VARIATION IN NESTLING PROVISIONING BEHAVIOR IN ACADIAN FLYCATCHERS
(Empidonax virescens)

By

Lashale D. Pugh

Submitted in Partial Fulfillment of the Requirements

For the Degree of

Master of Science

In the Department of Biological Sciences

YOUNGSTOWN STATE UNIVERSITY

August 2002

Variation in Nestling Provisioning Behavior in Acadian Flycatchers (*Empidonax virescens*)

Lashale D. Pugh

I hereby release this thesis to the public. I understand this thesis will be housed at the Circulation Desk of the University Library and will be available for public access. I also authorize the University or other individuals to make copies of this thesis as needed for scholarly research.

Signature:

Lashale D. Pugh, Student — 8/22/02 Date

Approvals:

Courtenay N. Willis, Thesis Advisor — 8/22/02 Date

Eric D. Mintz, Thesis Advisor — 8/22/02 Date

Carl F. Chuey, Thesis Advisor — 22 Aug 02 Date

Peter J. Kasvinsky, Thesis Advisor — 9/18/02 Date

ABSTRACT

Acadian Flycatchers (*Empidonax virescens*) at the Ravenna Training and Logistics Site in northeast Ohio were observed to determine if prey choice affects reproductive success. Arthropods fed to nestlings by specialist pairs (n=3 nests) and generalist pairs (n=5 nests) were identified using videotaped feedings of 7, 8, 9 and 10 day old nestlings. Specialists were classified as adult pairs for which 50% or more of the prey fed to nestlings consisted of a particular order or arthropods. Prey quality was determined by size, with each food item being classified as small (0 – 5 mm), medium (>5 – 10 mm), or large (>10 mm). Nestlings were weighed at 10 days of age as a measure of reproductive success.

For 4,727 feeding attempts, 1,715 (36%) prey were identified to order and 3,633 (77%) prey were sized. The predominant arthropods in the nestling diet were Dipterans (45%), Lepidopterans (21%), Hymenoptera (8%) and Phalangida (7%). Specialists tended to feed young less often than generalists, yet there was no difference in average nestling weight between specialist nests and generalist nests. Specialists fed prey from 5 – 9 orders whereas generalists fed prey from 7 – 11 orders. Specialists fed more large prey to nestlings and generalists fed more small and medium prey to nestlings. Therefore, it appears that the quality of prey may be more important than the quantity of prey fed to nestlings. In addition, specialists tended to spend more time at the nest when feeding, which would be adaptive for nest defense. These results suggest that a benefit of being selective may be a reduced risk of predation at the nest.

ACKNOWLEDGMENTS

I would like to thank Dr. Courtenay Willis for guiding me through this difficult part of my journey on a quest for knowledge. Dr. Eric Mintz, Carl Chuey, Dr. Andy Chang and Dr. Nicholas Mandrak also provided me with direction. The field work could not have been completed without the help of the field crew who carried equipment, set up the camera and checked nests, especially Trish Gundrum and Nick Borhurjak. Thank you to Jodi Haylett and Rob Adair for their assistance in identifying insects. Special thanks to Tim Morgan who allowed us access to the study site and provided the opportunity to do research in a beautifully wooded environment. My family also deserves a special thanks, in particular my mother, Leola Martin and aunt, Theresa Faircloth. Without their support during my time at Youngstown State University I would not have achieved such success. To my daughter, Joncquil Hope for time and attention sacrificed. To my cousin, Andre Faircloth, thank you for reminding me that an occasional diversion is okay. This research was supported in part by the Department of Biological Sciences at Youngstown State University and by a summer fellowship from The Greater Akron Audubon Society.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

The dietary habits of birds can provide information about their life history. By identifying the strategies that adult predators use to provide for their young, it may be possible to draw conclusions about the reproductive success of individuals within a population. Nestling provisioning strategies that provide a diet consisting of better quality prey items may result in increased fitness (Cairns 1987, Golet et al. 2000).

Goals and Objectives

The purpose of this research was to study variation in the nestling provisioning behavior of Acadian Flycatchers (*Empidonax virescens*) in northeast Ohio and to examine the relationship between feeding performance and reproductive success. My objectives are to: 1) identify common prey items in the nestling diet, 2) examine variation in nestling provisioning behavior, 3) compare feeding performance of specialist pairs and generalist pairs, and 4) determine if nestling fledging weights differ between specialist pairs and generalist pairs. The components of reproductive success are longevity, fecundity, mating success and offspring survival (Clutton-Brock 1988). This study evaluates potential offspring survival in relation to feeding strategies employed by adults when choosing prey for nestlings.

Optimal Foraging Theory is based on maximum energy gain, with the least amount of time and energy expenditure per food item (Emlen 1966, MacArthur and Pianka 1966) being optimal. Based on this theory one might suspect that a predator should concentrate on larger prey for maximum energy gain. When Pied Wagtails (*Motacilla alba yarrellii* Gould) were offered small, medium and large prey, the birds preferred medium sized prey (Davies 1977). Although small prey were easy to handle, they did not provide enough energy. Large prey took more time to handle, making them less profitable. Medium-sized prey were the most profitable given the time and energy it took to obtain each item. Specializing on medium-sized prey allowed the Pied Wagtails to forage optimally, maximizing energy intake (Davies 1977).

Overall, insectivorous birds have been found to feed on larger insects in greater proportions compared to their availability (Gibb and Betts 1963, Hespenheide 1971). This is may be due to the differences in foraging habits of different species (Holmes and Schultz 1988). Tree Swallows (*Tachycineta bicolor*) in particular have been identified as feeding on large insects in greater proportions compared to their availability (Hespenheide 1975, Turner 1982, Turner 1983, Dyrcz 1984, McCarty and Winkler 1999*b*). In a study of prey size selection by Tree Swallows, the number of large prey fed to nestlings was greater than the number of large prey captured when sampling arthropods (Quinney and Ankney 1985). Assuming that Acadian Flycatchers forage optimally, I expected the birds in my study to choose more large and medium-sized prey.

Feeding Strategies

It is believed that birds employ similar feeding strategies within a species (Strong 2000); however, factors that influence food availability may also influence nestling provisioning behavior, resulting in the use of different strategies (Morse 1971). For instance, changes in prey availability may lead to the use of different feeding strategies. The Band-rumped Swift (*Chaetura spinicauda*), Short-tailed Swift (*C. brachyuran*) and Rough-winged Swallow (*Stelgidopteryx ruficollis*) chose prey close to optimum size when food was abundant, but chose prey in a broader range of sizes when prey availability was limited (Hespenheide 1975).

Prey availability is affected by time of day and weather conditions, which may influence the type of prey selected for nestlings (Pinkowski 1978). Flying insects are most active in the early morning hours with activity decreasing by mid- to late-morning (Hespenheide 1975). Activity increases during midday when clouds are present mid-afternoon (Hespenheide 1975). Cooler temperatures cause flying insects to be less active which decreases their availability to aerially foraging birds (McCarty and Winkler 1999*a*). Acadian Flycatchers forage in the open areas under the open canopy (Maurer and Whitmore 1981) obtaining much of their prey by hover gleaning and aerial hawking (Sherry 1984), which is typical among Flycatchers.

The most prevalent strategies among birds are: generalist, specialist and opportunist. Below is a discussion of the diet associated with each strategy along with the advantages.

a. Generalist

Generalists have heterogeneous diets consisting of a wide breadth of prey items, which is common in migrant flycatchers (Sherry 1984). This strategy is associated with predators maximizing their opportunity to feed on ephemeral prey items and has been observed in flycatchers during the breeding season (Fitzpatrick 1980). To take advantage of available prey, predators should generalize when the encounter rate with profitable prey is low (MacArthur 1972). A study of the Great Tit *(Parus major)* found that when the density of more profitable prey is unpredictable the generalist strategy is employed (Krebs et al. 1977). Limited resources result in uncertainty regarding the availability of better quality prey. As a result, predators are expected to take advantage of whatever prey is present. Yellow Warblers (*Dendroica petechia*) were identified as generalists, eating prey in proportions similar to prey availability (Busby and Sealy 1979). Although generalists are not likely to exploit a particular type of prey as effectively as specialists, they have the advantage of being able to exploit a wide variety of prey types (Morse 1971).

b. Specialist

Homogeneous diets are associated with specialist feeders. Specializing is utilized when resources are abundant and predators can afford to be selective (Emlen 1966). In a study of Pigeon Guillemots (*Cepphus columba*), adults that specialized on large fish raised more nestlings than adults that fed smaller fish to nestlings (Golet et al. 2000). Choosing larger prey for their nestlings allowed adults to forage more efficiently and provide more energy per prey item than the same number of smaller prey items.

The main benefit to specializing is increased nestling survival. Those young raised on a specialist diet may weigh more due to the higher energy intake. One possible benefit of increased size would be increased chance of survival to adulthood. Feeding larger prey items would also result in adults making fewer visits to feed the nestlings. Fewer visits can reduce the risk of attracting predators to the nest.

c. Opportunist

Opportunist predators do not discriminate when choosing prey. However, when they encounter a patch of prey opportunists will maximize feeding opportunities by exploiting that particular patch (Fenton and Morris 1976, Fenton et al. 1977, Bell 1980, Rotenberry 1980). Opportunism provides insectivores an alternative to fluctuations in food supply and is more prevalent among migratory birds (Fitzpatrick 1980). Migration may have evolved as an adaptation to climatic changes allowing species to take advantage of food resources elsewhere when the weather changes (Morse 1971) or food supplies deteriorate (Clark 1962). For example, the Eastern Wood-Pewee *(Contopus virens)* and Acadian Flycatchers have more heterogenous diets than resident tropical species (Sherry 1984).

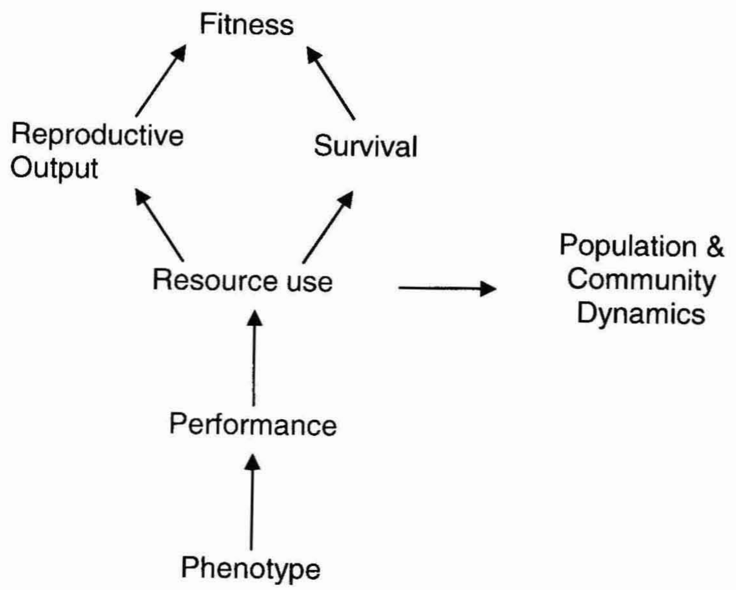
Differences in prey capture methods may explain opportunistic predation. Obtaining most of its prey from the forest floor, Ovenbirds (*Seiurus aurocapillus*) forage by walking slowly and gleaning prey from the surface of the leaf litter (Holmes and Robinson 1988, Van Horn and Donovan 1994, Burke and Nol 1998, and Strong 2000). Ovenbirds have been observed to feed opportunistically on ants in comparison to their abundance (Strong 2000). Antbirds (Formicariidae) are opportunistic in their exploitation of ant colonies (Willis 1966). An advantage of opportunistic feeding is an increase in feeding opportunities by exploiting patches of prey. Opportunism will not be examined as a strategy for the purpose of this study, since both specialists and generalists may exploit patches of prey.

