THE INFLUENCE OF FOOD AVAILABILITY AND HABITAT STRUCTURE ON
NEST SITE SELECTION OF THE ACADIAN FLYCATCHER

(Empidonax virescens)

By

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Submitted in Partial Fulfillment of the Requirements
for the Degree of
Master of Science
In the
Biological Sciences
Program

YOUNGSTOWN STATE UNIVERSITY
March 2001
The influence of food availability and habitat structure on nest site selection of the Acadian Flycatcher (Empidonax virescens)

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ABSTRACT

Food availability and habitat characteristics were examined in the vicinity of Acadian Flycatcher nests within a late-successional, Beech-Maple forest during the summer of 1999 at the Ravenna Training and Logistics Site in Portage County, Ohio. Flight interception (window) traps were placed at nest sites, non-nest sites, and upland sites to monitor the distribution of arthropods. Specimens were collected on a weekly basis, counted, sized and identified to family. Habitat characteristics were also measured at nest sites and non-nest sites.

For all arthropods combined, the quantity and quality of insects was significantly higher in riparian habitats in comparison to upland habitats, and was higher at nest sites than at non-nest sites, although not significantly. Of the 19 most abundant taxonomic groups of arthropods, Halictidae (Halictid bees), Apidae (bumblebees), Conopidae (thick-headed flies), Araneae (spiders), and Phoridae (scuttle flies) exhibited significantly greater mean abundances at nest sites than at upland sites. These results suggest that the distribution of insects in the forest plot I studied is not random. A higher abundance of Diptera and Hymenoptera, may enhance the quality of habitat for Acadian Flycatchers.

Nest sites tended to have a lower tree density, with subsequently less coverage of leaf litter than non-nest sites. This allowed for an open air space surrounding the nest. An open space surrounding the nest facilitates aggressive nest monitoring and defense behavior, which is common in flycatchers.
ACKNOWLEDGMENTS

Special thanks to Courtenay for not letting me fall out of the nest prematurely, sparking a two-year journey into education and philosophy. Also I would like to thank David B. MacLean and Carl F. Chuey for all your guidance and patience throughout my journey in academia thus far. I also thank my wife, Jennifer, for providing me with an unlimited onslaught of inspiration and devious attempts to keep me focused. I am indebted to my children, Riley and Isaac for providing me with the everyday adventure. Thanks to Nick Mandrak for catalyzing the growth of my knowledge and ability in modern statistical methods. Sincere thanks to Tim Morgan for his help as well as for his permission to study at the Ravenna Training and Logistics site. Special thanks to Dave Golden for spending time with me and minute Coleoptera. I also thank the fabulous Willis lab and field crew, including Mathew Philips, Trish Gundrum, Jody Haylett, Lashale Pugh, Barbara Adair, Jeremy Hutchison, Aimee Kasiewicz, and Beth Hudach, for their long hours of effort. I also thank my family and friends for their support.

This research was funded in part by grants from Sigma Xi Grants-In-Aid-of-Research, the Youngstown State University Research Council, Ohio Biological Survey, Akron Audubon Society, and the YSU Department of Biological Sciences.
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INTRODUCTION

Knowledge of avian life history traits, such as nest site selection, can provide insight into the factors that influence the reproductive success of birds. Predator avoidance has long been assumed to be the major factor influencing nest site selection (Wilson and Cooper 1998). However, abundance of food in a particular habitat may serve as an important cue used by birds in selecting nest sites (Holmes and Shultz 1987). It is also possible that physical landscape features and vegetation structure at the nest-site associated with food abundance may indirectly influence nest site selection (Smith and Shugart 1987, Burke and Nol 1998).

The purpose of this study was to examine the influence of food availability and habitat characteristics on nest site selection in the Acadian Flycatcher (*Empidonax virescens*) at the Ravenna Training and Logistics Site (RTLS). My objectives were to (1) determine if arthropod quality and quantity differ at nest sites and non-nest sites, (2) determine if habitat characteristics differ at nest sites and non-nest sites, (3) and, to initiate a survey of the distribution of arthropods available for insectivorous birds in the RTLS plot.

Factors Involved in Nest Site Selection

Recent studies have tested hypotheses regarding the influence of various factors that influence nest site selection (MacKenzie and Sealy 1981, Murphy 1983, Martin and Roper 1988, Morton et. al. 1993, Nolte and Fulbright 1996, Burke and Nol 1998). It is assumed that breeding birds choose habitats where there are sufficient resources available
for reproduction and survival (Steele 1993). The factors (or resources) that may be important to nest site selection are availability of food, foraging sites, the quantity and quality of nest sites, favorable microclimates, and places to avoid predators, parasites, and competitors (Cody 1981, Steele 1993). Studies of nest site selection have dealt primarily with three of these factors: (1) availability of food, (2) habitat structure, and (3) competition.

Food Availability

The role of food availability in habitat selection is a current subject of interest (e.g. Petit and Petit 1996, Burke and Nol 1998, Forsman et al. 1998). It has generally been assumed that predator avoidance is the main factor influencing nest site selection (Wilson and Cooper 1998). However, other hypotheses must be tested to gain insight into what other factors are influential to habitat selection in a particular species. It is rare to find studies that determine which resources are important during habitat selection in a particular species (Steele 1993). Habitat selection is a complex interaction between environmental and behavioral stimuli that ultimately attract an individual to take up residence within a given area (Petit and Petit 1996).

It is a common argument that food is superabundant during the breeding season (Wiens 1973, Morse 1978, Rotenberry 1980a, 1980b, Rosenberg 1982). However, this view does not account for energetic considerations, such as foraging time. Zebra Finches (Taeniopygia guttata) provided with low quality energy sources required increased search time, which resulted in a reduction of brood size and a decrease in juvenile survivorship. Brood reduction usually occurs within the first three days of hatching, and in many cases is a result of adults actively removing the youngest nestling or sibling competition.
The severe time and energetic demands of the nestling cycle limit the number of young that parents can raise, which ultimately affects fitness (Martin 1987). Availability of food in close proximity of the nest can relieve the intense energetic demands placed on parents provisioning chicks. Among Yellow Warblers (*Dendroica petechia*), females forage closer to the nest height during the early stages of nesting than the male, which may be due to a greater amount of nest centered activity (Busby and Sealy 1979). According to optimal foraging theory, birds should select territories that minimize metabolic costs and increase fitness during the nesting cycle, a time in which some birds function as central-place foragers (Orians and Pearson 1979).

Ovenbirds (*Seiurus aurocapillus*) represent a suitable species to test the food availability hypothesis. They concentrate foraging efforts on the insects and other arthropods in the leaf litter of the forest floor. Because they are considered generalist predators, all arthropods sampled from leaf litter can be considered possible prey items (Burke and Nol 1998). Studies have shown that Ovenbird territories were associated with significantly higher arthropod biomass than random or unoccupied sites (Smith and Shugart 1998, Burke and Nol 1998).

*Structural cues of food availability*

The possibility that habitat features associated with prey abundance may influence nest site selection indirectly has been termed the “structural cues hypothesis” (Smith and Shugart 1987). When birds arrive on the breeding habitat early in the spring, estimation of arthropod abundance may be difficult because many insects have not emerged and snow cover may still be present. Because birds may not be able to directly estimate food availability at the time when they arrive on the breeding grounds, structural cues
associated with high quality and quantity of prey may be important in nest site choice (Hilden 1965, Viestola et al. 1995).

Vegetation structure and physical features of the habitat, such as fragment size may influence factors that determine nest site quality. Small forest tracts may not reach the internal humidity necessary for maintenance of invertebrate food supplies (Southwood 1978). For Ovenbirds, pairing success was significantly greater in woodlots with increased core area (Burke and Nol 1998). Large woodlots with greater core area also contained sites with thicker leaf litter and increased relative humidity, characteristics that favor greater arthropod abundances on the forest floor (Ambuel and Temple 1983, Burke and Nol 1998).

