy cover management have a significant effect on the foraging resources available to forest-associated birds in coffee agroecosystems.

Introduction

Shade-grown coffee has gained widespread attention within the conservation community in past years, particularly as it has been documented to provide habitat and act as a refuge for migratory birds and other organisms that depend on forested habitat (Mas and Dietsch 2004). Many shade-grown coffees are marketed directly on the benefits described for migratory species, i.e. the Smithsonian's "Bird-friendly" coffee certification, (Tejeda-Cruz and Sutherland 2004). Some resident tropical bird species have also been noted to benefit from shade coffee, particularly with increasing forest loss over their range. Resident species, however, seem to exhibit much greater sensitivity to the process of agricultural intensification than migrants (Bierregaard et al. 1992, Petit et al. 1999, Perfecto and Armbrecht 2003, Tejeda-Cruz and Sutherland 2004).

A wide gradient of management systems exists in coffee, however, even within that which can be called shade-grown coffee. Shade-grown coffee can be broken down further into Rustic, Traditional Polyculture, Commercial Polyculture, and Shaded Monoculture (Moguel and Toledo 1999). The major differences between these varying management systems are the amount of shade cover, shade tree diversity, and structural complexity. Pruning of the shade trees and removal of epiphytes, a common practice on many shade coffee farms, also has a considerable effect on the structure and complexity of the habitat (Cruz-Angon and Greenberg 2005, Philpott 2005, Cruz-Angon et al. in press). Studies that include a gradient of these management systems indicate that a certain level of shade cover and structural complexity is necessary to maintain high levels of biodiversity among different taxa (Perfecto and Vandermeer 1994, Perfecto and Snelling 1995, Perfecto et al. 1997, Mas 1999).

Given that patterns of biodiversity loss exist along the intensification gradient, and that some shade coffee systems have been documented to provide habitat to resident forest birds, it would be valuable to understand what processes are behind these patterns. Since one of the main differences between coffee management types is amount of shade cover, the goal of this research was to determine what effects shade cover (and associated habitat complexity) has on the habitat quality for forest-associated birds foraging in coffee agroecosystems. Specifically, the availability of food resources was used as a measure of habitat quality that may be affected by varying shade levels. One could reasonably expect that foraging resources for forest-associated species would decline as the canopy of a coffee plantation is increasingly reduced. This would especially be true for species that feed on canopy insects and other arthropods, since it appears that as habitat complexity increases for a landscape, the diversity and abundance of canopy arthropods increases (Bunnell and Huggard 1999, Hijii et al. 2001, Ishii et al. 2004, Maleque et al. 2006).

Studying the availability of avian food resources can be difficult, particularly for insectivorous species (Hutto 1990). These can largely be attributed to issues of study-scale and differences in perception of resources between a researcher and the organism being studied (Hutto 1990, Smith and Rotenberry 1990). In an effort to address such issues, many avian researchers have argued that foraging behavior can effectively and predictably estimate food resources, since it provides a direct indication of avian feeding preferences and perception of prey (Robinson and Holmes 1982, 1984, Lyons 2005). Since the behaviors are based on the individual bird's perception of its resources, they eliminate the problems of study-scale and observer bias that are inherent in many arthropod sampling methods for evaluating avian food resources. In particular, prey attack rate (serving as an indicator of prey encounter rate) and foraging speed are behavioral variables that are frequently used as a proxy to indicate relative availability of food resources between habitats (Zach and Falls 1979, Pienkowski 1983, Delestrade 1999, Sheperd and Boates 1999, Lyons 2005). Lyons (2005) argues that in a habitat with higher food availability, a foraging individual would attack prey more frequently (because it is encountering prey more often) and it would forage more slowly (because it has an increased likelihood of encountering prey) than it would in a habitat with a lower availability of food.

The intention of this study is to evaluate the effects of shade management in coffee production on the availability of food resources, using the foraging behavior of two common forest-associated, insect-feeding species as an indication of food availability. The variation in food resources under different shade management regimes, may be one of the key factors determining the patterns of bird diversity that have been observed in coffee agroecosystems.

Methods

This study was carried out within two shaded coffee farms in the Soconusco region of the Sierra Madre Mountains in Chiapas, Mexico. Finca Irlanda (15°10' N, 92°20'W), a commercial polyculture according to the classification of Moguel and Toledo (1999) is a highly and diversely shaded farm under organic cultivation. Finca Hamburgo (15°10' N, 92°19' W) is managed in a much more intensive fashion, has less shade cover, and is dominated almost entirely be *Inga* species. Chemical fertilizers and pesticides are used on an infrequent basis at Finca Hamburgo (although no insecticides were applied during the course of this study), and it would fall into the category of a shaded monoculture (Moguel and Toledo 1999). Additional factors between the two farms are compared in Table 1, adapted from Mas and Dietsch (2004). These two farms are neighbors but are separated by an unmanaged forest fragment.

Two species of resident birds were selected for foraging study in these two farms, the Yellow-green Vireo (*Vireo flavoviridis*) and the White-winged Tanager (*Spermagra leucoptera*). Both species breed in the coffee farms of the Soconusco region (although the Yellow-green Vireo is a regional migrant), are common in the farms studied, forage on insects, and are generally associated with forest habitats (Howell and Webb 2005). Between these two species, the Yellow-green Vireo (YGVI) is more of an insect specialist (at least in the breeding period, as it will forage on fruits in the winter season), while White-winged Tanagers (WWTA) are observed foraging on fruits and seeds even in the breeding season. Part of the objective of this study was to examine the relationships to food resources of forest-associated resident species that do persist in intensified landscapes, to see if this could provide clues to understanding the processes underlying diversity patterns found with the coffee agroecological landscape.

Foraging data was collected between late May and late July in 2006, in the two shaded coffee farms in the Soconusco region of Chiapas, Mexico. Most foraging observations were taken between 0600 and 1200 Eastern Standard Time (EST). Established roads and trails throughout both farms were used for transects, as these were already dispersed at regular intervals throughout the farms, generally followed elevational terraces, and allowed better visual ability than straight-line transects through 2-3 meter tall coffee.