Performance Analysis

Performance analysis may provide insight into how strategies influence fitness. Performance has been used by ecomorphologists to explain an organism's ability to perform ecologically important tasks (Fig. 1) (Wainright and Reilly 1994). This model tries to explain the relationship between phenotype and performance relative to overall fitness (Huey and Stevenson 1979, Arnold 1983, Emerson and Arnold 1989, Wainright 1991). I use performance analysis to explain how nestling provisioning behavior may influence nestling fledging weight, a fitness correlate.

Using performance analysis for this study may provide insight into how foraging strategies influence fitness. The way that predators make use of the available resources can influence their reproductive output as well as their survival, which are related to overall fitness. An individual's own survival as well as the number of offspring that survive may depend on their use of the available resources. Examining the way that Acadian Flycatcher pairs use the available resources to feed their young, may provide insight into how their feeding strategies influence their fitness.

Figure 1. Flow chart showing the pathways influenced by individual fitness and population and community ecology. This diagram represents the performance analysis method used to relate an individual's phenotype to fitness. In this study, feeding performance was analyzed to see if it influenced nestling fledging weight, a fitness correlate (highlighted in red).


Fitness
Reproductive Output
Survival
Resource use
Population & Community Dynamics
Performance
Phenotype

Breeding Biology of the Acadian Flycatcher

The Acadian Flycatcher (*Empidonax virescens*), an insectivorous neotropical migrant that breeds locally, provides an excellent opportunity to study the effects of prey selection on reproductive success. In comparison with other insectivorous avian species at the study site, Acadian Flycatcher nests are typically found on low hanging branches making them easy to locate and monitor (Newman 1958, Mumford 1964, Walkinshaw 1966, Wilson and Cooper 1998, Adair 2001). As a member of the Tyrannid Flycatcher family (Tyrannidae), the Acadian Flycatcher is one of five *Empidonax* flycatchers found east of the Mississippi River. Unique song and habitat characteristics are helpful in distinguishing this species from other *Empidonax* flycatchers, which are difficult to identify visually.

The Acadian Flycatcher breeds throughout the eastern portion of the United States as far north as southern New York, Michigan, and Wisconsin and as far west as eastern Nebraska, Kansas and Texas (Beal 1912, DeGraaf and Rappole 1995). The male of this small migratory species arrives on the summer breeding ground prior to the female, from early- to mid-May (Mumford 1964). The breeding season begins in mid-May and lasts through August. Inhabiting the lower tree canopy and understory, they prefer damp, lowland forests with an understory and uplands with wooded ravines near streams (DeGraaf and Rappole 1995). Females build new nests or repair nests from previous seasons. Spider silk is used to anchor the nest to the branch and also holds nests together (Mumford 1964). Nest material may vary based on vegetation near the nest location. Nests are typically found in beech-maple associations in riparian habitat.

Preliminary data identified the following tree species as hosts for Acadian Flycatchers at RTLS: American Beech (*Fagus grandifolia* Ehrh.), Sugar Maple (*Acer saccharum* Marsh.), Witch Hazel (*Hamamelis virginiana* L.), Hop Hornbeam (*Ostrya virginiana* (Mill.) K. Koch), Red Maple (*Acer rubrum* L.), Bitternut Hickory (*Carya cordiformis* (Wang.) K. Koch), Wild Black Cherry (*Prunus serotina* Ehrh.), Oak (*Quercus spp.*) and Elm (*Ulmus spp.*) (Weishaupt 1971, Cooperrider et al. 2001). The nest often appears frail and the eggs may be visible through the nest bottom as nest materials appear loosely bound together, with long, loose plant material hanging underneath (Mumford 1964).

The female selects the nest site, although males will occasionally assist by visiting potential nest sites (Mumford 1964). Flying from fork to fork, the female will "sit" in a fork for varying lengths of time (Mumford 1964). Open space beneath the nest appears to be important, as birds often enter the nest by flying up from beneath or leave the nest by diving over the rim (Walkinshaw 1966). Nest height ranges from 1.5 - 11.5 m, with nests placed on a horizontal fork near the end of branches (Mumford 1964, Walkinshaw 1966, DeGraaf and Rappole 1995).

During courtship males chase the females (Mumford 1964). The male hovers above the female as she perches during nest construction (Ehrlich et al. 1988). During the solicitation pose, the female is perched on a branch with her beak open and wings slightly drooping. Copulation probably takes place as the male hovers over the female during the solicitation pose (Mumford 1964). The beginning of nest construction and the laying of the first egg are separated by approximately six days. Eggs are deposited one per day, with an average clutch size of three. Females incubate eggs for an average of 14 days.

Hatching occurs one egg at a time over a period of about 24 hours. The day of the first hatching is considered day one. At hatching, nestlings have no feathers. By day three nestlings are covered with white natal down. Feathers begin to emerge by day seven, and nestlings are completely feathered by day 10. At fledging (approximately day 14), the downy feathers have all been replaced by juvenile pennaceous feathers (Gill 1994).

For the first few days the female does most of the feeding. Males do not participate in brooding the nestlings although they do assist in feeding the young (Newman 1958). To keep the nest clean, fecal sacs are removed. To minimize predator attraction, they are taken away by the adults and dropped some distance from the nest.

The Acadian Flycatcher diet consists of beetles, moths, many types of lepidopteran larvae, damselflies, dragonflies, deerflies, harvestmen, mosquitoes, horseflies, spiders, wasps, ants and crane flies (Beal 1912, Mumford 1964). Available arthropods at the RTLS include a wide variety of Coleoptera, Arachnids, Collembolla, Ephemeroptera, Hemiptera, Homoptera, Hymenoptera, Diptera, Lepidoptera, Mecoptera, Orthoptera, Plecoptera, Psocoptera, Thysanoptera and Trichoptera (Williams and Hartzler 1999, Adair 2001).

The feeding behavior of the Acadian Flycatcher has been described as opportunistic (Sherry 1984). Migratory species, such as the Acadian Flycatcher, tend to have more heterogenous diets due to their opportunistic feeding behavior. Because the Acadian Flycatcher is a migratory species, it tends to have a heterogeneous diet (Sherry 1984). The Acadian Flycatcher is a suitable species for this type of study because it nests on low hanging branches making it accessible for video monitoring of nestling provisioning behavior. In addition, their feeding behavior of carrying prey to the nest one item at a time allows for easier identification of prey.

METHODS

Study Design

The goal of this study was to examine variation in nestling provisioning behavior and to determine how it affects nestling fledging weight, a fitness correlate. Feeding performance analysis was used to compare feeding performance of specialist pairs (n = 3 nests) and generalist pairs (n = 5 nests). Pairs were classified as specialists when 50% or more of the nestling diet was comprised of one taxonomic order and as generalists when they did not meet this criterion (Schoener 1971, Golet et al. 2000). Feeding performance variables used in this study include feeding rate (# feedings/h/# nestlings), amount of time spent feeding nestlings (# s at nest), amount of time spent sitting on nest (# s sitting on nest), and prey size. Size was determined by comparing length of prey to Acadian Flycatcher bill length (Pyle 1977). To determine whether nestling provisioning behavior affected fledging weight, nestlings were weighed at 10 days of age to approximate fledging weight, which was compared between specialist pairs and generalist pairs.

Video data of nest activity was collected to examine variation in nestling provisioning behavior and to determine whether prey composition varies between nests. Video was chosen as the data collection method to minimize disturbance and to prevent unnecessary disruption of reproductive success in this population.

Diet may be analyzed by a variety of methods: visual observations, emetics, artificial nestlings, ligatures, gut contents, fecal contents and automatic photography (Kleintjes and Dahlsten 1992). Results of a study comparing several methods of diet analysis determined that a greater number of prey were identified to species from film recordings than from other methods (Kleintjes and Dahlsten 1992). Data collection via video allows for better identification of soft-bodied prey which could be underrepresented by other methods. In addition, video monitoring provides information regarding other nest activity, including interactions between nestlings, time spent at nest by adults, number of trips over time, number of prey delivered and differences in parental behavior (Grundel 1984). Videography was been chosen for this study because it is non-invasive and it is the least stressful method, yet it allows a greater number of prey to be identified compared to more invasive methods.

To evaluate nestling provisioning behavior in this population I identified prey items fed to nestlings and compared feeding rates and nestling fledging weights to answer the following questions: 1) What common prey items are fed to nestlings in this population? 2) Is there variation in nestling provisioning behavior among Acadian Flycatchers? 3) Is there variation in feeding performance between specialist pairs and generalist pairs? 4) Are nestling fledging weights influenced by nestling provisioning strategies?

I expected the diet composition to be consistent with findings from previous studies and also with the arthropods available at the study site. Some variation in feeding performance was also expected. Specialist pairs were expected to have lower feeding rates because they would be expected to spend more time seeking out particular prey. I expected to find some adult pairs specializing on large prey, which would result in higher average nestling fledging weights. By selecting larger prey items for nestlings, a specialist provides more nutrition per feeding which could result in bigger nestlings. Focusing on one particular prey order could result in feeding items of greater nutritional value.

This study was designed to test the following null hypotheses:

1. Composition of the nestling diet will not vary between specialist pairs and generalist pairs.
2. Feeding performance will not vary between specialist pairs and generalist pairs.
3. Nestling fledging weight will not vary between specialist pairs and generalist pairs.

Study Site

This research was conducted in a late-successional beech maple forest located within the Ohio Army National Guard Training and Logistics Site in Portage County, Ohio (Fig. 2). The site is situated in Northeastern Ohio, encompassing 8,668 ha in a tract of land approximately 5.6 km wide and 17.7 km long and is currently jointly operated by the Operations Support Command (OSC) of the U.S. Army and National Guard Bureau (NGB). Operations at the installation date to 1940 during World War II and involved the production of military munitions and explosives. Presently, investigative and remediation activities are underway. Current use is a training and logistics site for the National Guard, Army Reserve, specialized forces, and local, state and federal law enforcement officials.

