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## **Foraging Behavior and Habitat Selection of Insectivorous Migratory Songbirds at Gulf Coast Stopover Sites in Spring.**

Chao-chieh Chen

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**FORAGING BEHAVIOR AND HABITAT SELECTION OF  
INSECTIVOROUS MIGRATORY SONGBIRDS AT  
GULF COAST STOPOVER SITES IN SPRING**

**A Dissertation**

**Submitted to the Graduate Faculty of the  
Louisiana State University and  
Agricultural and Mechanical College  
in partial fulfillment of the  
requirements for the degree of  
Doctor of Philosophy**

**in**

**The School of Forestry, Wildlife, and Fisheries**

**by**

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## **ABSTRACT**

Abundance of some species of Nearctic-Neotropical migrants has been declining dramatically since 1970. Most literature about Neotropical migrants is from the breeding grounds, and some is from the wintering grounds; very little is from stopover sites. I studied foraging behavior and habitat selection of insectivorous migratory songbirds at three stopover sites along northern coast of the Gulf of Mexico during spring migrations of 1993–1995.

Each migrant species had its unique combination of foraging behavior and habitat use during stopover. Migrants selected certain habitat strata and plant species and avoided others. The decrease of understory vegetation in the reduced plots had greater impact on foraging behavior of understory, subcanopy, and ground foragers, and less for canopy species.

Searching behavior has been studied less than attack behavior or foraging site because searching behavior is ephemeral and difficult to record. From the analysis of correspondence and cluster analyses, closely related species have similar searching behavior. Searching movements of migrants are greatly affected by various conditions such as site, plot, and flocking. Warblers (Parulinae) were found to be more flexible and more responsive to environmental conditions than were vireos.

It is important to study the properties of foraging sequences before one can select a reliable method to calculate foraging rates. The overall rate is more realistic than the sequential rate; the original sequences are more biased than the closed sequences.

However, the adjusted overall rate from the original sequences appears to be a compromise.



# **CHAPTER 1**

## **FORAGING ECOLOGY AND HABITAT SELECTION OF INSECTIVOROUS MIGRATORY SONGBIRDS AT GULF COAST STOPOVER SITES**

### **INTRODUCTION**

Abundance of many species of Nearctic-Neotropical migrants that include many songbirds, e.g., wood-warblers (Parulinae), vireos (Vireonidae), and flycatchers (Tyrannidae), which breed in the North America and winter in the Neotropics, has been declining dramatically since 1970 (Whitcomb 1977; Briggs and Criswell 1979; Hall 1984; Robbins et al. 1989; Terborgh 1989, 1992; Askins et al. 1990; Peterjohn et al. 1995). Conservation efforts directed at Neotropical migrants must be international because their life cycle covers many countries.

Many causes have been suggested for the decline. These include: (1) fragmentation of breeding habitat (Robbins 1980, Lynch and Whigham 1984, Dobkin 1994, Faaborg et al. 1995), (2) high rates of brood parasitism by Brown-headed Cowbirds, *Molothrus ater* (Mayfield 1977, Brittingham and Temple 1983, Robinson 1992, Robinson et al. 1995), (3) high rates of nest predation (Ambuel and Temple 1983, Wilcove 1985, Yahner and Scott 1988, Robinson 1992), (4) deforestation of wintering grounds in the Neotropics (Rappole and Morton 1985, Terborgh 1989, Rappole 1995), and (5) degradation of stopover sites (Martin and Karr 1990, Moore et al. 1990). These causal factors are not mutually exclusive, and the decline may be due to any of these factors, a combination of them, or some other factors or combination. The simultaneous decline of a group of species is of much more concern than the decline of a single

species; some common causes might be found for the simultaneous decline of many species. Recently, James and McCulloch (1995) provided some guidelines for inferring the causes of population trends of birds. Their study designs may be used to provide insight into this problem and deserve more attention.

Most literature concerning Neotropical migrants is from the breeding grounds, and some is from the wintering grounds; very little is from stopover sites. Stopover sites are now gaining more attention for their role in providing food resources for Neotropical migrants during migration (Martin and Karr 1990; Moore et al. 1990, 1995; Berthold and Terrill 1991). Because migration can be a critical period of natural selection for Neotropical migrants, the significant loss or degradation of en-route habitats is of concern.

“Chenier” is the term used in Louisiana for a relict beach ridge (Russell and Howe 1935). Cheniers are the only well-drained ground in the marshes bordering the Gulf of Mexico and are usually covered with woody plants. Consequently, cheniers are the only native forests in this vast marsh area, and they provide critical habitat for forest-dwelling migrants. For more description of the Chenier Plain, see Barrow et al. (in press) and Gosselink et al. (1979). The Chenier Plain, especially along the Louisiana and eastern Texas coast, is the first potential stop for many northbound, Neotropical migrants after trans-Gulf migration in the spring. Many Neotropical migrants stopover at these cheniers, especially during periods of inclement weather (Lowery 1945; Gauthreaux 1971, 1972; Moore and Kerlinger 1987). These cheniers are also among the most southern forested areas in the United States used by some wintering migrants such

as the Yellow-rumped Warbler (*Dendroica coronata*), the Ruby-crowned Kinglet (*Regulus calendula*), and the Solitary Vireo (*Vireo solitarius*).

Martin and Karr (1990) found that migrants used more types of foraging maneuvers during migration than during the breeding or wintering seasons. Several explanations can be made for the behavioral plasticity exhibited by migrants at stopover sites. First, as Hutto (1985a) pointed out, habitat use of migrating landbirds is determined by the benefit of using a particular migration route rather than habitat quality at stopover sites. Stopover habitats within a migration route are clearly more variable than the habitats on the breeding and wintering grounds. At stopover sites, migrants usually form flocks and wander around looking for food instead of settling at a particular spot soon after they land. Wandering behavior allows migrants to enter more different habitats than in breeding or wintering areas. Therefore, one would expect to observe more diverse foraging behaviors used by migrants en-route.

Second, high energy demand and food availability may contribute to the plasticity of foraging behavior of migrants at stopover sites. Although the most important task of migrants at stopover sites with respect to energy is to store fat (Hutto 1985a), the energy demand during migration is considered very high (Berthold 1975, Blem 1980). If adaptability (or flexibility) can result in more foraging opportunities, such strategy is likely to be adopted by migrants, especially by fat-depleted ones. Loria and Moore (1990) found that Red-eyed Vireos forage more intensively and with greater plasticity when they are lean after trans-Gulf migration. Martin and Karr (1990) also found that Chestnut-sided Warblers use more aerial maneuvers during nestling and

fledging periods than during the incubation period. Both examples indicate that birds may forage intensively or use more energetic maneuvers during periods of high energy demands. The limitation of food resources might also result in a high plasticity of foraging because flexibility may increase prey intake, especially scarce prey (Morse 1971). On the other hand, nutritional requirements during migration may be fulfilled better by some foods than others; as a result, the nutrition need may influence foraging behavior of birds (Bairlein 1990). Some migrants shift to different dietary regimes during migration; for example, fruit and nectar become important diet components prior to and during migration of many migrants, even insectivorous ones (Baird 1980, Jordano 1982, Martin and Karr 1986, Bairlein 1990).

Finally, migrants at stopover sites probably come from many different breeding grounds, or even a vast geographic area. One may actually take a sample from all of eastern North America when one does foraging behavior study at a northern Gulf coast site. Behavioral data could be more variable at stopover sites than from single sites on breeding or wintering grounds because geographic differences in foraging behavior of birds may remain in effect at stopover sites (Rabenold 1980, Emlen and DeJong 1981, Collins 1983, Block 1990, Petit et al. 1990a). In addition, plasticity of foraging behavior of migrants during migration may be determined by other factors such as predation (Kerlinger 1989, Lindström 1989), social behavior (Morse 1974, Craig 1989, Daily and Ehrlich 1994), morphology (Moermond 1979), or neophobia (Greenberg 1983, 1990).

Habitat selection of migrants en-route has been studied or reviewed by Parnell (1969), Bairlein (1983), Hutto (1985a, b), Martin and Karr (1986), Moore and Simons (1992), Moore et al. (1990, 1995), but knowledge about fine-scale habitat use is still lacking. We do not know how specifically migrants exploit stopover habitat. Migrants cannot expect to land on a predetermined “suitable” stopover site before they take off, especially during a nonstop flight such as trans-Gulf migration (Moore et al. 1995), because displacement of migrants due to wind drift is possible during such a long flight (Moore 1990). Migrants will eventually land somewhere within their migration routes and need to rest and refuel. Therefore, suitable stopover habitats are crucial to successful migration for Neotropical migrants (Blem 1980, Moore et al. 1995).

A hierarchical decision-making process has been applied in habitat selection of animals in general (Johnson 1980) and of migrants in particular (Hutto 1985a, Moore and Simons 1992). Most spring migrants arrive on the northern coast of the Gulf of Mexico in a fat-depleted condition due to the nonstop flight (Moore and Kerlinger 1987). Thus a suitable habitat for safely resting and replenishing fat reserves is crucial. If the probability of replenishment is low, migrants should search for another suitable stopover habitat (Lindström and Alerstam 1986, Martin and Karr 1986, Sandberg et al. 1988, Moore and Simons 1992).

Habitat change can have either beneficial or detrimental effects on birds. If a forest is disturbed, whether by nature or by humans, some birds benefit from the change, but others are harmed. Neotropical migrants, especially forest interior species, are among those that have suffered from environmental changes (Robbins 1980, Wilcove

1985). After change, both biotic and abiotic elements in a forest will change. Examples are (1) plant species composition, (2) vegetation structure, (3) insect abundance, and (4) the amount of sunlight received by the ground. Some disturbances from cattle grazing or understory clearing for pasture establishment have changed the habitat structure in the Chenier Plain. The loss of the understory vegetation of most cheniers along the Gulf coast is a major concern to conservationists because these cheniers are considered to be critical in providing food resources to the Neotropical migrants that stopover during spring and fall migrations.

The use of specific foraging tactics to acquire specific dietary needs is an important aspect of the foraging behavior of birds (Krebs and Kacelnik 1991). Maurer and Whitmore (1981) found differences in foraging behavior and foraging sites of five species of forest-dwelling birds in two habitats with different vegetation structure. Robinson and Holmes (1982) found that the foraging strategies of forest birds are influenced by branching patterns of the vegetation, the spatial arrangement of leaves, and other parameters of foliage structure. Other workers have also noticed that foraging behaviors are usually affected by vegetation structure and food resources (e.g., Davies 1977, Fitzpatrick 1981, Robinson and Holmes 1984, Holmes and Recher 1986, Lovette and Holmes 1995). One must first understand how each species uses its habitat before the relationship between birds and habitats can be determined (Robinson and Holmes 1982, 1984; Blake and Karr 1987; Barrow 1990). Thus information about foraging behavior and habitat use of migrants was collected to determine the effect of habitat change, because such study is one way to evaluate the quality of en-route habitats.

In this study, I (1) document foraging behavior of Neotropical migrants at the Gulf stopover sites during the spring migration, (2) determine habitat use patterns of Neotropical migrants, and examine whether migrants select certain habitat strata or plant species in accordance with their availability, and (3) determine the impact of understory change on foraging behavior of Neotropical migrants. This information can be useful to resource managers and others striving to restore stopover habitats along the northern coast of the Gulf of Mexico.

## **METHODS**

This study was part of a larger project on stopover ecology of Neotropical migrants at three sites on the Chenier Plain during the spring migrations of 1993–1995. Foraging data were collected during the spring migration seasons of 1993 through 1995; I did not use data from 1995 because I only spent a few weekends in the field then. During 1993, all foraging data were collected at one site, Grand Chenier, but during 1994, I traveled from site to site every week to equalize my effort among sites.

About 60 species of mostly Neotropical but some wintering migrants were recorded. Wintering migrants were abundant in early March and became scarcer as the migration season progressed; most wintering migrants had departed by the end of March. Neotropical migrants started to appear at mid-March and reached their peak numbers during the last week of April and the first week of May. The abundance of Neotropical migrants declined sharply after mid-May. During the migration season, thousands of Neotropical migrants were present in the study sites from time to time. The occurrence of these large numbers, “fallout,” often coincided with severe weather

conditions, especially thunderstorms as found by Lowery (1945, 1955) and Gauthreaux (1971).

### Study Area

I used three study sites along the northern coast of the Gulf of Mexico: (1) Grand Chenier, Cameron Parish, Louisiana; (2) Hackberry Ridge, Cameron Parish, Louisiana; and (3) Smith Point, Chambers County, Texas (Figure 1.1). The Grand Chenier site was a more mature and diverse coastal forest than the other two sites. The Hackberry Ridge site had a low canopy and consisted primarily of hackberry trees (*Celtis laevigata*). The Smith Point site had very thick understory and many live oaks (*Quercus virginiana*) in the canopy. For detailed description of the study sites, see Barrow et al. (in press).

Each study site consists of a “reduced” plot with a little to a moderate amount of understory, and a “normal” plot where the understory was denser. Each plot was intended to be a 100×300 m rectangular area, but this size plot could not be obtained at all sites because of the limited extent of woods available. Reduced and normal plots were adjacent at Grand Chenier, but separated at Hackberry Ridge (c.a. 1 km) and Smith Point (c.a. 100 m).

Each plot was oriented east-west, roughly parallel to the coastline. Within all study plots, I established grids marked with flags spaced every 25 m. Each flag was marked with a combination of a number (long axis) and a letter (short axis); these flags delineated the boundaries of many small blocks and several transect lines.





Figure 1.1. Study site location. Study sites were located along coastal forests in Louisiana and Texas. Site code GC = Grand Chenier, HB = Hackberry Ridge, and SP = Smith Point.

## **Recording Methods**

Foraging behaviors were recorded when opportunities occurred as I repeatedly traversed the study plots. Attempts were made to equalize effort in every part of the plot and not to concentrate sampling at any particular place. In addition, I tried not to gather data from the same bird more than once per day, e.g., not to stay at one spot too long, or to only observe individuals of different sexes or species at the same spot. Repeated sampling of individuals should be rare because most Neotropical migrants depart the night of their arrival (Gauthreaux 1971, 1972; Moore and Kerlinger 1987; Kuenzi et al. 1991).

I used “focal sampling” and “continuous recording” as recording methods (Martin and Bateson 1993). I quietly followed each bird encountered and entered observations into a tape recorder until the bird was lost from sight. If I could not determine what a bird was doing, I stopped recording. When making foraging behavior observations, I recorded data on attack behaviors, foraging sites, and searching movements (Chapter 2) of all insectivorous migrants encountered.

Some data were recorded on tape and the rest in a field notebook. After a bird was identified, I entered species, sex, if discernible, and time of day on the tape. I kept the recorder running. After saying “start,” I recorded in detail every attack behavior and searching movement until I was no longer able to do so, usually because the bird departed. At that moment, I said “stop.” After I had stopped the recorder, I recorded the following information in a field notebook: species, sex, time of day, if the bird was in a flock or solitary, bird density (high or low) in the plot (1994 only), and for the last

foraging location I recorded data on habitat strata, foraging substrate, foraging height, vegetation density [estimated vegetation volume within an imaginary 1-m-diameter sphere centered on the foraging bird, use 5% increments], perch diameter [ $< 1$  cm or  $> 1$  cm], crown position [inner or outer half of the crown], plant species, and information about that plant: plant height, DBH (diameter at breast height), and phenology. For ground foragers, like the Wood Thrush (*Hylocichla mustelina*), I recorded the percentage of herbs, fallen debris, leaf litter, water area, and mud (1994 only) within an imaginary 1-m-diameter circle centered on the last foraging site. For each foraging observation, I also sampled a random point for comparison. I used two different ways to find random points, one in 1993 and another in 1994. Because the first method may not have always been random in my study sites, I developed the second method to replace it the next year. The scheme used in 1993 to find a random point was to take a random direction ( $1 - 360^\circ$ ) and a random distance in number of paces ( $1 - 25$ ) from the location of the last attack of the bird. However, this method frequently got the same tree as the random plant if the tree used by the bird had a widespread crown. In contrast, the 1994 method was designed to find the random points without referring to the foraging location of birds except foraging height. I randomly selected a block to start with for each study plot, and then I went systematically around the whole plot. Each block ( $25 \times 25$  m) contained 100 points (or intersections) formed by dividing each side into 10 sections (2.5 m). When finding a random point, I referred to a pre-prepared random number table (00 – 99). The first digit was the random number for the side of the block on the long axis, and the second digit was for the other axis. After I located the random

point on the ground, I used a foraging height from a corresponding foraging observation to find the random plant. The random point data were measured separately from foraging observations but were conducted within the same week; actually, random points were usually measured the next day. For both methods, variables of plant species, height, DBH, and phenological characteristics, were recorded on the random plant. If the random point was for ground foragers, I recorded the percentage of herbs, fallen debris, leaf litter, water area, and mud (1994 only) within an imaginary 1-m-diameter circle on the ground. For each random point, I also recorded the presence or absence of vegetation for four habitat strata: ground cover, shrubs, subcanopy and canopy, within an imaginary 1-m-diameter cylinder extending from ground to the canopy.

For naming attack behaviors and foraging substrates, I used the scheme of Remsen and Robinson (1990). Terminology for habitat strata and foraging substrates are listed below because they were not identical to that in Remsen and Robinson (1990). Habitat strata were classified into five categories as ground, ground covers, shrubs, subcanopy, and canopy. They were defined based on vegetation layers rather than the absolute height. The range of height listed behind the habitat strata was already generalized; thus it might be different from site to site.

#### A. Ground

1. Bare ground (dry),
2. Mud (wet),
3. Water area,

.

4. Leaf litter, and

5. Fallen debris.

B. Ground cover (< 0.5 m, non-woody vegetation)

1. Grasses,

2. Herbs, and

3. Palmettos.

C. Shrubs (< 2 m, woody vegetation)

D. Subcanopy (2 – 10 m)

E. Canopy (> 10 m)

For habitat strata C – E, seven common substrates were listed as follows.

Conditions of substrates are specified after a slash.

1. Trunk / lichen, moss, or vine,

2. Branch (> 1 cm in diameter) / lichen, moss, or vine,

3. Twig (< 1 cm in diameter) / lichen, moss, or vine,

4. Leaf / dead, rolled, dead and rolled, lower surface, upper surface, or vine,

5. Flower / bud,

6. Fruit, and

7. Air / spider web.

Substrates recorded in this way could carry more information into data analysis.

For example, lichens on trunks or on twigs could be distinguished. Birds may use different attack behaviors at these two locations, and thus location of lichens may be more important than the lichens themselves. Another advantage of this recording

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method is that statistical analyses on substrates, their conditions, or a combination of them can be performed.

I obtained sequence and duration information from the tape with the aid of a stopwatch.

### **Data Analysis**

Although the original project was designed for Neotropical migrants, I had many observations on wintering migrants, which were also included in the analysis.

Wintering migrants included Yellow-rumped Warblers, Ruby-crowned Kinglets, and Solitary Vireos, as well as small numbers of Common Yellowthroats (*Geothlypis trichas*), Blue-gray Gnatcatchers (*Polioptila caerulea*), and White-eyed Vireos (*Vireo griseus*). Species such as Rose-breasted Grosbeak (*Pheucticus ludovicianus*) and orioles (*Icterus spurius* and *I. galbula*) that were not strictly insectivorous were excluded from the analysis because they had different foraging modes from truly insectivorous species. I kept the Tennessee Warbler (*Vermivora peregrina*) in the analysis, because they spent more time foraging on insects than on nectar.

A minimum sample of at least 30 individuals, about 150 sequential observations, is needed for analysis of foraging behavior (Morrison 1984). However, I included species with a minimum sample of 15 individuals, because these observations made up 1/4 the foraging data set in the project. I expect that all species included in this analysis should have sample sizes over the recommended one when the entire data set is analyzed. Based on this criterion, 33 species were included in this analysis (Table 1.1). I conducted separate analyses for ground foragers, because foraging sites of ground

Table 1.1. Insectivorous migratory songbirds with species codes, foraging strata, and sample sizes at Gulf coast stopover sites, 1993–1994. Bird names follow the AOU check-list (1983).

Family Common name (Scientific name)	Species code	Foraging strata	Observations
<b>Cuculidae</b>			
Yellow-billed Cuckoo ( <i>Coccyzus americanus</i> )	YBCU	Arboreal	18
<b>Tyrannidae</b>			
Acadian Flycatcher ( <i>Empidonax virescens</i> )	ACFL	Arboreal	24
Eastern Wood-Pewee ( <i>Contopus virens</i> )	EAWP	Arboreal	46
<b>Muscicapidae</b>			
Ruby-crowned Kinglet ( <i>Regulus calendula</i> )	RCKI	Arboreal	94
Blue-gray Gnatcatcher ( <i>Polioptila caerulea</i> )	BGGN	Arboreal	27
Gray-cheeked Thrush ( <i>Catharus minimus</i> )	GCTH	Ground	19
Swainson's Thrush ( <i>Catharus ustulatus</i> )	SWTH	Ground	34
Wood Thrush ( <i>Hylocichla mustelina</i> )	WOTH	Ground	43
<b>Mimidae</b>			
Gray Catbird ( <i>Dumetella carolinensis</i> )	GRCA	Ground	42
<b>Vireonidae</b>			
White-eyed Vireo ( <i>Vireo griseus</i> )	WEVI	Arboreal	31
Philadelphia Vireo ( <i>Vireo philadelphicus</i> )	PHVI	Arboreal	17
Red-eyed Vireo ( <i>Vireo olivaceus</i> )	REVI	Arboreal	182
<b>Parulinae</b>			
Blue-winged Warbler ( <i>Vermivora pinus</i> )	BWWA	Arboreal	41
Golden-winged Warbler ( <i>Vermivora chrysoptera</i> )	GWWA	Arboreal	21
Tennessee Warbler ( <i>Vermivora peregrina</i> )	TEWA	Arboreal	98
Northern Parula ( <i>Parula americana</i> )	NOPA	Arboreal	35
Yellow Warbler ( <i>Dendroica petechia</i> )	YWAR	Arboreal	23
Chestnut-sided Warbler ( <i>Dendroica pensylvanica</i> )	CSWA	Arboreal	48
Magnolia Warbler ( <i>Dendroica magnolia</i> )	MAWA	Arboreal	121
Yellow-rumped Warbler ( <i>Dendroica coronata</i> )	MYWA	Arboreal	147
Black-throated Green Warbler ( <i>Dendroica virens</i> )	BTNW	Arboreal	29
Blackburnian Warbler ( <i>Dendroica fusca</i> )	BLBW	Arboreal	22
Bay-breasted Warbler ( <i>Dendroica castanea</i> )	BBWA	Arboreal	142
Black-and-white Warbler ( <i>Mniotilta varia</i> )	BAWW	Arboreal	104
American Redstart ( <i>Setophaga ruticilla</i> )	AMRE	Arboreal	58
Prothonotary Warbler ( <i>Protonotaria citrea</i> )	PROW	Arboreal	21
Worm-eating Warbler ( <i>Helminthos vermivorus</i> )	WEWA	Arboreal	67
Ovenbird ( <i>Seiurus aurocapillus</i> )	OVEN	Ground	35
Northern Waterthrush ( <i>Seiurus noveboracensis</i> )	NOWA	Ground	33
Common Yellowthroat ( <i>Geothlypis trichas</i> )	COYE	Arboreal	28
Hooded Warbler ( <i>Wilsonia citrina</i> )	HOWA	Arboreal	47
<b>Thraupinae</b>			
Summer Tanager ( <i>Piranga rubra</i> )	SUTA	Arboreal	17
Scarlet Tanager ( <i>Piranga olivacea</i> )	SCTA	Arboreal	20

foragers were recorded differently from those of arboreal species. Ground foragers included in the analysis were the Gray-cheeked Thrush (*Catharus minimus*), Swainson's Thrush (*Catharus ustulatus*), Wood Thrush (*Hylocichla mustelina*), Gray Catbird (*Dumetella carolinensis*), Ovenbird (*Seiurus aurocapillus*), and Northern Waterthrush (*Seiurus noveboracensis*).

Foraging rate was defined as the number of attacks per minute (Robinson and Holmes 1982). Foraging rate was computed by dividing the number of attacks by the duration of a foraging sequence. Foraging rate was calculated for sequences with a duration of at least 20 seconds (*sensu* Robinson and Holmes 1982). I also calculated an average foraging rate for each species.

Most variables of foraging behavior are multinomial responses (categorical data), and they are usually recorded from the same bird. Such data can be constructed in a contingency table with two or several variables. Correspondence analysis is a tool to show graphically the association in a contingency table (Greenacre 1984, van der Heijden and de Leeuw 1985, Moser 1989) and is considered better than principal component analysis and factor analysis in most situations (Miles 1990).

Correspondence analysis (SAS Institute 1989) was performed on the frequencies of attack behavior with arboreal migrants. The same analyses were conducted for habitat strata, substrate, and plant species with arboreal species. However, categories of these variables were combined, or only categories with large counts were included. Because correspondence analysis is based on the Chi-square statistic, the average expected frequency for each cell should be  $\geq 5$  for reliable inference (Roscoe and Byars 1971,



Moser et al. 1990). Therefore, in attack behavior, I combined “reach” with “glean”, and “sally-hover” was incorporated into “sally-strike”. The habitat strata “shrubs,” “ground cover,” and “ground” were combined as “understory.” In foraging substrate, “branch” and “trunk” were combined into “bark.” In addition, the three main understory tree species, green hawthorn (*Crataegus viridis*), deciduous holly (*Ilex decidua*), and yaupon (*Ilex vomitoria*) were pooled together, and all vine species were combined into one category. Vine species included grape vine (*Vitis cinerea*), Japanese honeysuckle (*Lonicera japonica*), ladies eardrops (*Brunnichia cirrhosa*), poison ivy (*Toxicodendron radicans*), rattan-vine (*Berchemia scandens*), trumpet-creeper (*Bignonia radicans*), virginia-creeper (*Parthenocissus quinquefolia*), greenbrier (*Smilax tamnoides* and *S. rotundifolia*), and cherokee rose (*Rosa laevigata*). Other tree species included in the analysis are American elm (*Ulmus americana*), Chinaberry (*Melia azedarach*), Chinese tallow tree (*Sapium sebiferum*), cherry laurel (*Prunus caroliniana*), honeylocust (*Gleditsia triacanthos*), and red mulberry (*Morus rubra*). Plant species names follow Kartesz and Kartesz (1980).

In correspondence analysis, the distances between row points are a measure of the discrepancy between row profiles and are related to the Chi-square distances (Greenacre 1984, Greenacre and Hastie 1987, Moser 1989). The same principle can also be applied to column points. Because the distances between row and column points are not defined, it is meaningless to interpret them (Greenacre 1984, Greenacre and Hastie 1987). Row and column points are positively associated when they lie in the

same direction from the origin, and are negatively associated when they lie in the opposite direction.

For multidimensional contingency tables, multiple correspondence analysis is sometimes applied together with a loglinear (or logistic) model to explore the association in the tables (van der Heijden and de Leeuw 1985, Moser 1989, Moser et al. 1990). This approach usually results in more insight into the association among variables in such tables (Moser 1989) because the loglinear model shows the interaction between variables on the “variable level,” and correspondence analysis on the “category level” (van der Heijden and de Leeuw 1985). A loglinear model on the cross-classification table of attack behavior, habitat strata, and foraging substrate for the two most common taxa, warblers and vireos, was built to model the association among these variables (SAS Institute 1989, Agresti 1990, Stokes et al. 1995). Due to small sample size, attack behaviors were combined into two categories: leg-powered maneuvers and wing-powered maneuvers, or near-perch maneuvers and aerial maneuvers as in Remsen and Robinson (1990). Only canopy and subcanopy strata were retained in the model. Leaf, twig, and bark were included in the model as foraging substrates. A Burt table was constructed from those variables in the loglinear model; multiple correspondence analysis was then performed on the Burt table (Greenacre 1984). The three-dimensional plot that resulted from the multiple correspondence analysis was used to show the association of the contingency table graphically (van der Heijden and de Leeuw 1985, Moser 1989, Moser et al. 1990). Multiple correspondence analysis (SAS Institute 1989)

was also performed on habitat strata within study plots. The three-dimensional plot was used to show the association between plots and their vegetation profiles.

A loglinear model was also constructed to study the association between perch diameter and crown position among arboreal migrants. A simple linear regression was performed between foraging height and used plant height.

Analyses of habitat selection were conducted in two aspects: (1) comparison of habitat use patterns of migrants between normal and reduced plots; and (2) use and availability analysis at foraging site. The first analysis was conducted using only arboreal migrants. The Type I error (or  $\alpha$  level) used in the following tests was chosen to be 0.05. Likelihood ratio Chi-square tests (or G tests) were used to test if habitat strata were homogeneously used by migrants between control and reduced plots. The tests were conducted for each site and for all sites combined. Foraging heights as well as plant heights, DBH, and the ratios of foraging height to plant height were tested by  $t$  tests between normal and reduced plots. To test if the change of foraging height from normal plots to reduced plots was consistent for arboreal migrant species, a simple linear regression (SAS Institute 1989) was performed between foraging heights of migrant species in normal plots and their corresponding differences of foraging heights between reduced and normal plots. This analysis was only performed for canopy and subcanopy species.