Physical attributes of the landscape within the habitat can influence microclimate conditions. The aspect of a woodland area was found to be highly related to atmospheric moisture in a study of a temperate deciduous forest in northeast Ohio (Petit et al. 1985). Woodland insects have been shown to be present in greater abundances in moister areas, which could provide more food for insectivorous birds (Whittaker 1952).

Many insectivorous birds show affinities to flooded or riparian habitats. Prothonotary Warblers (Protonotaria citrea) preferred flooded habitats that contained a greater abundance of dipterans and mayflies than dry habitats (Petit and Petit 1996). Although abundance of prey items for Prothonotary Warblers fluctuated during the season, elevated peak abundances at flooded areas, due to aquatic insects, may influence selection of riparian nest sites (Petit and Petit 1996). Prey abundances were higher in flooded areas primarily due to mayfly and dipteran emergences and a greater abundance of spiders (Petit and Petit 1996). Although abundance of Lepidoptera, the principal prey item for
Prothonotary Warblers, was not significantly different between flooded and dry habitats, parents provisioning nestlings within flooded habitats benefited from a supplemental nestling food, provided at a minimal energetic cost (Petit and Petit 1996). 

**Other Factors related to Habitat Structure**

The role of habitat structure involves other factors that may influence nest site selection. Recent studies have cited the effects of predator avoidance and microclimate on nest placement, as well as the quantity and quality of suitable nest sites (Murphy 1983, Martin and Roper 1988, Wilson and Cooper 1998). Although the influence of these factors was not tested in this study, the following serves as an introduction to other aspects of the influence of habitat structure on nest site selection.

Predator avoidance has been shown to be influential in nest site selection (Murphy 1983, Martin and Roper 1988, Wilson and Cooper 1998). Birds have evolved two separate mechanisms of nest placement to avoid nest predation. One mechanism considered here is nest concealment, avoiding predators by placing nests in areas surrounded by dense vegetation. The other mechanism operates by placing nests in open areas, allowing birds to monitor and aggressively defend nests.

The most common mechanism of predator avoidance is nest placement (Murphy 1983, Martin and Roper 1988, Wilson and Cooper 1998). Nests placed in full, dense substrates with cover vegetation can be an important factor in reducing nest predation (Martin and Roper 1988). Hermit Thrush (*Catharus guttatus auduboni*) nests that experienced low predation rates were characterized by a significantly higher index of minimum side cover than highly predated nests (Martin and Roper 1988). Minimum side
cover provides an estimate of percent foliage cover 1 m from the nest in each cardinal
direction (Martin and Roper 1998).

Tyrannid Flycatchers provide an alternative example to the nest substrate and
cover density hypothesis, because nests in these birds often have minimal cover in order
to facilitate aggressive nest defense from predators (Murphy 1983). Scissor-tailed
Flycatchers (*Tyrannus forficatus*) nesting in San Patricio, Texas were shown to select
sites with minimal horizontal and vertical cover to allow for aggressive nest defense and
monitoring (Nolte and Fulbright 1996). This could be due, in part, to the strong influence
of avian predators that are not as deterred by nest placement as mammalian predators
(Nolte and Fulbright 1996). Small mammals, such as the Eastern chipmunks (*Tamias
striatus*), may also be able to predate nests placed at the distal end of small branches
(Courtenay Willis, personal observation).

Studies of nest site selection of two species of Tyrannid flycatchers, Eastern
Kingbird (*Tyrannus tyrannus*) and Acadian Flycatcher, have shown that nest placement
may involve a balance between minimizing nest loss due to predation and due to weather
(Murphy 1983, Wilson and Cooper 1998). Nests that are placed low on the tree and close
to the trunk are protected from extreme weather, but are easily accessible to predators
(Murphy 1983, Wilson and Cooper 1998). At the other extreme, nests that are placed
high in trees and placed away from the trunk are more likely to be lost to physical factors
(Murphy 1983, Wilson and Cooper 1998). Studies have shown that while predation may
influence nest placement, abiotic factors such as weather are also influential (Murphy
Nest placement may be an attempt by birds to rear chicks in a suitable microclimate. Wind, radiation, air temperature, and humidity are critical properties of microclimates and interact in complex and variable ways that influence avian biology (Walsberg 1981). Hermit Thrushes and their congeners prefer moister areas, such as nest trees at, or near, the bottom of woodland drainages (Martin and Roper 1988, Dilger 1956). Hermit Thrushes also orient nests to have a southwest exposure to take advantage of the warm afternoon sun at the cool, high elevation of the Mogollon rim in central Arizona (Martin and Roper 1988). Warbling Vireos (*Vireo gilvus*) of Sierra Ancha, Arizona, oriented nests beneath vegetation so that 47% of the solar radiation was reduced during hot afternoon hours as compared to that of the cool mornings (Walsberg 1981). Nolte and Fulbright (1996) found that abiotic factors such as storms, accounted for the greatest proportion of nest failure and successful nests had greater vertical cover to act as a buffer to the harsh climate.

The quality and quantity of suitable nest sites may also be a determining factor involved in nest site selection. Nest site requirements may include certain types of crotches, branching patterns, branch angles, cavities in dead and alive trees, intersecting shrub branches (Steele 1993). For example, Hooded Warblers (*Wilsonia citrina*) in bottomland hardwoods of South Carolina placed nests in crotches of the main stem and primary branches of the substrate plant, with the exception of one nest (Kilgo et. al. 1996). A suitable nest hole is an example of a key stimulus that induces selection of a nest site for cavity nesting birds (Hilden 1965). Although the habitat may be suitable, the patch will not be occupied without the presence of a suitable nest site.
Competition

Because many birds have specific nest site requirements, and often there are a limited number of suitable sites, competition for nest sites can be intense. Both interspecific and intraspecific competition have been shown to be important factors in populations of breeding birds, although intraspecific competition is often more intense (Hilden 1965, Mackenzie and Sealy 1981, Petit and Petit 1996).

Studies of nest site selection of sympatric Eastern Kingbird and Western Kingbird (Tyrannus verticalis) suggest that intraspecific competition is more intense than interspecific (MacKenzie and Sealy 1981). Interspecific aggression was observed only at the infrequent intrusion of a bird to its congeners nest tree in contrast, intraspecific aggression was noted in each species in the general vicinity of a nest (MacKenzie and Sealy 1981).

When suitable nest sites are limited, as often is the case with cavity nesters such as Prothonotary Warblers, interspecific competition from other species, such as Flying Squirrels and House Wrens (Troglodytes aedon), can influence nest site selection (Petit and Petit 1996). Prothonotary Warblers nesting in flooded bottomlands adjacent to the Tennessee River also experienced intraspecific competition, as older males may exclude younger males from the preferred, flooded habitats (Petit and Petit 1996). However, dominance may also be influenced by larger body size and brighter head plumage (Petit and Petit 1996). Although it is the female that ultimately chooses which territory to begin nest building, females will often avoid sub-optimal territories.

Heterospecific attraction provides an alternative view to theories of interspecific competition. According to the heterospecific attraction hypothesis, areas with increased
abundance of resident species are a sign of good quality or safe breeding patch (Forsman et al. 1998). An experimental manipulation of densities of resident tit species (*Parus* spp.) by winter feeding and removal by mist nets in Finnish Lapland, resulted in increased densities and numbers of the most abundant migrant species where resident numbers had been increased (Forsman et al. 1998). Two species that showed the most positive responses to the addition of tits, the Redwing (*Turdus iliacus*) and the Brambling (*Fringilla montifringilla*), have been reported to aggregate to breed in Fieldfare (*Turdus pilaris*) colonies to gain protection from predators (Slagsvold 1980). Because risk of predation has been shown to cause aggregation among birds, predation pressures may induce heterospecific attraction (Forsman et al. 1998).