The Acadian Flycatcher is a species that prefers moist wooded ravines. This study focuses primarily on the activities of Acadian Flycatchers that nest along the South Fork of Eagle Creek, a second order stream with a sandstone substrate that meanders through forest. Selective thinning of trees with a diameter at breast height (DBH) greater than 30.5 cm occurred in 1940. Located near the northern perimeter of the military installation, the 100 ha forest tract is fragmented by access roads (Fig. 3). Adjacent to the fenced northern perimeter is a rail line that is no longer in use (Fig. 4) and residential property in Windham Township. Cleveland is 56 km northwest of the site, and other nearby cities include Ravenna, Alliance, Windham and Paris Township. Youngstown is approximately 56 km east and Warren is approximately 40 km east of the site.

Figure 2. 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 along the South Fork of Eagle Creek.

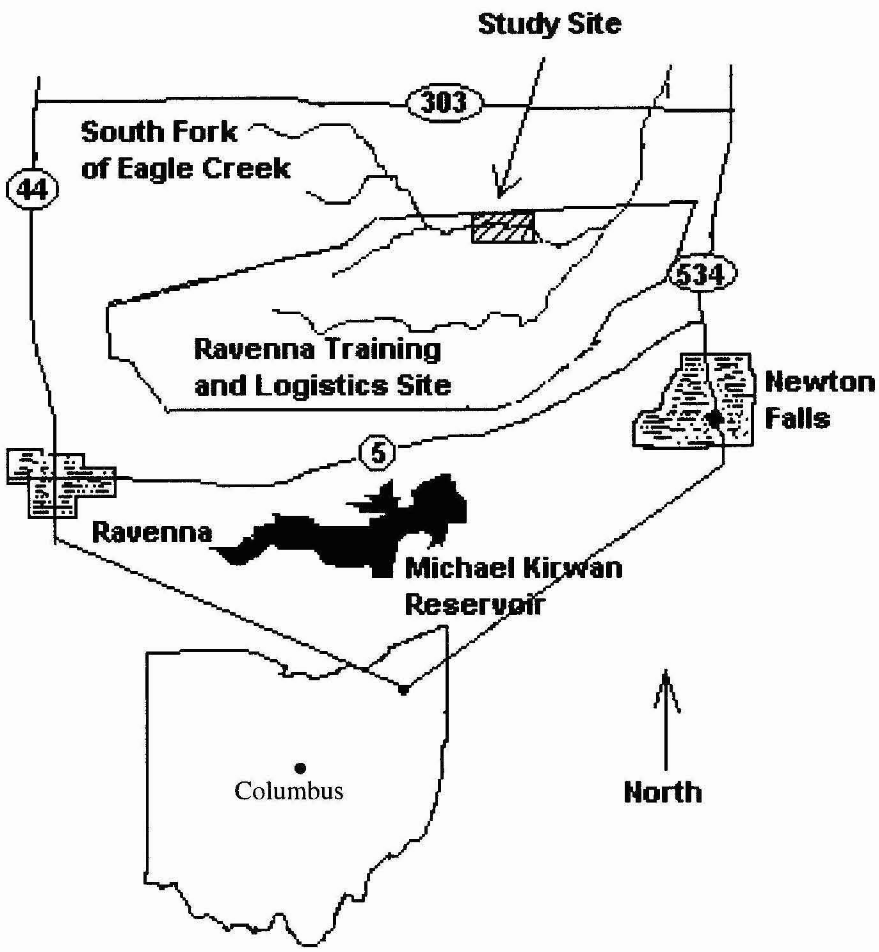

Study Site
303
South Fork
of Eagle Creek
44
534
Ravenna Training
and Logistics Site
Newton
Falls
5
Ravenna
Michael Kirwan
Reservoir
Columbus
North

Figure 3. Aerial photo of study site showing nest site locations in relation to each other. Nest locations are color coded by type. Generalist sites are indicated by red dots and specialist sites are indicated by blue dots. Two generalist nests were located in the same tree, resulting in overlap of two of the red dots.

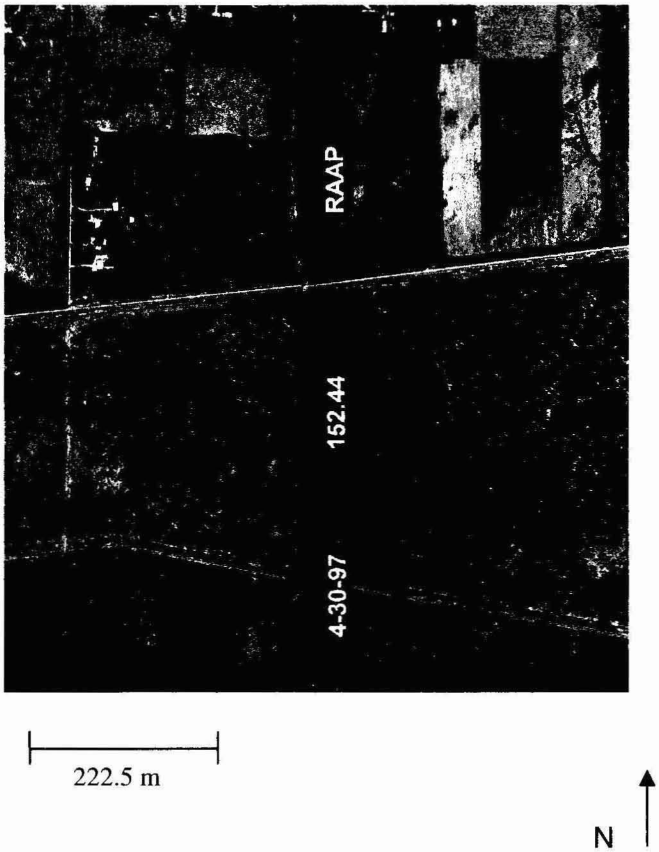
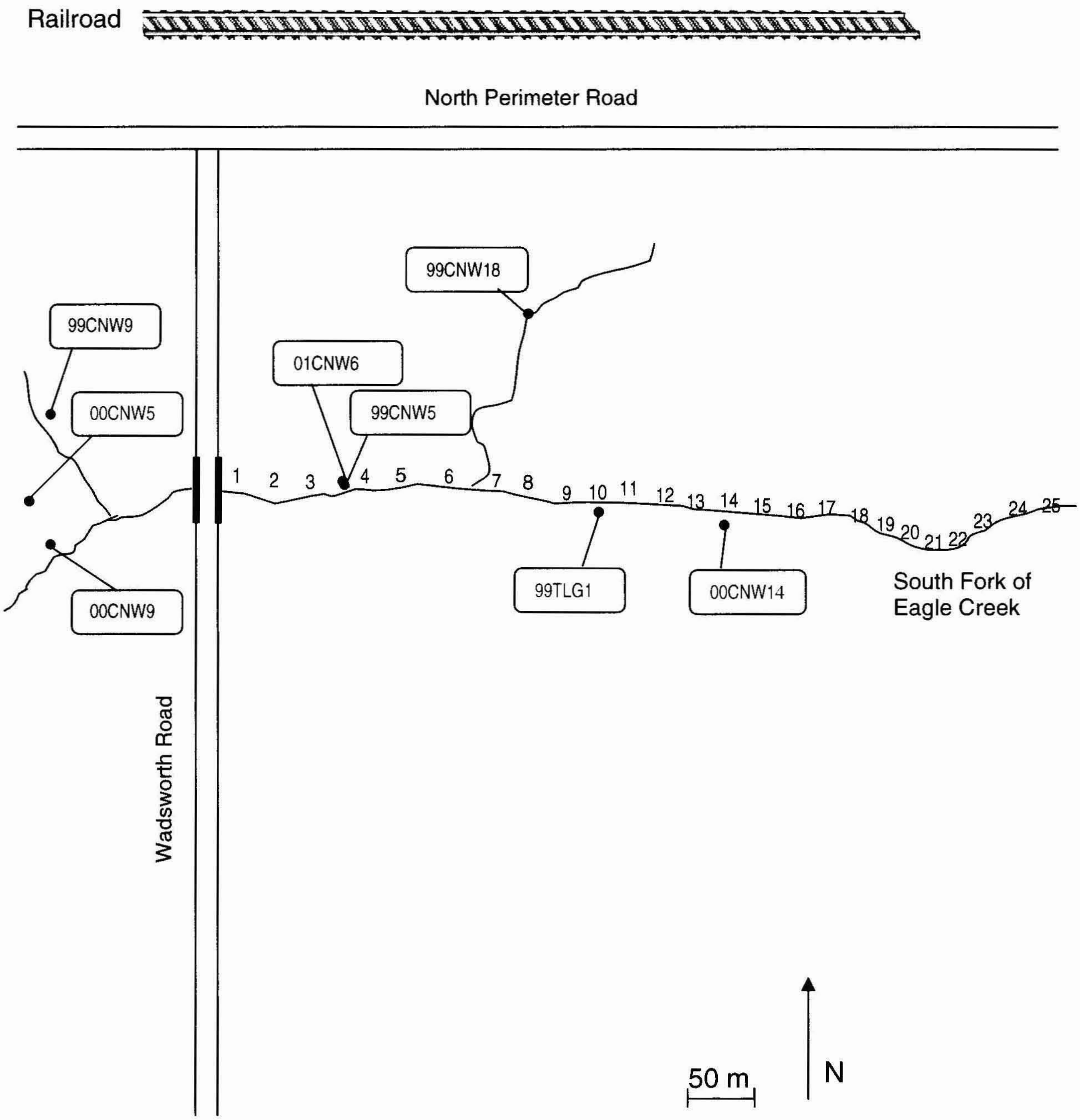

RAAP
152.44
4-30-97
222.5 m
N

Figure 4. Location of all nest sites used in this study and window trap sites used in a previous study along South Fork of Eagle Creek (Adair 2001). Generalist nest locations are indicated in red and specialist nest locations are indicated in blue.


Railroad
North Perimeter Road
Wadsworth Road
99CNW18
99CNW9
01CNW6
00CNW5
99CNW5
00CNW9
99TLG1
00CNW14
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
South Fork of
Eagle Creek
50 m
N

Data Collection

Nests were located and monitored using the Breeding Biology and Research Database (BBIRD) protocol (Martin and Guepel 1993, Martin et al. 1996). Search methods included observing adult behavior to determine nest location. Females carrying nest material were observed during nest construction. The location of the nests and distinguishing characteristics of host trees were recorded so that the nests could be found again. Nests were assigned a code including the last 2 digits of the year it was found, the initials of the person finding the nest and the number of the nest. Each nest was checked every 2 – 3 days to determine its status. Nests were considered active when under construction or when eggs or nestlings were present. Each active nest was monitored to determine the number of eggs laid, number of nestlings hatched, and the number of young that fledged. Data collected from nest monitoring was used to estimate nest success and reproductive success.