Several methods have been used to analyze use and availability data (e.g., Friedman 1937, Neu et al. 1974, Quade 1979, Johnson 1980), and each has its specific assumptions and constraints. For comparisons of these methods, see Alldredge and

Ratti (1986, 1992); for study design and statistical consideration of these methods, refer to Thomas and Taylor (1990). Recently, a new method (compositional analysis) was developed by Aebischer et al. (1993), and Manly et al. (1993) wrote a book trying to unify this topic through a resource-availability probability function. All use-availability analyses in this study followed Manly et al. (1993) because it seems to be more biological in its interpretation.

Use and availability analyses of habitat strata and plant species used by all arboreal migrants at each site and plant species used by the five most commonly recorded migrants were examined first by a Chi-square goodness-of-fit test (Alldredge and Ratti 1986, Manly et al. 1993, SAS Institute 1989). Selection indices and standardized selection indices were calculated for each category based on Manly et al. (1993). Those selection indices were tested with a simultaneous Bonferroni Z statistic to determine if they differed significantly from 1 (use = availability). The overall probability of committing a Type I error is 0.05. Because habitat strata and plant species were different from site to site, the tests were performed separately for each site. The criteria for including a category in the use and availability analysis is the same as for the Chi-square tests stated above. However, some statisticians consider it acceptable if there are no expected values  $< 1$  and no more than 20% of cells have an expected value  $< 5$  (Roscoe and Byars 1971, Dowdy and Wearden 1991). Because of small sample size for individual migrant species, I adopted the latter criteria. For those plant species that could not be treated as an individual category, I combined them as “others.” All cells under “others” had frequencies larger than 5.

Ground habitats were analyzed differently from the arboreal habitats because they were recorded as percentage instead of frequency. The distribution of resource data is usually not normal so that discriminant function analysis has limited value (Manly et al. 1993). Logistic regression does not require multivariate normality of the explanatory variables, and it was found to be more robust than discriminant analysis (Press and Wilson 1978, Moser et al. 1990); thus, I used a logistic regression model (SAS Institute 1989, 1995) to test if ground foragers selected particular microhabitats for foraging. This was a use-availability analysis and was conducted for each species and for all species combined. Ground habitats of all random points from the six species were combined as availability indices. I also used a logistic regression model (SAS Institute 1989, 1995) to test if ground foragers used different habitats from one another. Stepwise selection with significance levels for adding or removing variables of 0.30 was applied to select the best variables for discriminating habitat use among species. All statistical analyses on ground foragers were performed for only the 1994 data because an additional variable "mud" was only recorded in 1994 and it was an important variable for the Northern Waterthrush.

## RESULTS

### **Vegetation Profiles among Plots**

Vegetation profile or habitat strata differed more among sites than between plots because all normal plots were located closer to their corresponding reduced plots at each site rather than situated together (Figure 1.2). Plots from the same study site were very likely to be from the same plant community, even though a "normal" and a "reduced"

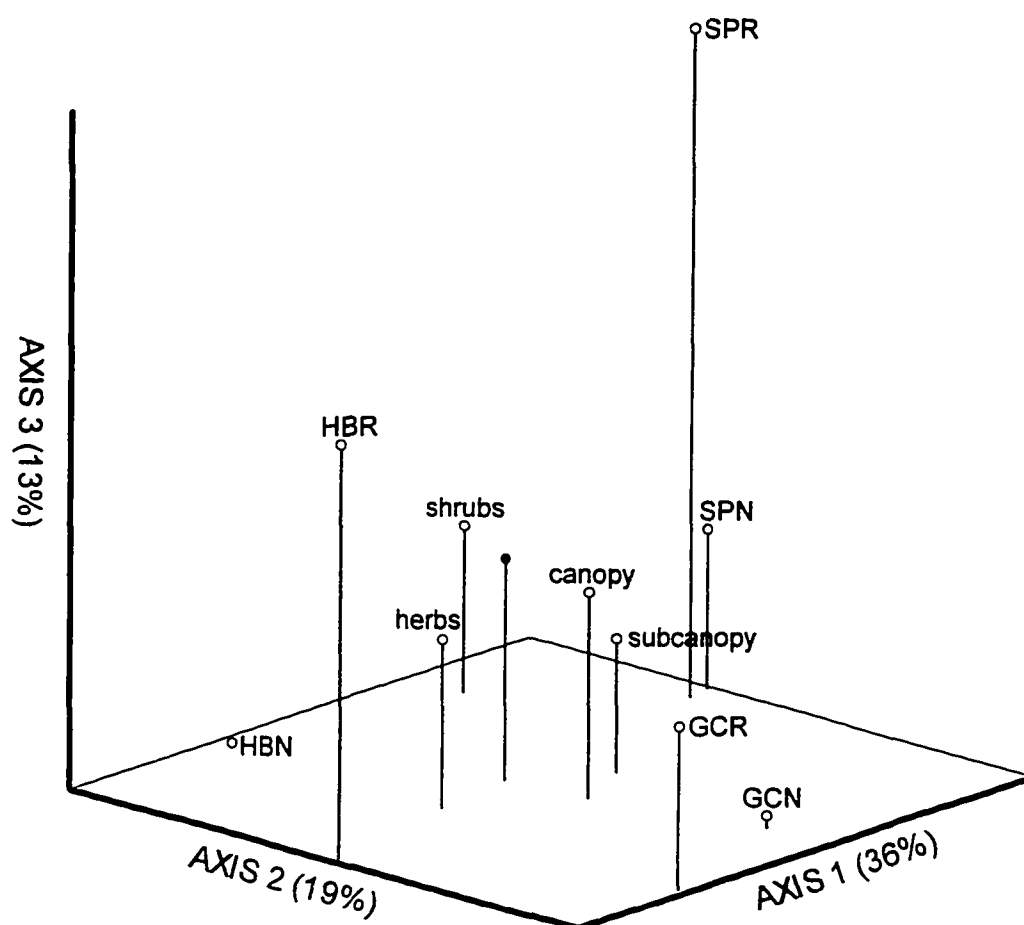


Figure 1.2. Correspondence analysis of habitat strata with study plots at Gulf coast stopover sites, 1994. Site codes are same as in Figure 1.1; plot codes, N = normal plot, and R = reduced plot. The origin is at the solid circle. Only presence of habitat strata are presented in the plot because absence points are in the opposite direction through the origin.

were assigned to them. However, subcanopy and shrubs levels were more associated with the normal plot than the reduced plot for all sites. Thus, all normal plots had denser subcanopy and shrub levels than their corresponding reduced plots. Grand Chenier had a more complete canopy layer than the other two sites. In contrast, Hackberry Ridge had more ground cover (herbs) than others. Similar results were found from univariate tests that compared proportions of habitat strata between the normal and reduced plots at each site in Barrow et al. (in press).

### **Foraging Behavior**

**Attack.** Although more than 30 species of migrants were included (Table 1.2), some clear trends were found. Attack behaviors of most arboreal migrants could be roughly divided into two categories, leg-powered maneuvers or wing-powered maneuvers. Glean was the most frequently used maneuver by leg-powered foragers, and reach and hang were used as complementary maneuvers to glean. An exception was the Worm-eating Warbler, which mainly used probes and was a dead-leaf specialist. BWWA, GWWA, and TEWA (see Table 1.1 for species codes) also used probes occasionally. Those species that used a greater proportion of aerial maneuvers mainly used sally-strikes, except for the Eastern Wood-Pewee, which sallied in the air more frequently. Sally-hover and sally were used to a lesser degree by wing-powered foragers. YBCU, AMRE, HOWA, and SCTA used similar amount of leg-powered and wing-powered maneuvers. Correspondence analysis revealed strong associations between the Eastern Wood-Pewee and sally, and between the Worm-eating Warbler and probe, which accounted for 62% of the Chi-square variation of the table of species by attack

Table 1.2. Percentages of attack behaviors of insectivorous migratory songbirds at Gulf coast stopover sites, 1993–1994. Attack behavior codes are GN = glean, RC = reach, HG = hang, PB = probe, FK = flake, FC = flutter-chase, FP = flush-pursue, SA = sally, SH = sally-hover, and SS = sally-strike. See Table 1.1 for species codes.

Species code	Attack behavior										n
	GN	RC	HG	PB	FK	FC or FP	SA	SH	SS	Other	
YBCU	50.0	2.9							47.1		34
ACFL							6.7	2.7	90.6		75
EAWP							71.7	1.1	27.2		350
RCKI	60.3	9.8	4.4				1.5	9.8	14.2		529
BGGN	51.1	13.5	3.8				3.0	15.1	13.5		133
GCTH	86.8				11.4					1.8	114
SWTH	95.4				4.6						86
WOTH	64.3				35.4					0.3	291
GRCA	21.6	0.3			78.1						380
WEVI	67.2	8.0	6.2					0.9	17.7		113
PHVI	56.8	2.3	9.1					7.9	23.9		88
REVI	48.2	5.8	11.1	0.2		0.2		3.9	30.6		620
BWWA	48.3	5.0	24.0	16.0				1.7	4.0	1.0	400
GWWA	58.9	2.7	19.9	13.7		0.7		0.7	2.0	1.4	146
TEWA	64.3	6.1	17.8	9.8			0.1	1.1	0.5	0.3	838
NOPA	74.2	4.5	11.5	5.3			0.4	0.8	2.1	1.2	244
YWAR	80.0	10.8	0.6					0.6	8.0		175
CSWA	69.0	7.7	3.4			0.4	0.4	2.1	17.0		235
MAWA	74.2	8.6	1.7	0.5		1.2	0.1	2.1	11.6		662
MYWA	76.0	5.6	2.0			0.2	3.3	1.8	8.8	2.3	1157
BTNW	69.1	6.8	2.6			1.6	3.1	5.8	11.0		191
BLBW	63.1	6.2	6.2	1.0		6.1	4.6	1.5	10.8		65
BBWA	76.7	6.6	5.5			1.3	0.6	0.9	8.3	0.1	678
BAWW	83.1	0.5	12.3			1.3			0.2	2.6	456
AMRE	35.4	2.4				21.2	13.7	2.3	25.0		212
PROW	64.6	11.7	11.2	1.2				2.5	6.7	2.1	240
WEWA	18.0	4.0	10.8	60.3		0.3	0.2		0.8	5.6	622
OVEN	86.2	0.7			12.4					0.7	145
NOWA	94.2				5.8						241
COYE	76.7	13.7	1.1				1.1	2.3	5.1		176
HOWA	42.8	3.6	1.2			3.0	5.4	4.8	35.6	3.6	166
SUTA	27.0	2.7					10.8		59.5		37
SCTA	43.2	2.7					2.7		51.4		37



behaviors. Because these four points were extreme outliers from the main cloud, I deleted the Eastern Wood-Pewee and the Worm-eating Warbler and did another correspondence analysis. The first three principal axes of the second correspondence analysis explained 98% of the total table variation (Figure 1.3). There was a strong association between sally-strike and ACFL, SCTA, HOWA, BGGN, and REVI. In addition to the Eastern Wood-Pewee, the American Redstart was more associated with sally than other species. In fact, the American Redstart used more flush-pursue and flutter-chase than sally; however, the latter two categories were not included in the analysis due to small sample size. BWWA, GWWA, and TEWA were highly associated with probe and hang. Interestingly, probe and hang were also related to each other, meaning that species that used probes were likely to use hangs as well. This also suggests that probe and hang could be combined in further analyses. A rare attack behavior “hang-probe” was only recorded for WEWA, TEWA, BWWA, GWWA, and PROW. Other positive associations were found between glean and all other arboreal migrants (Figure 1.3). Attack behaviors of ground foragers will be presented later.

Habitat strata. Most migrants except some ground foragers spent the majority of their time in the canopy and subcanopy (Table 1.3). Among these, the EAWP, PROW, WEWA, COYE, and HOWA used the subcanopy more frequently than the canopy. These species also foraged at the shrub level more than those species that mainly foraged in the canopy. On the other hand, the Common Yellowthroat and the Hooded Warbler foraged extensively in shrubs and subcanopy levels, and both also used ground cover more frequently than the other perch-gleaners. Species that used long sallies such

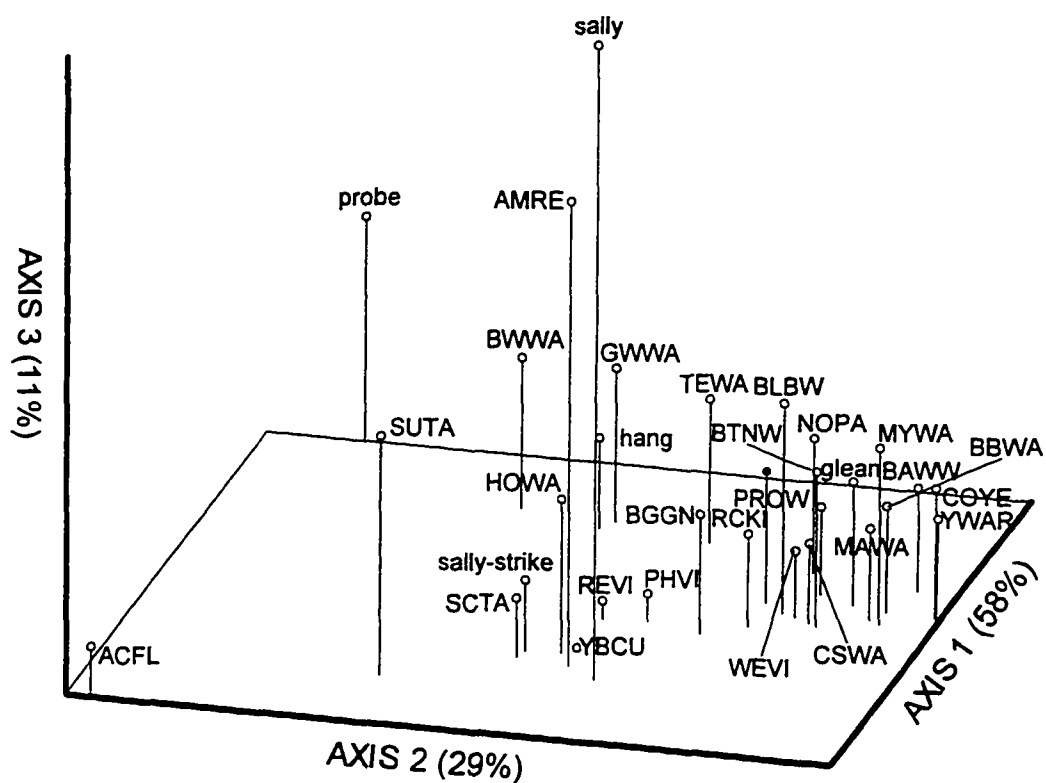


Figure 1.3. Correspondence analysis of attack behaviors with arboreal migrants at Gulf coast stopover sites, 1993-1994. The origin is at the solid circle. See Table 1.1 for species codes. Note that EAWP and WEWA are left out in this plot.

Table 1.3. Percentages of habitat strata used by insectivorous migratory songbirds at Gulf coast stopover sites, 1993–1994. Species codes given in Table 1.1.

Species code	Habitat strata					<i>n</i>
	Canopy	Subcanopy	Shrubs	Ground covers	Ground	
YBCU	77.8	22.2				18
ACFL	54.1	37.5	4.2	4.2		24
EAWP	32.6	43.5	8.7	15.2		46
RCKI	60.7	37.2	2.1			94
BGGN	92.6	7.4				27
GCTH					100.0	19
SWTH	26.5	8.8	2.9	2.9	58.9	34
WOTH				2.3	97.7	43
GRCA	28.6	4.8	7.1	4.8	54.7	42
WEVI	67.8	29.0	3.2			31
PHVI	76.5	23.5				17
REVI	84.6	14.3		1.1		182
BWWA	48.8	48.8	2.4			41
GWWA	76.2	23.8				21
TEWA	81.6	18.4				98
NOPA	94.3	5.7				35
YWAR	87.0	13.0				23
CSWA	72.9	27.1				48
MAWA	54.6	42.1	2.5	0.8		121
MYWA	82.3	17.7				147
BTNW	96.6	3.4				29
BLBW	81.8	18.2				22
BBWA	74.7	24.6	0.7			142
BAWW	71.1	27.9	1.0			104
AMRE	65.5	32.8	1.7			58
PROW	47.6	52.4				21
WEWA	43.3	49.2	4.5	1.5	1.5	67
OVEN		2.8		22.9	74.3	35
NOWA					100.0	33
COYE	7.1	21.4	53.6	17.9		28
HOWA	10.6	46.8	27.7	12.8	2.1	47
SUTA	52.9	35.3		11.8		17
SCTA	85.0	15.0				20

as the Eastern Wood-Pewee and the Summer Tanager also foraged in ground cover from time to time. Because habitat strata were reduced into three categories in the correspondence analysis, a two-dimensional plot could represent the association exactly (Greenacre 1984). The Common Yellowthroat mainly foraged in the understory. The row profile of the Common Yellowthroat had the largest value in the understory column; it was located in the direction of the understory and even far beyond it in the biplot (Figure 1.4). This association contributed most to the total table Chi-square variation. The Hooded Warbler had similar association to understory and subcanopy levels. Other species primarily foraged in trees and were ordered along the continuum between canopy and subcanopy. Of them, PROW, BWWA, and WEWA used the subcanopy more intensively than others.

Substrate. Leaf and twig were the two most common substrates used by arboreal migrants (Table 1.4). Eastern Wood-Pewees sallied in the air about 70% of the time. In contrast, Black-and-white Warblers most frequently foraged on branches; they restricted their foraging to bark. TEWA, NOPA, and BGGN used flowers as a substrate more frequently than others. On the other hand, the Gray Catbird and the Summer Tanager used more fruits, primarily red mulberries, than other insectivorous migrants. As in attack behavior, two particular pairs of strong association were found in the correspondence analysis; they were between the Eastern Wood-Pewee and the air and between the Black-and-white Warbler and bark. These two associations contributed about 62% of the total Chi-square variation of testing homogeneity between bird species and foraging substrates. Thus, a second correspondence analysis was performed without

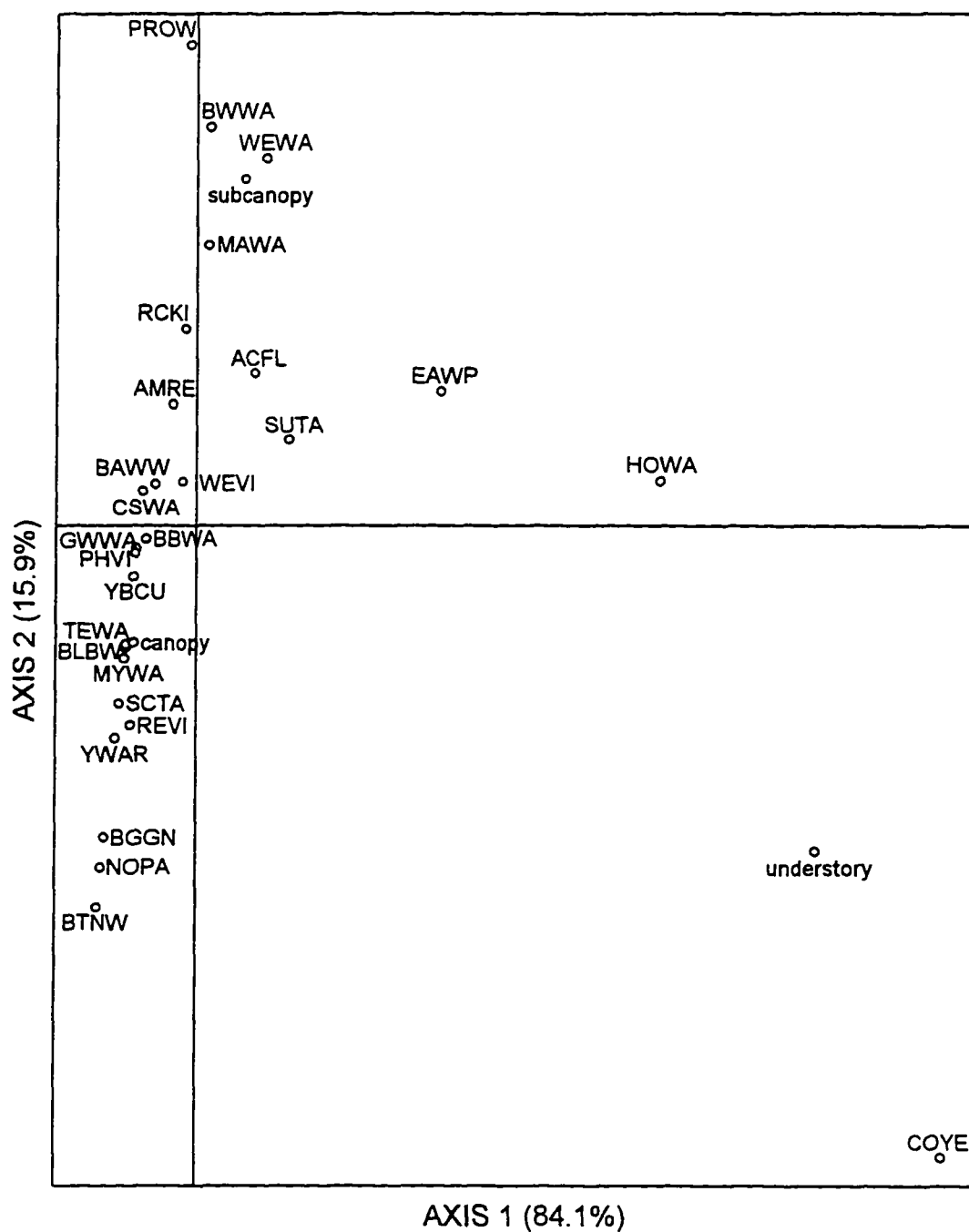


Figure 1.4. Correspondence analysis of habitat strata with 27 arboreal migrants at Gulf coast stopover sites, 1993-1994. See Table 1.1 for species codes.

Table 1.4. Percentages of foraging substrates used by insectivorous migratory songbirds at Gulf coast stopover sites, 1993–1994. See Table 1.1 for species codes.

Species code	Foraging substrate									n
	Air	Ground <sup>a</sup>	Leaf litter <sup>b</sup>	Trunk	Branch	Twig	Flower	Fruit	Leaf	
YBCU				5.6	5.6	5.6			83.2	18
ACFL	12.5								87.5	24
EAWP	69.6								30.4	46
RCKI	2.1				2.1	53.2	1.1		41.5	94
BGGN	3.7					29.6	22.2	3.7	40.8	27
GCTH		31.6	68.4							19
SWTH		8.8	50.0	8.8	8.8	8.8		6.0	8.8	34
WOTH		4.7	93.0						2.3	43
GRCA		2.4	54.8	7.1	2.4			26.2	7.1	42
WEVI					16.1	38.7	6.5		38.7	31
PHVI					5.9	11.7	5.9	5.9	70.6	17
REVI	0.5				1.7	9.3	1.7	2.2	84.6	182
BWWA							2.4		97.6	41
GWWA					4.7	19.1	14.3		61.9	21
TEWA					2.0	11.2	34.7		52.1	98
NOPA	2.8					28.6	22.9	8.6	37.1	35
YWAR						8.7	8.7		82.6	23
CSWA					4.2	29.2			66.6	48
MAWA					1.6	37.2	2.5		58.7	121
MYWA	1.4			0.7	8.8	35.4	13.6	3.4	36.7	147
BTNW					10.3	37.9	13.8		37.9	29
BLBW	4.6					31.8			63.6	22
BBWA	2.8				9.2	40.1		1.4	46.5	142
BAWW				11.5	73.1	14.4			1.0	104
AMRE	6.9			1.7	3.5	20.7			67.2	58
PROW					4.8	9.5			85.7	21
WEWA	1.5		1.5		11.9	7.5			77.6	67
OVEN	2.9	5.7	68.5		2.9				20.0	35
NOWA		81.8	18.2							33
COYE	3.6			3.6	3.6	42.8	3.6		42.8	28
HOWA	8.5		2.1	6.4	2.1	17.1	2.1		61.7	47
SUTA	5.9					11.8	5.9	23.5	52.9	17
SCTA	10.0					5.0	5.0	5.0	75.0	20

<sup>a</sup> Ground includes bare ground, mud, and water areas.

<sup>b</sup> Including fallen debris.

the Eastern Wood-Pewee, the Black-and-white Warbler, and the air, because the sample size of the air became very small when the Eastern Wood-Pewee was removed. The first two principal axes of the second correspondence analysis accounted for 90% of the total table variation (Figure 1.5). The association between the Tennessee Warbler and flowers contributed more to the total variation than any others. Also NOPA, BGGN, and GWWA were positively associated with flowers. All remaining species were roughly located along a gradient from leaves to bark and twigs. Within vireos, REVI and PHVI tended to foraged on leaves, but WEVI on twigs and branches. Bark, including the trunk and branches, was also positively associated with twigs because they shared more similar structural characteristics than to leaves.

Plant species. More than 90% of the table variation was explained by the first three principal axes in the correspondence analysis (Figure 1.6). Strong associations were found between Tennessee Warblers and honeylocusts, Hooded Warblers and understory tree species, Black-throated Green Warblers and live oaks, and Red-eyed Vireos and hackberry trees. Vine species and understory tree species were strongly associated with each other because these two groups of plants usually coexisted in the same stratum. As a result, migrants that foraged in understory trees were likely to forage in vines, and vice versa.

Perch diameter. All arboreal migrants except the Black-and-white Warbler primarily used perches with diameter  $< 1$  cm (Table 1.5). More than 90% of Black-and-white Warblers' perches were  $> 1$  cm, because they mainly foraged by climbing on branches and trunks (84.6%, Table 1.4). For other warbler species, the Hooded Warbler used

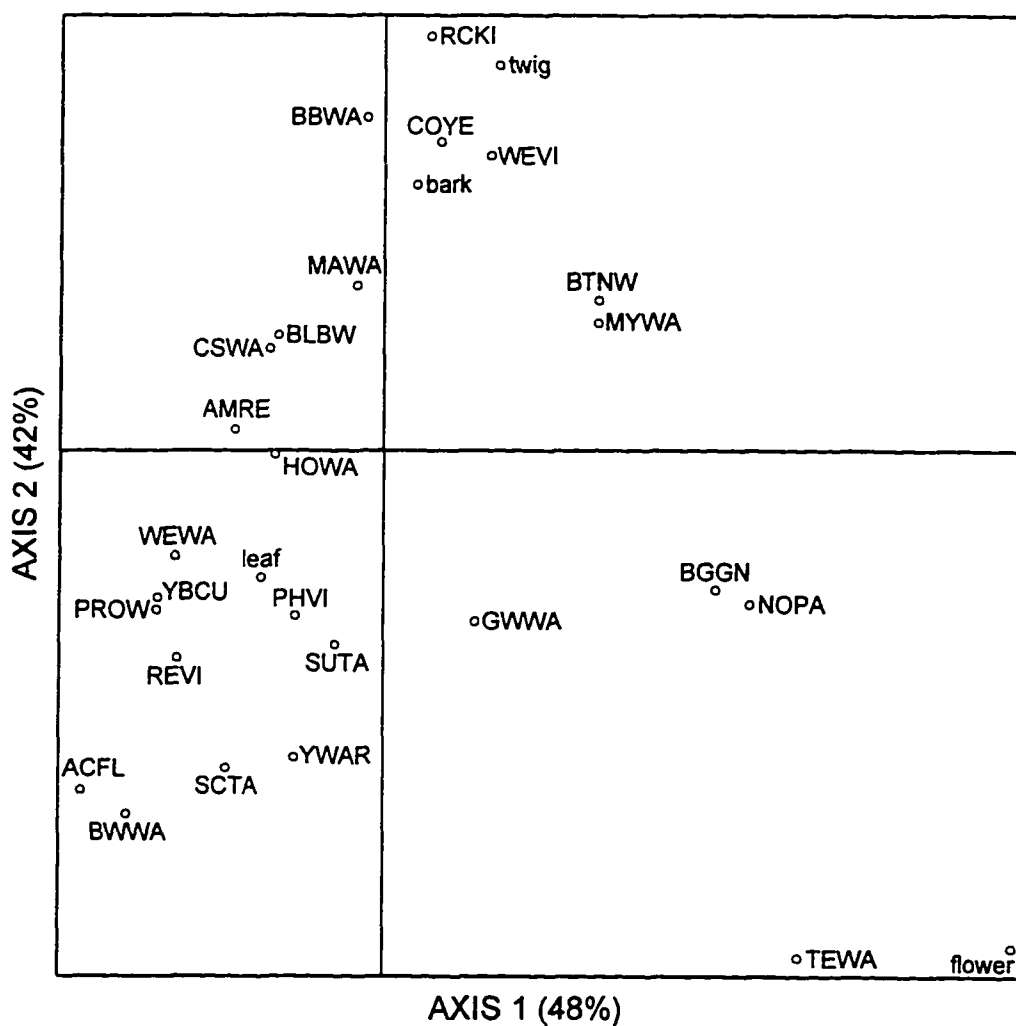


Figure 1.5. Correspondence analysis of foraging substrates with arboreal migrant species at Gulf coast stopover sites, 1993-1994. Branch and trunk are combined as "bark." Species codes are listed in Table 1.1. Note that EAWP and BAWW are left out in this plot.