A similar study, conducted in northeast Minnesota, showed that migrant birds responded positively to increased densities of resident birds (Black-capped Chickadee, *Parus atricapillus*, Red-breasted Nuthatch, *Sitta canadensis*, and White-breasted Nuthatch, *S. carolinensis*) of the same foraging guild (Monkkonen et al. 1997). The Red-eyed Vireo (*Vireo olivaceus*), and the Black-and-White Warbler (*Mniolilta varia*) are both arboreal insectivores belonging to the same foraging guild as the experimentally manipulated resident species, which suggests that food is an important factor in heterospecific attraction (Monkkonen et al. 1997). Results from studies of heterospecific attraction in Finnish Lapland and Minnesota may indicate that the cause of this behavior may be different on the two continents (Forsman et al. 1998, Monkkonen et al. 1997). The community structure, geographical location and other abiotic and biotic conditions may affect the relative importance and cause of heterospecific attraction (Forsman et al. 1998a).
Studies involving food web models have shown that the influence of predators on the processes that regulate species dynamics varies at different levels of productivity (Hairston et. al. 1960, Leibold 1989, Chase 1999a,b). Organisms that have access to an abundance of resources are regulated more by predation, while organisms that have a reduced amount of resources available are regulated more by food (Hairston et al. 1960).

**Food Availability Hypotheses: Direct or Indirect Cues?**

According to the direct cues hypothesis, birds select nest sites by assessing the quality and quantity of food, and they choose sites with abundant resources to ensure reproductive success. The influence of food can act as both an ultimate and a proximate factor in nest site selection. Ultimate factors are the characteristics of the habitat that are essential to the survival of the species. Examples of ultimate factors are food, habitat requirements related to the morphological and behavioral traits of the species, and protection from enemies and adverse weather (Hilden 1965). Proximate factors stimulate the species to choose a particular habitat, but do not necessarily relate to the survival or reproductive success of the species. Stimuli of the landscape or terrain, and other animals are some examples of proximate factors (Hilden 1965).

Food is generally thought of as an ultimate factor, but in some species has been found to influence nest-site selection directly acting as a proximate factor. For this study, arthropod abundance was measured within nest sites and non-nest sites in order to gain insight as to whether availability of food was functioning as a proximate factor.

Alternatively, birds may also use the vegetation structure as a proximate cue, to indirectly assess food availability. According to the indirect cues hypothesis, birds cue
into features of the habitat related to arthropod abundance rather than directly assessing food resources (Seastesdt and MacLean 1979). The structural cues hypothesis may be particularly relevant when arthropod prey may not have emerged, or may be difficult to assess at the time when migratory birds arrive on the breeding grounds early in the spring, when snow may still cover the ground (Hilden 1965).

**Relevance of the Species**

The Acadian Flycatcher represents a suitable species to test the influence of food availability on nest site selection. In comparison to most other insectivorous birds in this study site, Acadian Flycatcher nests are typically placed on low hanging branches (on average 4 m high), and are relatively easy to locate and monitor (Mumford 1964). The population at the RTLS appeared to be a good candidate for testing the influence of food availability because predation rates are typically lower compared to those reported in other studies by Wilson and Cooper (1998). Nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) is nearly absent (only one nest reported parasitism during Spring of 1999), which provides a unique chance to test alternative factors influencing nest selection (personal observation). The Acadian Flycatcher belongs to the Tyrannid Flycatcher family (*Tyrannidae*), and is one of the five species of *Empidonax* flycatchers present east of the Mississippi River. The *Empidonax* flycatchers of the eastern United States are known for the difficulty of identification by morphology alone, without noting song or habitat. They breed from, southeastern South Dakota across to southern New York, and north along the coast to Massachusetts, and south along the Atlantic coast to central Florida, to the gulf coast, and southern Texas and are currently expanding their
northern range (DeGraaf and Rappole 1995, Scott 1987). Acadian Flycatchers winter in Central and South America (Degraaf and Rappole 1995). Male Acadian Flycatchers arrive on breeding grounds in early May within their northern range, and begin establishing territories (Mumford 1964, Wilson and Cooper 1998). Males have been observed aggressively defending territories against intrusion by the Eastern Wood Peewee (*Contopus virens*), Least Flycatcher (*Empidonax minimus*), Ovenbird, and Cerulean Warbler (*Dendroica cerulea*) (Mumford 1964). Although there is little evidence that female Acadian Flycatchers defend territories, females have been observed actively defending the nest site (Mumford 1964).

Acadian Flycatchers feed by hovering at various substrates and hawking prey, concentrating foraging efforts in the open space between the lower canopy and forest floor (Maurer and Whitmore 1981). Based on foraging observations (n=1575) of Acadian Flycatchers at the RTLS, it was found that the average foraging perch height was 4 m. Insects are frequently picked from vertical tree trunks, the leaf surface, or clusters of dead leaves (Mumford 1964).

The diet of the Acadian Flycatcher consists of bees, wasps, ants, moths (both larval and adult), beetles and flies (Beal 1912). Data based on the stomachs contents of 100 Acadian Flycatchers collected in 14 states, District of Columbia and Canada from April to October showed that Hymenoptera were taken in the greatest numbers and that only 2.95% of all food was plant material (Beal 1912). In a concurrent study at the RTLS, microvideo recordings of nestling feedings were examined to identify prey items of Acadian Flycatchers at our site. The top ten identified prey items were 1. craneflies (Tipulidae) 32%, 2. adult and larval butterflies and moths (Lepidoptera) 15%,
3. harvestmen (Phalangida) 13%, 4. undetermined flies (Diptera) 8%, 5. hanging flies (Bittacidae) 6%, 6. undetermined beetles (Coleoptera) 5%, 7. undetermined bees and wasps (Hymenoptera) 4%, 8. undetermined damselflies and dragonflies (Odonata) 4%, 9. undetermined spiders (Araneae) 3%, 10. horseflies and deerflies (Tabanidae) 2% (Lashale Pugh and Courtenay Willis, preliminary data).

In a study of the diet of seasonally sympatric flycatchers in the Caribbean lowlands of Costa Rica it was found that migratory species, such as the Acadian Flycatcher, tended to have more opportunistic food exploitation patterns with heterogenous diets than non-migrating flycatchers. The results of the analysis did not suggest a preference to a certain prey type or characteristic, although prey of Acadian Flycatchers tended to have patchy and probably ephemeral distribution (Sherry 1984). Species that forage by flycatching (or hawking) tend to be more opportunistic than non-flycatching species for forest birds including the Acadian Flycatcher, Red-eyed Vireo (Vireo olivaceus), Black-throated Green Warbler (Dendroica virens), American Redstart (Setophaga ruticilla), and Scarlet Tanager (Piranga olivacea) in two forests with different vegetation structure in Tucker County, West Virginia (Maurer and Whitmore 1981).

Tests of the influence of food abundance and indirect food cues through habitat structure in birds with relatively wide foraging niches in complex environments, such as forests, have received little attention (Maurer and Whitmore 1981, Smith and Shugart 1987). Hypotheses addressing the direct or indirect influence of food availability on nest site selection are difficult to test when the species being studied use a wide variety of foraging substrates and foraging behavior (wide niche dimensions). Studies citing
evidence of the influence of food availability on nest site selection are often in habitats that are less diverse than forests structurally, such as Laplands (Seastedt and MacLean 1979), or in species with narrow niche dimension, such as the Ovenbird, which mainly forages in leaf litter (Burke and Nol 1998). Although the structurally complex nature of the forest plot at the RTLS makes comprehensive arthropod sampling difficult, if not impossible, sampling of the prey available to Acadian Flycatcher’s is possible due to the relatively low height and proximity to the nest at which they feed (C. Willis, personal observation).
METHODS

Study Design

To evaluate the influence of food availability and habitat structure on nest site selection of the Acadian Flycatcher, arthropods and vegetation were sampled within a forest plot. Arthropods were sampled to test for differences between insect quality and quantity at nest sites and non-nest sites. Because certain habitat features may be associated with insect abundance, habitat structure was also sampled to investigate indirect influences of food availability on nest site selection.