A Sony videocassette time-lapse recorder (model SVT-DL224) and LRTLV BOQKT Microcam 2 remote camera (model WAT 660D), and Sony T-160 VHS tapes were used to record nest activity in active nests when the nestlings were 7-10 days old (Fuhrman Diversified, Inc.). On day 5 or 6, the camera was mounted near the nest to allow the adults time to acclimate to the camera setup before video recording began. Rebar was used to anchor the camera pole to the ground, while ropes were used to stabilize the pole. The microvideocamera was covered with a camouflage sleeve and attached to a pole so that the camera lens was approximately 10 cm from the nest (Fig. 5). The power source was a marine

Figure 5. Microvideocamera setup used to record data at an Acadian Flycatcher nest. The camera is mounted on conduit and covered with a camouflage sleeve. The camera lens is positioned approximately 10 cm from the nest.

battery that was placed more than 20 m away from the nest tree along with the recording equipment (Fig. 6). Once the camera was in place, the adults were observed for 20 - 30 min to note whether they resumed normal feeding and nest attentiveness. If the adults did not resume their normal behavior, the camera was removed and a second attempt to mount the camera was made the following day. Adults that did not resume feeding within 30 min of camera setup on the second attempt were considered to be intolerant of the camera and no further attempts were made to video the nest.

Nestling provisioning behavior was recorded from 0600 – 1800h when nestlings were 7-10 d old. At least 24h of video was obtained per nest, and a total of 496 h of video was obtained for eight nests. No video was used from inclement weather days because prey may be less active which may affect adult foraging behavior. The nestlings were weighed on day 10 to approximate fledgling weights.

Rate of feeding (# feedings/h/# nestlings), time spent feeding nestlings (# s at nest), time spent sitting on the nest (# s sitting on nest) and prey size were determined from video replay. Video data on feeding behavior was collected from June – August in 1999, 2000 and 2001. Arthropods fed to nestlings were identified to family when possible (Borror and White 1970, Covell 1984, Arnett 1985, Borror et al. 1989, Haylett 2000, Grove et al. 2000, Adair 2001). The Youngstown State University entomology collection was used in conjunction with other sources for arthropod identification. Arthropods were also placed into one of three size categories as follows: small = 0 – 5mm, medium = > 5 – 10mm,

Figure 6. The video recorder was powered by a rechargeable marine battery. The monitor was used to ensure that the microvideocamera was mounted to provide adequate viewing of nest activity.

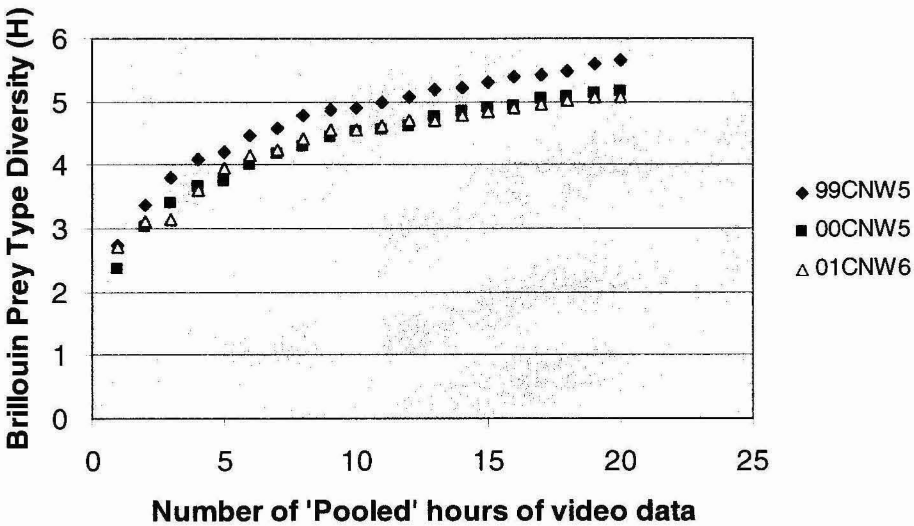
large = > 10mm. Size categories were based on the maximum bill length of the Acadian Flycatcher (10.1 mm) from nares to tip (Pyle 1997).

Statistical Methods

To determine the adequacy of sample size for number of hours of video data per nest, I used the Brillouin diversity index $H = (1/N)\ln(N!/n_1!, n_2! \ldots n_t!)$ where there are $n_1, n_2 \ldots n_t$ prey items in each of x different insect orders, with N total prey items per cumulative hour of video data (Pielou 1975, Sherry 1984)(Appendix 1). If video data from enough hours was collected, saturation curves of prey diversity would occur at X number of hours because additional video data on prey items fed would add little information to increase prey diversity. Based on this criteria, a sample size of at least 20 h of video per nest was determined to be appropriate (Fig. 7).

Chi-square contingency analysis was used to test the null hypothesis that the proportion of prey orders in the nestling diet did not differ between specialist pairs and generalist pairs (Zar 1996). Three orders were used for the analysis, (Lepidoptera, Diptera, and Araneae) because prey from these orders were fed at every nest. Chi-square contingency analysis was also used to test the null hypothesis that the proportion of large, medium and small prey in the nestling diet did not differ between specialist pairs and generalist pairs (Zar 1996). Mann Whitney U was used to compare feeding performance variables and nestling weights between specialist pairs and generalist pairs (SPSS Version 8.0).

Figure 7. Diversity of prey items (H) identified from videotaped feedings at three Acadian Flycatcher nest sites.


Brillouin Prey Type Diversity (H)
6
5
4
3
2
1
0
0
5
10
15
20
25
Number of 'Pooled' hours of video data
99CNW5
00CNW5
01CNW6

RESULTS

Composition of Nestling Diet

To determine what prey items are commonly fed to nestlings 184 h of video data were analyzed from eight nests: four nests in 1999 (99CNW5, 99CNW9, 99CNW18, 99TLG1), three nests in 2000 (00CNW5, 00CNW9, 00CNW14), and one nest in 2001 (01CNW6). From a total of 4,727 observed feedings, 1,715 (36%) prey items were identified from three classes of arthropods, 13 orders and 23 families (Table 1). The most common prey items were Diptera (45%), Lepidoptera (21%), Hymenoptera (8%), and Phalangida (7%)(Fig. 8a). There was a significant difference in the proportion of prey items from orders fed at specialist nests and generalist nests (Araneae, Diptera and Lepidoptera) ($\chi^2_{0.05,2}$ = 10.29). Specialists fed a larger proportion of Lepidoptera compared to generalists ($\chi^2_{0.05,1}$ = 8.54)(Figs. 8b and 8c).

Nestling Provisioning Behavior

Specialist pairs were identified at 00CNW5, 00CNW14 and 99TLG1 based on the criteria that 50% or more of the nestling diet was comprised of one order of arthropods (Table 2a). Adults at 00CNW5 specialized on Diptera. Adults at 99TLG1 and 00CNW14 specialized on Lepidoptera. At specialist nests, prey from 5 - 9 orders were fed to nestlings. The remaining five nests did not meet this criteria and were considered to be generalists (Table 2b). At generalist nests, prey from 7 – 11 orders were fed to nestlings.

Although both specialist and generalist pairs tended to feed the same types of prey items, they differed in the proportions fed. When comparing

Table 1. Number and percent frequency of prey items in the diet of nestling Acadian Flycatchers at all nests combined.

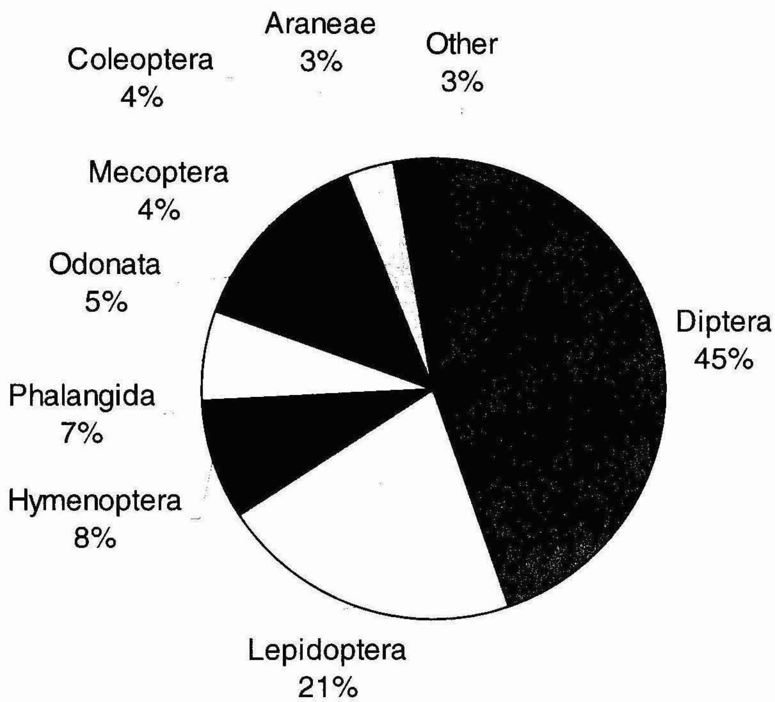
Taxon	Common Prey Items	#	%
Chilopoda	Centipede	1	<1%
Arachnida			
Phalangida	Daddy long legs	111	7%
Araneae	Spiders	56	3%
Insecta			
Coleoptera			
Elateridae	Click beetles	2	<1%
Meloidae	Blister beetles	1	<1%
Coccinellidae	Ladybugs	1	<1%
Undetermined	Beetles	66	4%
Diptera			
Asilidae	Robber fly	6	<1%
Calliphoridae	Blow fly	1	<1%
Tabanidae	Horseflies, Deerflies	22	1%
Tipulidae	Craneflies	570	33%
Culicidae	Mosquitoes	2	<1%
Undetermined	Flies	166	10%
Hymenoptera			
Ichneumonidae	Ichneumon wasps	36	2%
Formicidae	Ants	6	<1%
Undetermined	Bees, Wasps	99	6%
Lepidoptera			
Geometridae	Adult-2, larva-8	10	<1%
Lasiocampidae	Adult	3	<1%
Satyridae	Adult	3	<1%
Sphingidae	Adult	2	<1%
Noctuidae	Adult	1	<1%
Liparidae	Adult	2	<1%
Sesiidae	Adult	2	<1%
Undetermined	Adult-191, larva-148	339	20%