To collect foraging observations, observers walked through 15 500-meter transects on each farm, stopping every 50 meters and conducting a 10 minute observation period. During that period, if a foraging individual was detected, we followed it for as long as possible or up to five minutes, dictating its behavior and all movements into a portable voice recorder. If the focal individual went out of sight, this was noted into the recorder, and again noted if the individual reappeared. Observations were also recorded opportunistically if focal species were found foraging outside of established transects. Observations were conducted no more than 2-3 times on each transect to avoid multiple observations of the same individuals that would otherwise potentially skew results. The recorded data on movements, foraging activity, and other behaviors was transcribed from the tapes each evening, using a stopwatch to determine timed behavioral sequences.

For each foraging bout, the observer watched the foraging individual continuously and dictated all prey attack maneuvers, movements, and other behaviors into a micro-cassette recorder. Prey attack maneuvers included gleans, sally-hovers, sally-strikes, and aerial sallies (Remsen and Robinson 1990, Lovette and Holmes 1995, Lyons 2005). Gleans refer to any attack from a stationary position on a stationary prey item. Sally-hovers include attacks from a hovering position on stationary prey, and sally-strikes were similar but lacking the hovering motion.

Foraging movements involved hops, short flights (<1m), or long flights (>1m) (Robinson and Holmes 1982, 1984, Lyons 2005, Lebbin 2007). Time, foraging location (trunk, branch, foliage), foliage density (0-5, see Remsen and Robinson 1990), and shade tree species were also noted by the observer. Later, the tapes were transcribed and timed using a stopwatch. For each observation, the total time observed was determined using the stopwatch, as well as the timing of each "event" within the observation. If a bird disappeared from sight and was quickly resighted, the unobserved time was subtracted for the total time accumulation for the foraging bout. Prey attack maneuvers and movements were tallied, and they and all associated information (time, location, observer, etc) were entered into a database for analysis.

Shade trees were sampled from two randomly selected one-hectare plots in each farm from June-July of 2007. For each plot, a point was randomly selected in space to be the center of each 1 hectare plot. All trees with greater than 5 cm dbh (diameter at breast height) were identified and measured. Using this data, species diversity and abundance were calculated for each plot. Within each farm type, data from each of the two plots were averaged to provide farm-wide summary data.

Attack rates and foraging speed were computed by tallying the number of attack maneuvers or movements and then dividing by the amount of time spent foraging in each observation, and then compared using ANOVA and regression analyses (SPSS v. 13.0). Attack and movement rates were square root-transformed in order to fulfill assumptions of normality and homoschedasticity. Use of specific attack maneuvers (glean, hover, strike) and movements (hop, short flight, long flight) was also analyzed using χ^2 tests to determine if the varying habitat structures between the tree species or management types was having additional effects for the types of behavior that focal species displayed while foraging. Shade tree species used for foraging sites were compared with availability on both farms to see if shade tree diversity and identity affected foraging resources utilized. Specific foraging behaviors (attack rates and movement rates) were compared between, a) shade trees commonly utilized in the high shade farm, using non-parametric Kruskal-Wallis tests, and b) management types within tree species that are commonly found in both habitats, using multiple-factor regression analysis and ANOVA.

Results

Foraging observations were collected from 376 total individuals during the study period. Foraging observations of 92 Yellow-green Vireos (80.7 minutes of active foraging) and 39 White-winged Tanagers (40.3 minutes of active foraging) were collected in Finca Irlanda, the high shade farm. On the low shade farm, Finca Hamburgo, 54 Yellow-green Vireo observations (77.9 minutes) and 44 White-winged Tanager observations (62.6 minutes) were collected.

In both the high and low shade farms, trees of the *Inga* genus dominated the shade canopy (Table 2), mostly *Inga lauriana*, *I. micheliana*, *I. rodrigueziana*, and *I. vera*. In the high shade farm, 301 *Inga* sp. trees were found in the two one-hectare inventory plots, making up 69.2% of the trees within the plots. Other common trees in the high shade inventory plots included *Alchornea latifolia* with 33 individuals (7.6%), *Conostegia xalapensis*, *Nectandra* sp., *Veronia deppeana* with 14 individuals (3.2% each), *Yuca elephantipes*, *Trema micrantha*, *Albizia* sp. and *Schizolobium parahybum* with 6-11 individuals each (1.4-2.5%) (Table 2). There were 435 trees in total inventoried in the high shade farm plots.

In the low shade farm, 209 *Inga* sp. were found in the two one-hectare inventory plots, making up 68.9% of the trees found. Other common trees found in the low shade inventory included *Trema micrantha* (29 individuals, 9.6% of the total), *Conostegia xalapensis* (28 individuals, 9.2%), and *Yuca elephantipes* (20 individuals, 6.6%). No other tree genus made up more than 1% of the total count. In total, 303 trees were counted between the two inventory plots in the low shade farm.

Yellow-green Vireos foraging in high shade farms foraged in *Inga* sp. trees (or in a combination of *Inga* sp. with another tree species) with a lower frequency than those individuals foraging in low shade farms (~47% in high shade, ~73% in low shade), even though the percent availability of *Inga* was roughly similar in both farms based on vegetation surveys, roughly about 70%. In the high shade farm, other shade trees frequently utilized as foraging sites included *Trema micrantha* (12.8%), *Schizolobium parahybum* (7.7%), *Alchornea latifolia* (~7%), and *Albizia* sp. (3.8%). Among these shade trees, use is significantly different from the statistical availability of these shade trees, as determined from vegetation surveys (χ^2=67.1, df=5, p<0.0001). Analysis of standarized residuals indicated that the differences in use and availability for *Inga* sp. (-2.31), *Trema* sp. (+6.13), and *Schizolobium* sp. (+4.7) in the high shade farm are major drivers for the overall significant pattern.