Flight interception window traps were placed at 25 m intervals along a stream, its associated tributaries and also at upland sites in order to collect insects at nest sites and non-nest sites. Insect traps were oriented along the stream and tributaries because this area contained the greatest concentration of Acadian Flycatcher nests. Insect traps were placed at nest sites (n=22 traps), non-nest sites (n=22 traps), and upland sites (n=23 traps).

Plots for vegetation sampling were established at nests after fledging or nest failure. For both nest site plots (n=18) and non-nest site plots (n=18), 11.3 m and 5 m radius plots were established. In the 5 m plot, shrubs and saplings were counted and ground cover was measured. In the 11.3 m plot, trees were counted and the point-quarter sampling method was used to estimate tree density. Non-nest site plots were established 30 m away from the nest site in a random cardinal direction. As a result, non-nest site plots for vegetation sampling did not correspond to non-nest site plots for insect sampling.
This research was designed to investigate the hypotheses that arthropod quantity and quality and/or habitat characteristics influence the placement of nest sites by Acadian Flycatchers (*Empidona* virescens). Specifically, the null hypotheses were:

1. Arthropod abundance, size, and taxa does not differ at riparian nest, riparian non-nest, and upland sites.
2. Characteristics of the habitat do not differ at nest sites and non-nest sites.

**Study Site**

This study was conducted at the Ravenna Training and Logistics Site (RTLS) in Northeast Ohio (81° 04' N, 41° 13' W) (Figure 1). Fieldwork was oriented along 1 km of the South Fork of Eagle Creek, a second order stream at 299 m above sea level that flows west to east through our study site, which corresponded to the area with the greatest concentration of Acadian Flycatcher nests.

The stretch of South Fork of Eagle Creek included in this study is located near the northern perimeter of the military reservation, which encloses a 100 ha late successional hardwood stand. Dominant canopy species are American Beech (*Fagus grandifolia* Ehrh.) and Sugar Maple (*Acer saccharum* L.) (Weishaupt 1971). Most canopy species are currently over 80 years old, although some trees (DBH 30.5 cm) were harvested in 1940 (Tim Morgan pers. comm).
Figure 1. Location of the Ravenna Training and Logistics Site, Portage County, Ohio.

The enlargement shows the position of the RTLS in relation to surrounding transportation routes. The darkened region within the RTLS indicates the location of the study site.
Finding and Monitoring Nests

The study site was established as a BBIRD (Breeding Biology and Research Database) site in 1997. BBIRD provides a standardized method of collecting data on breeding biology and it allows for comparisons in studies among investigators and locations (Martin 1997). In the first year of the study, stations were marked using wooden stakes arranged at 50 m intervals in a grid system within a 10 ha beech-maple forest plot. These labeled station markers facilitate the relocation of nests without actually marking active nests, which can attract predators (Martin 1997).

For this study, nest searching began in May 1999, as soon as males arrived on the breeding grounds and began establishing territories. Singing males were spot-mapped, and female Acadian Flycatchers were observed for nest building behavior (i.e. carrying nesting material) (Martin and Geupel 1993). The distance and direction to the closest station marker of all new nests were recorded. After nest failure or fledging, nest microhabitat characteristics were measured. The primary and secondary tree species used for nest substrate were recorded. The primary and secondary tree species concealing the nest were recorded. The tree height, DBH, and health of the nest substrate was measured. The height of the nest, distance to the trunk, distance of the nest to the foliage edge, orientation of the nest, and the number and diameter of supporting branches was also recorded.
Estimating Arthropod Quantity and Quality

Flight-interception window traps are an effective way to measure the activity of flying arthropods (Hammond 1997). The window trap consisted of a 41 x 30 cm sheet of plexiglass with a 1 L plastic tray, mounted below it on two 1 x 1 in. wooden legs (Figure 2). The collection tray was filled with 1 L of 50-70% isopropyl alcohol. This trap is a smaller version of a conventional window trap as reported by Southwood (1978). Jonsson et al. (1986) reported that small window traps are less likely to be blown over by wind and easier to transport in the field.

Window traps were placed at three sites: (1) riparian nest sites (n=22 traps), (2) riparian non-nest sites (n=22 traps), (3) upland non-nest sites (n=23 traps). Window traps were placed at 25 m intervals along the South Fork of Eagle Creek, starting at the western boundary of the study plot (Wadsworth Rd.) and continuing east along the creek until the habitat changed into a scrub woods area. Traps were also placed in the first order tributaries adjoining South Fork of Eagle Creek, where Acadian Flycatcher nests were found. Upland trap sites were established by placing three traps at 25 m intervals perpendicular to nest traps along the creek or tributaries. Thus, upland sites of creek nest sites were oriented north-south and those of tributary nest sites were oriented east-west (Figure 3). Upland sites were placed on the northern side of the creek to avoid the logistical difficulty involved in placing traps on the exposed rock ravine bordering the stream to the south. For upland sites of nests on the tributaries, traps were established on the eastern side of the tributaries because the characteristic habitat did not change to the east of the two tributaries sampled.
Figure 2. Design and dimensions of flight interception window traps used to sample forest arthropods at nest sites, non-nest sites, and upland sites.
Figure 3. Location of all nest sites and window trap sites along South Fork of Eagle Creek. Trap sites are color coded by site type (nest (red), non-nest (black), or upland (green)). Prey availability and habitat structure was sampled at all nest sites labeled by black ovals. For nests labeled with green ovals, only habitat structure was sampled.
Flight interception traps were filled with alcohol and "set" on June 30 and were sampled throughout July 1998, corresponding to the time when birds in this forest are feeding nestlings. Arthropods were collected on July 7, 14, 21, and 28, 1999, placed in whirl-pac™ baggies, and preserved in 70% isopropanol until they could be processed. Back in lab, insects were pinned or placed on points for permanent storage in The YSU Insect collection, identified to family, counted, and placed into one of three size categories: 0-5 mm (small), >5-10 mm (medium), and >10 mm (large). These size categories were selected based on the size range (9.1-10.2 mm) of the Acadian Flycatchers beak (Pyle 1997).

**Measuring Nest Patch and Habitat Characteristics**

Habitat characteristics were measured according to BBIRD protocol (Martin et al. 1996). A total of 18 nest-site plots and 18 non-nest site plots were characterized from late July to mid-August 1999, after fledging or nest failure. Plots sampling vegetation at non-nest sites were established 30 m from the center nest site plots in a random cardinal direction. At each plot a central stake was placed in the ground under each nest or in the center of each non-nest plot and attached to four ropes extending to 5m and 11.3 m at 90° degree angles forming four equal quadrants (Figure 4). Within the 5 m plot, the following 21 habitat variables were measured: (1) The aspect (degrees determined by clinometer readings) and direction of slope (compass reading); (2) canopy cover (based on sightings within each quadrant using a convex spherical densiometer); (3) dominant and sub-dominant canopy species along with respective percent cover and top canopy height were estimated; (4) Numbers of stems > 50 cm were identified, put into size
Figure 4. BBIRD Plot design for vegetation sampling at nest sites and non-nest sites.

The circular plot consists of: (1) a 5m circular plot for shrub and sapling counts and measuring ground cover, and (2) an 11.3 m radius plot used for tree stem counts.
classes (<2.5, 2.5-8), and counted; (5) litter depth (mm); (6) percent ground cover constituents (13 variables) were estimated for each quadrant.