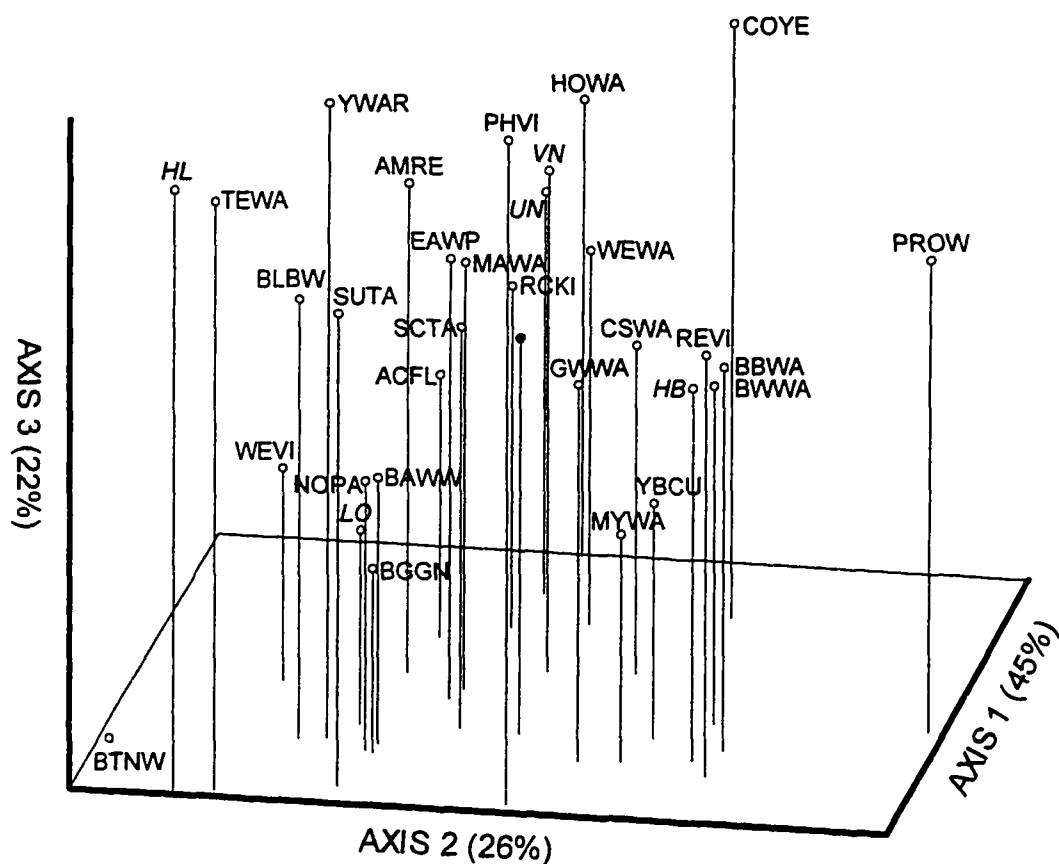


Figure 1.6. Correspondence analysis of plant species or groups of plants with arboreal migrants at Gulf coast stopover sites, 1993-1994. Plant codes: HB = hackberry; HL = honeylocust; LO = live oak; UN = understory species, including deciduous holly, green hawthorn, and yaupon; VN = all vine species. See Table 1.1 for bird species codes. The origin is at the solid circle.

Table 1.5. Percentages of perch diameter and crown position used by arboreal insectivorous migratory songbirds at Gulf coast stopover sites, 1993–1994. See Table 1.1 for species codes.

Species code	Perch diameter			Crown position		
	> 1 cm	< 1 cm	<i>n</i>	Inner	Outer	<i>n</i>
YBCU	27.8	72.2	18	27.8	72.2	18
ACFL	9.1	90.9	22	13.6	86.4	22
EAWP	34.8	65.2	46	6.8	93.2	46
RCKI	6.4	93.6	94	23.4	76.6	94
BGGN	3.7	96.3	27	14.8	85.2	27
WEVI	19.3	80.7	31	22.6	77.4	31
PHVI	5.9	94.1	17	11.8	88.2	17
REVI	6.1	93.9	179	17.4	82.6	178
BWWA	4.9	95.1	41	22.0	78.0	41
GWWA	4.8	95.2	21	19.0	81.0	21
TEWA	3.1	96.9	98	8.2	91.8	97
NOPA	0.0	100.0	35	20.0	80.0	35
YWAR	0.0	100.0	23	8.7	91.3	23
CSWA	6.2	93.8	48	8.3	91.7	48
MAWA	5.8	94.2	121	13.3	86.7	120
MYWA	12.9	87.1	147	15.6	84.4	147
BTNW	10.3	89.7	29	13.8	86.2	29
BLBW	0.0	100.0	22	13.6	86.4	22
BBWA	9.9	90.1	142	11.3	88.7	142
BAWW	90.4	9.6	104	27.9	72.1	104
AMRE	10.3	89.7	58	22.4	77.6	58
PROW	4.8	95.2	21	28.6	71.4	21
WEWA	18.2	81.8	66	18.5	81.5	65
COYE	15.4	84.6	26	33.3	66.7	24
HOWA	27.3	72.7	44	35.0	65.0	40
SUTA	6.2	93.8	17	20.0	80.0	17
SCTA	10.0	90.0	20	15.0	85.0	20

larger perches than all the remaining species. This was probably due to its frequent visits in understory vine tangles. Although the Common Yellowthroat was an understory species, it usually foraged in shrubs or reed patches. For vireos, the White-eyed Vireo used large perches more than the Red-eyed Vireo and the Philadelphia Vireo. It indicates that perch diameter may be related to the kinds of substrates used by the bird for near-perch gleaners. In this case, the White-eyed Vireo mainly attacked prey on branches and twigs; in contrast, the Red-eyed Vireo and the Philadelphia Vireo attacked prey mainly on leaves. The Acadian Flycatcher used more small perches than the Eastern Wood-Pewee because the Acadian Flycatcher's foraging activity was more concentrated on leaves and in the canopy level (Table 1.3).

Crown position. All arboreal migrants foraged more frequently in the outer half of tree crowns (Table 1.5). Species that used a high proportion of inner crown also used large perches more frequently ( $P < 0.0001$ , loglinear model). This is simply because the trunk and large branches are located in the inner part of trees, and more twigs and leaves are in the outer half of the crown. Thus perch diameter and crown position are related to each other structurally.

Foraging height. Because canopy heights differed dramatically from site to site, foraging height was not a good index to describe foraging niche in this study. Neither was the ratio between foraging height and tree height. Thus habitat stratum was a more appropriate indicator in this study. In fact, foraging height and habitat strata were highly related for most species. Species with foraging height under 2 m can be classified as understory species, from 3 to 6.8 m as subcanopy species, and beyond 6.8

m as canopy species (Table 1.6). Therefore, the Common Yellowthroat is an understory species according to its mean foraging height, 1.37 m, and the Hooded Warbler forages across understory and subcanopy and with mean foraging height 2.39 m.

Vegetation density. Worm-eating Warblers foraged in denser patches than all other arboreal migrants (Table 1.6). RCKI, BWWA, and GWWA also foraged in relatively dense areas. The Worm-eating Warbler was a dead-leaf specialist, and the Blue-winged Warbler and the Golden-winged Warbler also foraged on this substrate from time to time; observations on dead leaves occupied 61%, 15%, and 10% of total observations for WEWA, BWWA, and GWWA, respectively. If curled leaves were included, the figures become 75%, 17%, and 19% in the same order. Possibly, dead-leaves were more abundant in areas with dense vegetation that in turn had a higher probability to trap dead leaves (Gradwohl and Greenberg 1982, Remsen and Parker 1984). Species that used more aerial maneuvers, especially sally, tended to forage in sparser areas (for example, EAWP, ACFL, HOWA, and SUTA). Black-and-white Warblers also had low vegetation density because they foraged on the trunks or large branches where leaves were scarce.

Plant height and DBH. Height and DBH of plants used were highly related to habitat strata and to the plant species where birds foraged. Canopy species usually used trees with higher crown and larger DBH than subcanopy or understory species (Table 1.7). Although live oaks and hackberry trees had similar height, live oaks actually had larger DBH. For example, the Black-throated Green Warbler and the Red-eyed Vireo used plants with similar height, but the Black-throated Green Warbler used plants with larger

Table 1.6. Means, standard errors, and sample sizes for foraging height and vegetation density at foraging sites of arboreal insectivorous migratory songbirds at Gulf coast stopover sites, 1993–1994. See Table 1.1 for species codes.

Species code	Foraging height		Vegetation density (%)	
	$\bar{x} \pm SE$	<i>n</i>	$\bar{x} \pm SE$	<i>n</i>
YBCU	7.0 ± 0.8	18	40.6 ± 4.6	18
ACFL	5.6 ± 0.7	24	30.4 ± 3.5	24
EAWP	4.2 ± 0.4	46	12.6 ± 2.3	46
RCKI	6.6 ± 0.2	94	45.8 ± 1.9	94
BGGN	8.7 ± 0.6	27	40.0 ± 4.2	27
WEVI	6.2 ± 0.5	31	42.0 ± 3.3	30
PHVI	5.6 ± 0.5	17	35.9 ± 4.3	17
REVI	7.3 ± 0.2	182	35.1 ± 1.2	182
BWWA	5.6 ± 0.5	41	45.1 ± 3.2	41
GWWA	7.1 ± 0.6	21	44.3 ± 4.8	21
TEWA	6.9 ± 0.3	98	41.0 ± 1.8	98
NOPA	8.0 ± 0.4	35	34.0 ± 2.8	35
YWAR	9.1 ± 0.7	23	40.9 ± 2.9	23
CSWA	6.1 ± 0.3	48	40.0 ± 2.6	48
MAWA	5.0 ± 0.2	121	36.5 ± 1.5	121
MYWA	8.7 ± 0.2	147	32.7 ± 1.3	147
BTNW	8.1 ± 0.3	29	38.5 ± 2.3	29
BLBW	7.3 ± 0.7	22	39.1 ± 3.5	22
BBWA	5.7 ± 0.2	142	36.4 ± 1.3	142
BAWW	6.4 ± 0.3	104	23.8 ± 1.9	104
AMRE	5.3 ± 0.3	58	37.6 ± 2.6	58
PROW	5.6 ± 0.6	21	35.7 ± 4.6	21
WEWA	5.3 ± 0.3	67	46.2 ± 2.7	67
COYE	1.4 ± 0.3	28	37.9 ± 4.7	28
HOWA	2.4 ± 0.3	47	29.6 ± 3.0	47
SUTA	5.4 ± 0.8	17	30.0 ± 3.9	17
SCTA	7.4 ± 0.6	20	35.5 ± 3.4	20

Table 1.7. Means, standard errors, and sample sizes of height and DBH of plants used by arboreal insectivorous migratory songbirds at Gulf coast stopover sites, 1993–1994. See Table 1.1 for species codes.

Species code	Plant height		Plant DBH	
	$\bar{x} \pm \text{SE}$	<i>n</i>	$\bar{x} \pm \text{SE}$	<i>n</i>
YBCU	10.2 ± 0.6	18	26.5 ± 3.8	18
ACFL	8.5 ± 0.8	23	18.7 ± 2.5	23
EAWP	8.8 ± 0.6	43	25.5 ± 3.4	43
RCKI	9.2 ± 0.3	94	18.7 ± 1.7	94
BGGN	11.0 ± 0.6	27	36.9 ± 5.9	27
WEVI	10.1 ± 0.7	31	27.6 ± 4.6	31
PHVI	8.5 ± 0.4	17	25.2 ± 4.0	17
REVI	11.3 ± 0.2	180	28.7 ± 1.4	178
BWWA	9.2 ± 0.6	41	23.4 ± 3.6	41
GWWA	10.3 ± 0.6	21	31.8 ± 5.5	21
TEWA	10.0 ± 0.3	97	30.1 ± 2.2	97
NOPA	11.6 ± 0.5	35	38.2 ± 3.8	33
YWAR	11.4 ± 0.8	23	26.4 ± 3.9	23
CSWA	9.5 ± 0.4	48	25.4 ± 3.0	48
MAWA	8.7 ± 0.3	120	20.7 ± 1.8	119
MYWA	12.1 ± 0.3	147	40.6 ± 2.2	147
BTNW	11.9 ± 0.4	29	48.5 ± 4.7	29
BLBW	10.3 ± 0.7	22	25.6 ± 3.8	22
BBWA	9.8 ± 0.2	142	29.1 ± 1.7	142
BAWW	11.2 ± 0.4	104	36.7 ± 2.7	104
AMRE	9.2 ± 0.4	58	21.2 ± 2.4	57
PROW	8.8 ± 0.8	21	15.6 ± 3.6	21
WEWA	9.0 ± 0.5	65	21.7 ± 2.3	65
COYE	5.0 ± 0.8	24	7.9 ± 2.5	23
HOWA	6.5 ± 0.5	40	14.0 ± 2.8	39
SUTA	9.7 ± 1.3	15	24.5 ± 7.7	15
SCTA	10.6 ± 0.8	20	31.5 ± 5.4	19

DBH than the Red-eyed Vireo. In fact, the Black-throated Green Warbler mainly foraged in live oaks, and the Red-eyed Vireo frequented hackberry trees. Plant height was also highly related to foraging height ( $r = 0.75$ ,  $df = 1233$ ,  $P < 0.0001$ ).

Because foraging sites of ground foragers were recorded differently from those of arboreal migrants, they are presented here separately. All ground foragers used a combination of gleans and flakes to attack prey (Table 1.2). Flakes were actually used to find prey rather than attack them, but I treated them as an attack behavior here.

Among the six ground foragers, only Gray Catbirds used more flakes than gleans. All other species used flakes only as a complementary tool to gleans. The Swainson's Thrush and the Northern Waterthrush used flakes less often than the others. Most ground foragers did not forage in trees (Table 1.3), but the Swainson's Thrush and the Gray Catbird foraged above ground about 40% of the time. Two types of prey were used by ground foragers: visible or hidden prey. The attack behavior used to exploit each of these prey types were distinguished in Remsen and Robinson (1990) as surface maneuvers and subsurface maneuvers. Visible prey were found on bare ground, mud, water surface, and on the surface of fallen debris and leaf litter. On the other hand, hidden prey were exclusively under leaf litter and only exploited by flakes. Categories of ground habitat, e.g., herbs and mud, were recorded as percent area occupied within a 1-m-diameter circle. The total did not necessarily sum to 100%; it could be more than 100% (Table 1.8). The Northern Waterthrush usually foraged in areas with more mud and water than other species. WOTH, GRCA, and OVEN used ground with more leaf litter and fallen debris than others. The Ovenbird foraged in areas with the highest

Table 1.8. Mean percentages, standard errors and sample sizes of herbs, leaf litter, fallen debris, water, and mud within a 1-meter-diameter circle centered on the foraging site of ground foragers. See Table 1.1 for species codes.

Species code	<i>n</i>	Herbs (%)	Leaf litter (%)	Fallen debris (%)	Water (%)	Mud (%)
GCTH	19	36.1 ± 7.4	45.0 ± 8.3	11.8 ± 2.5	2.4 ± 2.1	25.6 ± 8.6 (18) <sup>a</sup>
SWTH	21	22.9 ± 6.2	70.0 ± 7.6	9.3 ± 1.4	7.1 ± 4.0	16.0 ± 10.2 (10)
WOTH	43	19.9 ± 3.9	88.4 ± 3.8	15.5 ± 1.5	0.7 ± 0.7	13.3 ± 6.6 (18)
GRCA	25	18.8 ± 3.8	80.4 ± 5.9	22.2 ± 2.8	0.0 ± 0.0	4.0 ± 4.0 (10)
OVEN	34	38.5 ± 4.9	76.9 ± 5.6	15.7 ± 2.4	0.0 ± 0.0	5.2 ± 4.1 (25)
NOWA	33	20.0 ± 4.0	29.9 ± 5.4	11.4 ± 2.6	34.2 ± 6.2	54.6 ± 7.4 (26)

<sup>a</sup> Mud was recorded only in 1994 and thus with smaller sample sizes.



percentage of herbs of the six species. The Gray-cheeked Thrush and Swainson's Thrush foraged in a manner like a combination of the other four species. I found a significant relationship among species and foraging habitat ( $P = 0.041$ ) by using a logistic regression. The amount of leaf litter was the best discriminator for telling species apart. When stepwise selection was performed, only leaf litter and fallen debris were retained in the model ( $P = 0.004$ ).

Foraging rates of ground foragers except the Ovenbird were higher than those for arboreal migrants (Table 1.9). The Gray Catbird had the highest foraging rate of all migrants because they used a high proportion of flakes, which were performed at high speed. Northern Waterthrushes also had high foraging rates because they usually picked up prey items from mud or water surface right away. Disregarding ground foragers, foraging rates can be ranked among taxa (family or subfamily) in descending order from warblers, vireos, flycatchers, tanagers, to the Yellow-billed Cuckoo. Within warblers, *Vermivora* species and the Northern Parula had higher foraging rates than others. Although the Worm-eating Warbler also had a high foraging rate, I could not determine if they caught prey for every probe. They probably would have a lower foraging rate if I exclude those probes where prey were not caught. The same reasoning applies to ground foragers that used flakes.

There is a strong association among the interaction of attack behavior, habitat strata, and taxa (Table 1.10,  $P = 0.032$ ), and also the interaction between attack behavior and substrate ( $P < 0.0001$ ) based on a loglinear model. From the multiple correspondence analysis, vireos used more wing-powered maneuvers, and more attacks

Table 1.9. Means, standard errors, ranges, and sample sizes for foraging rate of insectivorous migratory songbirds at Gulf coast stopover sites, 1993–1994. Species codes are listed in Table 1.1.

Species code	$\bar{x} \pm SE$	Range	<i>n</i>
YBCU	0.2 ± 0.1	0.0 – 2.1	54
ACFL	1.4 ± 0.2	0.0 – 3.3	26
EAWP	1.4 ± 0.1	0.3 – 3.7	55
RCKI	4.3 ± 0.3	0.0 – 17.8	108
BGGN	4.1 ± 0.5	0.0 – 11.2	34
GCTH	6.0 ± 0.9	2.1 – 11.3	12
SWTH	7.9 ± 1.1	3.8 – 14.6	9
WOTH	9.5 ± 1.5	2.4 – 23.8	19
GRCA	13.1 ± 3.6	0.0 – 51.6	19
WEVI	1.3 ± 0.2	0.0 – 6.1	75
PHVI	2.8 ± 1.0	0.0 – 25.7	25
REVI	2.7 ± 0.2	0.0 – 13.1	240
BWWA	5.6 ± 0.4	0.0 – 18.6	74
GWWA	6.2 ± 0.9	0.0 – 19.1	26
TEWA	6.1 ± 0.4	0.0 – 23.2	138
NOPA	6.4 ± 0.8	0.0 – 21.0	36
YWAR	5.4 ± 0.9	0.0 – 23.5	35
CSWA	3.1 ± 0.3	0.0 – 10.0	79
MAWA	4.5 ± 0.3	0.0 – 23.6	173
MYWA	5.0 ± 0.4	0.0 – 33.2	204
BTNW	2.6 ± 0.3	0.0 – 10.8	63
BLBW	2.3 ± 0.3	0.7 – 5.5	20
BBWA	4.1 ± 0.4	0.0 – 39.2	166
BAWW	4.4 ± 0.4	0.0 – 17.8	110
AMRE	3.6 ± 0.4	0.0 – 15.6	60
PROW	3.8 ± 0.4	0.0 – 12.0	50
WEWA	6.6 ± 0.5	0.0 – 21.6	85
OVEN	5.3 ± 0.5	0.8 – 10.0	22
NOWA	11.2 ± 1.4	0.0 – 24.6	19
COYE	4.0 ± 0.6	0.0 – 13.6	44
HOWA	2.4 ± 0.2	0.0 – 10.4	72
SUTA	0.8 ± 0.3	0.0 – 5.5	19
SCTA	0.7 ± 0.2	0.0 – 3.4	26

Table 1.10. Loglinear model of attack behaviors (ATTACK), habitat strata (STRATA), and foraging substrates (SUBSTRATE) between warblers and vireos (TAXA) at Gulf coast stopover sites, 1993–1994.

Source	df	Chi-square <sup>a</sup>	P
ATTACK	1	118.2	0.0000
STRATA	1	117.6	0.0000
SUBSTRATE	2	260.4	0.0000
TAXA	1	151.0	0.0000
ATTACK*SUBSTRATE	2	69.4	0.0000
SUBSTRATE*TAXA	2	27.1	0.0000
ATTACK*STRATA	1	0.8	0.3675
ATTACK*TAXA	1	5.7	0.0167
STRATA*TAXA	1	18.0	0.0000
ATTACK*STRATA*TAXA	1	4.6	0.0318
LIKELIHOOD RATIO	10	9.9	0.4495

<sup>a</sup> Likelihood ratio Chi-square tests.

on leaves than did warblers; they also foraged in the canopy more frequently than warblers (Figure 1.7). On the other hand, warblers tended to use more leg-powered maneuvers, more attacks on twigs or bark, and foraged more in the subcanopy. Vireos seldom foraged in the understory and ground levels, and thus I excluded these levels from the analysis.

### **Habitat Selection**

For arboreal migrants, when habitat strata ground, ground cover, and shrubs were combined as understory, use of habitat strata between normal and reduced plots differed significantly for all sites combined ( $G^2 = 44.7$ ,  $df = 2$ ,  $P < 0.001$ ). Migrants were more frequently recorded at the subcanopy level in normal plots and at the canopy level in reduced plots; there was not much difference at the understory level. When each site was examined separately, all had  $P < 0.001$  for the G test. The Grand Chenier and Smith Point sites had similar results to the all-site test; however, more migrants were recorded in the understory in the normal plot than that in the reduced plot at Hackberry Ridge.

Foraging height of all arboreal migrants combined was higher in reduced plots than in normal plots ( $t = 5.7$ ,  $df = 1416$ ,  $P < 0.0001$ ). Plants used were also taller in reduced plots than in normal plots ( $t = 8.1$ ,  $df = 1504$ ,  $P < 0.0001$ ), and plants used in reduced plots had higher DBHs as well ( $t = 14.1$ ,  $df = 1344$ ,  $P < 0.0001$ ). Canopy heights of both plots were similar at each site. These results are possibly due to the higher availability of saplings and shrubs in normal plots than reduced plots. In a test on the ratios of foraging height to tree height, normal and reduced plots did not differ

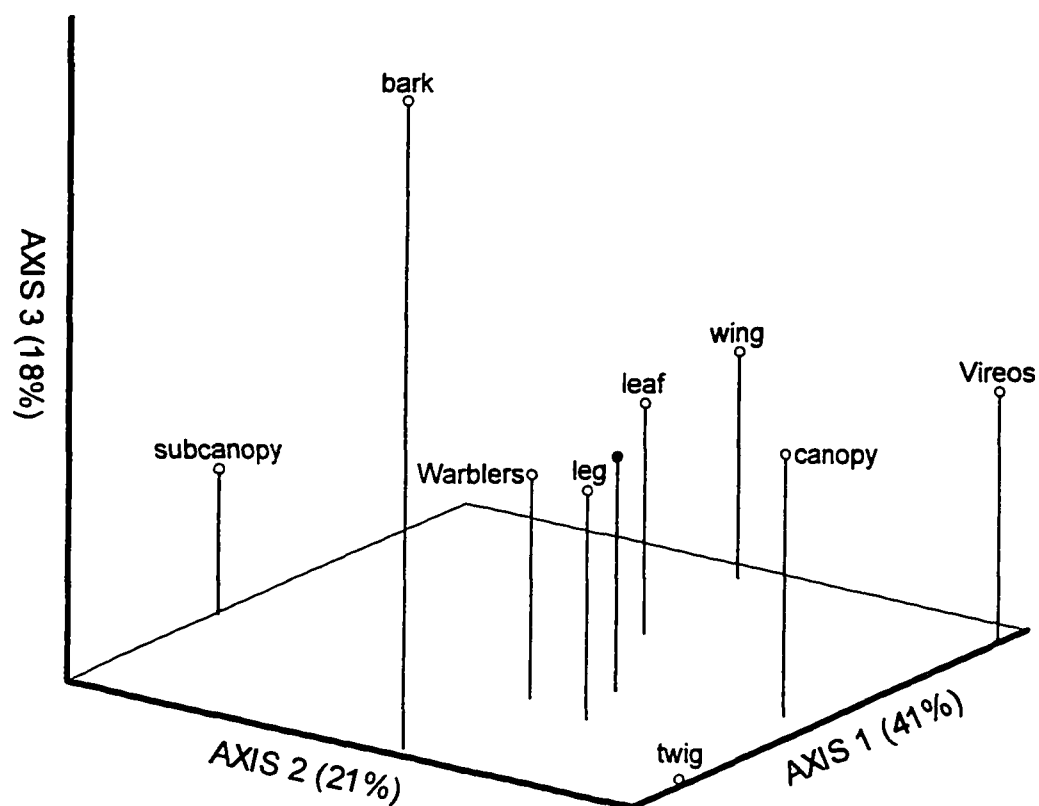


Figure 1.7. Multiple correspondence analysis of attack behaviors, habitat strata, and foraging substrates between warblers and vireos at Gulf coast stopover sites 1993-1994. "Wing" indicates wing-powered maneuvers, and so does "leg" for leg-powered maneuvers. The origin is at the solid circle.

significantly. In a simple linear regression model for arboreal migrants excluding the Common Yellowthroat and the Hooded Warbler (Figure 1.8), the difference of foraging height between reduced and normal plots was greater for subcanopy species than for canopy species. Subcanopy species foraged higher in reduced plots than in normal plots, but there was no clear trend in the difference of foraging height between plots for canopy species. Also there was greater overlap between the foraging heights of subcanopy and canopy species in reduced plots than in normal plots (Figure 1.9). Note that in this analysis the grouping of subcanopy and canopy species was based on the clear gap of foraging height in normal plots (about 6.8 m, Figure 1.8). The species composition of these two groups might differ slightly from that based on overall foraging height or habitat strata. On the other hand, Hooded Warblers and Common Yellowthroats foraged lower in reduced plots than in normal plots because these two species are more obligatory understory species; if they could not find understory patches in a plot, they might leave. In addition, understory patches in reduced plots were more localized and attached to the ground. In contrast, normal plots had more complete understory vegetation, extending from ground to subcanopy; this also provided more opportunities for foraging.

G tests between use and availability of habitat strata by arboreal migrants at each plot were all significant ( $P < 0.001$  for all plots). Canopy level at all sites was selected by arboreal migrants as well as subcanopy level in the normal plot at Smith Point (selection index  $> 1$ , Table 1.11). Subcanopy level in other plots and all shrubs level

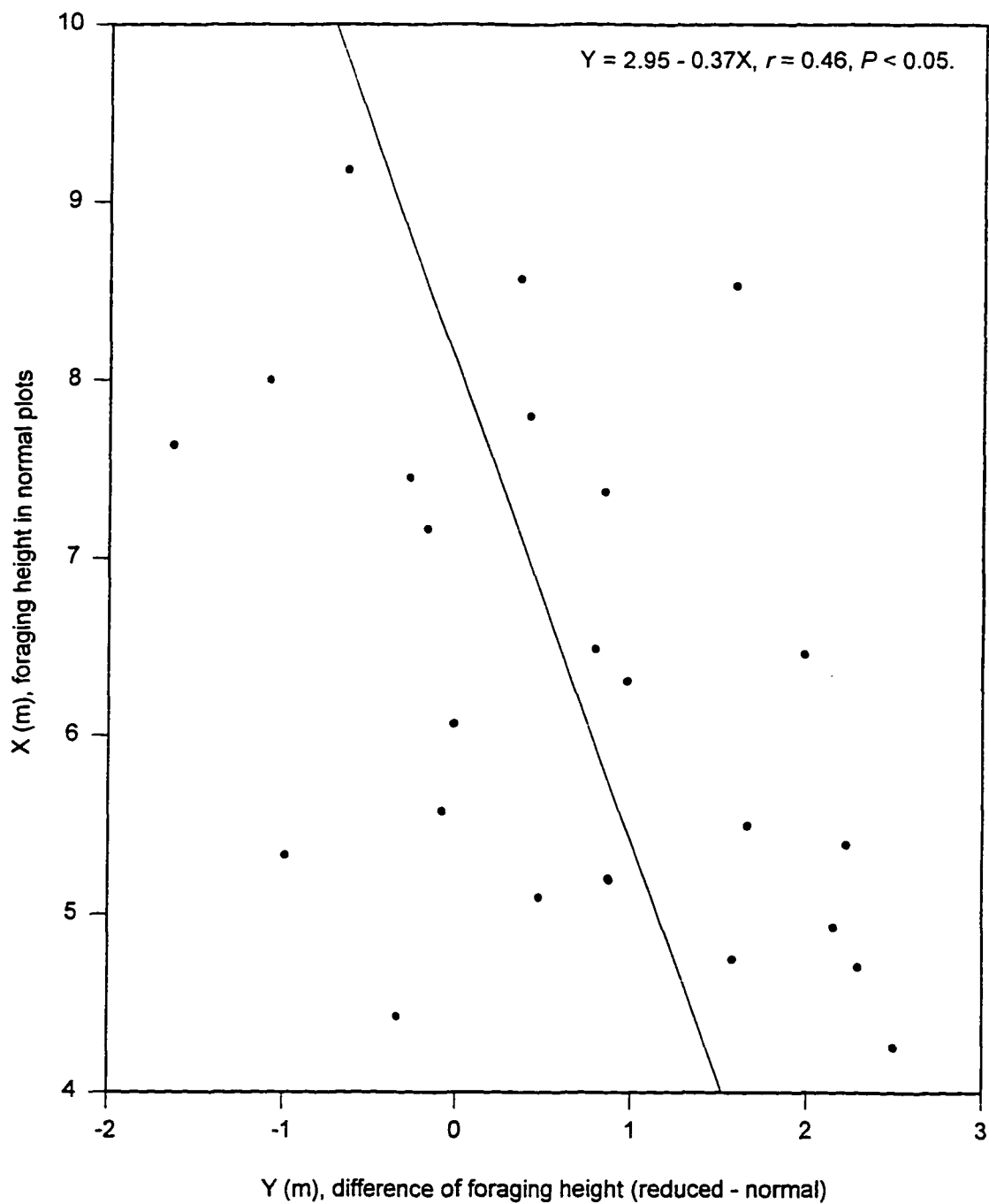


Figure 1.8. Simple linear regression between foraging height in normal plots and the difference of foraging heights between reduced and normal plots for subcanopy and canopy migrants at Gulf coast stopover sites, 1993-1994.