In the low shade farm, the other shade tree besides *Inga* sp. commonly used as a foraging site was *Trema sp.* (10.9%).Use of shade trees in the low shade farm was not significantly different from shade tree availability in the farm (χ^2=1.213, df=2, p=0.5461).

Foraging White-winged Tanagers in low shade farms utilized species of *Inga* sp. more frequently than in high shade farms (82.9% in low shade and ~52% in high shade). Other trees utilized by White-winged Tanagers in the high shade farm include *Trema* sp. (12%), *Albizia* sp. (4%), *Conostegia* sp. (4%), and *Cordea* (4%). The selection of trees by White-winged Tanagers for foraging sites in the high shade farm was not statistically different from shade tree availability on that farm ($\chi^2_{\text{corrected}}$ = 0.92, df=1, p=0.338). Additional trees besides *Inga* sp. utilized in low shade by White-winged Tanagers in the low shade farm include *Pinus* sp. (4.9%), *Cordea* sp. (2.4%), *Trema* sp. (2.4%). Shade tree use besides *Inga* sp. in the low shade farm was limited such that analysis was restricted to use of *Inga* sp. versus all other shade trees. The selection of trees for foraging sites by White-winged Tanagers in the low shade farm was significantly different from the availability of shade trees on that farm ($\chi^2_{\text{corrected}}$ = 4.87, df=1, p=0.0273), although analysis of standardized residuals did not indicate a strong influence of either group on this result.

In the high shade coffee farm, the shade trees in which foraging Yellow-green Vireos were found most frequently were *Inga* sp. (37 observations), *Trema* sp.(10 observations), *Alchornea* sp. (6 observations), and *Schizolobium* sp.(6 observations). A comparison between these trees did not reveal a significant difference in attack rate in the high shade farm (χ^2=4.745, df=3, p=0.191). Attack rates for each species were as follows: *Alchornea* sp. 2.69 attacks/min ± 0.744SE, *Inga* sp. 2.12 attacks/min ±0.396 SE, *Schizolobium* sp. 1.54 attacks/min ± 0.480 SE, and *Trema* sp. 3.45 attacks/min ± 0.594 SE. Mean foraging speeds for Yellow-green Vireos in each shade tree type were *Alchornea* sp. 17.21 moves/min ± 4.034 SE, *Inga* sp. 16.31 moves/min ± 1.658 SE, *Schizolobium* sp 6.29 moves/min ±1.889 SE, and *Trema* sp. 16.9 ±2.406 SE. The Kruskal-Wallis test statistic revealed significant differences in these foraging speeds

(χ^2=10.038, df=3, p=0.018), with the vireos foraging most slowly in *Schizolobium* sp. A post-hoc analysis comparing Least Significant Differences revealed significant pair-wise differences between *Inga* sp. and *Schizolobium* sp., and between *Trema* sp. and *Schizolobium* sp. Small sample sizes for each tree type may be hampering the accuracy of the overall Kruskal-Wallis test, and leading to an overstated p-value (in this case p=0.018).

Mean attack rate for individuals foraging in *Inga* sp. trees for the Yellow-green Vireo was 1.35 attacks/minute and 1.05 attacks/minute in the high and low shade farms respectively. This was statistically different between farm types (p=0.033, F=4.743, df=1).

Mean attack rate for White-winged Tanagers foraging in *Inga* sp. was 1.35 and 0.90 attacks/minute in the high and low shade farms. Differences in attack rates for the White-winged Tanagers were statistically significant compared between farm types (p=0.009, df=1, F=2.053). There was no significant influence of date or time of day on attack rates by either species, as indicated by regression analysis (p>0.05 for date and time of day).

Foraging speed was significantly different for Yellow-green Vireos foraging in *Inga* trees between farm types (p=0.009, df=1, F=7.121). Vireos moved on average significantly faster in the high shade farm (3.686 ±0.123 SE moves/minute) than the low shade farm (3.245 ± 0.111 SE moves/minute). Foraging speed was not different between White-winged Tanagers foraging in *Inga* trees in the high and low shade farms (p=0.745, df=1, F=0.107). Foraging speeds were very similar in the two farms, with foraging individuals making 3.517 ± 0.225 SE moves/minute in the high shade farm and 3.588 ± 0.102 SE moves/minute in the low shade farm. For both species, regression analysis indicated that there was no significant effect of date or time on foraging speed (p>0.05 for both date and time).

Mean attack rate for Yellow-green Vireos in *Trema* sp. was 1.69 ± 0.18 SE in the high shade farm and 0.81 ± 0.43 SE attacks/minute in low shade farm. This difference in attack rate was significantly different between the two habitats (F=10.433, df=1, p=0.006). Foraging speed was also significantly different between farms (4.12 ± 0.285 movements/minute in high shade farm and 3.10 ± 0.352 movements/minute in low shade farm) for Yellow-green Vireos foraging in *Trema* sp. (F=4.664, df=1, p=0.047).

Regression analysis did not indicate any significant influence of date or time of day on either variable ($p>0.05$ for both date and time). Low sample sizes prevented analysis of *Trema* sp. use by White-winged Tanagers.

Discussion

The differences between shade tree availability in the high shade farm and those actually used by foraging vireos indicate that there is a foraging value in increased diversity. The birds select favored foraging sites from those present within a local area, choosing some shade trees more or less frequently than those trees are available. This pattern does not occur in the low shade (and lower diversity) farm, where foraging sites selected by individual birds closely matches the availability of shade trees present. Such a dichotomy suggests that when presented with a higher diversity of choices for foraging sites, birds will choose favored sites from among the diversity, even when dominant trees, such as *Inga* sp., have been shown to be a quality foraging resource (Greenberg et al. 1997a, 1997b, Wunderle and Latta 1998, Dietsch et al. 2007). In the less diverse low shade farm, foraging vireos lacking this diversity in site selection adapt and forage where they can and select sites that more closely mirror the distribution of limited options available to them. Thus, the diversity of shade trees present in a coffee farm has a value for foraging vireos outside of amount and intensity of shade management. This may be a result of the insurance hypothesis (i.e., a higher diversity of shade trees increases the likelihood of including a shade tree species that presents a particularly high quality foraging resource) (Yachi and Loreau 1999), a continuity of fruiting phenology that attracts an increased diversity and abundance of arthropod prey (Carlo et al. 2004, Dietsch et al. 2007), or perhaps even better cover from potential avian predators. Particularly, it appears that shade trees such as *T. micrantha*, *S. parahybum, Miconia* sp., and *Cordia* sp. offer particularly desired foraging locations for the vireos observed in this study. These results are consistent with other studies that have found that increased tree diversity can promote and maintain increased bird diversity and abundance and may provide a mechanism for the observed patterns (Holmes and Robinson 1981, Rice et al. 1984, Robinson and Holmes 1984, Gabbe et al. 2002).