In the 11.3 m plot, 15 habitat variables were measured: (1) The numbers of woody stems in the following DBH size categories (in cm): 8-23, 23-38, >38; (2) the point quarter method was used to determine density and diversity of trees, snags, and shrubs. Variables included height, distance to center of quadrant, DBH (for trees and snags), crown width and perpendicular width (for shrubs).

**Statistical Analysis**

**Prey availability**

To examine the influence of prey availability on nest-site selection, differences in the number abundance of arthropods at nest-sites, non-nest sites, and upland sites were examined in three ways: (1) all arthropods combined, (2) small, medium, and large size categories, and (3) individual families of arthropods. These data were tested for normality (Kolmogorov-Smirnov test) and heterogeneity of variances (Levene’s test), to satisfy assumptions of the statistical tests. Data that were not normally distributed or showed significant heteroscedasticity of variances were log transformed (log(x+1)). Samples from July 21, 1999 were selected because it represented the most complete collection. Pooling data from successive weeks was not considered in order to avoid biases due to differences in emergence and peak abundance of insects, which may be associated with environmental factors such as temperature, moisture, and wind speed.
One-way analysis of variance (ANOVA) was used to compare relative abundance of all arthropods combined at nest site traps (n=22), non-nest traps (n=22), and upland traps (n=23) using Statistica (Statsoft 1998). Log transformed size-partitioned abundance data were normally distributed and displayed homogeneity of variances. To compare the number of small, medium, and large size categories at nest-sites, non-nest sites, and upland sites, a two-way ANOVA was performed. Log transformed abundance data were not normally distributed and displayed heterogeneity of variances. However, because ANOVA is typically robust, and the data did not deviate severely from the underlying assumptions (Levene’s test; F=1.341, p=0.269), the test was not considered invalidated (Zar 1999). The results of the two-way ANOVA were interpreted with caution.

To test for the influence of variation in arthropod taxa present at nest sites, non-nest sites and upland sites individual Kruskal-Wallis ANOVAs were performed for 19 of the top arthropod families. Because some families had too few individuals, these analyses were limited to 19 families in which total captures exceed 20 individuals (Hoback 1999). Log transformation of data was not sufficient in satisfying underlying assumptions of ANOVA, meriting the use of the non-parametric Kruskal-Wallis ANOVA. To examine multiple-comparisons, a non-parametric Tukey-type test was performed (Zar 1999). Discriminant Function Analysis (DFA) was used to detect the relative power of the abundance and presence of various insect taxa variables in discriminating between nest sites, non-nest sites, and upland sites. The Box M test for Homogeneity of variances showed significant heteroscedasticity (Box M=803.3, Chi-square=477.6, df=380, p=0.0005) for the log transformed variables. DFA can be an
effective means to explore data and caution was taken to not treat the analysis results as confirmatory (Williams 1983).

_Habitat Analysis_

Habitat variables from Acadian Flycatcher habitat sampled in August 1999 were analyzed using the Mann-Whitney test and principal components analysis (PCA). Log transformed data from the 19 habitat variables failed to satisfy the underlying assumptions of parametric methods of testing differences between means, meriting the use of the non-parametric Mann-Whitney test to individually test for differences in habitat variables at nest sites and non-nest sites.

Because the methods of measuring various habitat attributes are diverse, such as tree height, percent cover of forbes, and shrub density, all variables were transformed (proportional data: \((\arcsin + 0.5)\); ratio scale data: \(\log(x+1)\)) and standardized (subtract mean, divide by standard deviation). Data were standardized separately for nest sites and non-nest sites using within-group variances (Rohwer and Kilgore 1973). This method is appropriate when PCA is being used to separate groups where between-group variances may be large compared to within-group variances. Standardization based on total variance of both groups is problematic because it reduces the influence of variables with high variance.

PCA was used to detect variables displaying variability between nest sites and non-nest sites. Ordinations, such as PCA, determine which of the original variables are correlated and reduces a large set of variables, such as the various habitat characteristics,
to a smaller group in an attempt to aid in biological interpretation (MacKenzie and Sealy 1981, Murphy 1983).

In order to provide a statistical means for detecting if multivariate habitat variables differ between nest sites and non-nest sites, these variables were analyzed by a DFA. A DFA was performed on log transformed habitat variables to test if the habitat measurements would provide a mathematical means for separation of Acadian Flycatcher nest and non-nest site habitat characteristics (Manly 1986). The Box M test was not used to test for homogeneity of variances, because the covariance matrices could not be inverted (Statsoft 1998). To test variables for heteroscedasticity of variances, each variable was tested individually using Levene’s test. Of the 19 variables chosen for these analyses three showed significant heteroscedasticity, therefore, because this may invalidate the results of the DFA, a Mann-Whitney test was run on the factor loading of the first component of the PCA for habitat variables. The Mann-Whitney test provided an additional test to compare to the results of the DFA.
RESULTS

Prey Availability

Analyses of prey availability are based on the identification of 3,119 individuals, representing 108 families collected on July 21, 1999. A total of 1,258 arthropods were collected at (n=22) nest sites, 1,129 were collected at (n=22) non-nest sites, and 732 were collected at (n=23) upland sites. For all arthropods combined, significant differences between the mean abundance of insects collected at trap sites were detected (One-way ANOVA; F=3.70, df=64, p=0.030). The mean number of arthropods at nest sites was significantly greater than at upland sites (Tukey honest significant difference test for unequal N; p=0.025) (Figure 5). No significant differences were detected for any of the size classes between trap sites (One-way AVOVA; F=1.05, p=0.387). A greater mean number of small insects were found at nest sites (x=23) than at upland sites (x=14), but did not differ significantly (Tukey honest significant difference test for unequal n; p=0.089).

Of the 19 most abundant insect families, five showed significant differences between sites. All five arthropod taxa (Apidae, Halictidae, Phoridae, Conopidae, and Araneae) showed significantly greater mean number of individuals at nest sites than at upland sites. In addition, for Apidae and Araneae, the mean number of individuals at nest sites was significantly greater than at non-nest sites.
Figure 5. Comparisons of mean number of total insects (± 1 SD) from nest sites (n=22), non-nest sites (n=22), and upland sites (n=23). Means are labeled by letters representing significant differences as determined by one-way ANOVA (α=0.05).
(ANOVA, P=0.01, two-tailed)
Table 1. Mean number of insects (± 1 SD), standard deviations, and Kruskal-Wallis ANOVA results for the 19 most abundant arthropod families.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Site</th>
<th></th>
<th>Kruskal-Wallis ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>nest</td>
<td>non-nest</td>
<td>uplands</td>
</tr>
<tr>
<td>Arachnida</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Araneae</td>
<td>0.64 ±0.85</td>
<td>0.23 ±0.43</td>
<td>0.04 ±0.21</td>
</tr>
<tr>
<td>Coleoptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anobiidae</td>
<td>0.41 ±0.59</td>
<td>0.18 ±0.5</td>
<td>0.3 ±0.47</td>
</tr>
<tr>
<td>Byrrhidae</td>
<td>0.46 ±0.74</td>
<td>0.36 ±0.79</td>
<td>0.17 ±0.38</td>
</tr>
<tr>
<td>Elateridae</td>
<td>1.6 ±1.47</td>
<td>1.23 ±1.38</td>
<td>1.48 ±1.53</td>
</tr>
<tr>
<td>Eucnemidae</td>
<td>1.14 ±1.73</td>
<td>1.27 ±1.64</td>
<td>1.83 ±2.01</td>
</tr>
<tr>
<td>Mordellidae</td>
<td>7.09 ±6.73</td>
<td>7.64 ±7.89</td>
<td>4.26 ±4.93</td>
</tr>
<tr>
<td>Nitidulidae</td>
<td>5.68 ±4.55</td>
<td>4.68 ±4.45</td>
<td>7.13 ±4.42</td>
</tr>
<tr>
<td>Scolytidae</td>
<td>1.18 ±1.71</td>
<td>1.86 ±2.4</td>
<td>1.7 ±2.1</td>
</tr>
<tr>
<td>Staphylinidae</td>
<td>2.41 ±2.15</td>
<td>2.91 ±3.45</td>
<td>3.09 ±4.02</td>
</tr>
<tr>
<td>unidentified</td>
<td>0.36 ±0.73</td>
<td>0.59 ±0.85</td>
<td>0.13 ±0.34</td>
</tr>
<tr>
<td>Diptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conopidae</td>
<td>0.95 ±1.29</td>
<td>0.68 ±1.25</td>
<td>0.13 ±0.34</td>
</tr>
<tr>
<td>Muscidae</td>
<td>0.59 ±1.01</td>
<td>0.59 ±0.91</td>
<td>0.26 ±0.54</td>
</tr>
<tr>
<td>Phoridae</td>
<td>1.91 ±2.07</td>
<td>2.36 ±2.52</td>
<td>0.48 ±0.85</td>
</tr>
<tr>
<td>Hemiptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Miridae</td>
<td>0.95 ±0.95</td>
<td>0.55 ±0.91</td>
<td>0.3 ±0.47</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Apidae</td>
<td>1.05 ±1.17</td>
<td>0.41 ±0.85</td>
<td>0.3 ±0.47</td>
</tr>
<tr>
<td>Formicidae</td>
<td>0.64 ±0.95</td>
<td>0.59 ±0.85</td>
<td>0.26 ±0.68</td>
</tr>
<tr>
<td>Halictidae</td>
<td>16.14 ±21.49</td>
<td>15.45 ±23.46</td>
<td>2.22 ±1.76</td>
</tr>
<tr>
<td>Vespidae</td>
<td>0.55 ±0.91</td>
<td>0.14 ±0.35</td>
<td>0.26 ±0.54</td>
</tr>
<tr>
<td>Psocoptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>unidentified</td>
<td>0.36 ±0.66</td>
<td>0.5 ±0.67</td>
<td>0.26 ±0.69</td>
</tr>
</tbody>
</table>
Table 2. Dunn’s non-parametric Tukey-Type multiple comparison test for arthropod families.