Cont'd

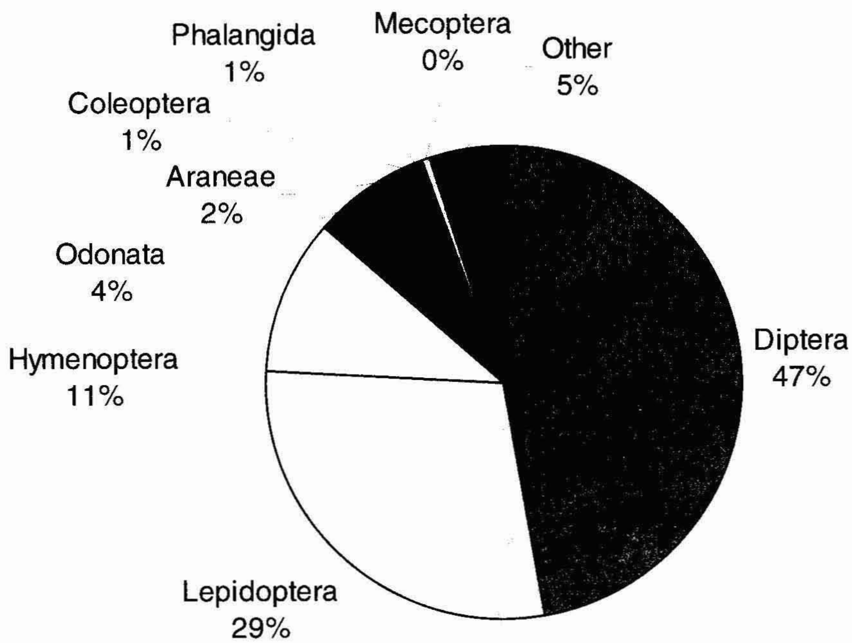
Taxon	Common Prey Items	#	%
Mecoptera			
Bittacidae	Hanging flies	69	4%
Panorpidae	Scorpionflies	3	<1%
Odonata			
Calopterygidae	Damselflies	2	<1%
Undetermined	Damselflies, Dragonflies	84	5%
Homoptera			
Cicadidae	Cicadas	11	<1%
Hemiptera	True Bugs	1	<1%
Neuroptera			
Undetermined	Lacewings	7	<1%
Orthoptera			
Acrididae	Grasshoppers	22	1%
Tettigoniidae	Katydids	1	<1%
Gryllidae	Crickets	4	<1%
Ephemeroptera		3	<1%
Total	Identified	1715	36%
	Unidentified	3012	64%

Figure 8. Proportions of prey orders in diet of nestling Acadian Flycatchers. (a) Common taxonomic orders of prey items fed to nestlings at all eight nests. (b) Common taxonomic orders of prey items fed to nestlings at specialist nests (n = 3). (c) Common taxonomic orders of prey items fed to nestlings at generalist nests (n = 5).

(a) All nests


Araneae
3%
Coleoptera
4%
Other
3%
Mecoptera
4%
Odonata
5%
Diptera
45%
Phalangida
7%
Hymenoptera
8%
Lepidoptera
21%

(b) Specialist Nests



(c) Generalist nests

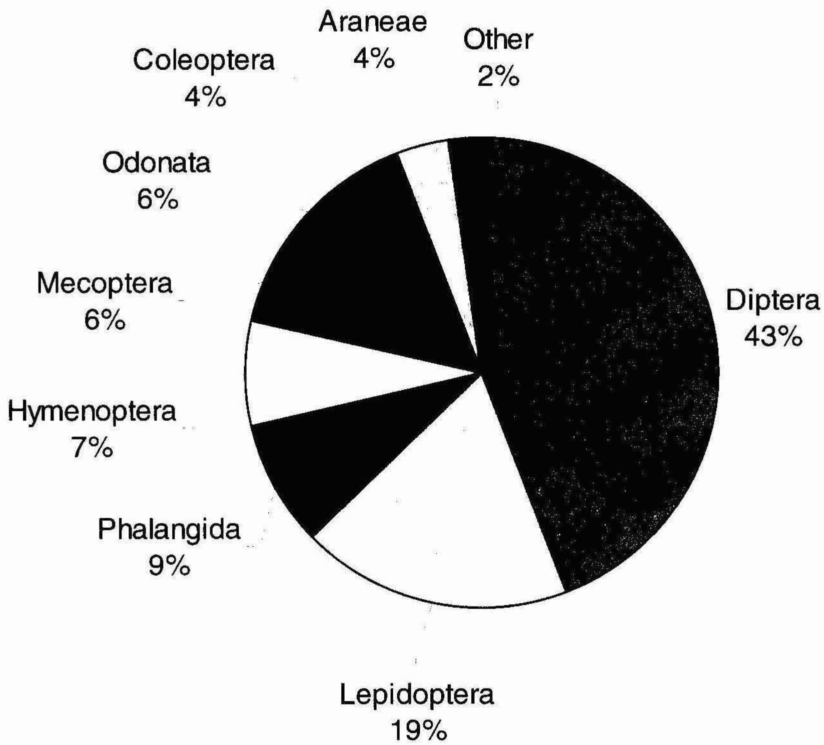


Table 2. Prey orders fed to nestling Acadian Flycatchers. (a) Nest sites that met the criteria for specialists are shown in blue. (b) Nest sites that did not meet the criteria for specialists are shown in red.

Table 2a **Specialists**

	99TLG1 (n=21h)		00CNW5 (n=22h)		00CNW14 (n=28h)	
Taxa	#	%	#	%	#	%
Chilopoda	0	0	0	0	0	0
Arachnida	5	4	7	3	3	3
Coleoptera	0	0	5	2	0	0
Diptera	42	33	146	63	27	28
Hymenoptera	6	5	35	15	7	7
Lepidoptera	63	50	19	8	48	51
Mecoptera	0	0	2	1	0	0
Odonata	1	1	16	7	0	0
Homoptera	0	0	0	0	0	0
Hemiptera	0	0	0	0	0	0
Neuroptera	1	0	0	0	0	0
Orthoptera	9	7	1	0	10	11
Ephemeroptera	0	0	2	1	0	0
Total # Prey ID	**127**		**233**		**95**	
Total % Prey ID		**7**		**14**		**6**

Table 2b **Generalists**

Taxa	99CNW5 (n=27h) #	%	99CNW9 (n=21h) #	%	99CNW18 (n=22 h) #	%	00CNW9 (n=22h) #	%	01CNW6 (n=23h) #	%
Chilopoda	1	0	0	0	0	0	0	0	0	0
Arachnida	60	18	15	14	19	8	29	8	29	12
Coleoptera	14	4	7	7	17	8	11	3	16	7
Diptera	144	42	42	40	105	47	141	41	120	49
Hymenoptera	18	5	9	8	21	9	45	13	0	0
Lepidoptera	64	19	23	22	33	15	56	16	56	23
Mecoptera	22	6	5	5	21	9	12	3	10	4
Odonata	16	5	5	5	0	0	38	11	8	3
Homoptera	0	0	0	0	6	3	5	1	0	0
Hemiptera	0	0	0	0	0	0	1	0	0	0
Neuroptera	1	0	0	0	2	1	2	1	3	1
Orthoptera	0	0	0	0	0	0	5	1	2	1
Ephemeroptera	1	0	0	0	0	0	0	0	0	0
Total # Prey ID	**341**		**106**		**224**		**345**		**244**	
Total % Prey ID		**20**		**6**		**13**		**20**		**14**

specialists and generalists, Diptera and Lepidoptera were the most important orders fed to nestlings. However, Hymenoptera was the third most important order fed by specialists, while Phalangida was the third most important order fed by generalists, followed by Hymenoptera (Figs. 8b and 8c).

A total of 3,633 prey items (77%) were placed into size categories for all nests (Table 3). At generalist nests 86% of prey were able to be sized while at specialist nests 55% of prey were able to be sized. Among all nests combined, medium prey were fed most often and accounted for 37% of prey that were able to be sized. At generalist nests, medium prey were fed in the greatest proportion and accounted for 40% of prey that were able to be sized. At specialist nests, large prey were fed in the greatest proportion and accounted for 53% of prey that were able to be sized. Generalists fed significantly more medium ($P = 0.025$) and small ($P = 0.025$) prey than specialists (Table 4)(Mann Whitney U).

Feeding Performance and Nestling Weight

When feeding rates were compared, specialists fed less often than generalists, although not significantly (Table 5)(Fig. 9)(Mann Whitney U; $P = 0.45$). When average sit times were compared, specialists spent more time sitting on the nest, although not significantly (Table 6)(Fig. 10) (Mann Whitney U; $P = 0.18$). When average visit times were compared, specialists spent more time visiting the nest, although not significantly (Table 6)(Fig. 10)(Mann Whitney U; $P = 0.18$). When average nestling weights were compared, there was no significant difference between specialist pairs and generalist pairs (Table 5)(Fig. 9)(Mann Whitney U; $= 0.89$).

Table 3. Comparison of the size of prey fed to nestling Acadian Flycatchers by generalists and specialists. The percentages of large, medium, and small prey are based on the number of prey that were able to be sized.

Nest ID	Large		Medium		Small		Sized		Unk. Size	
	#	%	#	%	#	%	#	%	#	%
Generalists										
99CNW5	213	22	448	47	293	31	954	90	108	10
99CNW9	61	14	134	31	232	54	427	97	13	3
99CNW18	190	38	188	38	120	24	498	90	58	10
00CNW9	223	41	178	33	143	26	544	92	46	8
01CNW6	164	37	194	43	89	20	447	66	232	34
	851	**30%**	**1142**	**40%**	**877**	**30%**	**2870**	**86%**	**457**	**14%**
Specialists										
00CNW5	218	62	86	25	47	13	351	43	468	57
00CNW14	95	39	81	33	68	28	244	77	73	23
99TLG1	93	55	47	28	28	17	168	69	76	31
	406	**53%**	**214**	**28%**	**143**	**19%**	**763**	**55%**	**617**	**45%**
Total	**1257**	**35%**	**1356**	**37%**	**1020**	**28%**	**3633**	**77%**	**1074**	**23%**

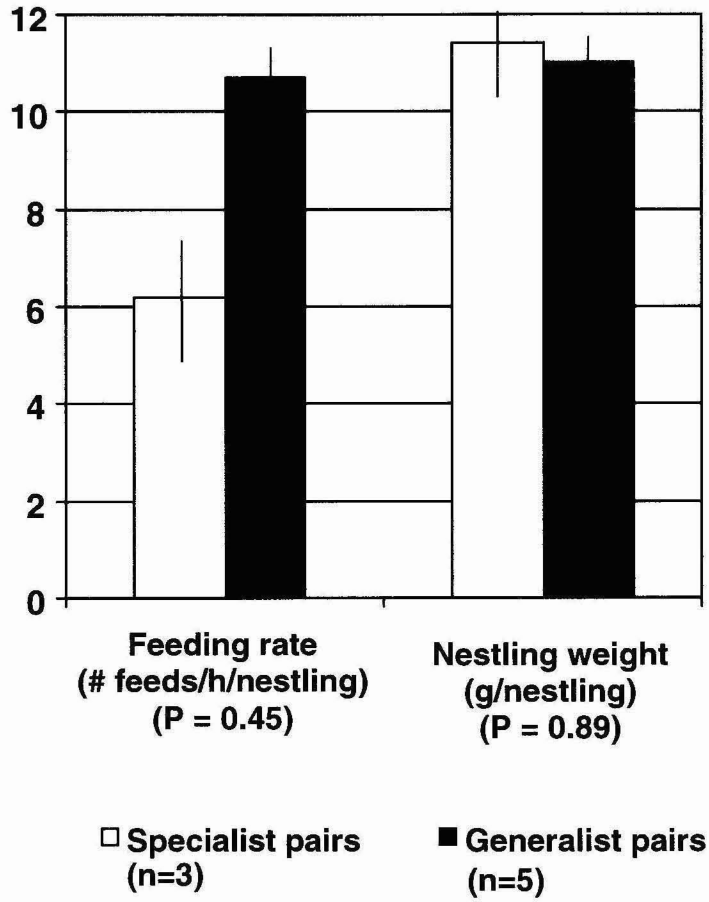
Table 4. Comparison of the average number of prey from each of three size categories fed to nestlings by generalists and specialists.