Results from foraging site selection in White-winged Tanagers present a different picture, although these results may be misleading due to the smaller sample sizes of foraging observations for this species. For this species, the selection for foraging sites within the high shade farm did not differ significantly from the availability of shade trees present, but there were significant differences between use of shade trees as foraging sites and the availability of those shade trees on the low shade farm. This difference was much weaker ($p=0.03$), however, than that observed for the selective usage of shade trees by foraging Yellow-green Vireos in the high shade farm ($p<0.0001$). It is possible that there are species-level differences between these two bird species in terms of foraging requirements and preferences that led to this variation, but to test this hypothesis would require additional study.

There is limited information available on the foraging requirements of both of these species, however Yellow-green Vireos are known to be more dependent on insects in the summer months than the more omnivorous White-winged Tanagers which will also forage on fruits and seeds (Howell and Webb 2005). The ability of White-winged Tanager to forage on a greater variety of food resources may contribute to the contrast in foraging site selection observed between it and Yellow-green Vireos in the high and low shade coffee farms. This is consistent with past studies that have concluded generalist species fare much better within intensified systems that more specialized ones, particularly in terms of foraging limitations (Thiollay 1995, Canaday 1996, Lindell et al. 2004).

Within the high shade farm, it was difficult to determine from specific foraging behaviors whether certain shade trees provided higher quality foraging resources or not. There was no difference among the most commonly used shade trees (*Alchornea* sp., *Inga* sp., *Schizolobium* sp., *Trema* sp.) in terms of attack rates, but foraging speeds were significantly different between both Inga sp. and Trema sp. compared with Schizolobium sp. Vireos foraging in Schizolobium sp. did so the most slowly, suggesting that it is providing a higher quality resource.

Whether or not the intensity of shade management affects foraging birds beyond simply the amount of tree diversity present was examined in the two shade trees most commonly used as foraging sites in both the high and low shade farms: *Inga* sp. and

Trema sp. By comparing foraging behavior indices within these shade trees between the two farms, the role of canopy cover in the availability of foraging resources is more direct.

The most common shade trees, those in the genus *Inga*, yielded the most foraging observations for both the Yellow-green Vireos and the White-winged Tanagers. For both species, attack rates were significantly higher when foraging in *Inga* trees in the high shade farm than in the low shade farm suggesting higher availability of prey. Similarly, when foraging in *Trema* sp., Yellow-green Vireos also exhibit a significantly higher attack rate when foraging in the high shade farm. Yellow-green Vireos also exhibit an increased speed of foraging in the high shade farm in both *Inga* sp. and *Trema* sp., which is contrary to original expectations that a more highly shaded habitat would encourage a slower rate of foraging due to increased likelihood of prey encounter. However, it is also possible that in a more highly shaded habitat birds would forage at an increased rate over a low shade habitat (as Yellow-green Vireos do in this study) due to a perceived decrease in predation risk by the foraging bird. If a bird feels more secure in terms of predation risk, it is possible that it will be more inclined to move about more actively while foraging (Lima and Bednekoff 1999, Whittingham and Evans 2004), resulting in the increased rate of foraging speed like the one observed for Yellow-green Vireos in the high shade farm. White-winged Tanagers, which due to sample size could only be compared in *Inga* sp., did not display a significant difference in foraging speed in *Inga* sp. between the high and low shade farm--foraging speeds between the two farms were in fact very similar.

These results suggest that in addition to responding to the diversity of shade trees available, the foraging activity of these birds is also directly affected by the intensity of shade management by impacting the rates of prey encounter and thus, by extension, prey abundance. This supports claims of increased arthropod diversity and abundance in high shade coffee farms (Perfecto and Vandermeer 1994, Perfecto et al. 1997, Moguel and Toledo 1999, Perfecto et al. 2003). Since direct measures of prey abundance for insectivorous birds are unreliable due to concerns of study scale and differences in perception, indices of foraging behavior that take the bird's perceptions and preferences directly into account may be the optimal method for determining food abundance. When studying species that forage high in the canopy, this becomes even more true, as there is a lack of canopy-level arthropod studies in the literature, likely due to difficulty of access. This is true of the coffee-arthropod literature as well as studies focused on more general canopy-arthropod communities but see Jedlicka (2006), Perfecto et al. (1997), and Philpott et al. (2004). Thus, these results indicate that variation in food availability is a significant factor in determining habitat quality for forest birds inhabiting coffee agroecosystems, and therefore may be critical in structuring patterns of avian diversity that have been documented along the intensification gradient of coffee management (Greenberg et al. 1997a, 1997b, Dietsch 2003).

Conclusion

While many studies have documented the avian diversity patterns associated with varying coffee management, a growing number have sought to determine why some forest species are able to persist even within intensely managed farms while others cannot. In this study, I examined two forest-associated species that are relatively common in both a high and low shade coffee farm. Despite their presence in both farm types, each is considerably more abundant in the high shade coffee farm (Dietsch 2003). The purpose of this study was to determine what, if any, type of effect of shade management these birds experience in food availability via indices of foraging behavior. Although the diversity of shade trees present in a farm affects avian foraging behavior and foraging site selection, shade management appears to have a significant effect on avian foraging behavior beyond that diversity.