<table>
<thead>
<tr>
<th></th>
<th>Halictidae</th>
<th></th>
<th>Apidae</th>
<th></th>
<th>Phoridae</th>
<th>Conopidae</th>
<th>Arachnida</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>nest</td>
<td>non-nest</td>
<td>upland</td>
<td>nest</td>
<td>non-nest</td>
<td>upland</td>
<td>nest</td>
</tr>
<tr>
<td>nest</td>
<td></td>
<td></td>
<td>0.02&gt;p&gt;0.01</td>
<td></td>
<td>0.05&gt;p&gt;0.02</td>
<td>0.02&gt;p&gt;0.01</td>
<td></td>
</tr>
<tr>
<td>non-nest</td>
<td>NS</td>
<td></td>
<td>0.05&gt;p&gt;0.02</td>
<td></td>
<td>NS</td>
<td>0.02&gt;p&gt;0.01</td>
<td></td>
</tr>
<tr>
<td>upland</td>
<td>0.02&gt;p&gt;0.01</td>
<td>NS</td>
<td></td>
<td>0.02&gt;p&gt;0.01</td>
<td>NS</td>
<td>NS</td>
<td>0.002&gt;p&gt;0.001</td>
</tr>
<tr>
<td>Phoridae</td>
<td>nest</td>
<td></td>
<td>0.05&gt;p&gt;0.02</td>
<td></td>
<td>NS</td>
<td>0.005&gt;p&gt;0.002</td>
<td></td>
</tr>
<tr>
<td>non-nest</td>
<td>NS</td>
<td></td>
<td></td>
<td></td>
<td>NS</td>
<td>NS</td>
<td>0.002&gt;p&gt;0.001</td>
</tr>
<tr>
<td>upland</td>
<td>0.05&gt;p&gt;0.02</td>
<td>NS</td>
<td></td>
<td>0.005&gt;p&gt;0.002</td>
<td>NS</td>
<td>NS</td>
<td>0.002&gt;p&gt;0.001</td>
</tr>
<tr>
<td>Arachnida</td>
<td>nest</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>upland</td>
<td>0.002&gt;p&gt;0.001</td>
<td>NS</td>
<td></td>
<td></td>
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</tbody>
</table>
The DFA correctly classified 72.7% of the variation at nest sites, 68.2% of non-nest sites, and 87.0% of upland sites (Wilk's Lambda= 0.30, approximate F=2.02, p< 0.003). The arthropod taxon that loaded highly, which were important to separation of nest, non-nest, and upland sites on the first root of the DFA were: Arachnida, Halictidae, Phoridae, and Conopidae. In addition, Apidae, Vespidae, and Nitidulidae loaded highly on root 2 (Table 3).

Multivariate habitat distances were greatest between nest sites and upland sites (F=2.84, p=0.002) and were greater for non-nest vs. upland sites (F=2.08, p=0.02) than for nest vs. non-nest sites (F=1.36, p=0.19). A scatter plot of root 1 vs. root 2 shows the separation of insect taxon found at nest sites from upland sites (Figure 6).

**Habitat Characteristics**

The mean abundance, standard deviation, and test results for the 19 habitat variables measured are summarized in Table 5. Percent cover of leaf litter was significantly lower at nest sites than at non-nest sites (Mann-Whitney U test; p=0.01). Also, the mean number of trees at nest sites was significantly lower than at non-nest sites (Mann-Whitney U test; p=0.01).

Principal component analysis on habitat variables at nest sites and non-nest sites produced 10 eigenvectors with eigenvalues greater than 1, cumulatively explaining 91.1% of the total variance. The unrotated factor loadings were used because of the relative ease in ecological interpretation of these loadings. Factor I had an eigenvalue of 8.2 and explained 24.2% of the total variation. High loadings on factor I included percent water, rock, leaf cover and leaf litter depth. Both rock and water cover loadings were
Table 3. Factor structure matrix coefficients of discriminant functions and arthropod family variables. Families are arranged alphabetically and grouped taxonomically.