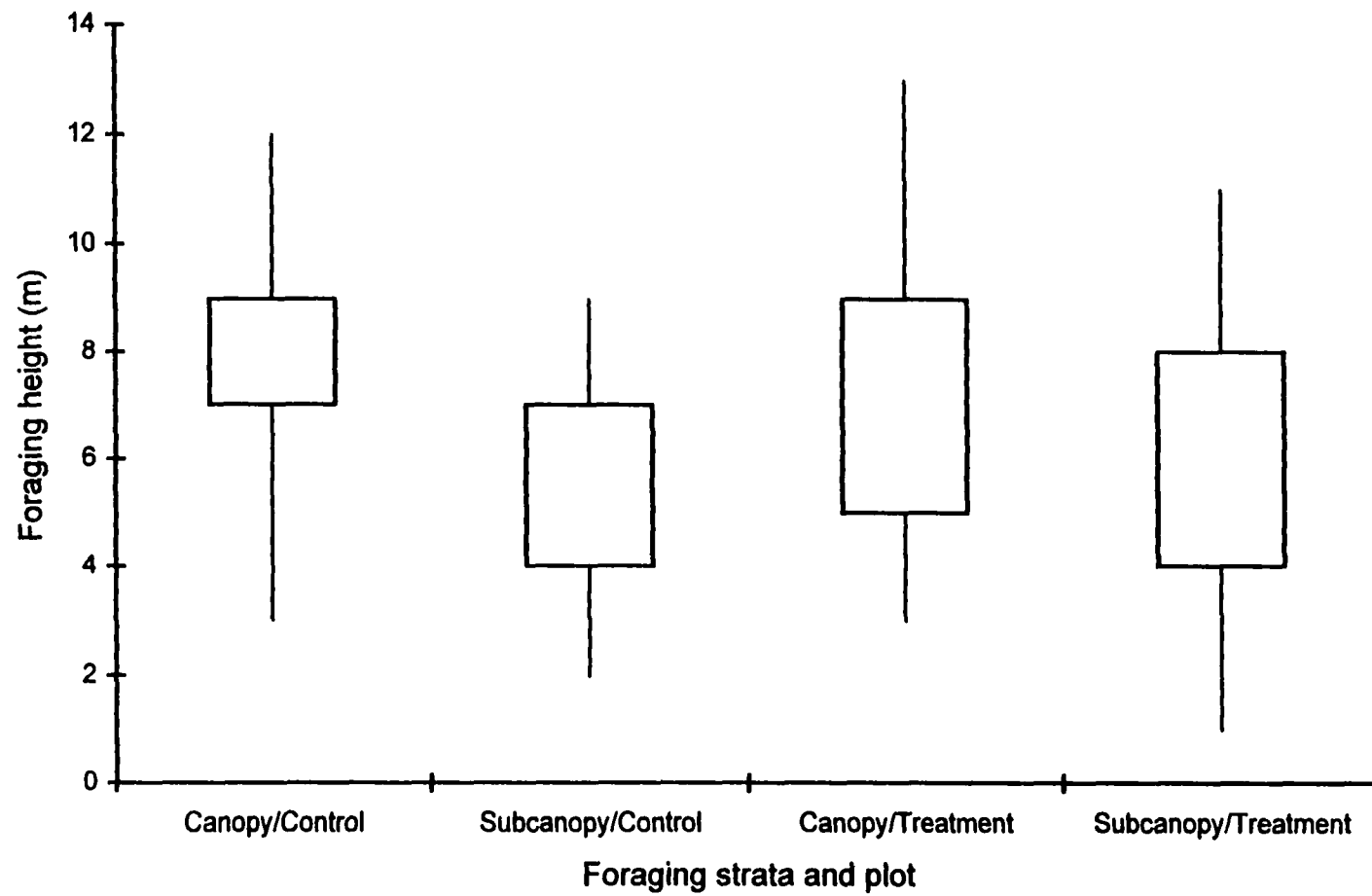


Figure 1.9. Foraging heights of canopy and subcanopy migrants between plots at Gulf coast stopover sites, 1993-1994. Boxes indicate quantile 1 to 3, and lines 90% limit.



Table 1.11. Habitat strata use and availability of all aboreal migrants in each plot at Gulf coast stopover sites, 1994.

Site, plot Habitat strata	Use (%)	Availability (%)	Selection index	Standardized index
<b>Grand Chenier, normal (411)<sup>a</sup></b>				
Shrubs	0.7	15.4	0.045*	0.019
Subcanopy	33.1	38.7	0.855	0.365
Canopy	66.2	45.9	1.441	0.616
<b>Grand Chenier, reduced (304)</b>				
Shrubs	2.0	2.7	0.741	0.289
Subcanopy	19.4	36.7	0.529*	0.206
Canopy	78.6	60.6	1.297*	0.505
<b>Hackberry Ridge, normal (268)</b>				
Shrubs	5.2	26.3	0.198*	0.073
Subcanopy	32.5	34.0	0.956	0.351
Canopy	62.3	39.7	1.569*	0.576
<b>Hackberry Ridge, reduced (278)</b>				
Shrubs	1.8	5.3	0.340*	0.154
Subcanopy	19.8	31.7	0.625*	0.283
Canopy	78.4	63.0	1.244*	0.563
<b>Smith Point, normal (111)</b>				
Shrubs	6.3	26.6	0.237*	0.085
Subcanopy	47.8	36.6	1.306	0.468
Canopy	45.9	36.8	1.247	0.447
<b>Smith Point, reduced (129)</b>				
Shrubs	8.5	27.0	0.315*	0.117
Subcanopy	20.2	32.4	0.623*	0.231
Canopy	71.3	40.6	1.756*	0.652

<sup>a</sup> Sample size of use; availabilities of habitat strata were calculated from all random points at each plot.

\* Indicates significant from simultaneous Bonferroni Z tests.

were avoided. This means that most arboreal migrants foraged in the subcanopy or canopy levels, and only a few species used the understory in this study.

G tests between use and availability of plant species by arboreal migrants at each site were all significant ( $P < 0.001$  for all sites). At Grand Chenier, honeylocust, deciduous holly, green hawthorn, poison ivy, and other species were selected; however, American elm, hackberry, live oak, and grape vine were avoided by arboreal migrants (Table 1.12). Honeylocusts and green hawthorns were also selected at Hackberry Ridge, but Chinaberries, live oak, grape vine, and others were avoided. Hackberry, red mulberry, and Japanese honeysuckle were used roughly according to their availability. Live oaks, which were avoided at Grand Chenier and Hackberry Ridge, were selected as well as yaupons and Japanese honeysuckles at Smith Point. In contrast, Chinese tallow trees, cherry laurels, and others were avoided. When selection indices were applied, poison ivy, honeylocust, other species, and green hawthorn were used twice as frequently as their availability if all plant species were equally available at Grand Chenier (Table 1.12). At Hackberry Ridge, honeylocust and green hawthorn were selected four times more than their availability. Japanese honeysuckles were selected more than twice as much as yaupon and live oaks; the latter two species were selected in similar degree at Smith Point.

Plant species that had large enough sample sizes to be analyzed in the G test were those common species or especially selected ones (Table 1.13). Only the Tennessee Warbler differed significantly in the goodness-of-fit test between use and availability of plant species. For Red-eyed Vireos, honeylocusts were highly selected,

Table 1.12. Plant species use and availability of all arboreal migrants within each study site at Gulf coast stopover sites, 1994.

Site			Selection	Standardized
Plant species	Use (%)	Availability (%)	index	index <sup>a</sup>
<b>Grand Chenier</b>				
American elm	6.7	19.3	0.347*	0.022
hackberry	21.7	31.4	0.691*	0.044
honeylocust	11.7	3.7	3.162	0.200
live oak	20.4	27.0	0.756	0.048
deciduous holly	3.0	2.0	1.500	0.095
green hawthorn	15.1	7.1	2.127	0.134
grape vine	2.0	3.1	0.645	0.041
poison ivy	3.7	1.0	3.700	0.234
others	15.7	5.4	2.907	0.184
Sample size	299	296		
<b>Hackberry Ridge</b>				
Chinaberry	0.2	2.6	0.077*	0.006
hackberry	62.7	62.7	1.000	0.079
honeylocust	11.7	2.9	4.034	0.321
live oak	3.8	5.6	0.679	0.054
red mulberry	2.7	2.6	1.038	0.082
green hawthorn	1.4	0.4	3.500	0.278
grape vine	14.4	16.8	0.857	0.068
Japanese honeysuckle	0.9	0.9	1.000	0.079
others	2.2	5.5	0.400*	0.032
Sample size	549	540		
<b>Smith Point</b>				
Chinese tallow	1.2	11.8	0.102*	0.014
live oak	72.5	57.6	1.259*	0.168
cherry laurel	2.9	13.4	0.216*	0.029
yaupon	14.8	9.7	1.526	0.203
Japanese honeysuckle	4.5	1.2	3.750	0.500
others	4.1	6.3	0.651	0.087
Sample size	243	238		

<sup>a</sup> Standardized indices are summed to 1 for each site.

\* Significant difference from simultaneous Bonferroni Z tests.

Table 1.13. Plant species use and availability of the five most frequently observed Neotropical migrants at Gulf coast stopover sites, 1994.

Migrant	Plant species	Use (%)	Availability (%)	Selection index	Standardized index <sup>a</sup>
<b>Red-eyed Vireo (78)<sup>b</sup></b>					
	Hackberry	57.7	59.0	0.978	0.146
	Honeylocust	10.3	2.6	3.962	0.591
	Live oak	11.5	11.5	1.000	0.149
	Others	20.5	26.9	0.762	0.114
<b>Tennessee Warbler (87)</b>					
	Grape vine	3.5	8.1	0.432	0.034
	Hackberry	28.7	43.7	0.657	0.051
	Honeylocust	34.5	3.4	10.147	0.790
	Live oak	20.7	18.4	1.125	0.088
	Others	12.6	26.4	0.477*	0.037
<b>Magnolia Warbler (74)</b>					
	Grape vine	9.5	16.2	0.586	0.134
	Hackberry	32.4	46.0	0.704	0.161
	Live oak	24.3	18.9	1.286	0.295
	Others	33.8	18.9	1.788	0.410
<b>Bay-breasted Warbler (107)</b>					
	Grape vine	15.0	13.1	1.145	0.318
	Hackberry	63.6	52.3	1.216	0.338
	Live oak	9.3	15.0	0.620	0.172
	Others	12.1	19.6	0.617	0.171
<b>Black-and-white Warbler (79)</b>					
	Grape vine	7.6	10.1	0.752	0.196
	Hackberry	30.4	30.4	1.000	0.261
	Live oak	38.0	27.9	1.362	0.355
	Others	24.0	31.6	0.759	0.198

<sup>a</sup> Standardized indices are summed to 1 for each migrant.

<sup>b</sup> Sample size are same for both use and availability.

\* Significant difference from simultaneous Bonferroni Z tests.

about four times as frequently as live oaks and hackberry trees, if all plant species were equally available. Tennessee Warblers selected honeylocust trees 10 times more than availability, and the intensity of use of honeylocust was 9 to 23 times more than that of all other plant species. MAWA, BBWA, and BAWW used the same categories of plant species: grape vine, hackberry tree, live oak, and others. Bay-breasted Warblers selected grape vine and hackberry and avoided live oak and others, whereas Magnolia Warblers used them in a reverse way, although the magnitude were not the same. "Others" consisted mainly of understory species such as green hawthorn, yaupon, and Japanese honeysuckle; the availability of these individual plants was very low. In contrast, Black-and-white Warblers selected live oak, avoided grape vine and others, and used hackberry exactly to its availability.

Ground foragers strongly selected certain microhabitat when foraging. All ground foragers except the Swainson's Thrush were found to forage selectively on ground with different microhabitat characteristics than random points (Table 1.14). All ground foragers avoided areas with dense vegetation. Variables that were good discriminators for separating use from availability differed from species to species. Gray-cheeked Thrushes and Wood Thrushes significantly avoided herbaceous areas. Gray Catbirds selected ground with more fallen debris, whereas Northern Waterthrushes selected water and muddy areas to forage and avoided vegetation areas. Ovenbirds slightly selected areas with more leaf litter ( $P = 0.09$ ).

Table 1.14. Comparison of use and availability of microhabitats of six ground foragers at Gulf coast stopover sites, 1994. All random points were combined as availability indices for comparisons. Variation presented are standard errors. Results of logistic regression are presented. Species codes are listed in Table 1.1.

Species	Use/availability	Herbs (%)	Leaf litter (%)	Fallen debris (%)	Water (%)	Mud (%)	Chi-square <sup>a</sup>	P
All species	Availability	66.1 ± 3.6	48.3 ± 4.3	9.4 ± 1.1	3.8 ± 1.6	11.3 ± 2.8		
	Use	32.8 ± 2.8	62.4 ± 3.7	14.7 ± 1.4	9.9 ± 2.3	22.9 ± 3.4	51.78	0.0001
GCTH (18) <sup>b</sup>	Use	37.8 ± 7.6	47.2 ± 8.5	11.9 ± 2.6	2.5 ± 2.2	25.6 ± 8.6	13.71	0.0176
SWTH (10)	Use	34.5 ± 9.3	65.0 ± 11.4	11.0 ± 2.3	12.0 ± 8.1	16.0 ± 10.2	7.19	0.2071
WOTH (18)	Use	29.7 ± 7.2	80.6 ± 7.7	15.3 ± 2.6	0.0 ± 0.0	13.3 ± 6.6	20.12	0.0012
GRCA (10)	Use	20.5 ± 6.0	95.0 ± 2.2	31.0 ± 5.3	0.0 ± 0.0	4.0 ± 4.0	29.22	0.0001
NOWA (26)	Use	22.7 ± 4.9	30.8 ± 6.2	11.7 ± 3.3	34.2 ± 7.0	54.6 ± 7.4	66.06	0.0001
OVEN (25)	Use	46.2 ± 5.5	79.0 ± 6.6	14.4 ± 2.6	0.0 ± 0.0	5.2 ± 4.1	14.50	0.0127

<sup>a</sup> Likelihood ratio Chi-square tests.

<sup>b</sup> Sample size.

## DISCUSSION

### Foraging Behavior

Each migrant species has its unique combination of attack behavior, habitat strata, and substrate use (Appendix). However, there was less difference in the use of perch diameter and crown position.

If a species uses a particular substrates for more than 75% of its foraging attempts (Remsen and Parker 1984), then it can be considered as a specialist in foraging. The Worm-eating Warbler can be considered as a dead-leaf specialist, the Black-and-white Warbler as a bark specialist, and the Wood Thrush as a leaf litter specialist. Other arboreal migrants mainly foraging on live foliage.

The Worm-eating Warbler, which is a dead-leaf specialist on the wintering grounds, only uses this substrate about 11% of the observations on the breeding grounds (Greenberg 1987). In this study, the Worm-eating Warbler used dead leaves in a manner similar to that in the overwintering period. The Worm-eating Warbler searched for dead leaves most of the time during the spring migration, but Greenberg (1987) found that the Worm-eating Warbler mainly forage in live-foliage at a breeding location in Maryland. How is such a dramatic change possible just within a week or a month? Greenberg (1987) also found that the relative abundance of dead and live leaves between the temperate and tropical study sites are very similar. However, the change in the relative abundance and type of dead and live leaf arthropods may be responsible for the behavioral shift of the Worm-eating Warbler (Remsen and Parker 1984, Greenberg

1987). Accordingly, dead leaves were probably profitable to the Worm-eating Warbler during spring migration at Gulf coast stopover sites.

Blue-winged Warblers and Golden-winged Warblers occasionally foraged on dead or curled leaves. It appears that these two species exploited freshly dead or curled leaves in leaf clusters instead of suspended leaf litter that was the main foraging substrate of the Worm-eating Warbler. The size of dead leaves that used by Blue-winged Warblers and Golden-winged Warblers appeared to be smaller compared to those used by Worm-eating Warblers. The difference between the characteristics of dead leaves used by these two groups may be explained by the bill size of these species (Remsen and Parker 1984).

### **Habitat Selection**

Most migrants select en-route habitat similar to their breeding habitat (Parnell 1969, McCann et al. 1993, Moore et al. 1995). For example, after trans-Gulf flight, most forest-dwelling migrants elected to land in woods rather than marshes or fields. When a smaller scale is considered, habitat structure (e.g., strata) becomes important. For example, Hackberry Ridge had a clearly distinguishable difference in understory vegetation between normal and reduced plots, and more migrants were recorded foraging in understory level in normal plots than in reduced plots. However, the contrast of understory vegetation between plots was not so clear at Grand Chenier and Smith Point, and migrants used understory level in similar frequencies between plots at these two sites. MacArthur (1964) found that vegetation density or layer structure had great influences on the diversity of breeding birds. This effect may be present at



stopover sites as well. Thus the presence of a certain habitat strata could be considered as an intrinsic factor of suitable stopover habitats. Another example is the Hooded Warbler that was more often encountered in normal plots ( $n = 30$ ) than in reduced plots ( $n = 17$ ). In addition, most observations in reduced plots were from Smith Point, where thick understory was present in both plots.

Subcanopy migrants foraged significantly lower in normal plots than in reduced plots (Figure 1.8). This might be due to the relatively contiguous vegetation from understory to canopy in normal plots. This also implies that the impact of habitat degradation due to grazing and browsing by cattle and deer affected not only understory species, but also subcanopy species. The degree of impact is probably lower for subcanopy species because subcanopy vegetation is less damaged than understory vegetation, and subcanopy species were abundant in both normal and reduced plots. However, in the long run, plant species composition may change due to differential grazing and regeneration.

Ground foragers used areas with far fewer herbs or grasses than random points (Table 1.14). All reduced plots, especially at Hackberry Ridge, had much more ground cover than the normal plots (Figure 1.1). Grasses are usually associated with strong sunlight. Reduced plots had much less understory and subcanopy vegetation. This might result in high penetration of sunlight onto the ground level that would benefit the growth of grassy or herbaceous vegetation in reduced plots. All ground foragers except the Swainson's Thrush were encountered more frequently in normal plots than in reduced plots ( $G^2 = 11.1$ ,  $df = 5$ ,  $P = 0.049$ ). This indicates that the alteration of

understory vegetation also has a great impact on ground foragers in addition to understory and subcanopy species. The change of ground vegetation probably altered the microhabitat and hence the prey types. Besides the availability of prey, dense ground vegetation may reduce the visibility for detecting predators.

In addition to habitat structure, some migrants appeared to be attracted by certain plant species in this study. Thus, plant species composition is an important index of suitable stopover habitats. Holmes and Robinson (1981) also noticed the important association between bird and plant species on a temperate breeding ground. Such relationships can be widespread because morphological constraint of birds might restrict them to forage in plant species that are relatively more profitable to them (Graber and Graber 1983, Holmes and Schultz 1988). The adaptation to forage in trees with particular foliage structures may be responsible for the selection of plant species by birds (Holmes and Robinson 1981, Holmes and Schultz 1988); however, Hutto (1985a, b) found that food availability also plays a critical role in determining where migrants forage. Migrants are rather opportunistic; they probably select specific food sources rather than specific tree species. In fact, those trees species, e.g., honeylocust, hackberry, and live oak, used intensively by migrants tended to harbor more insects than others (Barrow and Spengler, unpubl. data).

### **Plant Species Use**

Honeylocust and green hawthorn were selected wherever present. Live oaks were selected for at Smith Point, but selected against at both Grand Chenier and Hackberry Ridge. At Smith Point, live oaks and Chinese tallow trees occupied most of

the canopy. This site had no honeylocust, green hawthorn, or hackberry, those species used intensively by arboreal migrants at the other two sites (48.5% and 75.78% for Grand Chenier and Hackberry Ridge, respectively). Chinese tallow trees were strongly avoided by migrants; they were used for only 1.2% out of 11.8% at Smith Point. This implies that live oak is probably not the first-choice tree. But if other better selections are omitted, live oak can be a substitute. However, care must be taken to distinguish between a resource that is highly favored but rare and seldom used and a resource that is less favored but is the only one available and thus comprises a larger proportion of use (Petrides 1975, White and Garrott 1990, Manly et al. 1993). Live oak is an example for the latter case. In fact, live oak and hackberry tree combined accounted for about 60% of the availability at all sites, and they were used for 40–70%. Thus the high availability of these two tree species may outweigh the preference for some more favorable trees that occur at a very low density (Emlen 1966, Manly et al. 1993) because the cost for searching rare plant species can be significantly higher than for common species (Barrow et al. in press).

Honeylocusts were used intensively by some migrants, especially the Tennessee Warbler. Honeylocusts contain diverse prey types for various migrants. Besides numerous insects, flowers and nectar were also abundant during late migration season; these resources were especially important for occasional nectarivores, e.g., the Tennessee Warbler. Honeylocusts also harbor another nutrient food resource; almost every leaf bud contains a pupa. Some migrants, including Indigo Buntings (*Passerina*

*cyanea*), Rose-breasted Grosbeaks, and Blue Grosbeaks (*Guiraca caerulea*), feed frequently on such leaf buds.

Although red mulberry was also an important tree species in providing food during migration, its main contribution is its fruits. However, the fruiting period is relatively short and late in the migration season, and many resident species used this resource as well. Warblers were seldom observed eating fruits in red mulberry, which might be due to their morphological constraint. On the other hand, mulberry provides important food resources for larger migrants such as vireos, Gray Catbirds, orioles, tanagers, and Rose-breasted Grosbeaks. Thrushes occasionally ate mulberries in the canopy or picked those that dropped on the ground.

Although the toothache tree (*Zanthoxylum clavaherculis*) may be a common native plant on the Chenier Plain historically (Barrow et al. in press), there were just a few in the study plots. Migrants were seldom recorded foraging in this tree. However, an insect outbreak specific to this tree has been recorded in the past (Hine 1906). The importance of toothache-tree to migrants needs further study.

Most vine species, including poison ivy, provide important foraging substrates for migrants. Vines themselves as well as the environment that they create are important factors to make them profitable patches for migrants. Vine tangles have been found to be an important foraging substrate for some breeding migrants in a bottomland hardwood forest in northern Louisiana (Barrow 1990). Many vines grew on understory tree species. Although competition may take place between the two, they actually form a special microhabitat for birds. The Hooded warbler was not the only species that used

this particular habitat. Other species like RCKI, WEWA, AMRE, MAWA, and CSWA all used this habitat frequently. Because vine tangles usually harbor abundant dead leaves (Gradwohl and Greenberg 1982), they are also important food patches for the Worm-eating Warbler. These species were more frequently encountered in normal plots because of more understory vegetation there. Thus the decrease of understory vegetation of stopover sites are most likely to affect these migrants.

### **Community Consideration**

In such a huge bird community, we may wonder how migrants interact with one another. Although competition among individuals has been considered high at stopover sites (Moore and Yong 1991), I actually seldom observed aggressive behavior among birds even on fallout days. Some possible explanations are suggested here. Niche segregation is probably the most convincing reason. As illustrated in Figure 1.7, warblers and vireos are separated from each other well in terms of ecological niche. Species-specific habitat selection is considered common during stopover (this study, Parnell 1969, Bairlein 1983, Holmes and Robinson 1988). The use of foraging maneuvers, habitat strata, substrates, plant species, and prey, all differ among species. Thus, aggressive encounters between individuals are greatly reduced (Berthold 1993). However, competition through food depression is apparent (Moore and Yong 1991) because migrants with similar diet and strong energy demands are concentrated in a small area (this study, Hutto 1985b, Moore and Simons 1992). Loria and Moore (1990) reported that migrants replenish energy reserves more slowly during periods of high migrant density.

Subcanopy migrants expanded their foraging heights upward in reduced plots (Figure 1.9), where the subcanopy and shrub levels were much sparser than that in normal plots. This resulted in greater overlap in foraging heights between canopy and subcanopy species in reduced plots and could hence increase competition between the two groups. Competition among migrants at stopover sites may imply that suitable habitats are scarce or patchily distributed. Consequently, the reduction in weight gain may force migrants, especially fat-depleted ones, to stay longer during stopover (Biebach 1985, Biebach et al. 1986, Moore and Kerlinger 1987) and to delay further their arrival on the breeding grounds (Yong and Moore 1993, Moore et al. 1995).

Although evidence for stopover territoriality was found for the Northern Waterthrush (Rappole and Warner 1976), little field data support the presence of territorial behavior for arboreal migrants (but see Bibby and Green 1980, and Sealy 1988, 1989). Based on a theoretical model of territory behavior, the economic defendability of a territory decreases when intrusions increase (Brown 1964, Gill and Wolf 1975). This can partly explain why aggressive behavior is rare during stopover.

### **Comments about Methodology**

Use and availability analysis is frequently used to determine resource selection or avoidance by animals, especially in wildlife management (e.g., Neu et al. 1974, Johnson 1980, Aebischer et al. 1993). When the absolute availability of resources are not measurable, a random sample is usually taken to estimate the availability. However, a simple and appropriate sampling scheme for estimating resource availability in avian foraging is still lacking. Thus, a comparison between the two sampling methods used in

this study may provide some insights for later studies. One disadvantage of the first method (used in 1993) is the selection of a maximum pace. A random pace(s) from 1 to 25 was taken from the location where the last foraging maneuver was recorded. It was not uncommon to record the same tree used by the migrant as the random plant if the tree had a widespread crown. This indicates that the maximum of 25 paces is probably too short for plots with many large trees and less understory vegetation. Further, if the random plant is within 25 paces (average 12.5 paces) of the plant used, then the random plant probably will still be within the foraging patch of the bird. If random points are measured from the same patch in which the birds are foraging, then they are not independent. Second, the random plant that I sampled was related to the foraging location of birds. This means that what I used as a random plant to some degree depended on the used plant. For example, little understory vegetation grew under live oaks, and thus the chance to get shrubs as random plants was low when birds were recorded foraging in live oaks. On the other hand, shrubs and/or saplings usually grew with one another. As a result, it was very likely to sample shrubs or saplings as random plants when birds foraged in shrubs or saplings. Third, random points were located on a two dimensional plane, the ground, based on the first method. Because I did not have another coordinate for the third dimension, the height, several candidates were usually possible for a selected point. An herb, a shrub, a sapling, and a tree could all overlap at the same location. In such a situation, an herb or a shrub was usually chosen because they outnumbered saplings and trees. As a result, many palmettos (*Sabal minor*) were counted as random plants even when the bird that I used to get the random point was a

canopy species. Finally, it is difficult to reach an availability index from such data set. When calculating the availability index, basal area or other density indices are often incorporated to correct frequency data (Holmes and Robinson 1981, Barrow et al. in press). Although the final index may be a better choice to represent the absolute availability, it also includes further uncertainty from sampling errors.

Due to these drawbacks of the first method, a revised method was developed later in 1994. Some advantages of this method are described as follows. First, random plants are sampled separately from used plants. A different sampling scheme was used to choose random plants that had no connection with the used plants except the foraging height. The foraging height of birds was used as the third coordinate to locate random points in the three-dimensional space. Second, because random plants were chosen based on the distribution of foraging height of the migrants, only plants within the potential foraging range of migrants had the chance to be included in the random plants data set. Therefore, these data can also be used to compare use and availability of plants for each migrant species (Table 1.13). The disadvantage of this method is that the resultant availability probably cannot represent the plant community well because the random sample will be biased by the composition of bird species observed. For instance, more canopy species were observed in this study, and hence more random plants were sampled from the canopy stratum. In fact, the availability of plants recorded in such a way might make more sense in terms of potential use because I leave out those plants that will never be used according to the foraging height of birds. Third, frequency alone is enough to perform use-availability analysis. Because we use three



coordinates to locate the random point, there is only one choice for the random point in the space under the canopy. As a result, I do not have to measure basal area or density indices of plants in the study plots. In a sense, this method actually takes volume into account. Finally, because the movements of migrants are ephemeral, it is more efficient to concentrate on collecting foraging behavior when many migrants appear in the study plot and work on the random plants later on.

A detailed survey of every stem was conducted in 1995 to find the absolute availability of plants at all sites. More understanding will result if we compare data from the two sampling methods with the actual availability. Another possible method is to use a random height instead of the foraging height of birds to find the random plant.

Some attack behaviors such as probe and flake are actually not attack behaviors. Although Remsen and Robinson (1990) classified these behaviors as subsurface maneuvers under attack behavior, such behaviors are actually used to find prey instead of attacking them. Thus “exploratory maneuver” is probably a better term for such behavior. Other exploratory maneuvers like gape, peck, pry, and pull were also recorded in this study. When these maneuvers are counted as attack behavior, they are indiscernibly included in calculating foraging rate. Thus we usually overestimate foraging rates of those species that use such behaviors. Gray Catbirds were often observed using consecutive flakes up to 20 times and then using a glean to attack the prey. Thus flake is definitely an exploratory maneuver rather than an attack behavior. As a result, when one calculates foraging rate, he should not include flakes. However, other subsurface maneuvers probably function as an exploratory maneuver first, and

attack behavior as well if they detect prey. As a result, it is difficult to tell whether birds catch prey or not when they use probes or gapes. Greenberg (1987) used the action of bill-wipe upon removal from a dead leaf to determine successful probes of Worm-eating Warblers and found that success rate is about 7% on the breeding grounds, and 5% on the wintering grounds.