From analysis of site selection by these foraging birds, it appears that some trees in particular may provide high quality foraging resources for insectivorous birds, which include *Trema* sp., *Schizolobium* sp., *Miconia* sp., and *Cordia* sp. For farmers that are seeking to maintain populations of insectivorous birds, these may be good selections for shade trees in addition to the widely-used *Inga* sp. In addition, from comparisons of foraging behavior within the two most-frequently used shade trees, *Inga* sp. and *Trema* sp., the intensity of management also plays a significant role in the availability of food resources for insectivorous birds.

Minimizing the intensity of shade management, therefore, may encourage populations of insectivorous forest birds by providing a higher quality habitat than is available in low shade coffee farms. This may have significant impacts on the observed ability of insectivorous birds to contribute to pest control and outbreak prevention (see Perfecto et al. 2004) by attracting them to the coffee habitat and maintaining their foraging requirements in between potential pest outbreaks.

Figures

	Finca Irlanda (High Shade)	**Finca Hamburgo (Low Shade)**
Management Type	Commercial Polyculture	Shaded Monoculture
Tree Species Richness	3.8	2.0
Tree Abundance	8.8	4.3
Trees with Epiphytes (%)	17%	6.3%
Average Tree Height (m)	9.0	7.9
Average Tree DBH (cm)	11.4	8.8
Canopy Cover (%)	58.8%	14.5%
Altitude (m)	1004	1018
Slope (%)	28.3	41.8
Aspect (°)	142.3	272.0
Management Index (scored out of total of 7)	4.5	5.71

Table 2. Comparison of habitat variables for high and low shade coffee farms adapted from Mas and Dietsch (2003).

Shade Tree	**Average #/ha**	**% of Total**
a) High Shade Farm		
Total *Inga* sp.	150.5	69.2
I. lauriana	5.5	2.5
I. micheliana	96	44.1
I. rodrigueziana	18	8.3
I. vera	24.5	11.3
Other *Inga* sp.	6.5	3.0
Alchornea latifolia	16.5	7.6
Conostegia xalapensis	7	3.2
Nectandra sp.	7	3.2
Veronia deppeana	7	3.2
Yuca elephantipes	5.5	2.5
Trema micrantha	5	2.3
Albizia sp.	4	1.8
Schizolobium parahybum	6	1.4
Other	12	5.5
High Shade Total	**217.5**	**100**
b) Low Shade Farm		
Total *Inga* sp.	104.5	68.9
I. micheliana	71.5	47.2
I. vera	9	5.9
I. rodrigueziana	24	15.8
Trema micrantha	29	9.6
Conostegia xalapensis	28	9.2
Yuca elephantipes	20	6.6
Other	17	5.6
Low Shade Total	**151.5**	**100**

Table 3. Common shade trees in high and low shade coffee farms determined from two 1-ha sampling plots in each farm.

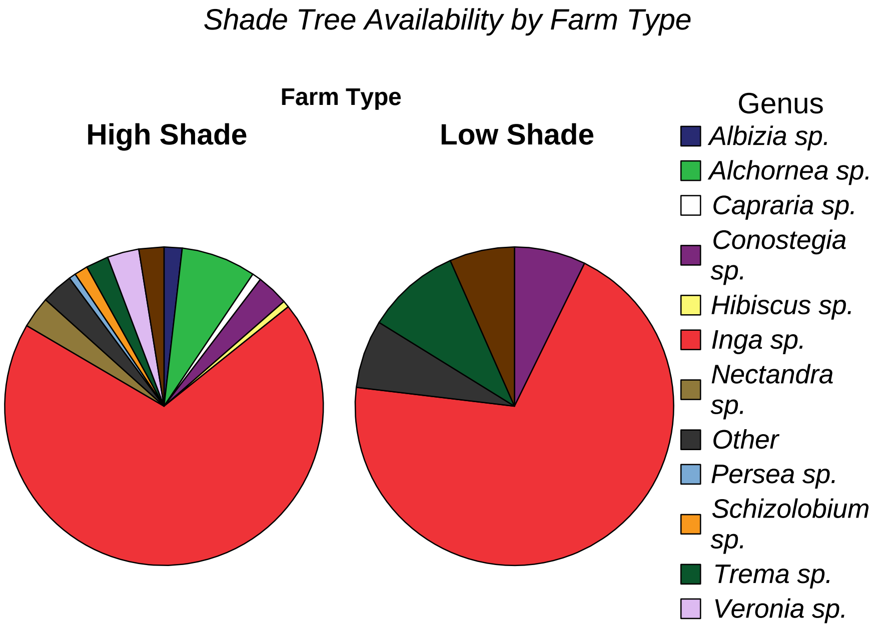

Figure 1. Percentage of shade tree distribution by farm type.

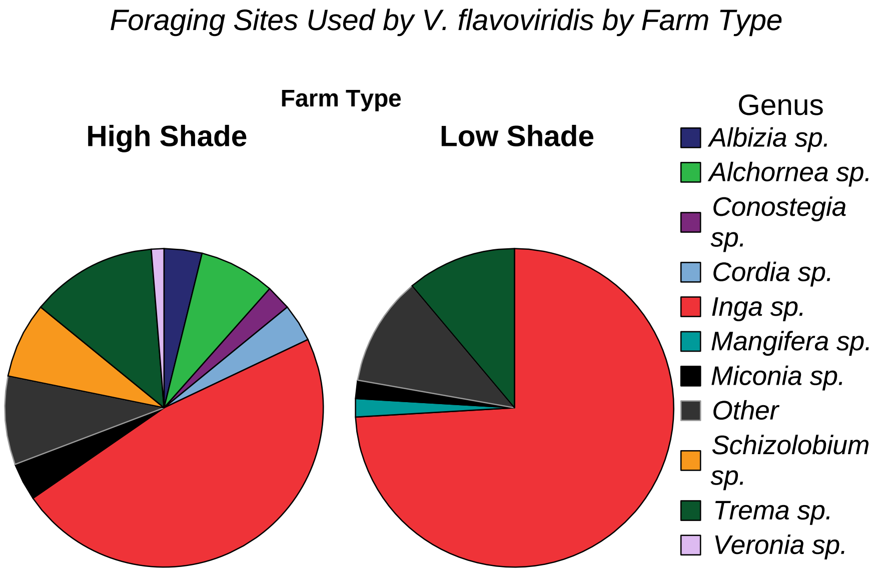

Figure 2. Percentage of use of shade trees selected for foraging sites by Yellow-green Vireos in high and low shade coffee farms.