Nest ID	**# Large /h/# nestlings**	**# Medium /h/# nestlings**	**# Small /h/# nestlings**
Generalists			
99CNW5	2.6	5.5	3.6
99CNW9	1.5	3.2	5.5
99CNW18	2.9	2.8	1.8
00CNW9	3.4	2.7	2.2
01CNW6	2.7	3.2	1.5
X ± 1 SD	2.6 ± 0.7	3.5 ± 1.2	2.9 ± 1.7
Specialists			
00CNW5	2.5	1.0	0.5
00CNW14	1.6	1.4	1.2
99TLG1	1.5	0.7	0.4
X ± 1 SD	1.9 ± 0.6	1.0 ± 0.4	0.7 ± 0.4

Table 5. Average feeding rate (X $\pm$ 1 SD) and nestling weight (X $\pm$ 1 SD) for generalists and specialists.

Nest ID	N	# Nestlings	Average Feed rate (#/h/nestling)	Average Nestling Wt. (#g/nestling)
Generalists				
99CNW5	27	3	13.21	11.1 g ± 0.5 g
99CNW9	21	2	10.48	10.2 g ± 0.4 g
99CNW18	22	3	8.42	11.5 g ± 0.8 g
00CNW9	22	3	8.94	10.9 g ± 0.7 g
01CNW6	20	3	11.35	11.3 g ± 0.06 g
X ± 1 SD	22.4 ± 2.7	2.8 ± 0.45	10.48 ± 1.9	11.1 g ± 0.7g
Specialists				
00CNW5	22	4	9.31	10.8 g ± 0.7 g
00CNW14	29	2	5.47	12.0 g ± 0.5 g
99TLG1	21	3	4.03	NA
X ±1 SD	24 ± 4.4	3 ± 1.0	6.27 ±2.7	11.2 g ± 0.9 g

Figure 9. Comparison of average feeding rate (X $\pm$ 1SE) and average nestling weights (X $\pm$ 1SE) for specialist pairs (n=3) and generalist pairs (n=5). Results for specialists are shown in yellow and results for generalists are shown in blue.

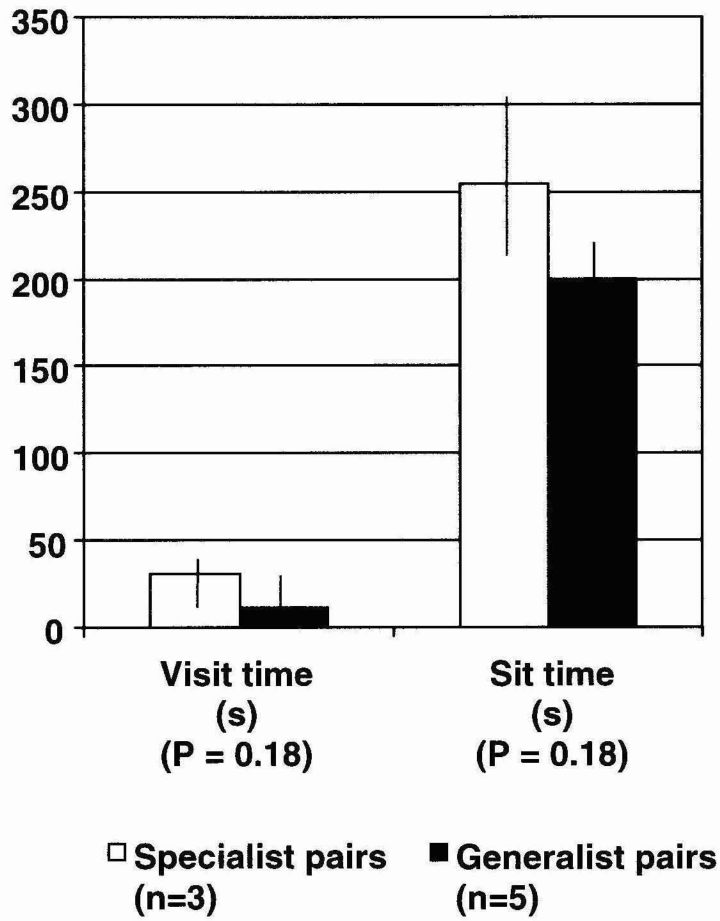


Mann Whitney U test

Table 6. Comparison of average visit time (X $\pm$ 1SD) and average sit times (X $\pm$ 1SD) for generalists and specialists.

Nest ID	N (h)	Average Visit Time (s)	Average Sit Time (s)
Generalists			
99CNW5	27	12	144
99CNW9	21	9	254
99CNW18	22	7	213
00CNW9	22	8	193
01CNW6	20	18	139
X ± 1SD	**22.4 ± 2.7**	**11 ± 4.4**	**201 ± 48.3**
Specialists			
00CNW5	22	11	163
00CNW14	29	17	298
99TLG1	21	129	407
X ± 1SD	**24 ± 4.4**	**34 ± 66.5**	**256 ± 122.2**

Figure 10. Comparison of time spent visiting the nest ($X \pm 1$ SE) and sitting on the nest ($X \pm 1$ SE) for specialist pairs (n=3) and generalist pairs (n=5). Results for specialists are shown in yellow and results for generalists are shown in blue.



(Mann Whitney U test)

DISCUSSION

Composition of Nestling Diet

The composition of the nestling diet was consistent with results of previous studies that included the Acadian Flycatcher (Beal 1912, Mumford 1964, Sherry 1984). In this study, Diptera were identified as the most important food source fed to nestlings because they comprised the greatest proportion of the nestling diet and were fed at every nest. Tipulidae was the most frequently fed dipteran, probably due to their large size or digestibility. Studies on migratory songbirds have also found Diptera to be an important food source, probably because they exist in large numbers near moist areas and are relatively slow-moving and easy to catch (Quinney and Ankney 1985, Bull and Beckwith 1993, McCarty and Winkler 1999*b*).

Dipterans accounted for 74% of the prey in the boluses of Tree Swallows feeding nestlings (Quinney and Ankney 1985). Diptera was the second most important order fed to nestlings by Vaux's Swifts, and had the greatest representation of families (Bull and Beckwith 1993). Diptera was also the most important food source for nestling Tree Swallows in a study on diet selectivity (McCarty and Winkler 1999*b*). Lepidoptera, the second most important food source fed to nestlings in this study, are also important for Least Flycatchers (*Empidonax minimus*), Red-eyed Vireos (*Vireo olivaceus*) and Black-throated Green Warblers (*Dendroica virens*) (MacArthur 1959, Royama 1970, Robinson and Holmes 1982, Holmes and Schultz 1988). Lepidoptera larva may provide more food value per prey item due to their large size or digestibility (Holmes and Schultz 1988).

Hymenoptera were the third most important food source fed in this study. Hymenoptera have been identified as important prey for flycatchers (Sherry 1984). Due to the importance attributed to Hymenoptera by other studies (Beal 1912), it was interesting that they were not more important in this study. It is possible that they were not able to be identified as easily as some other prey. Phalangida have not previously been identified as a food source for Acadian Flycatchers. It was surprising that they were so prominent in the nestling diet, especially since Phalangida emit a noxious odor when disturbed.

Results from a preliminary study using fecal sac analysis to identify prey consumed by nestlings identified Araneae and Coleoptera in greater proportions than were identified by this study (Pugh et al. 2001). Fecal sac analysis is biased toward identification of hard-bodied prey, since body parts like mandibles, elytra and tarsi remain intact (Ralph et al. 1985, Jenni et al. 1990). Microvideography is biased toward larger more visible soft-bodied prey such as Diptera and Lepidoptera. Microvideography, used in conjunction with other methods such as fecal sac analysis, may provide the most information on nestling diet.

Nestling diet is influenced by prey availability and prey capture methods. An earlier study at the RTLS using flight intercept window traps to evaluate prey availability identified many of the prey fed in this study (Adair 2001). Due to the hawking and gleaning methods of prey capture employed by the Acadian Flycatcher some of the arthropods at the study site may not be suitable for capture. Acadian Flycatchers hover above a substrate to capture prey. This method is suitable for capturing flying prey like Diptera, which were fed in the greatest proportion at all nests in this study (Maurer and Whitmore 1981). Acadian Flycatchers often exploit prey that are attracted by rapid regrowth of vegetation in or near tree-fall gaps (Sherry 1984).

Nestling Provisioning Behavior

An expectation for this study was that specialists would feed more large prey to nestlings than generalists. Although this was not the case, specialists fed nestlings a greater proportion of large prey compared to medium or small. Specialists also fed from a smaller diversity of orders which indicates that they were cueing in on particular prey of higher quality as opposed to taking the easy, more abundant prey. This may help to explain why generalists fed a large proportion of daddy longlegs to nestlings which are abundant prey and distributed widely, whereas specialists fed Hymenoptera.

Increased abundance of arthropods at the riparian edge compared to upland areas may make riparian habitat more attractive as nesting habitat for Acadian Flycatchers (Adair 2001). All of the pairs in this study nested in the riparian zone. Adults that forage in these areas may forage more efficiently. Foraging efficiency is associated with specialist behavior. Pigeon Guillemots that specialized on large fish foraged more efficiently and had higher reproductive success than those that did not (Golet et al. 2000).

Pigeon Guillemots that specialized chose large fish for their nestlings (Golet et al. 2000). Tree Swallows also selected large prey more often for their nestlings (McCarty and Winkler 1999*b*). The size of a prey item can influence the amount of time than an adult spends at their nest. For example, specialist pairs appear to feed nestlings less often than generalist pairs. By feeding more large prey adults were able to spend more time at the nest protecting nestlings from predators. Results for average sit times for specialists are biased due to the long periods of time spent visiting the nest by the female at 99TLG1.

Feeding Performance and Nestling Weight

There was no significant difference in weight between nestlings at specialist and generalist nests. Therefore, the strategy that adults use for provisioning nestlings did not appear to affect nestling weight in this study. However, results of this study could also be due to the small sample sizes.