Perch diameter is usually recorded as  $< 1$  or  $> 1$  cm (this study, Barrow 1990) or separated into several categories by size (e.g., Craig 1989, Moyer 1993). On the other hand, some researchers (e.g., Block 1990) recorded perch substrates instead of perch size. And still others (e.g., Petit et al. 1990b, Sillett 1994, Kratter 1995) recorded both perch substrate and perch size. Although I recorded perch diameter as in Barrow (1990), I actually think that perch substrate has more biological meaning because we lose some information when we only record perch diameter. The association between perch and foraging substrates cannot be found from such a data set. A bird hanging on a vine has the same category of perch diameter as a bird gleaning from a twig. Attack behavior, foraging substrate, and perch substrate are to some degree associated with one another. But researchers are seldom aware that perch substrate can actually affect attack behavior. Although perch substrate and foraging substrate are highly correlated with each other (see Block 1990), birds do not always attack the substrate on which they perch. A strong association can be easily found between perching on twigs and attacking on leaves, and glean is usually employed in such situations. However, perch size may be helpful when very different sizes of birds are included in a study (e.g., Sillett 1994).

## CONSERVATION APPLICATIONS

Most migrants fly over the 40–50 km width of the coastal marshes and land in inland forests when weather conditions are fair (about 80% of the time)(Gauthreaux 1971). During inclement weather, however, almost all migrants are forced to land in coastal cheniers. Unfortunately, forested areas on the cheniers are restricted and confined by marshes and pastures. In addition, many woodlands are only a few hectares in extent and still in a state of continuous loss (Moore and Simons 1992, Barrow et al. in press). Thus conservation efforts in this area becomes critical because any further loss of stopover habitat may affect the survival of Neotropical migrants. Many researches have found that intrinsic quality of stopover habitat is related to the length of stay and rate of fat deposition of migrants (Martin 1980, Bairlein 1983, Hutto 1985b). If migrants cannot find enough food to continue migration, then they probably stay longer. The delay of arrival on the breeding ground may result in their relegation to lower-quality territories (Moore et al. 1995) or even loss of breeding opportunities (Sherry and Holmes 1989).

Some conservation implications can be made from this study. Such implications primarily center on within-habitat level rather than between-habitat scale. First, understory vegetation is an important feature for a suitable stopover habitat. The presence of understory level provides more and diverse habitat for migrants, especially ground, and understory species. In all normal plots, which had more extensive understory, more ground and understory foragers were recorded during foraging observation. Subcanopy and canopy species also had more concentrated and less

overlapped foraging bands in the normal plots than in the reduced plots. The loss of understory vegetation due to cattle or deer grazing and browsing is widespread because most cheniers are privately owned and managed for cattle. In contrast, the creation or increase of understory vegetation will improve the suitability of stopover habitat for migrants.

Second, some trees are usually kept for shade; in some pastures, several hectares of woods are retained for that purpose. In such woody tracts, understory vegetation is more likely to exist. Cattle were found to rest or overnight in woods with more vines and understory than woods with clear understory (pers. observ.). This may mean dense vegetation provides better shading during the daytime and warmer shelter at night. These speculations deserve further study. However, numerous tracks and direct observations during the study period agree with the hypothesis. This also implies that the increase of understory vegetation or structural complexity of woods can benefit both migrants and cattle. If this is verified, the establishment of more wooded tracts can be encouraged. Such projects will be promising for migrant conservation at Gulf coast stopover sites for both spring and fall migrations.

Third, plant species composition was found important for most migrants. Plant species such as honeylocust, green hawthorn, red mulberry, hackberry, live oak, yaupon, and most vine species contribute many foraging opportunities for migrants. An important feature of these plant species is that they all bear flowers or fruits during spring migration. Besides nectar and fruits, they also attract many insects. Structurally, vine tangles in the understory layer are an important feature that creates great foraging

opportunities for migrants, including species that search for dead leaves (Gradwohl and Greenberg 1982). In addition, a diverse plant community also ensures foraging opportunities to migrants. For example, honeylocusts will benefit smaller migrants, especially warblers. On the other hand, red mulberries provide fruits for larger migrants, such as Gray Catbirds and Rose-breasted Grosbeaks. Moreover, temporal diversity of plant species is also important to migrants. Caterpillar irruption on hackberry trees usually takes place before the peak of spring migration. In contrast, honeylocusts are used heavily in the late migration season. Whenever a restoration or rehabilitation project is designed (see Barrow et al. in press), plant species composition should be taken into account. Tree and vine species that can create temporal and spatial diversity of food resources for migrants are recommended.

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## **CHAPTER 2**

### **ANALYSIS OF SEARCHING MOVEMENTS OF INSECTIVOROUS MIGRATORY SONGBIRDS AT GULF COAST STOPOVER SITES**

#### **INTRODUCTION**

Remsen and Robinson (1990) classified foraging behavior of birds in terrestrial habitats into five basic components: search, attack, foraging site, food, and food handling. They said that “searching behavior includes those movements used to search for food or substrates that hide food; ..., “search” ends once food or food-hiding substrates are sighted and attacked” (Remsen and Robinson 1990). Searching behavior can be roughly divided into scanning and movement (O'Brien et al. 1990). Scanning, the action of head and eyes, which are used to spot prey, is not considered in this study, in part because it is nearly impossible to collect. In fact, I concentrated only on searching movements, or between-foraging-site movements as in Remsen and Robinson (1990).

Searching behavior has been studied less than attack behavior or foraging site because searching behavior is difficult to record. In addition, searching behavior is subtle and not as easy to distinguish as attack behavior or foraging site. However, searching behavior can be as important as or even more important than attack behavior in foraging birds because most birds spend more time searching for prey than attacking, and they must find food before they attack it. Searching behavior might provide a better view on the entire foraging process and give insight into more detailed decisions that birds make during foraging. Searching data are also helpful in ecomorphological



studies. Attack behavior has been found to have a close relationship with morphological characteristics of birds (e.g., Miles and Ricklefs 1984, Leisler and Winkler 1985). Such a relationship may also exist with searching behavior, but there is little literature on this topic.

The use of specific foraging tactics to acquire specific dietary needs affects foraging behaviors of birds (Krebs and Kacelnik 1991). Prey type and the distribution and abundance of prey might influence how birds search for them and affect foraging behavior (e.g., Davies 1977, Griffiths 1980, Graber and Graber 1983, Holmes and Schultz 1988, Lovette and Holmes 1995). Eckhardt (1979) observed two guilds of insectivorous birds in the Colorado Rocky Mountains and found that one group of birds have higher searching rates and have a foraging repertoire associated with passive prey, whereas another group of birds have lower searching rates and have a foraging repertoire associated with active prey. Huey and Pianka (1981) also found that widely foraging desert lizards generally eat more prey that are sedentary, unpredictably distributed, and clumped than do sit-and-wait lizards.

In addition to being affected by body size and type of attack behavior, distances of searching movements might be correlated with scanning diameter of birds (O'Brien et al. 1989, 1990). Optimal length and direction of movements can be predicted in some situations if we know the scanning diameter of animals (O'Brien et al. 1990). However, birds seldom forage in ideal conditions, and they must adapt to the changing nature of external conditions. Adaptability (or flexibility) thus results in more foraging possibilities, and possibly in higher survivorship (Lewontin 1978). As Hutto (1985)

pointed out, habitat use of migrating landbirds is rather determined by the extrinsic benefit of using a particular migration route than the habitat's intrinsic quality at stopover sites. Stopover habitat is presumably more diverse and unpredictable than the habitat on the breeding and wintering grounds. Consequently, birds might tend to use more diverse, and flexible foraging behavior at stopover sites (this study, Martin and Karr 1990).

Searching rate has been shown to be positively correlated with foraging rate in field studies (Robinson and Holmes 1982) and in theoretical foraging models (Schoener 1971, Stephens and Krebs 1986). Hutto (1990) recommended this index for its ease in measuring birds that forage in dense vegetation, and Lovette and Holmes (1995) used this index along with three other foraging variables to determine the relative availability of prey. In addition, from the standpoint of energy, searching movements may cost even more energy than attacking does for most perch-gleaners. Searching rate should be a useful index to describe foraging mode and may give insight into some aspects of foraging ecology (Eckhardt 1979, Remsen and Robinson 1990).

Searching behavior of forest birds has only been analyzed in a few studies (Williamson 1971; Morton 1980; Fitzpatrick 1981; Robinson and Holmes 1982, 1984; Holmes and Recher 1986; Lovette and Holmes 1995). In most studies, searching behavior was treated as a subset of foraging behavior and presented in a descriptive way. Both Robinson and Holmes (1982, 1984) in New Hampshire and Holmes and Recher (1986) in Australia found that searching tactics of insectivorous birds are related to vegetation structure and prey availability. Fitzpatrick (1981) found that visual field

complexity and prey dispersion characteristics are the two most important factors affecting searching strategies of tyrant flycatchers. How searching movements of birds are affected by external factors is still unclear.

“Chenier” is the term used in Louisiana for a relict beach ridge (Russell and Howe 1935). Cheniers are the only well-drained ground in the marshes bordering the Gulf of Mexico and are usually covered with woody plants. Consequently, cheniers are the only native forests in this vast marsh area, and they are critical habitat for forest-dwelling migrants. For more description of the Chenier Plain, see Barrow et al. (in press) and Gosselink et al. (1979). The Chenier Plain, especially along the Louisiana and eastern Texas coast, is the first potential stop for many northbound, Neotropical migrants after trans-Gulf migration in the spring. Many Neotropical migrants stopover at these cheniers, especially during periods of inclement weather (Lowery 1945; Gauthreaux 1971, 1972; Moore and Kerlinger 1987). These cheniers are also among the most southern forested areas in the United States used by some wintering migrants such as Yellow-rumped Warblers (*Dendroica coronata*), Ruby-crowned Kinglets (*Regulus calendula*), and Solitary Vireos (*Vireo solitarius*).

In this chapter, I analyze searching movements of birds as part of my studies of foraging ecology. First, I use correspondence and cluster analyses to study the relationships among migrants based on their searching movements. Second, I examine the effect of various factors such as site, plot, and flocking on the searching movements of birds.

## METHODS

This study was part of a larger project on stopover ecology of Neotropical migrants at three sites on the Chenier Plain during the spring migrations of 1993–1995. When documenting foraging behavior, I recorded searching movements, attack behaviors, and foraging sites of all insectivorous migrants. Because only data on searching movements are used in this chapter, I describe only the methods I used pertaining to searching movements.

Data on searching movements were collected mainly in the spring migration seasons of 1993 and 1994; during 1995, few data were collected. About 60 species of mostly Neotropical but some wintering migrants were recorded. Wintering migrants were abundant in early March and became scarcer as the migration season progressed; most wintering migrants had departed by the end of March. Neotropical migrants started to appear at mid-March and reached their peak numbers during the last week of April and the first week of May. The abundance of Neotropical migrants declined sharply after mid-May. During the migration season, thousands of Neotropical migrants were present in the study sites from time to time. The occurrence of these large numbers, “fallout,” often coincided with severe weather conditions, especially thunderstorms (Lowery 1945, 1955; Gauthreaux 1971).

### Study Area

I used three study sites along the northern coast of the Gulf of Mexico: (1) Grand Chenier, Cameron Parish, Louisiana; (2) Hackberry Ridge, Cameron Parish, Louisiana; and (3) Smith Point, Chambers County, Texas. The Grand Chenier site was a more

mature and diverse coastal forest than the other two sites. The Hackberry Ridge site had a low canopy and consisted primarily of hackberry trees (*Celtis laevigata*). The Smith Point site had very thick understory and many live oaks (*Quercus virginiana*) in the canopy. Plant species names are those of Kartesz and Kartesz (1980). For detailed description of the study sites, see Barrow et al. (in press).

Each study site consists of a “reduced” plot with a little to a moderate amount of understory, and a “normal” plot where the understory was denser. Each plot was intended to be a 100×300 m rectangular area, but this size plot could not be obtained at all sites because of the limited extent of woods available. Reduced and normal plots were adjacent at Grand Chenier, but separated at Hackberry Ridge (c.a. 1 km) and Smith Point (c.a. 100 m).

Each plot was oriented east-west, roughly parallel to the coastline. Within all study plots, I established grids marked with flags spaced every 25 m. Each flag was marked with a combination of a number (long axis) and a letter (short axis); these flags delineated the boundaries of many small blocks and several transect lines.

I started data collection on searching movements at the mid-migration season and only at Grand Chenier in 1993. In 1994, I traveled from site to site every week to equalize my effort among sites. In 1995, I spent about a week at Smith Point because I had less data from this site from previous years.

### **Recording Methods**

Searching movements were recorded along with other foraging behaviors when opportunities occurred as I repeatedly traversed the study plots. Attempts were made to

equalize effort in every part of the plot and not to concentrate sampling at any particular place. In addition, I tried not to gather data from the same bird more than once per day, e.g., not to stay at one spot too long, or to only observe individuals of different sexes or species at the same spot. Repeated sampling of individuals should be rare because most Neotropical migrants depart the night of their arrival (Gauthreaux 1971, 1972; Moore and Kerlinger 1987; Kuenzi et al. 1991).

I used “focal sampling” and “continuous recording” as recording methods (Martin and Bateson 1993). I quietly followed each bird encountered and entered observations into a tape recorder until the bird was lost from sight. If I could not determine what a bird was doing, I stopped recording. After a bird was identified, I recorded species, sex, if discernible, and time of day on the tape. I kept the recorder running. After saying “start,” I recorded in detail every searching movement and attack behavior as well as the distances (cm, by comparing to the body length) of the first observation of each kind of searching movements until I was no longer able to do so, usually because the bird departed. At that moment, I said “stop” and noted whether the bird was in a flock. Since 1994, I also recorded the species of tree the bird was in and whether any vines were in the area where the bird had been foraging. Bird density (high or low) was recorded in a field notebook with other information on foraging site. I obtained sequence and duration information from the tape with the aid of a stopwatch.

For classifying searching movements, I applied the scheme of Remsen and Robinson (1990) and made some modifications:

Hop -- movements made only by legs,

Flutter -- movements made mainly by legs and with the support of wings, and

Fly -- movements made by the beating of wings.

During 1994, I further divided flights into two types: flights within patches and flights between patches (Jander 1975). A patch could be a tree or a group of connected trees. Those flights used to pass a gap onto another tree or patch were for transporting rather than searching and thus they were not included in the analysis. I stopped recording when a bird started to fly out of the foraging patch.

### **Data Analysis**

Although the original project was designed for Neotropical migrants, I had many observations on wintering migrants, which were also included in the analysis. Wintering migrants included Yellow-rumped Warblers, Ruby-crowned Kinglets, and Solitary Vireos, as well as small numbers of Common Yellowthroats (*Geothlypis trichas*), Blue-gray Gnatcatchers (*Poliophtila caerulea*), and White-eyed Vireos (*Vireo griseus*). I included only arboreal insectivorous species in this chapter because all had similar searching modes. I excluded ground foragers such as thrushes (*Hylocichla* and *Catharus* spp.), Gray Catbirds (*Dumetella carolinensis*), Ovenbirds (*Seiurus aurocapillus*), and waterthrushes (*Seiurus motacilla* and *S. noveboracensis*). Species such as Rose-breasted Grosbeak (*Pheucticus ludovicianus*), and orioles (*Icterus spurius* and *I. galbula*) that were not strictly insectivorous were also excluded because they had different searching modes from truly insectivorous species. Bird names follow the American Ornithologists' Union (1983).

A minimum sample of at least 30 individuals, about 150 sequential observations, is needed for analysis of attack behavior or foraging site (Morrison 1984).

Unfortunately, there is no such source for minimum sample requirement for searching behavior. In a given period of time, many more searching movements were recorded than attack behaviors for most species. Thus, I included only species with  $\geq 20$  individuals or with total sequential observations of searching movements larger than 200. Furthermore, I used only searching sequences with duration  $\geq 10$  seconds. There were 31 species that met the sample size requirements (see Table 2.1).

Searching rate was defined as the number of searching movements per minute (Robinson and Holmes 1982). Searching rate was computed by dividing the total number of searching movements within a sequence by sequence duration. Searching rate was calculated for all sequences, and an average searching rate was calculated for each species.

Correspondence analysis (SAS Institute 1989) was performed on the frequencies of searching movements among species. Cluster analysis with complete linkage (SAS Institute 1989) was used to group the 31 migrant species based on frequencies of flight, searching rates, and hopping distances.

The distances between row (species) points are a measure of the discrepancy between row profiles and are related to the Chi-square distances (Greenacre 1984, Greenacre and Hastie 1987, Moser 1989). The same principle can also be applied to column (searching movement) points. Because the distances between row and column points are not defined, it is meaningless to interpret them (Greenacre 1984, Greenacre



Table 2.1. Number and relative frequencies of searching movements and searching rates of insectivorous migratory songbirds at Gulf coast stopover sites, 1993–1995. Searching rate is equal to number of movements per minute.

Family Common name (Scientific name)	Species code	Observations	Searching movement			Total	Searching rate $\bar{X} \pm SE$
			Hop (%)	Flutter (%)	Fly (%)		
<b>Cuculidae</b>							
Yellow-billed Cuckoo ( <i>Coccyzus americanus</i> )	YBCU	56	454 (74.4)	31 (5.1)	125 (20.5)	610	6.0 $\pm$ 0.6
<b>Tyrannidae</b>							
Acadian Flycatcher ( <i>Empidonax virens</i> )	ACFL	27	12 (17.4)	0 (0.0)	57 (82.6)	69	1.7 $\pm$ 0.3
Eastern Wood-Pewee ( <i>Contopus virens</i> )	EAWP	56	13 (18.8)	0 (0.0)	56 (81.2)	69	0.3 $\pm$ 0.1
<b>Muscicapidae</b>							
Ruby-crowned Kinglet ( <i>Regulus calendula</i> )	RCKI	128	2378 (82.5)	158 (5.5)	346 (12.0)	2882	24.7 $\pm$ 0.8
Blue-gray Gnatcatcher ( <i>Polioptila caerulea</i> )	BGGN	41	869 (85.4)	38 (3.7)	111 (10.9)	1018	26.6 $\pm$ 1.4
<b>Vireonidae</b>							
White-eyed Vireo ( <i>Vireo griseus</i> )	WEVI	80	1192 (80.9)	104 (7.1)	177 (12.0)	1473	17.9 $\pm$ 0.8
Solitary Vireo ( <i>Vireo solitarius</i> )	SOVI	23	238 (68.6)	23 (6.6)	86 (24.8)	347	11.3 $\pm$ 1.1
Yellow-throated Vireo ( <i>Vireo flavifrons</i> )	YTVI	18	331 (81.3)	31 (7.6)	45 (11.1)	407	16.2 $\pm$ 1.7
Philadelphia Vireo ( <i>Vireo philadelphicus</i> )	PHVI	28	366 (75.9)	19 (4.0)	97 (20.1)	482	13.5 $\pm$ 1.1
Red-eyed Vireo ( <i>Vireo olivaceus</i> )	REVI	291	2639 (78.0)	255 (7.5)	488 (14.5)	3382	14.6 $\pm$ 0.3
<b>Parulinae</b>							
Blue-winged Warbler ( <i>Vermivora pinus</i> )	BWWA	96	1228 (81.0)	89 (5.9)	199 (13.1)	1516	24.6 $\pm$ 1.2
Golden-winged Warbler ( <i>Vermivora chrysoptera</i> )	GWWA	31	469 (83.5)	31 (5.5)	62 (11.0)	562	22.9 $\pm$ 1.7
Tennessee Warbler ( <i>Vermivora peregrina</i> )	TEWA	175	2029 (86.3)	94 (3.9)	239 (9.8)	2425	20.2 $\pm$ 0.8
Northern Parula ( <i>Parula americana</i> )	NOPA	51	649 (84.6)	34 (4.4)	84 (11.0)	767	21.9 $\pm$ 1.4
Yellow Warbler ( <i>Dendroica petechia</i> )	YWAR	50	670 (84.8)	51 (6.5)	69 (8.7)	790	25.9 $\pm$ 1.4
Chestnut-sided Warbler ( <i>Dendroica pensylvanica</i> )	CSWA	98	1877 (88.1)	93 (4.4)	159 (7.5)	2129	29.9 $\pm$ 1.2
Magnolia Warbler ( <i>Dendroica magnolia</i> )	MAWA	221	4225 (88.3)	230 (4.8)	330 (6.9)	4785	30.9 $\pm$ 0.7
Yellow-rumped Warbler ( <i>Dendroica coronata</i> )	MYWA	237	3774 (81.3)	273 (5.9)	596 (12.8)	4643	20.5 $\pm$ 0.6
Black-throated Green Warbler ( <i>Dendroica virens</i> )	BTNW	75	1617 (84.9)	116 (6.1)	172 (9.0)	1905	24.9 $\pm$ 1.2
Blackburnian Warbler ( <i>Dendroica fusca</i> )	BLBW	26	680 (87.1)	18 (2.3)	83 (10.6)	781	26.9 $\pm$ 2.1
Bay-breasted Warbler ( <i>Dendroica castanea</i> )	BBWA	192	3856 (88.9)	135 (3.1)	348 (8.0)	4339	25.9 $\pm$ 0.6
Cerulean Warbler ( <i>Dendroica cerulea</i> )	CERW	28	502 (83.2)	27 (4.5)	74 (12.3)	603	24.6 $\pm$ 1.2
Black-and-white Warbler ( <i>Mniotilta varia</i> )	BAWW	131	3015 (91.9)	76 (2.3)	191 (5.8)	3282	32.3 $\pm$ 1.0
American Redstart ( <i>Setophaga ruticilla</i> )	AMRE	71	1284 (84.1)	49 (3.2)	194 (12.7)	1527	26.6 $\pm$ 1.3
Prothonotary Warbler ( <i>Protonotaria citrea</i> )	PROW	59	938 (80.7)	92 (7.9)	132 (11.4)	1162	18.9 $\pm$ 1.0
Worm-eating Warbler ( <i>Helmitheros vermivorus</i> )	WEWA	96	1591 (85.7)	75 (4.1)	190 (10.2)	1856	20.9 $\pm$ 0.8
Common Yellowthroat ( <i>Geothlypis trichas</i> )	COYE	56	739 (88.3)	41 (4.9)	57 (6.8)	837	21.2 $\pm$ 1.1
Hooded Warbler ( <i>Wilsonia citrina</i> )	HOWA	89	859 (73.7)	44 (3.8)	263 (22.6)	1166	18.2 $\pm$ 0.9
Canada Warbler ( <i>Wilsonia canadensis</i> )	CAWA	27	513 (89.1)	6 (1.0)	57 (9.9)	576	35.7 $\pm$ 2.4
<b>Thraupinae</b>							
Summer Tanager ( <i>Piranga rubra</i> )	SUTA	20	118 (68.6)	8 (4.7)	46 (26.7)	172	4.6 $\pm$ 0.9
Scarlet Tanager ( <i>Piranga olivacea</i> )	SCTA	26	203 (73.6)	12 (4.3)	61 (22.1)	276	5.4 $\pm$ 0.9
All species	31 spp.	2603	39328 (84.1)	2253 (4.8)	5194 (11.1)	46775	21.7 $\pm$ 0.2

and Hastie 1987). However, row and column points are positively associated when they lie in the same direction from the origin, and are negatively associated when they lie in the opposite direction. Correspondence analysis and resulting plots are often used as a complementary tool to analysis of logistic or loglinear models (e.g., van der Heijden and de Leeuw 1985, Moser 1989, Moser et al. 1990). Because I am interested in the association between searching movements and those conditions, I will focus only on this association hereafter.

Environmental conditions: study site, plot, tree size, and presence of vines; internal difference: sex; and social behavior: flocking, and bird density were tested with searching movements for the hypothesis of independence. For tree size, hackberry and live oak were classified as large trees, and green hawthorn (*Crataegus viridis*) and yaupon (*Ilex vomitoria*), which are understory species, were classified as small trees. Type I error (or  $\alpha$  level) was chosen to be 0.05 for all tests. Likelihood ratio Chi-square tests (SAS Institute 1989) were used to evaluate the relationship of searching movements with those variables individually. ANOVA or *t* tests (SAS Institute 1989) were used to test if searching rates and movement distances of birds differed among different levels of variables. Duncan's multiple-range tests (SAS Institute 1989) were used to test if searching rates and distances of birds varied from site to site. These analyses were performed only for data in 1994 because I stayed at only one site in both 1993 and 1995. In addition, because searching movements differed significantly among families of birds, I did a separate analysis for each family or subfamily. Only warblers and vireos had large enough samples to be analyzed.

For multidimensional contingency tables, multiple correspondence analysis is sometimes applied together with a loglinear (or logistic) model to explore the association in the tables (van der Heijden and de Leeuw 1985, Moser 1989, Moser et al. 1990). This approach usually results in more insight into the association among variables in such tables (Moser 1989) because the loglinear model shows the interaction between variables on the “variable level,” and correspondence analysis on the “category level” (van der Heijden and de Leeuw 1985). Logistic models (SAS Institute 1989, Agresti 1990) were built to model the association between searching movements and those variables for warblers and vireos. Tree size was not included in this analysis because of its small marginal frequency for vireos on small trees. Searching movements of birds can be considered as a response variable that will be related to those conditions (explanatory variables) through a logistic model (Agresti 1990). Due to different amounts of missing data for sex, presence of vines, and density of birds, eight logistic models were built to maximize sample size for each combination of variables. Burt tables were constructed from those variables except sex in the logistic models for both warblers and vireos; multiple correspondence analyses were then performed on the Burt tables (Greenacre 1984). Three-dimensional plots resulting from multiple correspondence analyses were used to show the association among variables graphically.

## RESULTS

Relative frequencies of hops differed among taxa: warblers (85.0%), vireos (77.0%), tanagers (71.1%), and flycatchers (18.1%)(Table 2.1); the trend in searching

rate was similar, 24.9 movements per minute for warblers, 14.7 for vireos, 5.0 for tanagers, and 1.0 for flycatchers (Table 2.1). In contrast, flight was employed by the above taxa in an almost opposite pattern to hops. Flycatchers used flights intensively, 82.6% for the Acadian Flycatcher and 81.2% for the Eastern Wood-Pewee, respectively. Among warblers, Hooded Warblers had the highest relative frequency of flight, more than twice that for other warblers (Table 2.1). Flutters were rare (< 5%) for most species; flycatchers did not use flutters (Table 2.1).

Distances traveled during searching movements were generally proportional to a bird's body size (Table 2.2). Warblers had a mean hopping distance of 12 cm, vireos, 16 cm, and the Yellow-billed Cuckoo, the largest species in this study, 23 cm. Average fluttering distance was 31 cm for warblers, 39 cm for vireos, and 66 cm for the Yellow-billed Cuckoo. Flying distances were also greatly influenced by the type of attack behavior a species used. Species that used predominantly aerial maneuvers tended to have longer flights than perch-gleaners. Mean flying distance was 109 cm for warblers, 110 cm for vireos, 252 cm for the Yellow-billed Cuckoo, and 432 cm for flycatchers (Table 2.2). Among warblers, the Hooded Warbler had the longest average flight distance, which may be due to its frequent use of aerial maneuvers (Chapter 1, Barrow 1990, Waynor 1995). Blue-gray Gnatcatchers and Ruby-crowned Kinglets had similar searching modes as warblers. In contrast, Yellow-billed Cuckoos searched in a manner closer to that of tanagers and vireos.

Table 2.2. Distances (in cm) of searching movements of insectivorous migratory songbirds at Gulf coast stopover sites, 1993–1995. Data under “Fly” were within patch flights and only recorded in 1994 and 1995. See Table 2.1. for species codes.