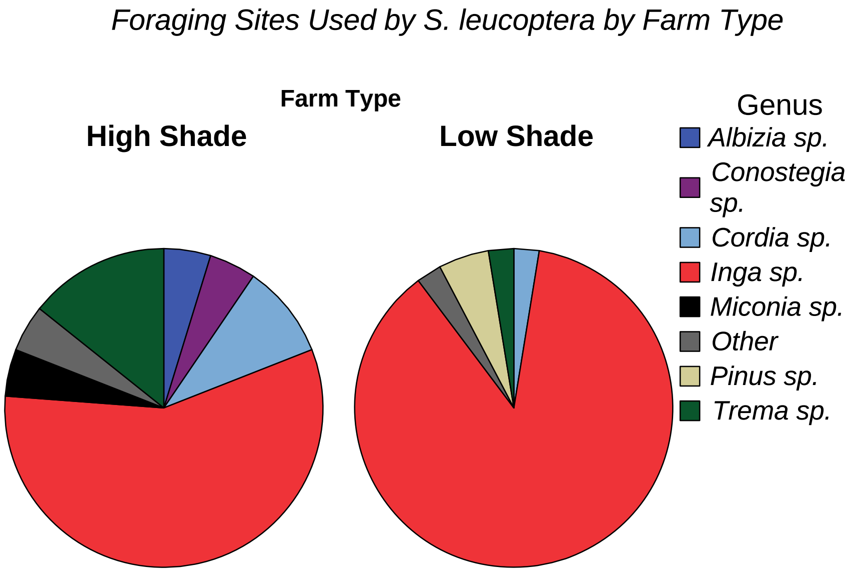

Figure 3. Percentage of use of shade trees selected for foraging sites by White-winged Tanagers in high and low shade coffee farms.

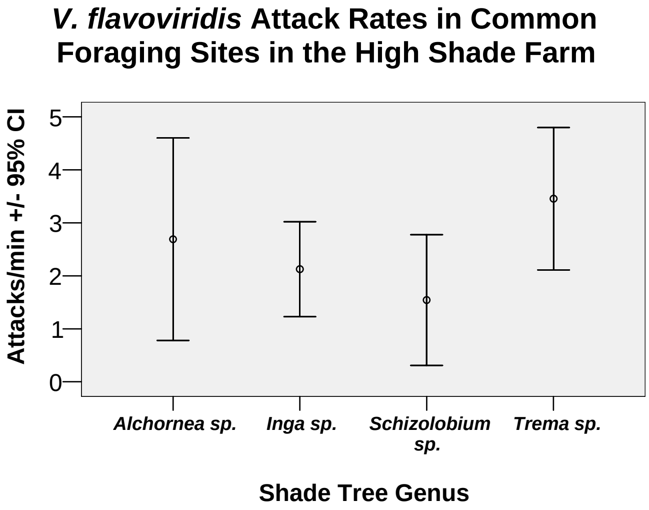

Figure 4. Attack rates of Yellow-green Vireos among the shade trees commonly selected as foraging sites within the high shade farm.

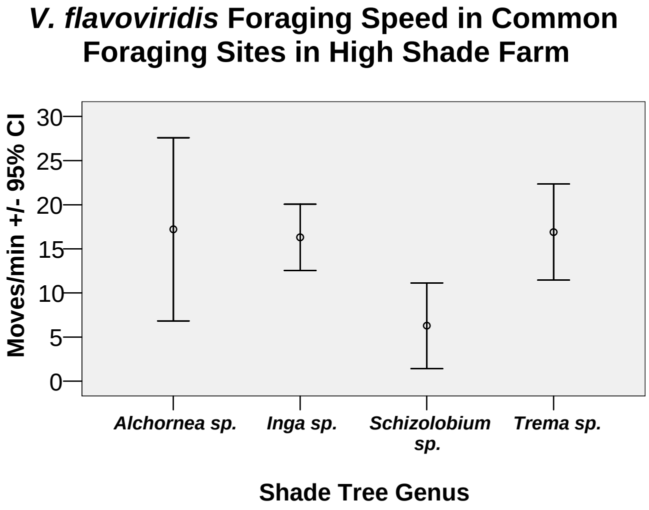

Figure 5. Foraging Speed of Yellow-green Vireos between shade trees commonly selected as foraging sites within the high shade farm.

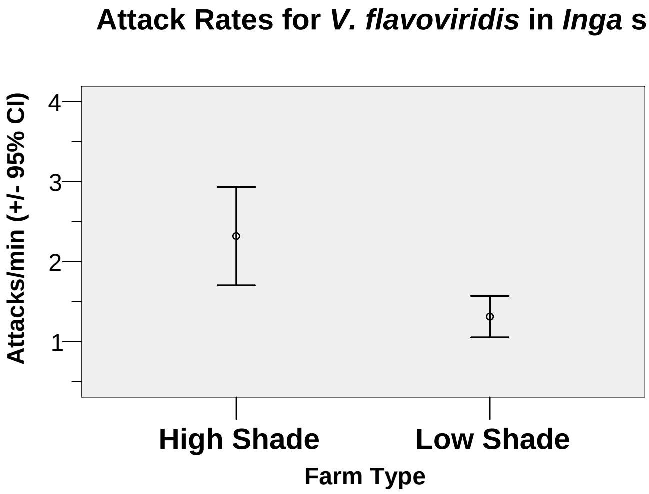

Figure 6. Attack rates for Yellow-green Vireos in Inga sp. in high and low shade coffee farms.