A more important factor may be nest defense. Specialists spent more time at the nest, feeding and sitting on the young, which would allow for increased vigilance. Specialists also tended to make fewer visits to the nest to feed young, presumably because they spent more time seeking out particular prey. Fewer visits to the nest would be adaptive because it would reduce the likelihood of attracting predators to the nest. By choosing better quality prey rather than a greater quantity of prey, adults are able to spend more time caring for and defending their young. Food may be so abundant that it is not a limiting resource.

Likely predators at the RTLS include chipmunks and Blue Jays, Great Horned Owl, Barred Owl, Red-tailed Hawks and Woodpeckers. Chipmunks (Courtenay Willis, *personal observation*) are likely mammalian predators as Acadian nests are located at the ends of very slender branches making them inaccessible to heavier mammals (Wilson and Cooper 1998). Acadian Flycatcher nests have open space below for aggressive defense against predators. Blue Jays are the most common avian predators of young birds (Darveau et al. 1997). They sit in the treetops observing the activity of potential prey and have been observed pecking a chick in a nest (Courtenay Willis, personal observation). Birds and snakes were the most common predators of Acadians in Arkansas (Wilson and Cooper 1998). Red squirrels are also assumed to be major predators of songbird nests (Vander Haegen and Degraaf 1996, Darveau et al. 1997, Sloan et al. 1998, Bayne and Hobson 2002).

The results presented here lead to several conclusions. Although Acadian Flycatchers are often considered to be generalists, some specialization does appear to occur. Specialization may allow for better nest defense since however, specialization does not appear to influence nestling fledgling weight or fitness. Finally, quality appears to be more important than quantity when choosing prey for nestlings.

Further research needs to be done to clarify the trends that have been documented in this study. In addition, there is a need to address the question of when is it adaptive to specialize? How important are environmental conditions and seasonality in influencing the foraging behavior of adults? In this study, Two of three specialist nests were identified in a wetter than normal year (2000) which suggests that environmental conditions may influence foraging behavior. Specialist nests were also found later in the season as opposed to generalist nests which tended to be found earlier in the season. One female is suspected of not changing strategies in different years. Nests at 01CNW6 and 99CNW5 were likely built by the same female, which was banded in 2000. In both years this nest was identified as a generalist nest, and both years happened to be very dry.

REFERENCES

Adair, Jr., R. T. 2001. The Influence of Food Availability and Habitat Structure on Nest Site Selection of the Acadian Flycatcher (*Empidonax virescens*). Master's thesis. Youngstown State University. Youngstown, Ohio.

Arnett, R. H. 1985. American Insects: A Handbook of the Insects of America North of Mexico. Van Nostrand Reinhold Co. New York, New York.

Arnold, S. J. 1983. Morphology, Performance and Fitness. American Zoologist 23: 347-361.

Bayne, E. M and K. A. Hobson. 2002. Effects of Red Squirrel (*Tamiasciurus hudsonicus*) Removal on Survival of Artificial Songbird Nests in Boreal Forest Fragments. American Midland Naturalist 147: 72-79.

Beal, F. E. L. 1912. Food of our More Important Flycatchers. U. S. Department of Agriculture. Washington, DC.

Bell, G. P. 1980. Habitat Use and Response to Patches of Prey by Desert Insectivorous Bats. Canadian Journal of Zoology 58: 1876-1883.

Borror, D. J. and R. E. White. 1970. A Field Guide to Insects. Houghton Mifflin. New York, New York.

Borror, D. J., C. A. Triplehorn, N. F. Johnson. 1989. An Introduction to the Study of Insects, Sixth edition. Saunders College Publishing. Fort Worth, Texas.

Bull, E. L. and R. C. Beckwith. 1995. Diet and Foraging Behavior of Vaux's Swifts in Northeastern Oregon. Condor 95: 1016-1023.

Burke, D. M. and E. Nol. 1988. Influence of Food Abundance, Nest-site Habitat, and Forest Fragmentation on Breeding Ovenbirds. Auk 115(1): 96-104.

Busby, D. G. and S. G. Sealy. 1979. Feeding Ecology of a Population of Nesting Yellow Warblers. Can. J. Zool. 57: 1670-1681.

Cairns, D. K. 1987. The Ecology and Energetics of Chick Provisioning by Black Guillemots. The Condor 89: 627-635.

Clark, D. P. 1962. An Analysis of Dispersal and Movement in *Phaulacridium vittaturn* (Sjost) (Acrididae). Australian Journal of Zoology 10: 382-99.

Clutton-Brock, T. H. ed. 1988. Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems. University of Chicago Press. Chicago, Illinois.

Cooperrider, T. S., A. W. Cusick and J. T. Kartesz, Eds. 2001. *Seventh Catalog of the Vascular Plants of Ohio*. Ohio State University Press. Columbus, Ohio.

Covell, C. V. 1984. A Field Guide to Moths of Eastern North America. Houghton Mifflin Co. Boston, Massachusetts.

Darveau, M., L. Belanger, J. Huot, E. Melancon and S. Debellefeuille. 1997. Forestry Practices and the Risk of Bird Nest Predation in a Boreal Coniferous Forest. Ecol. Appl. 7: 572-580.

Davies, N. B. 1977. Prey Selection and Social Behavior in Wagtails (*Aves: monticillidae*). Journal of Animal Ecology 46: 37-57.

DeGraaf, R. M. and J. H. Rappole. 1995. Neotropical Migratory Birds: Natural History, Distribution, and Population Change. Cornell University Press. Ithaca, New York.

Dyrcz, A. 1984. Breeding Biology of the Mangrove Swallow *Tachycineta abilinea*and the Grey-Breasted Martin *Progue chalybea* at Barro Colorado Island, Panama. Ibis 126: 59-66.

Ehrlich, P. R., D. S. Dobkin and D. Wheye. 1998. The Birders Handbook: A Field Guide to the Natural History of North American Birds. Simon and Schuster. New York, New York.

Emlen, J. M. 1966. The Role of Time and Energy in Food Preference. American Naturalist 100: 611-617.

Emerson, S. B. and S. J. Arnold. 1989. Intra- and Interspecific Relationships Between Morphology, Performance, and Fitness. In Complex Organismal Functions: Integretation and Evolution in Vertebrates, eds. D. B. Wake and G. Roth. 295-314. Wiley. New York, New York.

Fenton, M. B., N. G. H. Boyle, T. M. Harrison and D. J. Oxley. 1977. Activity Patterns, Habitat Use, and Prey Selection by Sympatric Insectivorous Bats. Biotropica 9: 73-85.

Fenton, M. B. and G. K. Morris. 1976. Opportunistic Feeding by Desert Bats (*Myotis* spp.). Canadian Journal of Zoology 54: 526-530.

Fitzpatrick, J. W. 1980. Wintering of North American Tyrant Flycatchers in the Neotropics. Pages 67-78 in A. Keast and E. S. Morton, Eds. Migrant Birds in the Neotropics: Ecology, Behavior, Distribution and conservation. Smithsonian Institution Press. Washington, D. C.

Gibb, J. A. and M. M. Betts. 1963. Food and Food Supply of Nestling Tits (*Paridae*) in Breckland Pine. Journal of Animal Ecology 32: 489-533.

Gill, F. B. 1994. Ornithology Second Edition. W. H. Freeman and Company. New York, New York.

Golet, G. H., K. J. Kuletz, D. D. Roby and D. B. Irons. 2000. Adult Prey Choice Affects Chick Growth and Reproductive Success in Pigeon Guillemots. Auk 117(1): 82-91.

Groves, D., S. Reader, J. M. Forshaw, G. Shea and M. Moulds eds. 2000. Animal Kingdom. Barnes and Noble Books. New York, New York.

Grundel, R. 1984. The Foraging Behavior of Parent Mountain Chickadees Parus gambeli: Factors Influencing Prey Selection and Notes on the Bird's Role in Regulating Insect Populations. Ph.D. thesis, University of Texas. Austin, Texas.

Haylett, J. 2000. Distribution of Frass Produced by Larval Lepidoptera in a Hardwood Canopy. Master's thesis. Youngstown State University. Youngstown, Ohio.

Hespenheide, H. A. 1971. Food Preference and the Extent of Overlap in Some Insectivorous Birds, With Special Reference to The Tyrannidae. Ibis 113: 59-72.

Hespenheide, H. A. 1975. Selective Predation by Two Swifts and a Swallow in Central America. Ibis 117: 82-99.

Holmes, R. T. and S. K. Robinson. 1988. Spatial Patterns, Foraging Tactics, and Diets of Ground-foraging Birds in a Northern Hardwoods Forest. Wilson Bulletin 100: 377-394.

Holmes, R. T. and J. C. Schultz. 1988. Food Availability for Forest Birds: Effects of Prey Distribution and Abundance on Bird Foraging. Canadian Journal of Zoology 68: 720-728.

Huey, R. B. and R. D. Stevenson. 1979. Integrating Thermal Physiology and Ecology of Ectotherms: A Discussion of Approaches. American Zoologist 19: 357-366.

Kleintjes P. K. and D. L. Dahlsten. 1992. A Comparison of Three Techniques for Analyzing the Arthropod Diet of Plain Titmouse and Chestnut-Backed Chickadee Nestlings. Journal of Field Ornithology 63(3): 276-285.

Krebs, J. R., J. T. Erichsen and M. I. Webber. 1977. Optimal Prey Selection in the Great Tit *(Parus major)*. Animal Behavior 25: 30-38.

Jenni, L., P. Ruetimann, and S. Jenni-Eiermann. 1990. Recognizability of Different Food Types in Faeces and Alimentary Flushes of *Sylvia* Warblers. Ibis 132: 445-543.

MacArthur, R. H. 1959. On the Breeding Distribution Patterns of North American Migrant Birds. Auk 76: 318-325.

MacArthur, R. H. 1972. Geographical Ecology: Patterns in the Distribution of Species. Harper and Row. New York, New York.

MacArthur, R. H. and E. R. Pianka. 1966. On Optimal Use of a Patchy Environment. American Naturalist 100: 603-609

Martin, T. E. and G. R. Geupel. 1993. Nest-Monitoring plots: Methods for Locating Nests and Monitoring Success. Journal of Field Ornithology 64(4): 507-519.

Martin , T. E., C. J. Conway and W. M. Hochachka. 1996. BBIRD Field Protocol. Montana Cooperative Wildlife Research Unit, Missoula, Montana.

Maurer, B. A. and R. C. Whitmore. 1981. Foraging of Five Bird Species in Two Forests with Different Vegetation Structure. Wilson Bulletin 93(4): 478-490.

McCarty, J. P. and D. W. Winkler. 1999*a*. Relative Importance of Environmental Variables in Determining the Growth of Nestling Tree Swallows *Tachycineta bicolor*. Ibis 141: 286-296.

McCarty, J. P. and D. W. Winkler. 1999*b*. Foraging Ecology and Diet Selectivity of Tree Swallows Feeding Nestlings. The Condor 101: 246-254.