Species code	Searching movement					
	Hop		Flutter		Fly	
	<i>n</i>	$\bar{x} \pm \text{SE}$	<i>n</i>	$\bar{x} \pm \text{SE}$	<i>n</i>	$\bar{x} \pm \text{SE}$
YBCU	65	22.7 ± 1.7	24	65.8 ± 6.2	44	251.8 ± 24.7
ACFL	3	23.3 ± 6.7	0	–	21	341.0 ± 76.4
EAWP	4	10.5 ± 5.1	1	50.0 ± –	22	523.6 ± 100.1
RCKI	83	12.3 ± 9.0	65	25.7 ± 1.5	67	97.2 ± 9.6
BGGN	27	16.8 ± 4.2	17	23.8 ± 2.9	27	84.3 ± 8.6
WEVI	46	15.5 ± 2.0	36	39.7 ± 3.6	33	115.2 ± 15.5
SOVI	8	20.6 ± 4.2	5	42.0 ± 5.8	12	96.7 ± 16.7
YTVI	19	17.3 ± 2.8	8	38.8 ± 4.8	10	108.0 ± 13.5
PHVI	25	11.5 ± 1.4	11	35.5 ± 5.3	26	113.5 ± 20.7
REVI	156	13.2 ± 0.8	110	38.2 ± 1.6	76	121.3 ± 10.6
BWWA	40	11.4 ± 1.1	26	31.0 ± 1.8	21	81.0 ± 7.7
GWWA	15	8.0 ± 1.1	14	33.6 ± 3.6	9	80.0 ± 8.8
TEWA	74	9.3 ± 0.8	39	29.1 ± 1.8	45	91.8 ± 5.6
NOPA	25	10.4 ± 1.6	10	22.5 ± 4.0	30	92.0 ± 13.7
YWAR	21	11.4 ± 1.8	20	36.5 ± 2.7	12	72.5 ± 5.8
CSWA	63	13.1 ± 1.2	40	32.0 ± 2.8	26	111.9 ± 18.7
MAWA	126	12.7 ± 1.4	90	29.1 ± 1.2	71	84.6 ± 11.4
MYWA	140	9.5 ± 0.6	101	28.9 ± 1.3	170	128.9 ± 7.7
BTNW	52	10.3 ± 1.1	41	28.4 ± 2.2	36	80.0 ± 5.2
BLBW	21	12.0 ± 1.8	7	25.7 ± 3.2	29	74.1 ± 9.4
BBWA	126	10.2 ± 0.6	71	35.5 ± 4.1	102	98.3 ± 7.7
CERW	13	11.2 ± 1.3	7	31.4 ± 4.0	11	152.7 ± 40.4
BAWW	86	11.2 ± 2.4	41	31.7 ± 2.4	43	122.6 ± 22.4
AMRE	45	12.8 ± 1.3	20	35.5 ± 2.9	38	106.6 ± 18.7
PROW	23	12.0 ± 2.6	22	29.5 ± 3.2	15	113.3 ± 13.5
WEWA	39	10.9 ± 1.3	24	40.0 ± 3.6	23	129.6 ± 25.0
COYE	30	17.1 ± 3.4	12	28.3 ± 4.4	7	165.7 ± 60.9
HOWA	43	16.2 ± 2.0	17	36.2 ± 3.3	51	190.0 ± 19.0
CAWA	18	8.7 ± 1.2	3	26.7 ± 3.3	11	95.5 ± 23.4
SUTA	9	10.6 ± 2.5	2	32.5 ± 17.5	9	344.4 ± 88.4
SCTA	15	12.0 ± 2.0	7	57.1 ± 9.2	20	161.0 ± 22.2

### Searching Movements among Species

Correspondence analysis of frequencies of searching movements among species (see Table 2.1) illustrated the influence of the intensive use of flights by flycatchers on the total Pearson  $\chi^2$  statistic ( $\chi^2 = 1730$ ,  $df = 60$ ,  $P < 0.001$ ) under the hypothesis of homogeneity (Figure 2.1). Thus, besides flycatchers, tanagers, YBCU, HOWA, PHVI, and SOVI were positively associated with flights. Other vireos and the Prothonotary Warbler were positively associated with flutters. In contrast, those remaining species, especially warblers, were positively associated with hops (Figure 2.1). Also note that flight and hop were related to the first axis, and flutter was more associated with the second axis.

Three clear groups were found in the cluster analysis based on searching movements: warblers, vireos and tanagers, and flycatchers (Figure 2.2). From the cluster analysis, species were grouped roughly according to their familial relationships. However, there were some exceptions. The Hooded Warbler was clustered with vireos and tanagers instead of warblers, and the Solitary Vireo was closer to tanagers than other vireos. The Ruby-crowned Kinglet and the Blue-gray Gnatcatcher were grouped with warblers, whereas the Yellow-billed Cuckoo was close to vireos and tanagers. Furthermore, two subgroups could be identified within warblers: CAWA, BAWW, MAWA, and CSWA as one subgroup, and all the other warblers except the Hooded Warbler as another subgroup. The former subgroup was characterized by high searching rates (Table 2.1). Another division separated the vireos and tanagers.

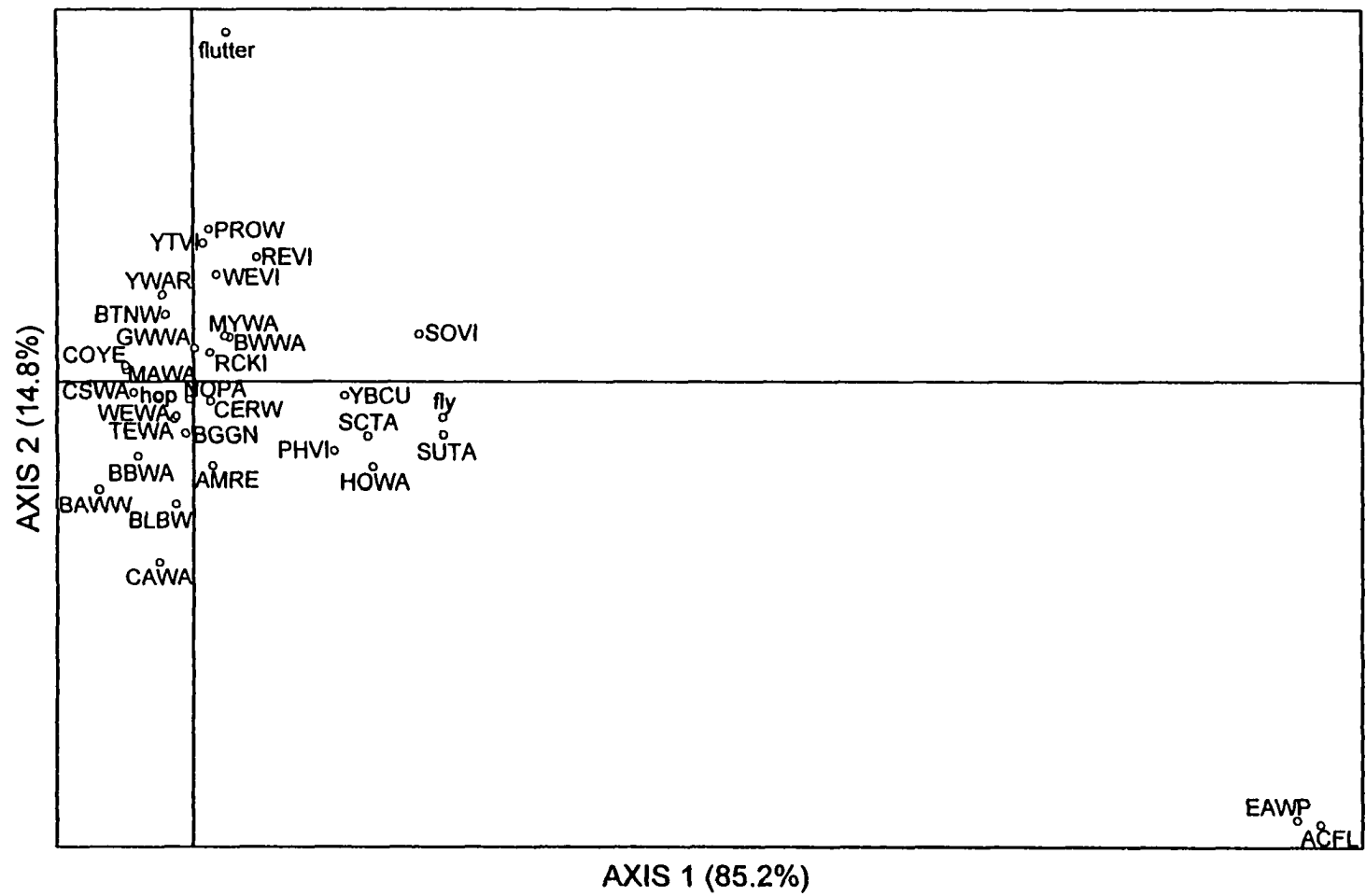


Figure 2.1. Correspondence analysis of searching movements with 31 migrants at Gulf coast stopover sites, 1993-1995.

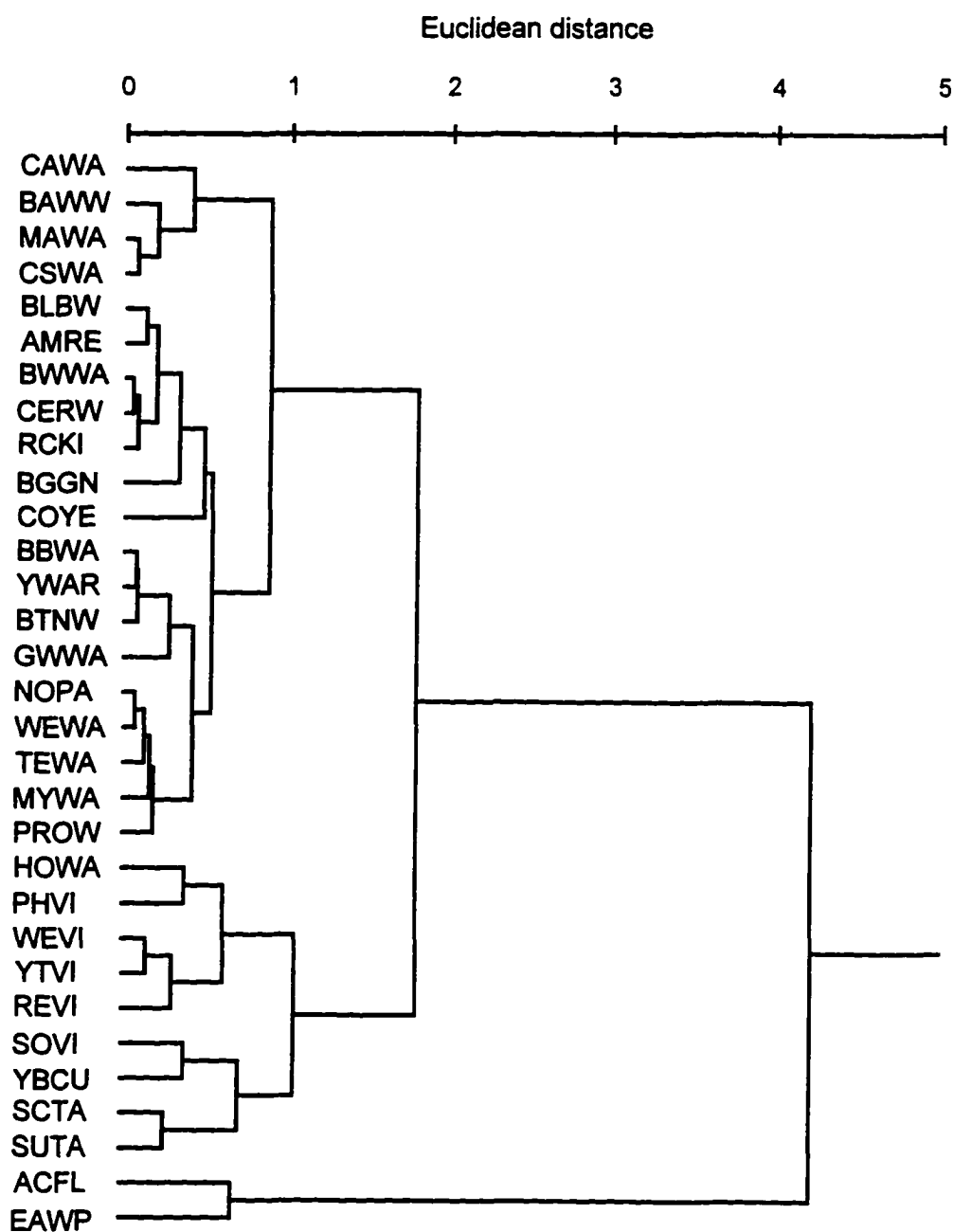


Figure 2.2. Cluster dendrogram of 31 migrants based on frequencies of flight, searching rates, and hopping distances.



However, the Solitary Vireo and the Yellow-billed Cuckoo were clustered with each other; as a group they were closer to tanagers than to other vireos (Figure 2.2).

### **Conditions Affecting Searching Movements**

Because the results differed for warblers and vireos, they will be presented separately. Significant differences were found in both frequencies and rates of searching movements but not in searching distances for both warblers and vireos. Eight out of 21 tests were significant for warblers, whereas 2 out of 17 tests were significant for vireos (Tables 2.3, 2.4).

Site. Warblers used more hops but less flutters and flights at Hackberry Ridge and Smith Point, and the opposite at Grand Chenier ( $P < 0.001$ , Table 2.3). Searching rates of warblers differed among sites ( $P < 0.001$ , Table 2.4) and also differed from site to site based on Duncan's multiple-range tests. Flying distances of vireos did not differ between Grand Chenier and Hackberry Ridge, and between Hackberry Ridge and Smith Point, but flying distances between the two groups differed based on Duncan's multiple-range tests even though the  $P$  value for the  $F$  test was about 0.1.

Plot. More hops and flights were recorded in normal plots than reduced plots for warblers ( $P < 0.001$ , Table 2.3). Searching rate of warblers was faster in normal plots than that in reduced plots ( $P = 0.002$ , Table 2.4). Vireos had shorter fluttering ( $P = 0.08$ ) and flying ( $P = 0.10$ ) distances in normal plots than in reduced plots.

Tree size. Warblers used more hops and less flutters and flights in small trees than in large trees ( $P = 0.007$ , Table 2.3). Searching rate of warblers was faster in small trees than in large trees ( $P = 0.102$ , Table 2.4).

Table 2.3. Differences of frequencies of searching movements of migrating warblers and vireos among different levels of conditions at Gulf coast stopover sites, 1994.

Condition Level	Warblers					Vireos				
	Hop	Flutter	Fly	$G^2$	$P$	Hop	Flutter	Fly	$G^2$	$P$
<b>Site</b>										
Grand Chenier	4880	216*	855*			541	28	137		
Hackberry Ridge	11079*	403	1243			1412	64	284		
Smith Point	6300*	205	654	117.38	0.001	792	38	150	5.7	0.226
<b>Plot</b>										
Normal	10654*	333	1359*			1420	69	297		
Reduced	11605	491*	1395	20.96	0.001	1325	61	274	0.1	0.951
<b>Tree size</b>										
Large	10920	473*	1224*			1310	68	268		
Small	1575*	44	157	9.79	0.007	27	2	3	1.5	0.479
<b>Presence of vines</b>										
No	14665	587*	1746*			1589	82*	369*		
Yes	3901*	107	384	22.97	0.001	662*	22	123	6.8	0.033
<b>Sex*</b>										
Females	4757	133	541							
Males	9933	316	1223	3.49	0.175					
<b>Flocking</b>										
Flock	9147	405	1151			632	28*	182*		
Solitary	2745	124	339	0.13	0.940	319*	9	49	14.7	0.001
<b>Bird density</b>										
High	9732*	273	1163			1270	62	282		
Low	12527	551*	1589*	38.40	0.001	1475	68	289	1.9	0.389

\* Indicates that frequency of movement is larger than the expected value.

\* Only made for warblers because most of them are discernible by sex.

Table 2.4. Searching rates of migrating warblers and vireos under different conditions at Gulf coast stopover sites, 1994.

Condition Level	Warblers				Vireos			
	<i>n</i>	$\bar{x} \pm SE$	<i>F</i> or <i>t</i>	<i>P</i>	<i>n</i>	$\bar{x} \pm SE$	<i>F</i> or <i>t</i>	<i>P</i>
<b>Site</b>								
Grand Chenier	315	22.1 $\pm$ 0.6			54	13.2 $\pm$ 0.7		
Hackberry Ridge	634	24.5 $\pm$ 0.4			111	14.4 $\pm$ 0.5		
Smith Point	340	27.1 $\pm$ 0.7	16.9	0.001	59	15.1 $\pm$ 0.9	1.4	0.239
<b>Plot</b>								
Normal	621	25.6 $\pm$ 0.5			112	14.3 $\pm$ 0.6		
Reduced	668	23.6 $\pm$ 0.4	3.2	0.002	112	14.4 $\pm$ 0.6	- 0.1	0.945
<b>Tree size</b>								
Large	557	25.2 $\pm$ 0.4			102	14.5 $\pm$ 0.6		
Small	68	27.8 $\pm$ 1.6	- 1.7	0.102	3	13.1 $\pm$ 2.1	0.4	0.686
<b>Presence of vines</b>								
No	761	24.9 $\pm$ 0.4			134	14.1 $\pm$ 0.5		
Yes	195	27.3 $\pm$ 0.8	- 2.7	0.007	37	14.5 $\pm$ 1.0	- 0.3	0.754
<b>Sex<sup>a</sup></b>								
Females	258	25.8 $\pm$ 0.7						
Males	533	25.8 $\pm$ 0.5	0.1	0.947				
<b>Flocking</b>								
Flock	513	23.6 $\pm$ 0.5			53	13.1 $\pm$ 0.7		
Solitary	124	22.3 $\pm$ 1.0	1.2	0.225	25	11.7 $\pm$ 1.3	1.0	0.317
<b>Density</b>								
High	563	25.1 $\pm$ 0.4			112	14.8 $\pm$ 0.5		
Low	726	24.2 $\pm$ 0.4	1.6	0.118	112	13.8 $\pm$ 0.6	1.3	0.209

<sup>a</sup> Only made for warblers because most of them are discernible by sex.

Presence of vines. More hops and fewer flutters and flights were observed in areas with vines than in areas without vines ( $P < 0.05$  for both warblers and vireos, Table 2.3).

The searching rate of warblers was higher in areas with vines ( $P = 0.007$ , Table 2.4).

Fluttering distance of warblers was shorter in area with vines ( $P = 0.06$ ).

Sex. Statistical tests were only done for warblers because most warblers are discernible to sex; vireos were not. No significant difference was found for all tests.

Flocking. Vireos hopped more when foraging alone, and they fluttered and flew more when foraging in flocks ( $P < 0.001$ , Table 2.3). Warblers fluttered shorter distances when foraging in flocks than when alone ( $P = 0.06$ ).

Bird density. Warblers employed more hops but fewer flutters and flights during period of high bird density ( $P < 0.001$ , Table 2.3). Warblers also used longer hops in high bird density periods ( $P = 0.09$ ).

From logistic models, I found that searching movements of warblers were more affected by those variables stated above than were vireos (Table 2.5). Most fitted models had 3-factor interactions for warblers, whereas 2-factor interactions were sufficient to explain the association in vireos. In other words, vireos searched in a manner less dependent on external conditions than did warblers. For both warblers and vireos, strong positive associations were found among hops and solitary foragers, and Smith Point, and between flights and Grand Chenier, and foragers in flocks (Figures 2.3, 2.4). Flutters also had a strong association with high bird density for vireos.

Table 2.5. Logistic models of searching movements with various conditions for warblers and vireos at Gulf coast stopover sites, 1994. Codes for explanatory variables are S = SITE, P = PLOT, D = DENSITY, X = SEX, V = VINE, and F = FLOCK. All interaction terms are significant and with  $P < 0.05$  except (SPD) for vireos.

Variables in the model	Warblers		Vireos	
	Best fitted model	<i>P</i>	Best fitted model	<i>P</i>
SITE, PLOT, DENSITY	(SPD)	–	(SPD)	–
SITE, PLOT, DENSITY, SEX	(SPD,SPX,PDX)	0.2707	NA	
SITE, PLOT, DENSITY, VINE	(SD,SV,PD,PV,DV)	0.2833	(SP,SD,DV)	0.3878
SITE, PLOT, DENSITY, FLOCK	(SPD,PF)	0.4534	(SD,PD)	0.6587
SITE, PLOT, DENSITY, SEX, VINE	(SPD,SPX,SPV,SDX,PDX)	0.9564	NA	
SITE, PLOT, DENSITY, SEX, FLOCK	(SPD,SPX,PF,XF)	0.4529	NA	
SITE, PLOT, DENSITY, VINE, FLOCK	(SVF,SD,PF)	0.8780	(DV,PF,S)	0.3527
SITE, PLOT, DENSITY, SEX, VINE, FLOCK	(SPD,SPX,SDX,PDX,SXF,PF,DV,XV)	1.0000	NA	

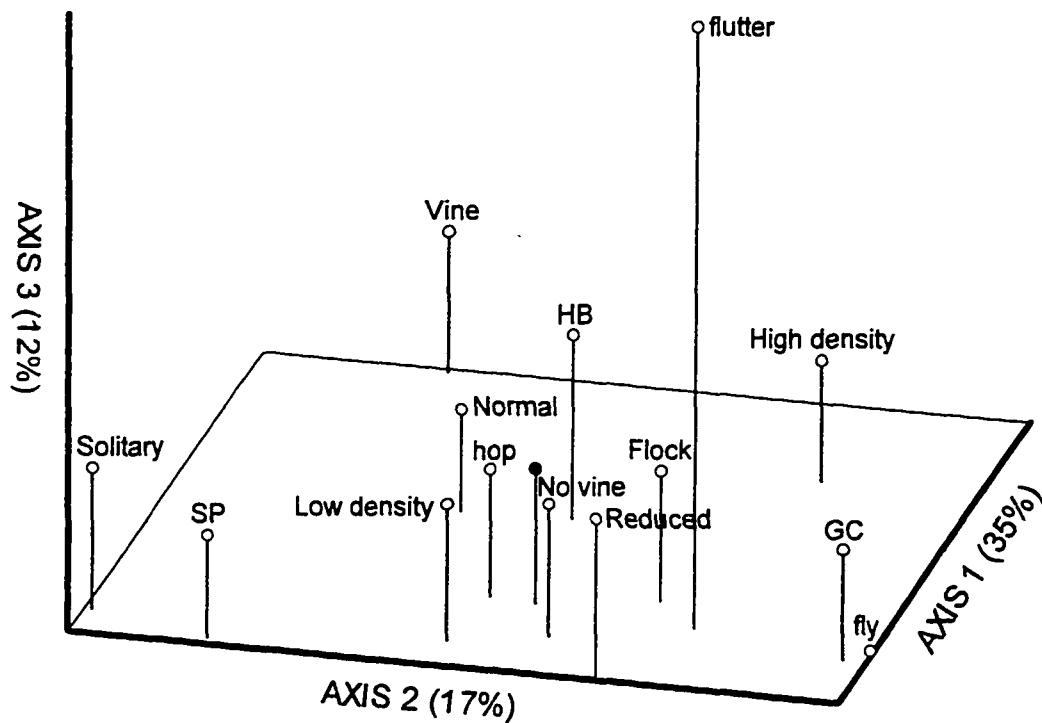


Figure 2.3. Correspondence analysis of searching movements with site, plot, presence of vines, density of birds, and flocking for warblers at Gulf coast stopover sites, 1994. Site codes: GC = Grand Chenier, HB = Hackberry Ridge, and SP = Smith Point. The origin is at the solid circle.

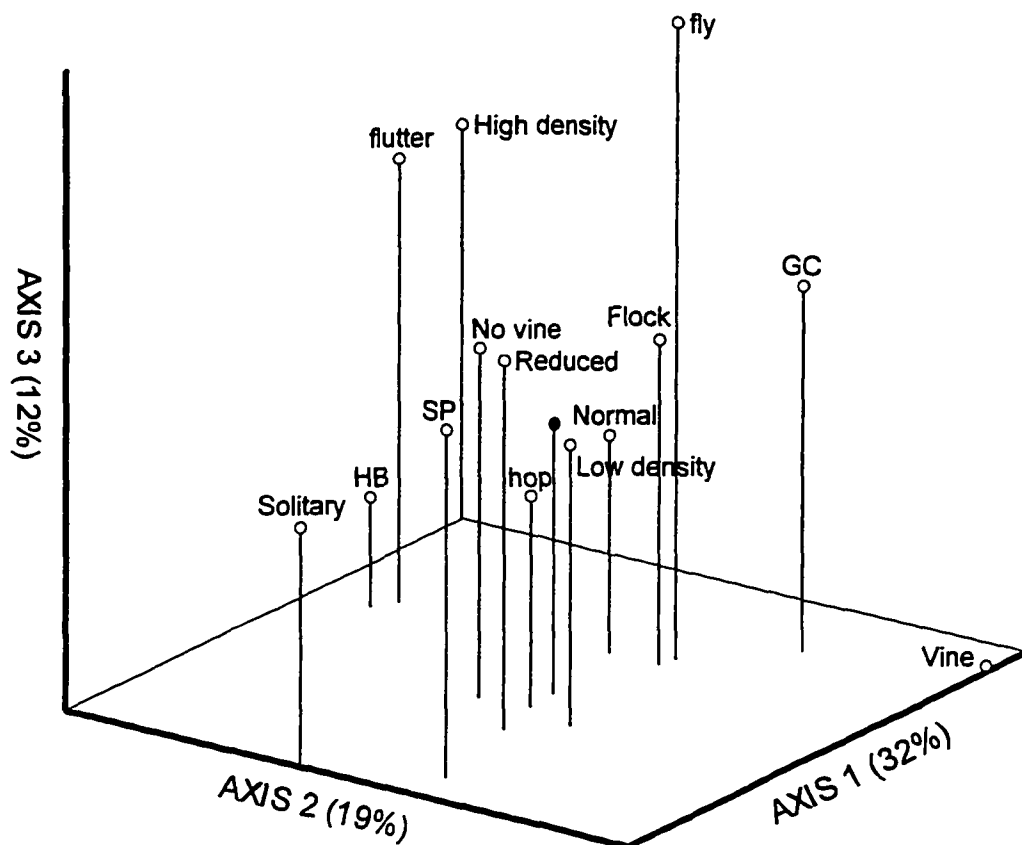


Figure 2.4. Correspondence analysis of searching movements with site, plot, presence of vines, density of birds, and flocking for vireos at Gulf coast stopover sites, 1994. See Figure 2.3 for site codes. The origin is at the solid circle.

## DISCUSSION

Searching rates, frequencies and distances of searching movements of birds might be related to one another to some degree. More hops usually resulted in higher searching rates; shorter movements were also associated with higher searching rates. Thus it is probably best to examine these three variables at the same time. Unfortunately, searching movements are actually too fast to be recorded in a great detail through a pair of binoculars. Video-taping foraging and subsequent analysis can be a potential tool for such a task.

A researcher can use multivariate analyses to provide a clear view of the community structure of these migratory songbirds in terms of how they search for prey (Figures 2.1, 2.2). In my data set, species are grouped roughly according to their presumed relationship. Obviously, closely related species have similar searching modes. O'Brien et al. (1990) concluded that all searching behavior can be placed on a "stop-and-go" continuum with one extreme "widely foraging" and another "sit-and-wait" (Huey and Pianka 1981). Many Accipitridae species (e.g., hawks, harriers) are widely foraging species, and most flycatchers (Tyrannidae and Muscicapidae) sit and wait for prey. Many species in this study are in between and can be called "saltatory searchers" (Evans and O'Brien 1988). The ordination of these species along the continuum can be roughly represented by Figure 2.2, because duration of pauses, and the speed and length of movements, which O'Brien et al. (1990) considered important to describe saltatory behavior, are similar to those variables that I used in the cluster analysis. Moreover, the position of these species along the continuum between "widely

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foraging” and “sit-and-wait” might be related to a species’ morphological characteristics. Such relationships deserve further examination because searching behavior could affect the evolution of morphological characters.

External conditions, such as vegetation structure and prey availability, have been found to influence searching movements of birds (Robinson and Holmes 1982, 1984; Holmes and Recher 1986). In addition, social behavior such as flocking and density of birds, also affected searching movements.

Vegetation structure accounts for a set of opportunities and constraints that influence how and where birds forage and, as a consequence, may affect the success of a bird species exploiting habitats and thus influence the community structure of birds in these habitats (Robinson and Holmes 1982, 1984; Holmes and Recher 1986; Barrow 1990). Vegetation Structure was correlated with searching movements of birds, especially searching frequencies and rates. Among three study sites, vegetation was densest in Smith Point, intermediate in Hackberry Ridge and least dense in Grand Chenier. All normal plots were denser than reduced plots. Small trees had more compact vegetation structure than large trees, and denser vegetation was found in areas with vines than in areas without vines. Birds used more hops and shorter movements and therefore a higher searching rate in denser vegetation (Tables 2.3, 2.4). The distances by which potential perches are separated in small trees or areas with vines are shorter than distances in large trees or areas without vines. This might be the reason why birds hopped more and had shorter movements at these locations. The same effect also can be applied to larger scales of habitat such as study plot and site. A similar

result was found in American Redstarts and Red-eyed Vireos that take more flights in white ash (*Fraxinus americana*) than other tree species because white ash has lower vegetation density and a more even distribution of leaves (Robinson and Holmes 1984). On the other hand, compact vegetation structure might make it difficult for birds to search for prey and thus reduce their scanning diameter. If this is true, birds will spend less time at a certain spot and move onto the next spot faster than in more open habitats. Robinson and Holmes (1982) hypothesized that the constraints imposed by the structure of the vegetation may affect the foraging traits of birds and hence influence their selection of habitat and the overall community structure.

The Yellow-billed Cuckoo is a good species to illustrate the relationship between searching mode and prey characteristics. The Yellow-billed Cuckoo can be considered a typical saltatory searcher. They mainly forage on large caterpillars; as a result, prey abundance is usually less than the abundance of small caterpillars. The best search strategy for cuckoos is a mix of “sit-and-wait” and “widely foraging.” Yellow-billed Cuckoos usually sit on a perch and scan for a while, sometimes as long as several minutes. Scanning radius is probably very large, maybe even beyond 1 m, because cuckoos use sally-pounce or take several quick hops to catch prey far away from their perch location. Large caterpillars are more visible and easier to detect than small ones when they move; that is why “sit-and-wait” works for the Yellow-billed Cuckoo. Due to the relatively lower abundance of large caterpillars, cuckoos have to move to a new patch after a while. The saltatory search strategy actually describes the searching movements of the Yellow-billed Cuckoo: high frequency of flights, long movements,

and low searching rates. From a net energy gain simulation model on white crappie (*Pomoxis annularis*), O'Brien et al. (1989) predicted that short moves are associated with maximum net energy gains when animals feed on small prey, and that longer moves maximize energy gain for large prey or a mixture of large and small prey. "Sit-and-wait" is probably efficient in terms of energy gain when movement rates of prey are high, because species that tend to use "sit-and-wait" tend to eat prey that are active or large in size (Eckhardt 1979, Griffiths 1980).