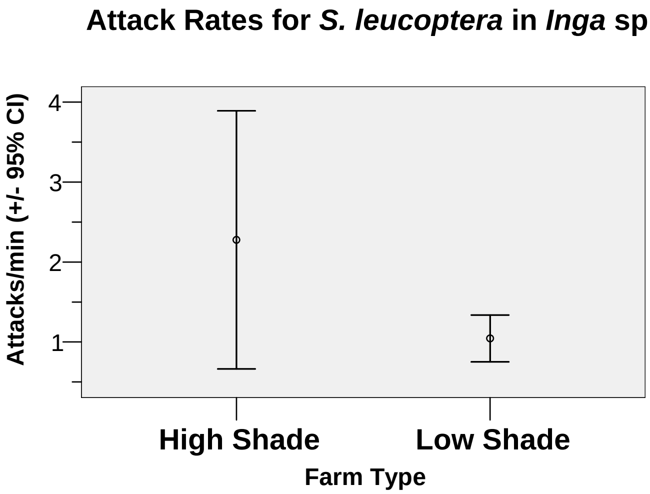

Figure 7. Attack rates for White-winged Tanagers in Inga sp. in high and low shade coffee farms.

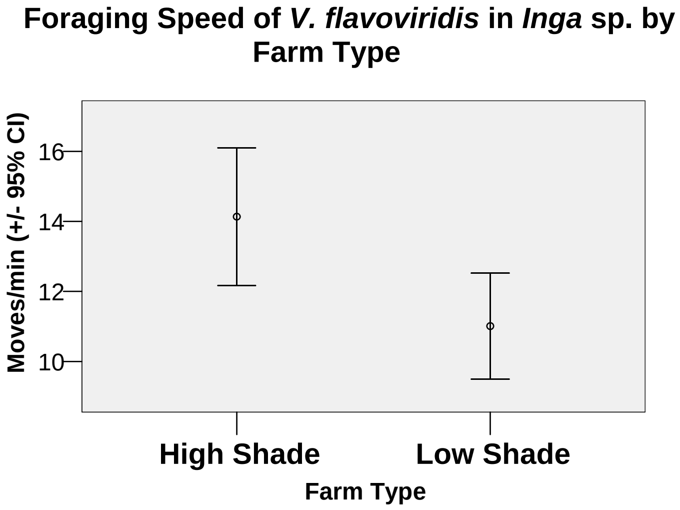

Figure 8. Average foraging speed of Yellow-green Vireos in Inga sp. in high and low shade coffee farms.

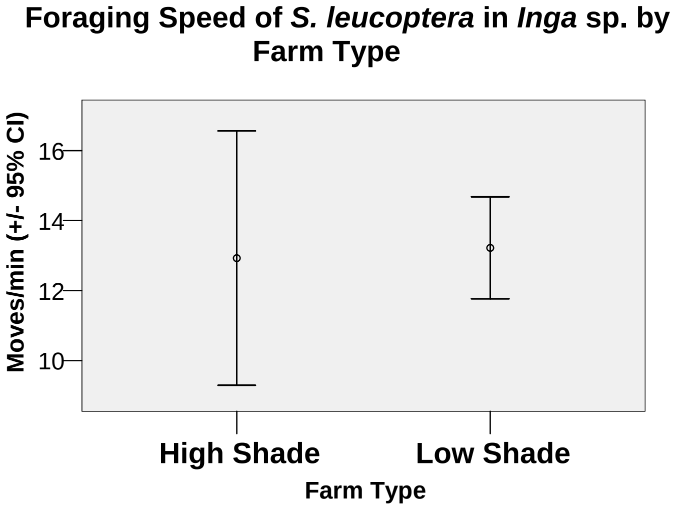

Figure 9. Average foraging speed of White-winged Tanagers in Inga sp. in high and low shade coffee farms.

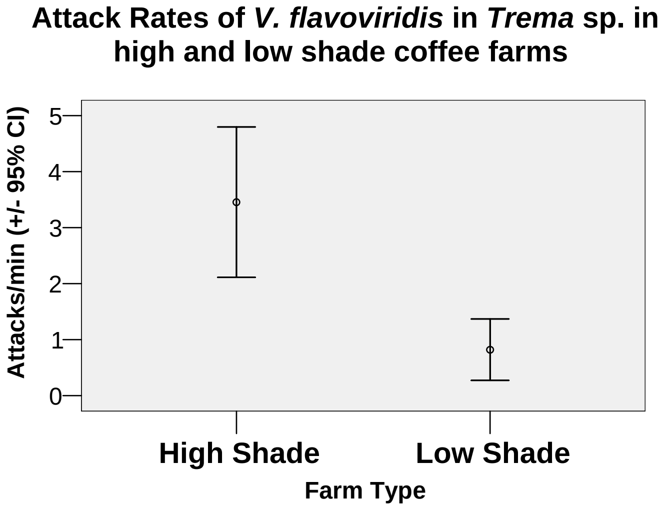

Figure 10. Average attack rates of Yellow-green Vireos in Trema sp. in high and low shade coffee farms.

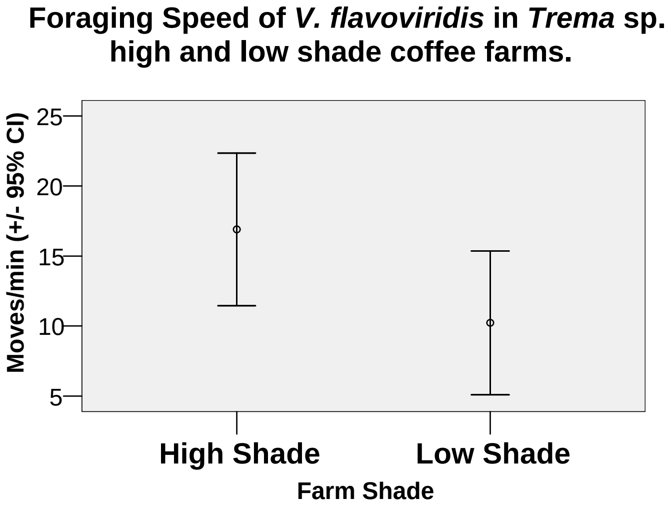

Figure 11. Average foraging speed of Yellow-green Vireos in Trema sp. in high and low shade coffee farms.