Morse, D. H. 1971. The Insectivorous Bird as an Adaptive Strategy. Annual Review of Ecology and Systematics 2: 177-200

Mumford, R. E. 1964. The Breeding Biology of the Acadian Flycatcher. University of Michigan. Ann Arbor, Michigan.

Newman, D. L. 1958. A Nesting of the Acadian Flycatcher. Wilson Bulletin 70: 130-144.

Pielou, E. C. 1975. Ecological Diversity. Wiley and Sons. New York, New York.

Pinkowski, B. C. 1978. Feeding of Nestling and Fledgling Eastern Bluebirds. Wilson Bulletin 90(1): 84-98.

Porter, L. N. 1907. The Breeding Habits of *Empidonax virescens* in Connecticut. Auk 24: 99.

Pyle, P. 1997. Identification Guide to North American Birds. Slate Creek Press. Bolinas, California.

Pugh, L. D., C. N. Willis and T. L. Gundrum. 2001. A Comparison of Microvideography and Fecal Sac Analysis for Analyzing the Arthropod Diet of Acadian Flycatchers. Ohio Journal of Science 101(1): 15.

Quinney, T. E. and D. D. Ankney. 1985. Prey Size Selection by Tree Swallows. Auk 102(2): 245-250.

Ralph, C. P., S. E. Nagata and C. J. Ralph. 1985. Analysis of Droppings to Describe Diets of Small Birds. J. Field Ornithol. 56: 165-174.

Robinson, S. K. and R. T. Holmes. 1982. Foraging Behavior of Forest Birds: the Relationships Among Search Tactics, Diet, and Habitat Structure. Ecology 63: 1918-1931.

Rotenberry, J. T. 1980. Dietary Relationships Among Shrub-steppe Passerine Birds: Competition or Opportunism in a Variable Environment? Ecological Monographs 50: 93-110.

Royama, T. 1970. Factors Governing the Hunting Behaviour and Selection of Food by the Great Tit (*Parus major* L.). Journal of Animal Ecology 39: 619-659.

Sherry, T. W. 1984. Comparative Dietary Ecology of Sympatric, Insectivorous Neotropical Flycatchers (Tyrannidae). Ecological Monographs 54: 313-338.

Schoener, T. W. 1971. Theory of Feeding Strategies. Annual Review of Ecology and Systematics 2: 369-404.

Sloan, S. S., R. T. Holmes and T. W. Sherry. 1998. Depredation Rates and Predators at Artificial Bird Nests in an Unfragmented Northern Hardwoods Forest. Journal of Wildlife Management 62: 529-539.

SPSS. 1998. Version 8.0 SPSS Inc. Chicago, Illinois

Strong, A. M. 2000. Divergent Foraging Strategies of Two Neotropical Migrant Warblers: Implications for Winter Habitat Use. Auk 117(2): 381-391.

Turner, A. K. 1982. Optimal Foraging by the Swallo (*Hirundo rustica*, L.): Prey Size Selection. Animal Behavior 30: 862-872.

Turner, A. K. 1983. Food Selection and Timing of Breeding of the Blue-and-White Swallow *Notiochelidon cyanoleuca* in Venezuela. Ibis 125: 450-462.

Vander Haegen, W. M. and R. M. Degraaf. 1996. Predation on Artificial Nests in Forested Riparian Buffer Strips. Journal of Wildlife Management. 60: 542-550.

Van Horn, M. A. and T. M. Donovan. 1994. Ovenbird (*Seiurus aurocapillus*). *In* The birds of North America, no. 89. (A. Poole and F. Gill Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Wainright, P. C. 1991. Ecomorphology: Experimental Functional Anatomy for Ecological Problems. American Zoologist 31: 167-194.

Wainwright, P. C. and S. M. Reilly eds. 1994. Ecological Morphology. The University of Chicago Press. Chicago.

Walkinshaw, L. H. 1966. Studies of the Acadian Flycatcher in Michigan. Bird Banding 37(4): 227-257.

Weishaupt, C. G. 1971. Vascular Plants of Ohio: A Manual for Use in Field and Laboratory. Kendall/Hunt Publishing Company. Dubuque, Iowa.

Williams, R. and D. Hartzler. 1999. Survey of the Coleoptera at the Ravenna Training and Logistics Site 1999. Ohio State University, OARDC. Wooster, Ohio.

Willis, E. O. 1966. The Role of Migrant Birds at Swarms of Army Ants. The Living Bird 5: 187-231.

Wilson, R. R. and R. J. Cooper. 1998. Acadian Flycatcher Nest placement: Does Placement Influence Reproductive Success? The Condor 100: 673-679.

Zar, J. H. 1996. Biostatistical Analysis. 3rd ed. Prentice Hall, Upper Saddle River, New Jersey.

Appendix 1

99CNW5

Hour

1	2.742095190 = (1/36)ln(36!/3!,5!,1!,1!,1!)
2	3.388560950 = (1/71)ln(71!/4!,6!,2!,3!,1!,1!,1!,1!)
3	3.800602868 = (1/108)ln(108!/7!,7!,4!,4!,1!,1!,1!,4!,1!)
4	4.101014029 = (1/150)ln(150!/12!,8!,6!,4!,1!,4!,1!,6!,1!)
5	4.203130434 = (1/177)ln(177!/18!,9!,7!,4!,1!,6!,1!,7!,1!)
6	4.466039857 = (1/231)ln(231!/24!,9!,12!,4!,3!,7!,3!,7!,1!)
7	4.597701669 = (1/266)ln(266!/31!,11!,15!,6!,4!,8!,4!,7!,2!)
8	4.776352586 = (1/319)ln(319!/39!,13!,15!,9!,6!,13!,5!,7!,2!)
9	4.888902109 = (1/369)ln(369!/47!,15!,18!,9!,6!,14!,6!,8!,2!)
10	4.889865682 = (1/393)ln(393!/56!,16!,20!,9!,6!,14!,6!,7!,2!)
11	4.984585599 = (1/424)ln(424!/61!,16!,25!,11!,7!,16!,6!,7!,2!)
12	5.089407818 = (1/467)ln(467!/65!,17!,27!,12!,7!,18!,6!,7!,2!)
13	5.195416928 = (1/504)ln(504!/66!,22!,27!,12!,7!,18!,6!,7!,2!)
14	5.231032996 = (1/544)ln(544!/74!,23!,28!,12!,9!,18!,6!,8!,2!)
15	5.300027510 = (1/580)ln(580!/78!,26!,29!,12!,11!,18!,6!,8!,2!)
16	5.384523384 = (1/625)ln(625!/84!,30!,32!,12!,11!,20!,6!,8!,2!)
17	5.423344157 = (1/672)ln(672!/93!,31!,34!,13!,11!,20!,6!,9!,2!)
18	5.489291960 = (1/715)ln(715!/100!,33!,38!,14!,11!,21!,8!,9!,2!)
19	5.586013942 = (1/759)ln(759!/101!,37!,40!,15!,12!,21!,9!,9!,2!)
20	5.663253803 = (1/810)ln(810!/106!,38!,43!,15!,12!,26!,9!,1!,9!,2!)

00CNW5

Hour

1	2.359928273 = (1/32)ln(32!/7!,3!,2!)
2	3.023307214 = (1/69)ln(69!/13!,3!,4!)
3	3.403673927 = (1/106)ln(106!/19!,3!,4!,3!,3!)
4	3.657037591 = (1/144)ln(144!/27!,4!,4!,6!,4!)
5	3.757728864 = (1/173)ln(173!/35!,4!,4!,6!,6!,2!)
6	4.012059817 = (1/216)ln(216!/40!,4!,4!,8!,8!,2!)
7	4.191802399 = (1/253)ln(253!/46!,4!,4!,8!,14!,2!)
8	4.309280363 = (1/286)ln(286!/52!,4!,6!,10!,15!,2!)
9	4.434135332 = (1/319)ln(319!/57!,4!,7!,11!,18!,2!.2!)
10	4.517121487 = (1/355)ln(355!/62!,4!,7!,11!,18!,2!,2!)
11	4.556049145 = (1/394)ln(394!/72!,4!,7!,12!,18!,2!,2!)
12	4.620694225 = (1/434)ln(434!/81!,4!,9!,12!,19!,3!,2!)
13	4.746687605 = (1/476)ln(476!/84!,5!,9!,13!,21!,3!,2!)
14	4.835890867 = (1/510)ln(510!/88!,5!,10!,15!,23!,3!,2!)
15	4.913542612 = (1/541)ln(541!/92!,5!,10!,16!,27!,3!,2!)
16	4.939696978 = (1/575)ln(575!/101!,5!,12!,16!,28!,3!,2!)
17	5.047217971 = (1/618)ln(618!/105!,6!,12!,18!,32!,4!,2!)
18	5.074016346 = (1/631)ln(631!/106!,6!,12!,18!,33!,4!,2!)
19	5.121680834 = (1/672)ln(672!/112!,6!,13!,18!,33!,4!,2!)
20	5.161478275 = (1/724)ln(724!/123!,7!,13!,18!,34!,5!,2!)

01CNW6
Hour

1 2.725161627 = (1/41)ln(41!/5!,2!,3!)
2 3.126163202 = (1/67)ln(67!/11!,2!,7!)
3 3.133951866 = (1/72)ln(72!/13!,2!,7!)
4 3.610136585 = (1/101)ln(101!/14!,4!,10!,3!,2!,2!)
5 3.953952636 = (1/132)ln(132!/19!,5!,16!,7!,2!,2!)
6 4.146484298 = (1/167)ln(167!/23!,6!,18!,7!,2!,2!)
7 4.251717081 = (1/191)ln(191!/27!,6!,20!,8!,2!,2!)
8 4.417966249 = (1/229)ln(229!/31!,6!,21!,11!,2!,2!)
9 4.548229372 = (1/250)ln(250!/32!,6!,25!,11!,2!,3!)
10 4.565406659 = (1/258)ln(258!/33!,6!,25!,11!,2!,3!)
11 4.621797248 = (1/298)ln(298!/42!,7!,25!,13!,2!,3!)
12 4.687908669 = (1/311)ln(311!/44!,10!,27!,13!,2!,3!,2!)
13 4.710375940 = (1/332)ln(332!/48!,10!,27!,13!,2!,3!,2!)
14 4.777416847 = (1/353)ln(353!/50!,10!,29!,13!,3!,3!,2!)
15 4.849361964 = (1/378)ln(378!/53!,12!,30!,14!,3!,3!,2!)
16 4.912142705 = (1/414)ln(414!/62!,14!,31!,17!,6!,3!,2!)
17 4.960051873 = (1/443)ln(443!/68!,14!,32!,20!,6!,3!,2!,2!)
18 5.016532397 = (1/482)ln(482!/77!,15!,36!,21!,6!,3!,2!,2!)
19 5.078531411 = (1/510)ln(510!/82!,15!,39!,23!,7!,3!,2!,3!)
20 5.085297693 = (1/533)ln(533!/88!,15!,39!,24!,7!,3!,2!,3!)