Food resources are actually distributed in a hierarchical structure, e.g., substrate, patch, and habitat (Hutto 1985, Bell 1991). Locomotory movements and scanning for prey within a patch can be defined as "local search," and between patches movements as "ranging" (Jander 1975). Since 1994, I separated flights into within-patch flights and between-patch flights. Data from between-patch flights should not be included in statistical analysis of "local search" behavior because between-patch flights are ranging instead of local search; one should exclude them when computing frequency, rate, and distance of flights. However, between-patch flights can be an important variable to record when we are interested in "ranging." Unfortunately, I did not distinguished the two types of flights until 1994, and thus data under "fly" in Table 2.1 actually incorporated a few between-patch flights from 1993. But the number is very small; its influence could be neglected.

Flocking, and high density of birds are spatial and temporal events when many birds occur in a relatively restricted area at the same time. Both can be considered as social behaviors because they are related to interactions among individuals.

Flocking was a common social behavior during spring migration on the Chenier Plain. Foraging flocks usually moved very rapidly from tree to tree; in contrast, solitary foragers tended to stay longer in the same tree. Individuals in a flock used slightly more flights and flutters than solitary foragers (Table 2.3). When birds forage in a flock, more eyes and bills are at work simultaneously in a patch; as a result, prey are depleted much faster and it is less profitable for birds to stay (e.g., Charnov et al. 1976, Krebs and Cowie 1976, Stephens and Krebs 1986). In addition, the presence of other individuals could result in competition, threat, or at least individual distance changes that might induce a forager to search in a more restricted space (Morse 1970, Moore and Yong 1991). Morse (1970) found that birds reduce their foraging space in proportion to flock size. Moreover, foragers in a flock might not even search a patch as thoroughly as solitary foragers because of the constant movement of flocking individuals.

Density of birds in a plot changed from day to day, and sometimes during a day. Relatively high density of birds often occurred in the afternoon hours or during a fallout. Because most migrants reach the Gulf coast in the afternoon (Lowery 1955; Gauthreaux 1971, 1972; Moore et al. 1990), small- to large-scale movements of migrants were often found during that time of day. High density of birds could last several days as a result of fallout that resulted mainly from weather storms. High density of birds was a totally different situation from flocking. During high density periods, birds were actually compacted into a limited space; the density of birds suddenly increased 10-fold or even 100-fold. Consequently, individual distance or available space for birds was reduced sharply. Because migrants were everywhere in a plot, it might be more efficient for a

bird to search thoroughly on a location instead of covering more space as a flock would. Staying at one place might also reduce intra- and inter-species conflicts when the possibilities of interaction were so high (Moore and Yong 1991). During high density periods, birds usually stayed in the same tree for a longer time and hopped around more frequently than during low density periods (Table 2.3).

Sex dimorphism in plumage is common in warblers (Parulinae), and males tend to be slightly larger than females (Pyle et al. 1987). Although the difference in morphology between sexes is subtle, it might actually induce difference in foraging characteristics. Males and females might have different searching strategies that can be explained by morphological constraints or niche segregation as shown in some studies (e.g., Morse 1968, Williamson 1971, Ornat and Greenberg 1990, Parrish and Sherry 1994). In my comparison between sexes, I found no significant difference between females and males.

Warblers were more affected by external conditions than vireos (Table 2.5). On the other hand, warblers were more flexible and responsive to the change of external condition than vireos. Although warblers have a higher attack rates than vireos (Chapter 1), the comparison is not valid if the two groups actually eat different sizes of insects. The difference in body size, foraging tactics, prey, and habitat preference between warblers and vireos might all contribute to some degree to the result, but most importantly, warblers were more intensive arboreal searchers, especially on twigs, than vireos. Therefore, warblers were affected more by vegetation structure simply because they used it more. Holmes and Robinson (1981) also noted that vegetation structure

strongly affects the foraging behavior of perch-gleaners, but had little influence on species that sally (or hover) to catch prey. Similarly, species that use more hops (i.e., warblers) might be influenced more by vegetation structure.

Optimal foraging theory has been used to explain the results of many studies (e.g., Davies 1977, Stephens and Krebs 1986, Stephens 1990). Results of some studies have been considered to prove optimal foraging theory (e.g., Cowie 1977, Kacelink 1984, Schmid-Hempel et al. 1985), but others have not (e.g., Hughes and Elner 1979, Wetterer and Bishop 1985). I argue here that birds probably do not forage optimally all the time. But under certain circumstances, they may do so; for example, during the period of feeding young, and prior to and during migration. At my study sites, birds foraged all day long, and I seldom found them taking a rest. My study plots might not even be at the most critical location, because the birds are already past the gulf. Thus I speculate that the best time to study optimal foraging theory is the period prior to the taking of a long non-stop overwater flight.

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### **CHAPTER 3**

## **COMPARISONS OF DIFFERENT METHODS IN CALCULATING AVIAN FORAGING RATES**

### **INTRODUCTION**

Foraging (or attack) rate is a useful variable in avian foraging studies. It is often defined as the number of attacks per minute (e.g., Eckhardt 1979, Robinson and Holmes 1982). Attack behavior is the action that birds use to reveal or capture prey after a food item, or food-concealing substrate, is sighted (Remsen and Robinson 1990). A continuous recording of attack behaviors through time will allow the calculation of foraging rate. Foraging rate along with foraging maneuvers and site characteristics is used to describe foraging behavior at the species level (Remsen and Robinson 1990). Foraging rate of birds has been used as a variable that differs between sexes (Morse 1981), among different stages of the breeding season (Robinson 1986), among tree species (Robinson and Holmes 1984), and the relationship with searching rate (Robinson and Holmes 1982) and weather conditions (Murphy 1987). Foraging rate is also an important element in various models of optimal foraging theory (Charnov 1976, Stephens and Krebs 1986).

Two methods to calculate foraging rate are found in the literature. In one method, a foraging rate is calculated for each observed foraging sequence by dividing the number of attacks by the duration of the foraging sequence; the foraging rate for a species is the average of the rates for all sequences recorded for that species (Morton 1980, Robinson and Holmes 1982, Barrow 1990). In another method, the total number of attacks and the total duration for each species are calculated first, and the foraging

rate for a species is then calculated based on the total number of attacks and total duration (Morse 1968, Eckhardt 1979, Robinson and Holmes 1984, Robinson 1986). The foraging rate calculated by the former method is often called the “sequential rate” and the rate calculated by the latter method is called the “overall rate.” In the sequential rate, each foraging sequence is treated as an independent observation and further statistical tests are then possible (Robinson and Holmes 1982). In contrast, in the overall rate the species is considered to be an independent unit, and all observations from the same species can be recomposed. In other words, when one collects a foraging sequence, one simply cuts off a small section of events from a continuous foraging activity, and all observations from the same species should be connected to reconstruct the foraging sequence. Although Krebs et al. (1974) used intervals to calculate foraging rate in Black-capped Chickadees (*Parus atricapillus*), this method is seldom used in field studies.

Although migrants actively foraged all day long at the Gulf coast stopover sites, their foraging rate was not constant. Several factors affecting foraging rate might include circadian rhythms (Meier and Russo 1985), food distribution and abundance (Hutto 1981, Holmes and Schultz 1988), the depletion of prey (Charnov et al. 1976, Bibby and Green 1980), tree species (Robinson and Holmes 1984), and foraging maneuvers (Morse 1968). Birds actually forage in a dynamic pattern, spatially and temporally. All foraging observations of birds are just a small sample of such dynamic foraging; the sampled sections can be from any part of the continuous sequence. We may collect a fast sequence at one time, or a slow sequence at another time; we may

collect a sequence that has equal foraging intervals or one with intervals changing at a constant rate. In fact, foraging is likely to have stochastic components (Oaten 1977, Green 1980, Stephens and Charnov 1982). In addition, visibility of the birds to the observers (Wagner 1981, Bradley 1985) may influence the foraging rate as well. It is likely that birds search differently in dense vegetation areas versus more open areas. It is possible that sequential rates are overestimated for conspicuous species or early migrants because they could be easily followed to many attacks in more open perches or in early spring when leaves are not present.

Foraging rate has been a controversial topic in optimal foraging theory (Templeton and Lawlor 1981, Turelli et al. 1982, Stephens and Krebs 1986) because there is no way to calculate the average foraging rate without any assumptions. In addition, foraging might be a stochastic event (Oaten 1977, Green 1980, Stephens and Charnov 1982) that may not be possible to represent by a single value. The main purpose of calculating foraging rates is to find an estimated index that is a reliable estimator in a long-term basis. Although the foraging rate of birds may be estimated by many ways, the study of the properties of foraging sequences and the application of statistical theories may enable us to find a reasonable foraging rate estimator.

Sequential rates and overall rates are similar (this study), but they may not be as unbiased as foraging rates calculated by methods introduced in this analysis. In this study, data on time intervals between any two attack behaviors were collected, and as a result, the calculation of foraging rates from intervals is possible. I will compare three new estimates of foraging rate with the two formally used rates. I believe that such

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comparisons will give insights into some subtle differences in the properties of foraging rates and help to find a more reliable foraging rate estimator.

## METHODS

This study was part of a larger project on stopover ecology of Neotropical migrants at three sites on the Chenier Plain during the spring migrations of 1993–1995. Foraging data used herein were collected during the spring migration seasons of 1993 and 1994. Foraging data of 1993 were all collected at one site, Grand Chenier, but during 1994, I traveled from site to site every week to equalize my effort among sites.

About 60 species of mostly Neotropical but some wintering migrants were recorded. Wintering migrants were abundant in early March and became scarcer as the migration season progressed; most wintering migrants had departed by the end of March. Neotropical migrants started to appear in mid-March and reached their peak numbers during the last week of April and the first week of May. The abundance of Neotropical migrants declined sharply after mid-May.

### Study Area

I used three study sites along the northern coast of the Gulf of Mexico: (1) Grand Chenier, Cameron Parish, Louisiana; (2) Hackberry Ridge, Cameron Parish, Louisiana; and (3) Smith Point, Chambers County, Texas. The Grand Chenier site was a more mature and diverse coastal forest than the other two sites. The Hackberry Ridge site had a low canopy and consisted primarily of hackberry trees (*Celtis laevigata*). The Smith Point site had very thick understory and many live oaks (*Quercus virginiana*) in the canopy. For detailed description of the study sites, see Barrow et al. (in press).

Each study site consists of a “reduced” plot with a little to a moderate amount of understory, and a “normal” plot where the understory was denser. Each plot was intended to be a 100×300 m rectangular area, but this size plot could not be obtained at all sites because of the limited extent of woods available. The reduced and normal plots were adjacent at Grand Chenier, but separated at Hackberry Ridge (c.a. 1 km) and Smith Point (c.a. 100 m).

Each plot was oriented east-west, roughly parallel to the coastline. Within all study plots, I established grids marked with flags spaced every 25 m. Each flag was marked with a combination of a number (long axis) and a letter (short axis); these flags delineated the boundaries of many small blocks and several transect lines.

### **Recording Methods**

Foraging behaviors were recorded when opportunities occurred as I repeatedly traversed the study plots. Attempts were made to equalize effort in every part of the plot and not to concentrate sampling at any particular place. In addition, I tried not to gather data from the same bird more than once per day, e.g., not to stay at one spot too long, or to only observe individuals of different sexes or species at the same spot. Repeated sampling of individuals should be rare because most Neotropical migrants depart the night of their arrival (Gauthreaux 1971, 1972; Moore and Kerlinger 1987; Kuenzi et al. 1991).

I used “focal sampling” and “continuous recording” as recording methods (Martin and Bateson 1993). I quietly followed each bird encountered and entered observations into a tape recorder until the bird was lost from sight. If I could not



determine what a bird was doing, I stopped recording. The Eastern Wood-Pewee (*Contopus virens*) usually could be followed for more than 10 minutes. In some cases, it seemed I could follow it indefinitely; I stopped the recording after an attack if I felt that I had gotten a long enough sequence ( $> 10$  minutes).

I recorded data on all insectivorous migrants encountered. After a bird was identified, I recorded species, sex, if discernible, and time of day on the tape. I kept the recorder running. After saying “start,” I recorded in detail every attack behavior until I was no longer able to do so, usually because the bird departed. At that moment, I said “stop.” In some situations, when birds took a long flight into another tree or patch, I stopped the recording as well. Connected vegetation from different plants was considered as a patch. For naming attack behaviors, I used the scheme of Remsen and Robinson (1990). I obtained sequence and duration information from the tape with the aid of a stopwatch. I replayed the tape and started the stopwatch when I heard “start;” then I wrote down the time whenever an attack was heard. I computed the length of intervals between any two attacks and the length of the closed sequence from the first attack to the last attack (Figure 3.1). The time before the first attack (pre section) and the time after the last attack (post section) were calculated for sequences with at least two attacks. For sequences with  $\geq 3$  intervals, I also computed the duration of the first three intervals, starting with the first attack and ended with the fourth attack.

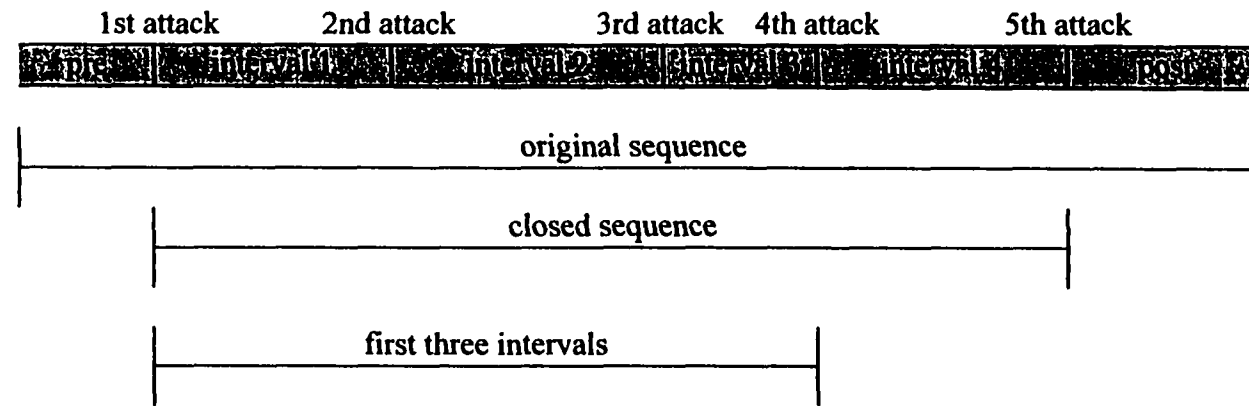


Figure 3.1. A simplified foraging sequence to illustrate how different sections of foraging sequences were used to calculate different foraging rates.

## Calculation

The unit of foraging rate is the same for all methods and is the number of attacks per minute. Two different methods of calculation have been used for the original sequences (Figure 3.1) in the literature:

1. In the sequential rate method, the ratio of number of attacks to duration of each sequence is calculated first; all of these for a species are averaged to obtain a mean foraging rate for each species. It is usually assumed that the beginning and ending points of a foraging sequence are random. There were some sequences with a 0 rate, which indicates that birds actively searched for prey but without any attacks. Most workers exclude sequences with short duration, e.g., 20 sec. (e.g., Robinson and Holmes 1982, Barrow 1990) when they calculate the sequential rate. Lovette and Holmes (1995) used only sequences with at least two attacks.
2. In the overall rate method, the rate is equal to the total number of attacks divided by the total duration of foraging for a particular species. In other words, all foraging sequences of a particular species are connected together first, and the foraging rate is calculated by dividing the total number of attacks by the total foraging duration of the recomposed sequence. This rate is also equal to the ratio of the mean number of attacks divided by the mean length of the foraging sequences. Statistically, the overall rate is considered to be a better ratio estimator of the data than the sequential rate (Manly et al. 1993). Theoretically, the overall rate is more realistic because it enables us to evaluate the outcome of a series of foraging decisions (Stephens and Krebs 1986). Some workers

used overall rate because they found that many foraging sequences were short, under 30 seconds (e.g., Robinson and Holmes 1984).

The sequential rate was only computed for the original sequences, but the overall rate was calculated for original sequences, closed sequences, intervals, and the first three intervals (Figure 3.1). Closed sequences are sequences without the pre and post time sections; the sections of time before the first attack and after the last attack are deleted. Overall rates of closed sequences are calculated in the same way as for the original sequences except that closed sequences have one less attack than the original sequences. The overall rate of intervals for a particular species is computed by taking the total number of intervals and the total length of all intervals first, and then computing the overall rate from the two. This rate is exactly the same as the overall rate of closed sequences. I will use only the overall rate of closed sequences hereafter. Foraging rates of the first three intervals were included in this analysis because observing for only three intervals (or four attacks) may be a more efficient way to collect data than observing as long as possible. Similarly, the first 5 or 10 intervals could have been used to calculate foraging rate, but the number of observations would have decreased. Because the mean length of the pre and post sections was longer than the mean intervals for most species, it appears to be reasonable to count each as one attack. A modified overall rate resulted from this adjustment; I call this rate the “adjusted overall rate.”

The last three methods discussed (overall rates from closed sequences and the first three intervals, and the adjusted overall rate) are used to calculate foraging rate for the first time. I used them in my attempt to determine if any other alternative methods

can give more reliable foraging rates than the two methods normally used for the original sequences.

### **Data Analysis**

I used only sequences with duration of  $\geq 20$  seconds for original sequences. For closed sequences, I used sequences with at least two attacks regardless of duration. A minimum sample of at least 30 individuals is needed for analysis of foraging behavior (Morrison 1984). I used only species with  $\geq 50$  original sequences in this analysis to make sure that I would have enough sequences with at least three intervals. Even with  $\geq 50$  original sequences, only eight species had more than 30 sequences with at least three intervals. I did use the Prothonotary Warbler (*Protonotaria citrea*) that had only 21 sequences, and both the Eastern Wood-Pewee and the Blue-winged Warbler (*Vermivora pinus*) that had 29 sequences for the first three intervals. Other species in the analysis include Ruby-crowned Kinglet (*Regulus calendula*), Red-eyed Vireo (*Vireo olivaceus*), Magnolia Warbler (*Dendroica magnolia*), Yellow-rumped Warbler (*Dendroica coronata*), Bay-breasted Warbler (*Dendroica castanea*), Black-and-white Warbler (*Mniotilta varia*), and Worm-eating Warbler (*Hemitheros vermivorus*). The Tennessee Warbler (*Vermivora peregrina*) was excluded from the list because it usually foraged on flowers. The spatial arrangement of flowers might bias the foraging rate of the Tennessee Warbler and complicate the analysis of comparisons with strictly insectivorous species. Bird names follow the check-list of the American Ornithologists' Union (1983).

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Because foraging data are not normally distributed, the arithmetic mean might not represent the actual mean well. Logarithmically transformed (Neter et al. 1990) sequential rates are normally distributed or nearly so. Means from logarithmical transformation (geometric means) of sequential rate were calculated for the original sequences and closed sequences.

The correlation coefficient (SAS Institute 1989) was used to determine if the coefficient of variation of sequential rates of original sequences was related to the range (maximum minus minimum) of the five foraging rates resulting from the different methods of calculation of foraging sequences. The Type I error (or  $\alpha$  level) is set at 0.05 for all tests.

The length of the first three intervals was compared to that of the last three intervals to see if the first three intervals of foraging sequences was shorter than the last three intervals. In other words, I tested if birds foraged faster in early section of a sequence than the later counterpart. This analysis was only performed for those sequences with  $\geq 6$  intervals and for all 10 species combined. Because length of intervals was not normally distributed, I tested  $\log(\text{length of the first three intervals} / \text{length of the last three interval}) = 0$  using a paired  $t$  test (SAS Institute 1989).

## RESULTS

### The Properties of Foraging Sequences

Two different trends were discernible in the scatter plot of sequence duration by number of attacks when all 10 species were included (Figure 3.2): some sequences extended from the origin to the right; and in the other extreme, sequences extended from

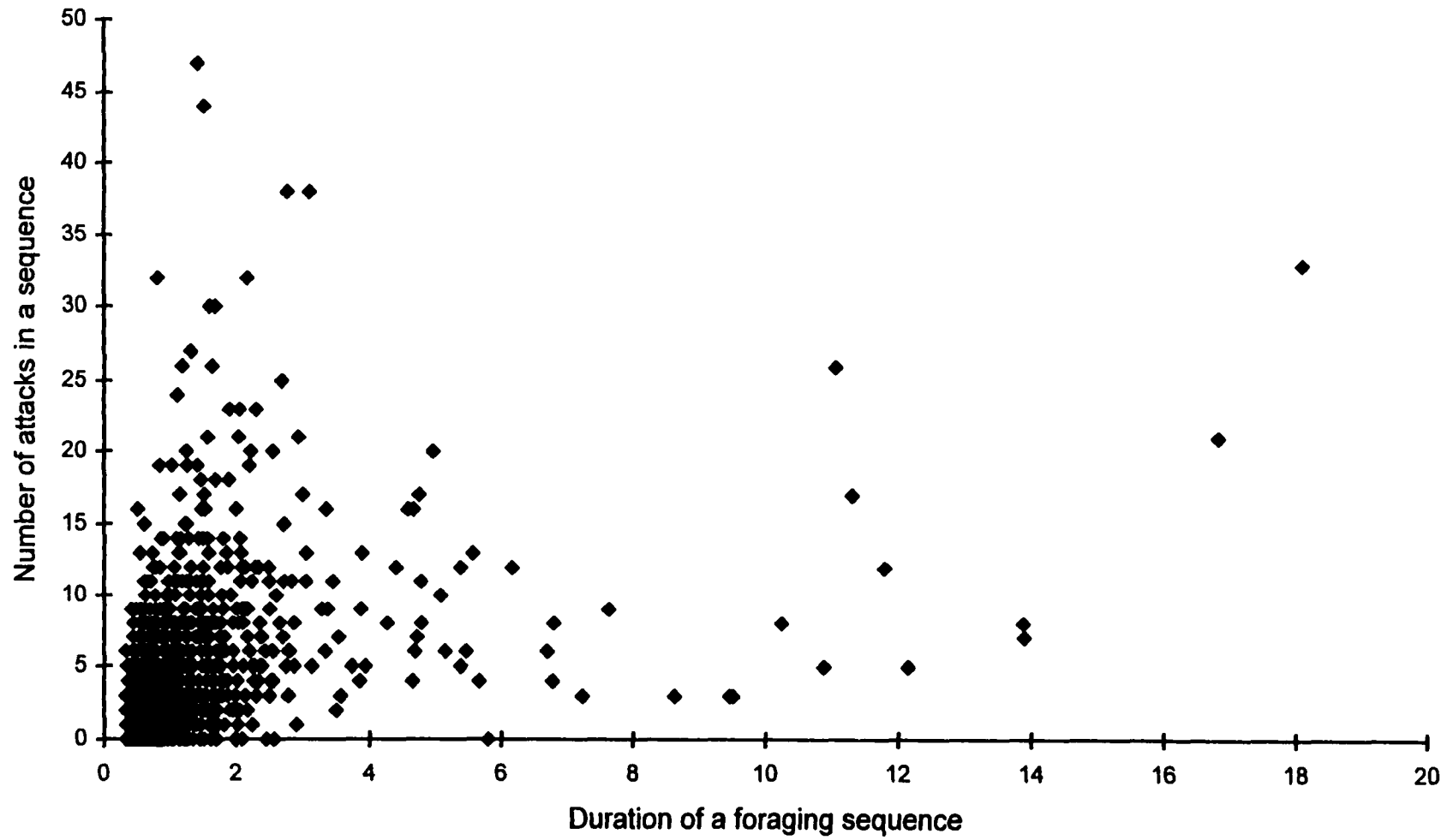


Figure 3.2. Number of attacks and duration (in minute) of foraging sequences of 10 insectivorous migratory songbirds at Gulf coast stopover sites, 1993-1994.

the origin to the upper part along the *Y* axis. The first trend represented those individuals that foraged slowly and could be followed for a long time. Those points beyond 6 minutes exclusively belonged to the Eastern Wood-Pewee, which foraged from open perches and could be easily followed for more than 10 minutes. The second trend consisted of observations from those pearch-gleaners that foraged fast, and were difficult to follow; the duration of these was shorter, usually under 3 minutes. Those points that exceeded 25 attacks were mostly from Yellow-rumped Warblers. They could be observed easily in the early season when leaves had not come out.

Because the sequential rate was calculated by dividing the number of attacks by the sequence duration, the resulting rate should be positively related with the numerator (number of attacks) and negatively related with the denominator (sequence duration). Foraging rates were roughly positively correlated with the number of attacks (Figure 3.3). The more attacks in a sequence, the higher the foraging rate was. The scatter plot formed a fan shape that extended from the origin to the right upper corner. This happens because foraging rates were more variable when the number of attacks were highest. Foraging rates were negatively correlated with the sequence duration in a quadratic form (Figure 3.4). The longer the sequence duration was, the lower the foraging rate was. Birds definitely did not forage at a constant rate because the clouds of points should form a horizontal line in both figures if they had done so.

The mean lengths of the pre and post sections were longer than the mean interval for most species (Figure 3.5). The Eastern Wood-Pewee was the only species with shorter mean post section than the mean interval, which may be due to my arbitrary



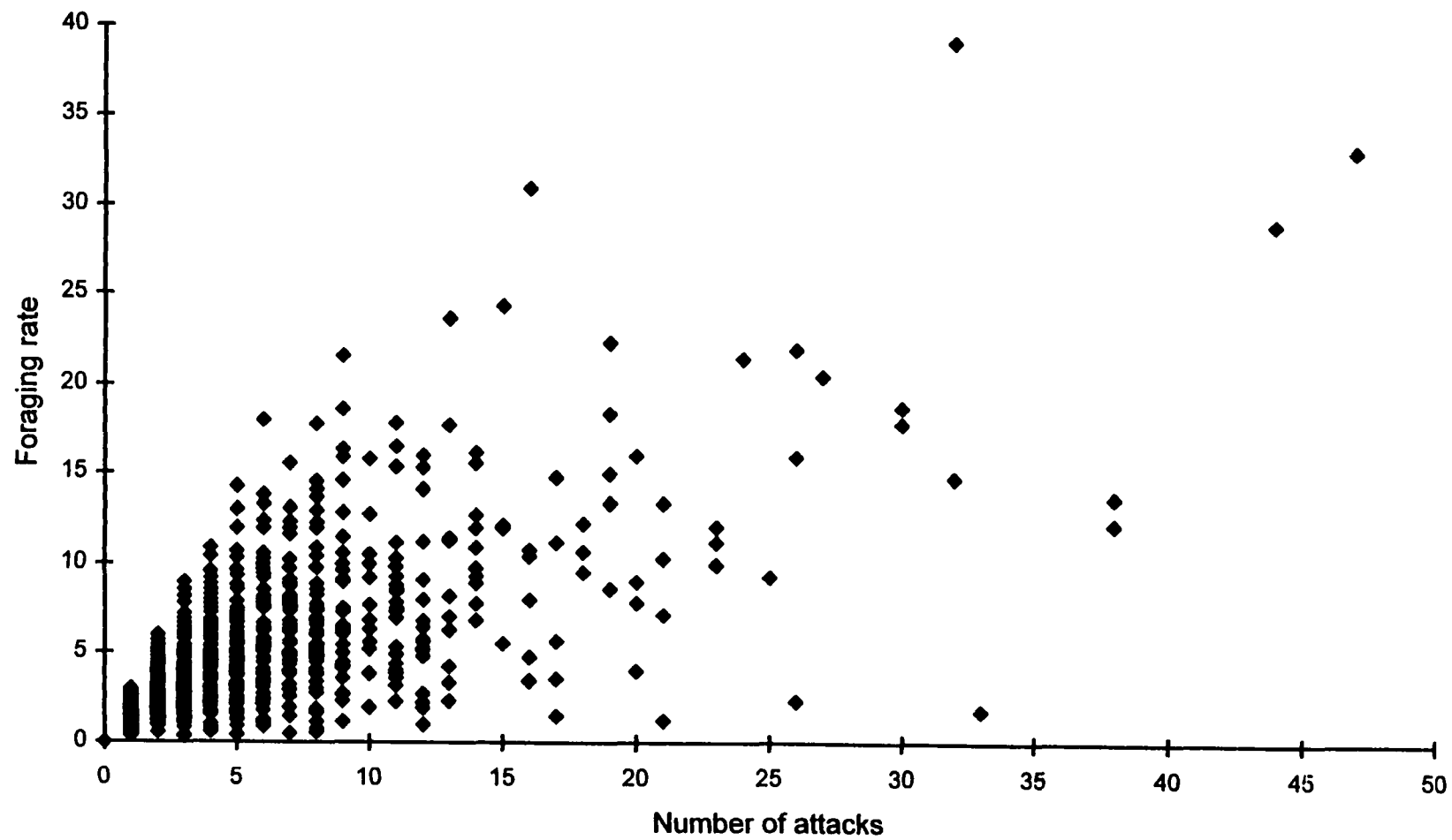


Figure 3.3. Scatter plot of foraging rates with number of attacks of foraging sequences at least 20 seconds in length for all 10 species combined at Gulf coast stopover sites, 1993-1994.