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Chapter 4

Conclusions

Many studies have shown increased diversity and abundance of birds in shaded coffee farms, and indicate that such coffee farms may have a key role in the conservation of birds and other tropical wildlife in an increasingly fragmented landscape (Donald 2004). A growing focus in the literature on this topic is aimed at determining which factors drive these patterns of diversity, and which elements of shaded coffee farms are important in providing a refuge for tropical birds in the face of widespread habitat loss and degradation (Pomara et al. 2003, Tejeda-Cruz and Sutherland 2004, Cruz-Angon and Greenberg 2005, Philpott et al. 2005, Gleffe et al. 2006, Jedlicka et al. 2006).

For many birds, the breeding season represents one of the greatest times of energy limitation (Martin 1987, Martin 1992). The requirements of an individual feeding itself as well as its nestlings and possibly a mate make for an intensive period of foraging activity. Agricultural areas have become an integral part of the conservation landscape, and may considerably affect the availability of foraging resources. The process of agricultural intensification has had widespread effects on the viability of wildlife populations, and insectivorous birds represent one group of particular conservation concern (Sekercioglu et al. 2002, Gray et al. 2007). The literature documenting the effects of agricultural intensification, particularly in coffee, on their food sources—arthropods—is extensive (Donald 2004). Given the considerable energy constraints that many birds face in the breeding season, it is important to understand how processes of agricultural intensification affect the availability of their foraging resources.

In this research, I have used several variables of foraging behavior to assess the quality of habitat presented by two shaded coffee farms under different management intensities. I also collected data on the body condition of birds inhabiting these two farms as an additional view into the habitat quality of these two farms. In my studies, I focused on two species of forest-associated breeding birds that successfully inhabit both types of coffee farms studied (a commercial polyculture and a shaded monoculture), the Yellow-green Vireo and the White-winged Tanager. My results indicate that on average, individuals of these species foraging in the high shade commercial polyculture exhibit a significantly higher attack rate, indicating a higher rate of prey encounter and thus a higher prey availability, than in the lower shade shaded monoculture. While my analysis of body condition data did not reveal consistent patterns between these two farms to corroborate these behavioral results, limited capture rates and sample sizes prevent any strong conclusions about the effects of the apparent discrepancy in food availability on body condition between these farm types.

While it appears that foraging birds are experiencing an increased availability of food resources in the high shade farm, there are several aspects of farm management that could be affecting this pattern. In the second part of this thesis, I looked at two aspects of coffee management—shade tree diversity and canopy management (cover and density)—to determine if they affected the overall patterns of food availability already observed. When comparing the shade trees used by foraging individuals with the proportional availability of those trees, I found that in the higher shade (and higher diversity) farm, birds were not simply using whichever trees were around based on their on-farm distribution. They used more types of rare shade trees at an increased rate and seemed to avoid (although still heavily depend on) the most dominant shade trees, those in the genus *Inga*. This was different in the low shade (and lower diversity) farm, where the trees that foraging individuals used did not differ from the proportional distribution of shade trees (also largely dominated by *Inga* sp., but with much fewer rare species). These results seem to indicate a value of increased shade tree diversity for foraging birds, as it allows birds to seek out preferred foraging locations from a range of tree types. This may be a result of the sampling hypothesis (i.e., a higher diversity of shade trees increases the likelihood of including a shade tree species that presents a particularly high quality foraging resource) (Loreau 1998) a continuity of fruiting phenology that attracts an increased diversity and abundance of arthropod prey (Carlo et al. 2004, Dietsch et al. 2007), or perhaps even better cover from potential avian predators.

Does canopy management play a role in food availability beyond that presented in the diversity of shade trees present? I attempted to answer this question by examining foraging behavior within the two most common shade trees on both farms—*Inga* sp. and *Trema* sp. Results from this analysis indicated that for Yellow-green Vireos, but not for

White-winged Tanagers, individuals foraging in the high shade farm exhibit a significantly higher attack rate than individuals foraging in the low shade farm within both *Inga* sp. and *Trema* sp.—again indicating an increased availability of food resources even within the same shade tree type. Variation between the two focal species may be due to differences in habitat preferences, as Yellow-green Vireos appear to have a stronger association with forest habitat than the White-winged Tanagers exhibit.

As biodiversity-friendly certification programs become more common and familiar to consumers, it is important to understand how organisms are interacting in these agricultural environments. Shade-grown coffee represents a potentially great opportunity for bird conservation, but our understanding of how the process of intensification affects the necessary foraging and breeding resources for forest birds is still limited. This study indicates that there is a significantly higher availability of foraging resources in a high shade commercial polyculture than a low shade shaded monoculture, and that both shade tree diversity and canopy management are playing an important role in determining the availability of those resources. Results from body condition data suggest that this variation in resource availability may be affecting overall bird health, but more data and study would be needed to assess that relationship appropriately. In addition, attention should be given to which types of shade trees provide the highest quality habitat for biodiversity. In this study, it appears that some shade trees, such as *Trema* sp., *Schizolobium* sp., *Miconia* sp., and *Cordia* sp. In addition to the widely used *Inga* sp, encouraging these species in shaded coffee farms may increase the habitat value for foraging birds.

In general, more studies of specific habitat use patterns by forest birds (and other organisms as well) will be helpful in understanding how and why biodiversity is structured the way it is along the intensification gradient for various agricultural land-uses. In turn, these studies will allow informed decisions regarding sustainable farming practices and appropriate criteria for biodiversity-friendly certification programs.

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