<table>
<thead>
<tr>
<th>taxa</th>
<th>Root 1</th>
<th>Root 2</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Arachnida</strong></td>
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<tr>
<td>Araneae</td>
<td>-0.38</td>
<td>0.26</td>
</tr>
<tr>
<td><strong>Coleoptera</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anobidae</td>
<td>-0.02</td>
<td>-0.27</td>
</tr>
<tr>
<td>Byrrhidae</td>
<td>-0.16</td>
<td>-0.05</td>
</tr>
<tr>
<td>Elateridae</td>
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<td>Eucnemidae</td>
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<td>0.02</td>
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<td>Mordellidae</td>
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</tr>
<tr>
<td>Nitidulidae</td>
<td>0.23</td>
<td>-0.28</td>
</tr>
<tr>
<td>Scolytidae</td>
<td>0.06</td>
<td>0.16</td>
</tr>
<tr>
<td>Staphylinidae</td>
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<td>-0.31</td>
</tr>
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<td>unidentified</td>
<td>-0.17</td>
<td>0.27</td>
</tr>
<tr>
<td><strong>Hymenoptera</strong></td>
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<td></td>
</tr>
<tr>
<td>Apidae</td>
<td>-0.28</td>
<td>-0.39</td>
</tr>
<tr>
<td>Formicidae</td>
<td>-0.21</td>
<td>0.06</td>
</tr>
<tr>
<td>Halictidae</td>
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<td>0.04</td>
</tr>
<tr>
<td>Vespidae</td>
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<td><strong>Diptera</strong></td>
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<td>Muscidae</td>
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<td>Mirtidae</td>
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<td>-0.22</td>
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<tr>
<td><strong>Psocoptera</strong></td>
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<td></td>
</tr>
<tr>
<td>unidentified</td>
<td>-0.11</td>
<td>0.19</td>
</tr>
</tbody>
</table>
Figure 6. Plot of discriminant scores of nest site, non-nest site and upland sites of multivariate arthropod assemblage.
Table 4. Means (± 1 SD) for habitat variables at Acadian Flycatcher nest sites and non-nest sites.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Nest (N=17)</th>
<th>Non-nest (N=17)</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter</td>
<td>17.8 (13.2)</td>
<td>24.1 (15.2)</td>
<td>0.21</td>
</tr>
<tr>
<td>High canopy</td>
<td>0.84 (0.07)</td>
<td>0.87 (0.03)</td>
<td>0.23</td>
</tr>
<tr>
<td>Total canopy</td>
<td>0.88 (0.03)</td>
<td>0.88 (0.02)</td>
<td>0.97</td>
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<tr>
<td>Grass</td>
<td>0.05 (0.05)</td>
<td>0.05 (0.04)</td>
<td>0.66</td>
</tr>
<tr>
<td>Sedge</td>
<td>0.06 (0.13)</td>
<td>0.02 (0.02)</td>
<td>0.16</td>
</tr>
<tr>
<td>Forbes</td>
<td>0.13 (0.10)</td>
<td>0.10 (0.09)</td>
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<tr>
<td>Shrub</td>
<td>0.09 (0.11)</td>
<td>0.05 (0.12)</td>
<td>0.13</td>
</tr>
<tr>
<td>Fern</td>
<td>0.04 (0.07)</td>
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<tr>
<td>Moss</td>
<td>0.06 (0.09)</td>
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<td>0.07 (0.11)</td>
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</tr>
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<td>Rock</td>
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<td>0.06 (0.12)</td>
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<td>Leaf</td>
<td>0.43 (0.33)</td>
<td>0.73 (0.31)</td>
<td>0.01*</td>
</tr>
<tr>
<td>Brush</td>
<td>0.87 (0.73)</td>
<td>0.12 (0.07)</td>
<td>0.15</td>
</tr>
<tr>
<td>Shrubs (small)</td>
<td>163.7 (231.6)</td>
<td>114.8 (180.9)</td>
<td>0.48</td>
</tr>
<tr>
<td>Shrub (large)</td>
<td>1.6 (2.9)</td>
<td>2.1 (2.9)</td>
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</tr>
<tr>
<td>Trees</td>
<td>11.7 (6.2)</td>
<td>17.2 (5.9)</td>
<td>0.01*</td>
</tr>
<tr>
<td>Snags</td>
<td>0.88 (1.3)</td>
<td>1.18 (1.2)</td>
<td>0.31</td>
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</table>
negative, while leaf cover and leaf litter depth loaded positively. Factor II had an eigenvalue of 5.1 and explained 14.9% of the total variation. Density of small shrubs had a high negative loading on factor II, and large shrubs and snags had moderate positive loadings. The factor loadings for each nest and non-nest site for factors I and II were plotted to display the variation between the two groups (Figure 7). Both nest sites and non-nest sites showed considerable amounts of variation and overlap. Along the axis corresponding to factor I, nest sites fell relatively evenly distributed on either side of the origin. For non-nest sites, 76% fell to the right of the origin. Along factor II, 59% of nest sites fell above the origin, while nest sites distributed evenly on either side of the origin.

Nest sites with high percent cover of water and reduced leaf cover (strong riparian influence) tended to load negatively on factor 1, while those without water or with very little water cover and with high percent cover of leaf litter loaded positively (strong upland influence). A Mann-Whitney U test was run on the loadings on factor 1 for habitat variables for nest sites and non-nest sites to test for differences in loadings along factor 1. No significant differences were found (Mann-Whitney U Test; U=133.5, p=0.70).

The results of the discriminant function analysis on 19 habitat variables was not significant (Wilk’s Lambda= 0.37859, approx. F (19, 14)=1.21, p< 0.364).
Figure 7. Ordination of nest sites and non-nest sites from the first two factors of the principal component analysis of habitat variables.
DISCUSSION

Prey Quantity and Quality

The quality and quantity of prey within the territory of a breeding bird is likely to function as an important ultimate factor by influencing the evolution of behavior and traits related to the acquisition of food (Hilden 1965). Availability of prey may also act as a proximate factor, influencing habitat choice either directly or indirectly by features, such as vegetation structure, that may correspond to food availability (Hilden 1965).

Prey availability may be an important factor in the nest site selection of Acadian Flycatchers within this Beech-Maple forest. For all arthropods combined, the mean abundance of insects was higher at nest sites than at upland sites, suggesting that the distribution and abundance of insects in a forest is not random. Acadian Flycatchers at the RTLS may be using arthropod abundance as one means of assessing high quality nest sites.

Results from this study support studies of other Neotropical migratory birds that appear to select nest sites based on food availability. Insect biomass was greater at nest sites than at random sites in a study of the Ovenbird nesting in a Beech-Maple forest in southern Ontario (Burke and Nol 1998). Prothonotary Warblers nesting in west-central Tennessee show preference to the flooded areas adjacent to the Tennessee river compared to nearby drier bottomland sites (Petit and Petit 1996). The lower nesting success of Prothonotary Warblers in dry habitats appeared to be related to lower food availability in the drier bottomlands (Petit and Petit 1996). Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) in eastern Washington state chose marshes with high rates of emerging odonates, but individual territories did not show correlations between
rates of emergences and Yellow-headed Blackbird density (Orians and Wittenberger 1991). Yellow-headed Blackbirds may assess food availability for the entire marsh, because of the polygynous mating system, females are not defended from adjacent males territories, and forage considerable distances from the nest.

When each insect size class was compared by site, no difference was detected. However, insects in the smallest size class showed a trend similar, but not significant, to that of overall arthropod abundance. It is probable that the presence of small insects influences the quality of a habitat because small insects are assumed to be the most profitable of all size classes, as they often occur in large patches (Quinney and Ankney 1985). Strong statistical support of negative relationships between insect size and abundance is often debated and results may be artifacts of sampling (Gaston and Lawton 1998). Small insects tend to be common, widespread, and widely fluctuating, but the form of the interspecific relationship between abundance and body size is largely debated (Blackburn and Gaston 1997, Gaston and Lawton 1998).

It is possible that the flight-interception window traps were inadequate in sampling large insects. Some insects that Acadian Flycatchers were observed feeding to chicks on microvideo recordings, such as large Lepidopterans, Tipulids, and Odonates, were rarely collected by the trap (C. Willis, unpublished data). There are few studies that address the effectiveness of window traps for sampling various taxa and sizes of insects (Jonsson et al. 1986, Hammond 1997).

Of 22 taxa (20 families and 1 Sub Orders) identified from microvideo recordings and nestling fecal sacs, 15 of them were included in both window trap samples and the diet of Acadian Flycatchers at our study site. The taxa included harvestmen
(Phalangida), broad-nosed weevils (Curculionidae), click beetles (Elateridae), leaf-mining beetles (Chrysomelidae), robber flies (Asilidae), blow flies (Callophoridae), horseflies and deerflies (Tabanidae), craneflies (Tipulidae), ichneumon wasps (Ichneumonidae), ants (Formicidae), geometrid moths (Geometridae), wood nymphs (Satyridae), sphinx moths (Sphingidae), noctuid moths (Noctuidae) and various bees and wasps (families of Hymenoptera).

There were seven families that were present in the nestling diet but not in window trap samples. These groups included tent caterpillar moths (Lasiocampidae), tussock moths (Lymantriidae), hanging flies (Bittacidae), broad-winged damselflies (Calopterygidae), cicadas (Cicadidae), grasshoppers (Acrididae), and leaf-footed bugs (Cor piedae). Many of the insect families that were not collected by flight interception window traps were too large to be successfully sampled by this method. Hanging flies and grasshoppers were collected in a preliminary study using sweep netting to collect arthropods. Although sweep netting may have been a better method to sample certain insects found in the Acadian Flycatcher nestling diet, it is difficult to standardize and simultaneously sample throughout a study site (Courtenay Willis, Jodi Haylett and Robert Adair, preliminary data).

It is probable that the increase in abundance of arthropod groups that are aquatic or exploit vegetation at the riparian edge may enhance the quality of habitat for Acadian Flycatchers. The results from a preliminary study of food items parents fed to nestlings showed that craneflies (Tipulidae) were an important item in the diet. Also, other unidentified flies, wasps, and bees were important prey items. Bumble bees (Apidae) and sweat bees (Halictidae) were found in greater numbers at the South Fork of Eagle Creek,
where riparian vegetation provides their food source. Scuttle flies (Phoridae) and thick-headed flies (Conopidae) were found in greater numbers at riparian sites. Many scuttle flies and thick-headed flies are reported to be larval parasites of Hymenoptera and also may be indirectly attracted by the riparian vegetation that their hosts feed on (Borrer, Triplehorn and boognish). Unidentified spiders (Araneae) were also found in nestling diet, and are more abundant at riparian sites. As predators, spiders may benefit by the increase in bees, wasps, and flies at riparian sites.

Acadian Flycatchers have been reported to be opportunistic in their foraging behavior, probably selecting a variety of active ephemeral prey types, while other flycatchers may choose taxa-related prey characteristics, such as social Hymenoptera or evasive Diptera (Sherry 1984). It is probable that the seasonal rise in productivity at riparian sites during the breeding season of the Acadian Flycatcher may be one of the factors that enhance the quality of riparian nest sites.

Due to the fact the results of this study are based on the initial year of sampling to assess available prey for Acadian Flycatchers, it is impossible to determine variation in insect abundance and community structure due to differences in precipitation, temperature, and wind speed. Compared to previous years, 1999 was a drier breeding season, which may have affected the prey availability for insectivorous birds in this region.

**Habitat Structure**

Nest sites were characterized by a lower density of trees and subsequently less coverage of leaf litter than non-nest sites. By selecting forest patches with more space in
between trees, Acadian Flycatchers are able to orient nests on the distal ends of branches creating an open air space beneath the nest, which allows these birds to monitor and defend nests against predators. For Acadian Flycatchers nesting in an Oak-Hickory forest in Michigan, open space beneath the nest was found to be important to nest site selection (Mumford 1964). Aggressive nest defense is common in many of the Tyrannid flycatchers, and placing nests in open regions with more air space facilitates monitoring and maneuvering to attack intruders (Nolte and Fulbright 1996, Murphy 1983).

Alternatively, the open space beneath the nest may be an attempt to conceal the nest from above. Acadians often enter the nest by flying up from beneath it, and nests are most easily seen from below (Mumford). At our site, Beech trees were used as the nest substrate more often than expected despite the abundance of other suitable trees (Courtenay Willis, Preliminary data). Due to the fact that Acadian Flycatchers approach the nest from below and exit the nest by diving over the rim, the use of Beech and Hemlock is common, because few shrubs or small trees grow beneath them (Walkinshaw 1966).

According to the results of the PCA, it appears that Acadian Flycatchers may be choosing sites that represent a trade off between sites with riparian features, such as cover of water and rock, and sites with increased leaf litter and shrub density. Habitat characteristics at nest sites showed a great deal of variation, and the combination of variables measured were not sufficient in predicting if a given area was a nest site or a non-nest site.
**Future Research Needs**

This study was not designed to examine the relationship between insect quality and quantity and habitat characteristics. A future study that included replications of plots that sampled arthropods and vegetation would allow for tests of the correlation between these two variables at nest sites and non-nest sites. An understanding of the arthropod-plant relationship would facilitate the testing of the structural cues hypothesis, and perhaps provide insight into whether birds nest near a certain plant physiognomy or host species that support a greater quantity and quality of arthropods (Kimmins 1996). The relationship between arthropods and habitat structure could also be further elucidated by a more thorough knowledge of the natural history of forest arthropods. To assess the functional role of arthropods as a food source for breeding birds, a better understanding of life history traits, such as lifespan, reproductive rates, and foraging guild membership for individual species is needed. Due to the lack of taxonomic keys and expertise, species level identifications were not feasible for this study.

In this study of the arthropod community using family level identification, many families showed characteristic non-random distributions throughout the forest. Hoback et al. (1999) noted that while absence of family-level differences does not imply species-level differences, an occurrence of family-level differences does imply species-level differences. Studies of community structure measured at taxonomic levels above species have been a controversial issue, but they do offer potential benefits when studying diverse groups such as insects and other arthropods (Hoback et al. 1999). Family-level identifications can be achieved in much less time than species level identifications due to
the relative ease in identification. In addition, maximum data per sample can be used, assuming that all specimens can be identified to family (Hoback et al. 1999).

Another consideration to be made in designing studies to test the influence of various factors on nest site selection is to examine the dependence of the effects of the spatial scale at which the data was collected (Orians and Whittenberger 1991, Pribil and Picman 1997). For Yellow-headed Blackbirds, increased rates of emerging odonates appeared to influence selection between marshes, but not individual territories. At the level of individual territories, an increased vegetation density appeared to be an important factor. These results suggest that interpretations of habitat selection may be dependent on the scale at which the data is collected (Orians and Whittenberger 1991).

Acadian Flycatchers at the RTLS may represent a unique opportunity to examine alternative factors influencing nest site selection because predation rates are average. In the study area the occurrence of nest parasitism by Brown-headed Cowbirds is very low. Although food availability appears to be an influential factor in nest site selection, habitat selection is not thought of as a response to a single factor, but rather a complex outcome of many operating environmental and behavioral interactions (Hilden 1965, Petit and Petit 1996). In the future, studies of the influence of various factors such as moisture, age, and sexual selection on nest site selection could provide valuable information regarding the conservation of this species. An increased level of moisture may provide cues as to the quality of habitat. It has been demonstrated in a variety of woodland types that areas of increased moisture support greater insect abundance (Whittaker 1985). Also, the age of nesting birds may influence the choice of nest sites, assuming that older males are able to exclude younger males from quality sites. For the Prothonotary
Warbler, older males dominate flooded habitats, which contain more food resources than dry habitats (Petit and Petit 1966). Mate choice may also contribute to the female’s selection of a nest site, morphological traits such as larger body size and brighter head plumage that correspond to genetically “fit” males may influence the females settlement on a territory (Petit and Petit 1996).

Conclusion

Factors influential to nest site selection appear to be dependent on the scale at which data is collected (Orians and Whittenberger 1991, Pribil and Picman 1997). When prey availability is examined on a coarse scale between riparian and upland zones, an increased number of arthropods may be influential in the selection of nests located in riparian sites.

On a finer scale, examination of both nest and non-nest sites along the riparian corridor, the number of arthropods appears to be continuous. Due to the observation that the prey available may be similar throughout the entire riparian corridor, it could be speculated that Acadian Flycatchers discriminate between sites along the riparian zone by choosing those with lower tree density, reduced leaf litter and characteristics such as an open air space beneath the nest substrate branch.

Determining the importance of prey availability on nest site selection of the Acadian Flycatcher may not always be clearly demonstrated by a limited study. The impact of other factors such as predator avoidance, availability of preferred areas and other habitat features might also influence the settlement pattern in this species.
REFERENCES


APPENDIX

ARTHROPOD TAXA DATA
Table 1. Arthropod taxa collected by flight interception traps on July 21, 1999. Taxonomic groups are listed alphabetically. Abundance values are listed as total abundance collected at nest, non-nest, and upland sites. Asterisks denote families used for statistical analysis.

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<th>non-nest</th>
<th>upland</th>
<th>total</th>
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* Total including Silphidae (carrion beetles)