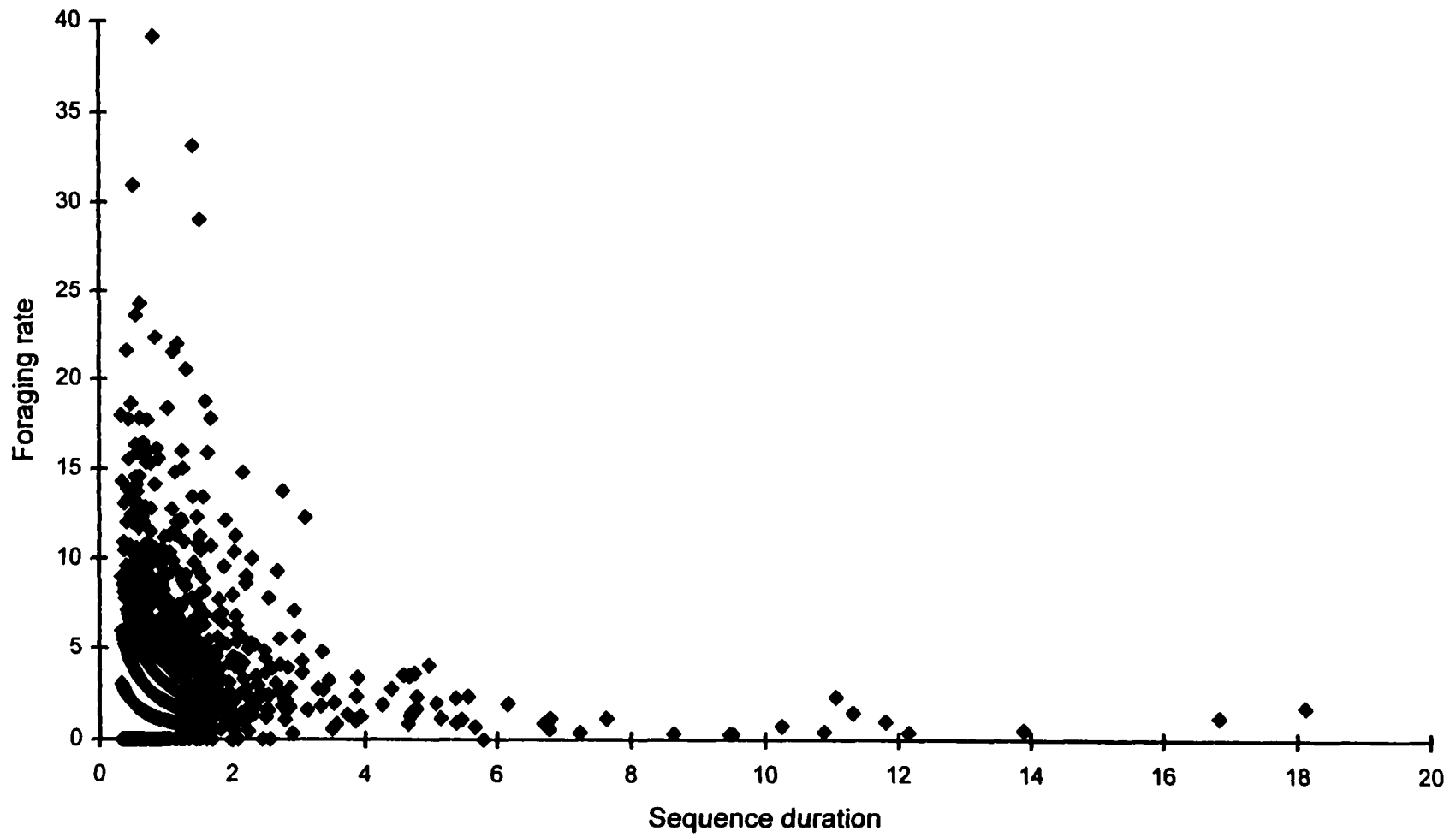


Figure 3.4. Scatter plot of foraging rates with duration of foraging sequences at least 20 seconds in length for all 10 species combined at Gulf coast stopover sites, 1993-1994.

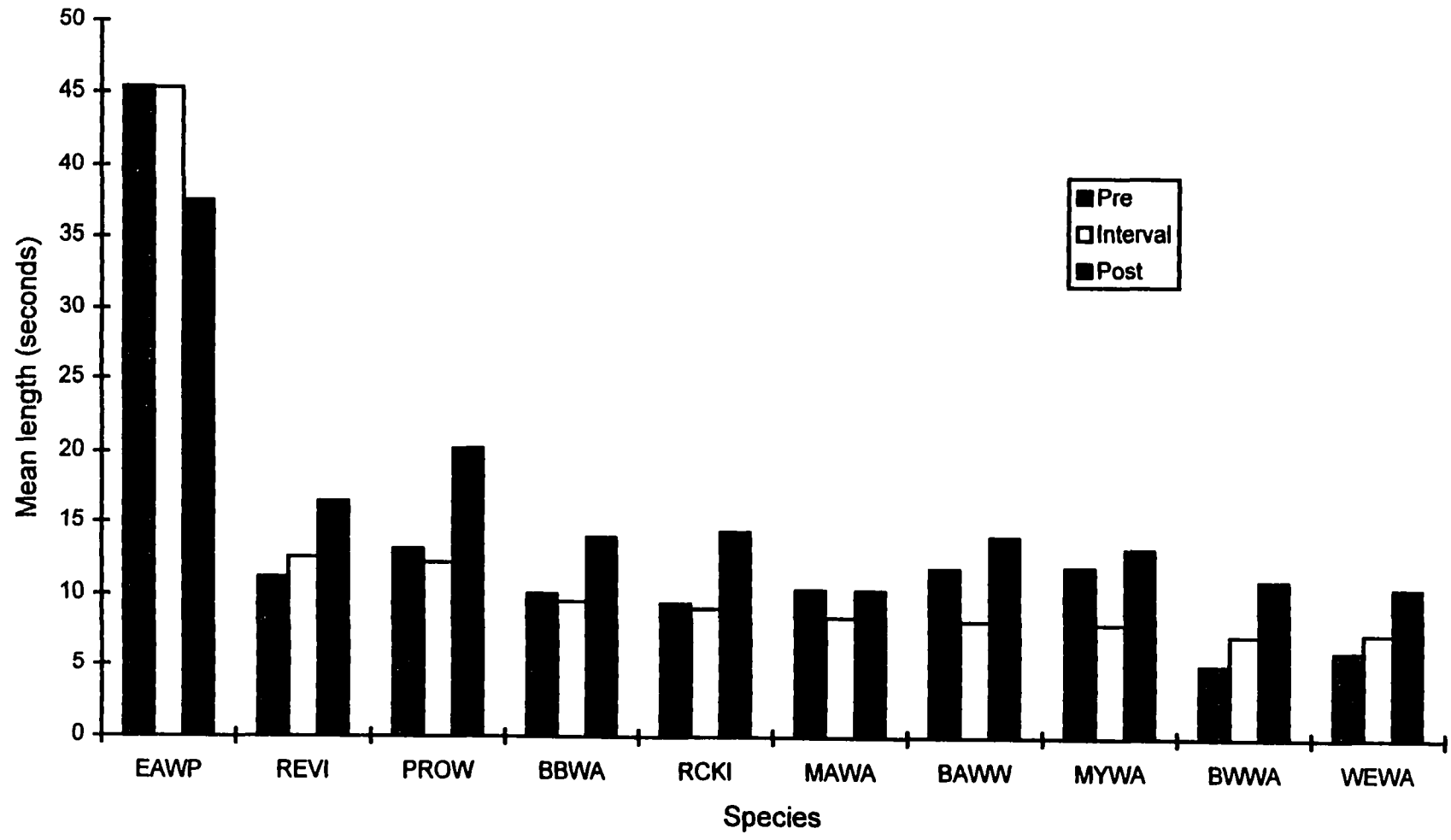


Figure 3.5. Mean lengths of pre, post sections, and intervals for 10 insectivorous migratory songbirds at Gulf coast stopover sites, 1993-1994.

ending of long sequences. In contrast, the Red-eyed Vireo, the Blue-winged Warbler, and the Worm-eating Warbler had shorter mean length of the pre section than the mean interval. The mean length of the pre section was shorter than the mean length of the post section for all species except the Eastern Wood-Pewee and the Magnolia Warbler. For the latter species, the two were almost the same.

When the cumulative frequency of number of attacks was plotted for all 10 species combined, an exponential curve was formed (Figure 3.6) because there were many more foraging sequences with small number of intervals than with large number of intervals. This shows that it is difficult to follow birds for more than 10 intervals.

The first three intervals were shorter than the last three intervals for all species combined (paired  $t = 2.52$ ,  $df = 260$ ,  $P = 0.012$ ). This implies that birds foraged faster in the early section than in the later section of a foraging sequence. For individual species, the same trend was found for the Bay-breasted Warbler ( $df = 30$ ,  $P < 0.05$ ), the Blue-winged Warbler ( $df = 19$ ,  $P < 0.05$ ), the Ruby-crowned Kinglet ( $df = 29$ ,  $P < 0.1$ ), and the Worm-eating Warbler ( $df = 33$ ,  $P < 0.1$ ). No significant differences were found for other species.

### **Foraging Rates from Different Methods**

Overall rates and sequential rates from original sequences were closer to each other than to the other three rates (Table 3.1, Figure 3.7). Overall rates from closed sequences were higher than those from the original sequences for all species except the Eastern Wood-Pewee. The adjusted overall rate from the original sequences fell in between those from the original sequences and those from the closed sequences for all

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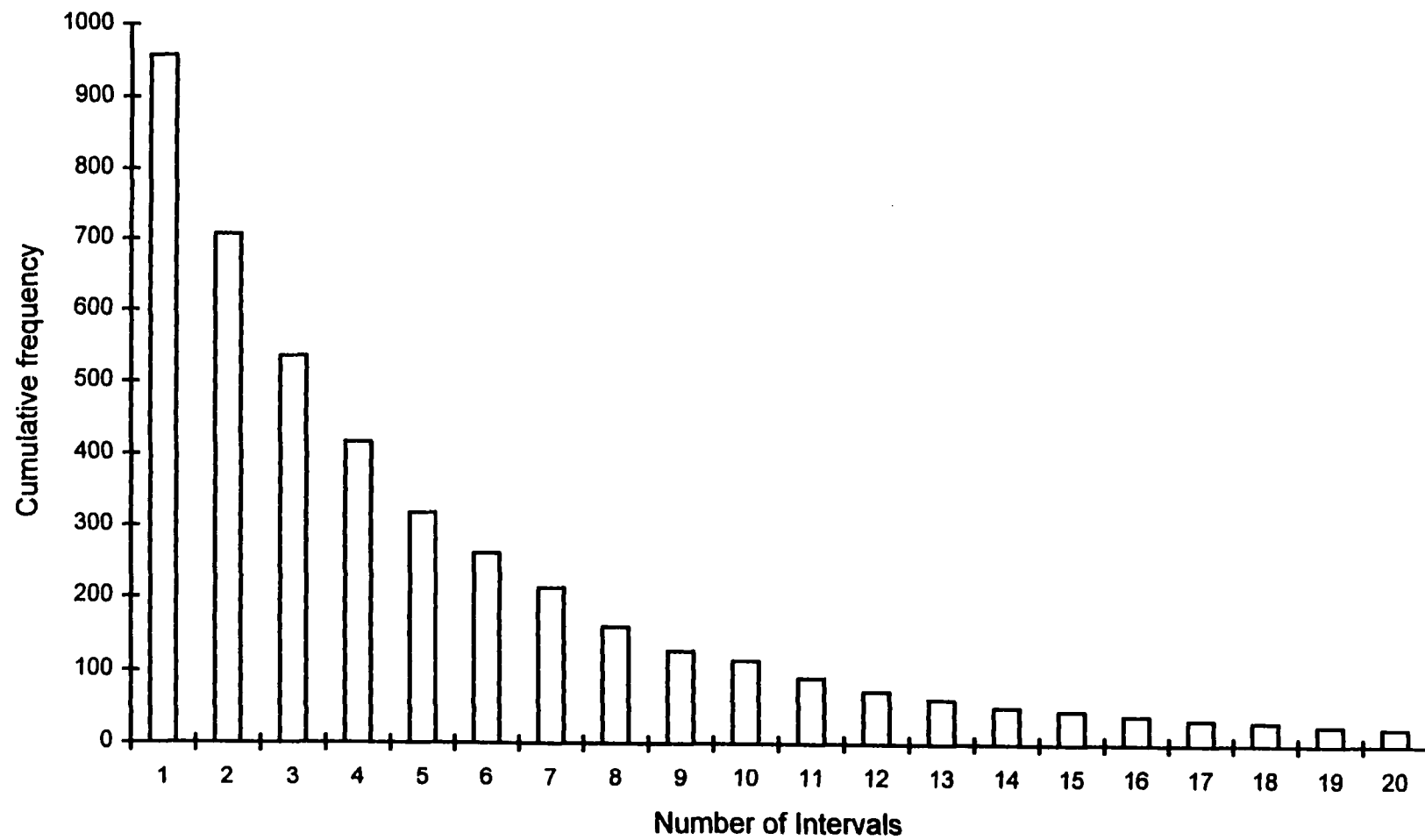


Figure 3.6. Cumulative frequency of number of intervals of foraging sequences for 10 species combined at Gulf coast stopover sites, 1993-1994.

Table 3.1. Comparison of foraging rates from different calculating methods for 10 insectivorous migratory songbirds at Gulf coast stopover sites, 1993–1994. Unit of foraging rate is equal to number of attacks per minute.

Species	Original sequences				Closed sequences <sup>a</sup>		First three intervals	
	Sequential rate <sup>b</sup>	Overall rate	Adjusted overall rate <sup>c</sup>	<i>n</i>	Overall rate	<i>n</i>	Overall rate	<i>n</i>
Eastern Wood-Pewee	1.4 ± 0.1	1.2	1.3	55	1.3	50	1.2	29
Red-eyed Vireo	2.7 ± 0.2	2.4	3.4	240	4.8	150	5.6	33
Prothonotary Warbler	3.8 ± 0.4	3.4	4.1	50	4.9	39	4.8	21
Bay-breasted Warbler	4.1 ± 0.4	4.0	5.0	166	6.3	116	8.1	47
Ruby-crowned Kinglet	4.3 ± 0.3	4.6	5.6	108	6.6	82	6.9	43
Black-and-white Warbler	4.4 ± 0.4	4.4	5.5	110	7.3	89	7.8	38
Magnolia Warbler	4.5 ± 0.3	4.4	5.7	173	7.0	132	7.7	51
Yellow-rumped Warbler	5.0 ± 0.4	4.8	5.7	204	7.4	153	6.6	79
Blue-winged Warbler	5.6 ± 0.4	6.0	7.2	74	8.3	66	8.8	29
Worm-eating Warbler	6.6 ± 0.5	6.7	7.7	85	8.1	80	8.0	47

<sup>a</sup> After deleting pre and post sections of the original foraging sequences.

<sup>b</sup> Variation is standard error.

<sup>c</sup> Pre and post sections each counted as one attack.

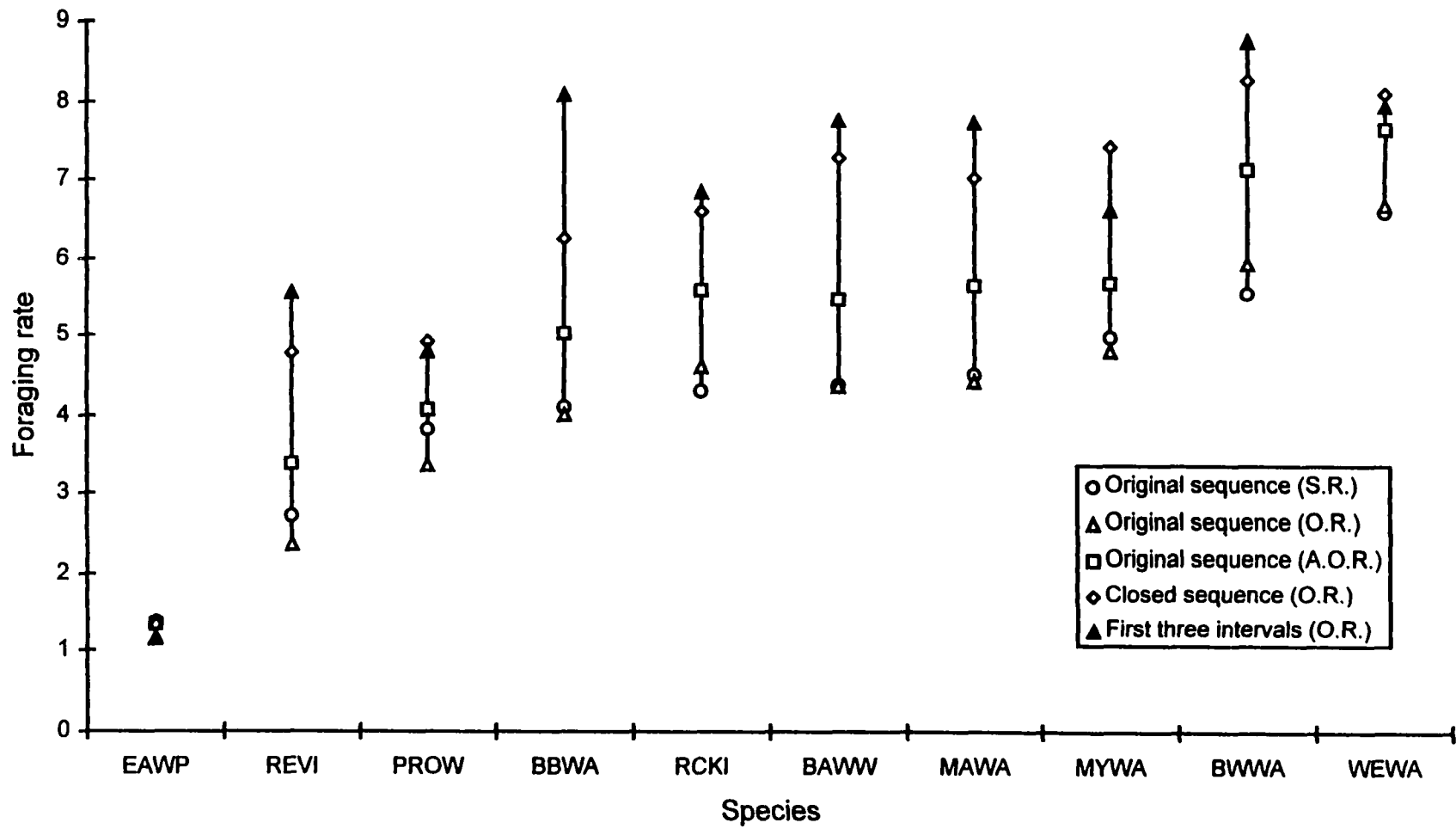


Figure 3.7. Comparison of five different foraging rates among 10 migrant species at Gulf coast stopover sites, 1993-1994. S.R. indicates sequential rate, and A.O.R. adjusted overall rate.

species except the Eastern Wood-Pewee. Although foraging rates from the first three intervals were closer to those from the closed sequences, the closeness varied from species to species. It appears that the overall rate from the first three intervals was more variable than all the other rates.

Compared to the overall rates, foraging rates from a logarithmic transformation of the sequential rate or adjusted sequential rate were lower for the original sequences for most species. In contrast, it was the opposite for the closed sequences. The magnitude of the difference between overall rates and transformed rates was similar for both original and closed sequences (Figure 3.8).

The coefficient of variation of the sequential rate and the difference between the greatest rate and the smallest rate of the five rates were correlated to each other among species ( $r = 0.64$ ,  $P < 0.05$ ). The higher the coefficient of variation is, the greater the range of the five foraging rates (Table 3.2).

## DISCUSSION

Although migrants actively foraged all day long on the Chenier Plain, they seldom foraged at a constant rate, presumably because prey type and abundance are different from tree to tree (Holmes and Schultz 1988). Even in the same tree, prey are presumably patchily distributed. Foraging rate will slow down when prey are depleted through time in a patch (Charnov et al. 1976, Bibby and Green 1980). On the other hand, satiation might also play a role here and slow down the foraging rate (McCleery 1977, Graber and Graber 1983). The former is probably true because birds usually



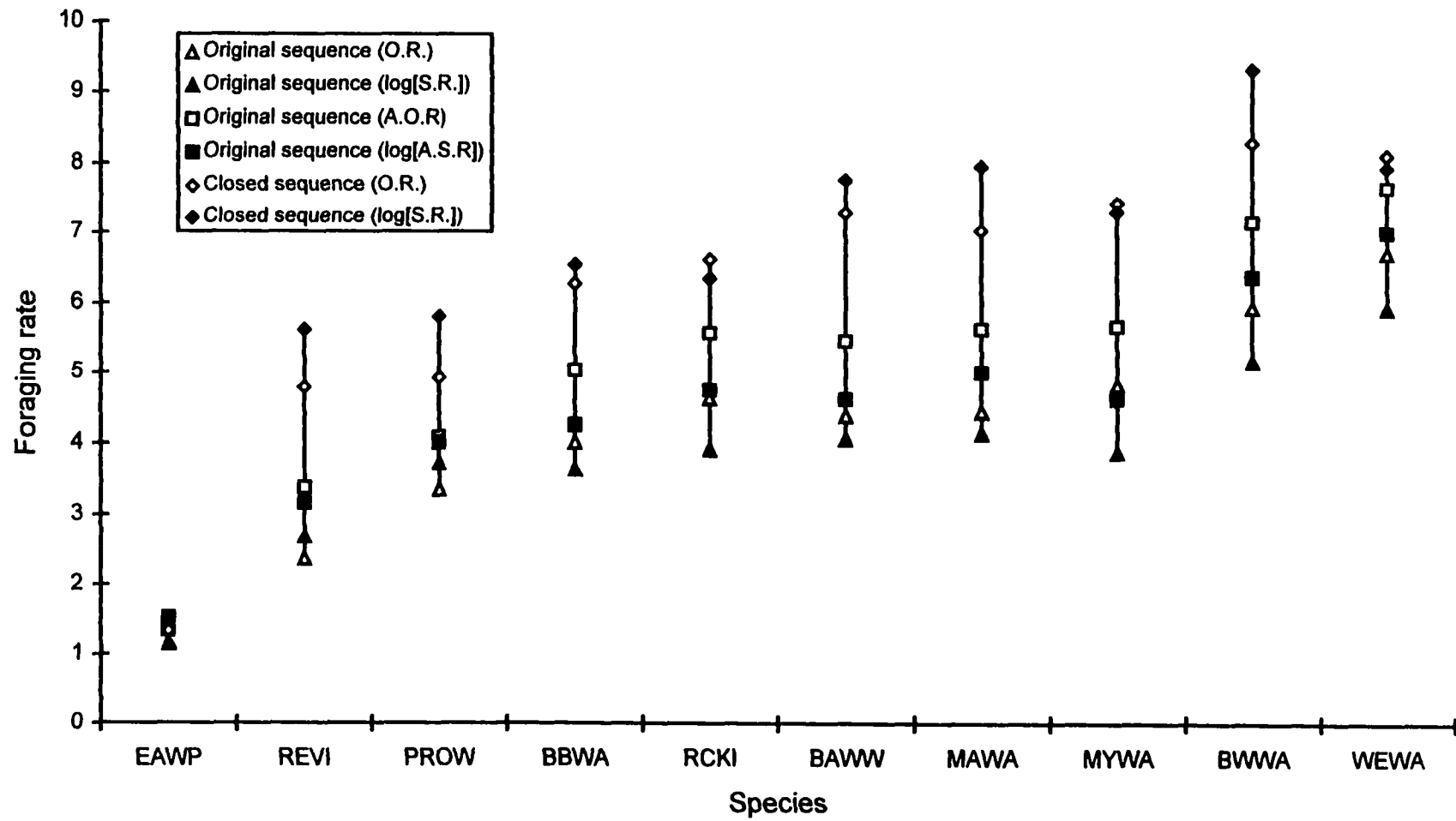


Figure 3.8. Comparison of overall rate with its corresponding log-transformed sequential rate for original sequences, and closed sequences of 10 migrants at Gulf coast stopover sites, 1993-1994.

Table 3.2. Sample sizes, means, standard deviations, coefficients of variation (CV), and the differences between the greatest rate and the smallest rate (Diff.) of sequential rates of 10 insectivorous migratory songbirds at Gulf coast stopover sites, 1993–1994. Correlation coefficient ( $r$ ) between CV and Diff. is equal to 0.6, and  $P < 0.05$ . Species are ranked by CV.

Species	$n$	Mean	SD	CV	Diff.
Eastern Wood-Pewee	55	1.4	0.8	56.4	0.2
Blue-winged Warbler	74	5.6	3.4	60.3	3.2
Worm-eating Warbler	85	6.6	4.2	62.8	1.5
Prothonotary Warbler	50	3.8	3.1	80.8	1.6
Ruby-crowned Kinglet	108	4.3	3.6	82.8	2.5
Magnolia Warbler	173	4.5	3.9	85.3	3.3
Black-and-white Warbler	110	4.4	4.0	91.2	3.4
Red-eyed Vireo	240	2.7	2.6	95.8	3.2
Bay-breasted Warbler	166	4.1	4.7	113.1	4.1
Yellow-rumped Warbler	204	5.0	5.7	113.1	2.6

spent more time searching in the latter part of foraging sequences. This may explain why the mean post section is longer than the mean interval for most species.

For sequential rates, both the sequence duration and the number of attacks in a sequence are variables. Each covaries with foraging rates in a different manner (Figures 3.3, 3.4). Sequence duration is a source of variation because short sequences tend to have higher sequential rates than longer ones (this study, Graber and Graber 1983). As a result, if the observations of a certain species contains more short sequences than long sequences, then the sequential rate may be biased. On the other hand, long sequences have a higher probability of having long intervals and thus a lower foraging rate. The number of attacks in a sequence is positively correlated with the sequential rate. However, the relationship becomes more diffuse when the number of attacks increases (Figure 3.3). In fact, both effects from the sequence duration and the number of attacks may be offset by each other if both variables are randomly distributed.

Unfortunately, foraging data are usually not normally distributed; therefore, the arithmetic mean is not an appropriate estimator of central tendency for such data. In fact, foraging data may have exponential or lognormal distributions, and geometric or harmonic means appear to be better estimators for such distributions (Neter et al. 1990). For original and closed sequences, geometric means of sequential rates are similar to the overall rate (Figure 3.8). Mathematically, overall rates of intervals or the first three intervals are equal to their corresponding harmonic means of interval lengths. Clearly, most workers have not been aware of the underlying distribution of foraging data when they calculated foraging rates and they used arithmetic means.

In calculating the overall rate, because we sum all foraging sequences first, there is probably no need to exclude short sequences. However, most workers subjectively delete those short sequences before they calculate the sequential rate (e.g., Robinson and Holmes 1982, Barrow 1990, Lovette and Holmes 1995). Sequences used to calculate the sequential rate should have a duration longer than the mean interval length. For example, the Red-eyed Vireo had a mean interval length of 13 seconds; if foraging sequences less than 13 seconds are included, one can obtain a 0 rate based on the distribution of interval lengths. In general, a criterion of 20-30 seconds is reasonable for perch-gleaners, and one minute for flycatchers.

Although all five foraging rates were from the same data set, only the sequential rate, overall rate, and adjusted overall rate of the original sequences used the entire data set; the other two methods (closed sequences and the first three intervals) used only a portion of the original data set. This partly contributes to the difference in the final figures of each rate. The sequential rate and the overall rate of the original sequences were almost the same for most species. In reality, different individuals forage differently even if they belong to the same species. Some tend to be faster and others slower; such variation makes the overall rate and sequential rate differ from each other. Statistically, the overall rate is considered a better ratio estimator than the sequential rate because the sequential rate is easily affected by some extreme observations. If we are interested in the long-term trend of foraging, the overall rate appears to be a more realistic estimator because the overall rate is a long-term average-rate maximizer (Stephens and Krebs 1986). Both foraging rates from the original sequences were lower

than the other three foraging rates for all species except the Eastern Wood-Pewee. This result was mainly due to the inclusion of 0- and 1-attack sequences in the original sequences (Table 3.3). The resulting 0 rate or very low rate from 1-attack-sequences contributed greatly to the lower foraging rate from original sequences. In addition, the inclusion of the pre and post sections in the original sequences also contributed to the lower rate because both sections were much longer than expected.

The overall rates of closed sequences were calculated after leaving out those sequences with 0 or 1 attacks and after deleting the pre and post sections of each foraging sequence; consequently, such foraging rate would be higher than those from the original sequences. Because the portion of uncertainty have been removed, overall rates from closed sequences can be considered as less biased foraging rate estimators than those from the original sequences. However, overall rates of closed sequences might be overestimated because of the exclusion of 0- and 1-attack sequences.

If birds forage at a constant rate, the sum of the pre and post sections should be roughly close to the mean interval for any species given that the starting point and the ending point of foraging sequences are random. However, this was not true in this study. The mean lengths of the pre and post sections were both longer than the mean intervals for most species. This implies that birds do not forage constantly all the time or there were some observer errors. Foraging birds might be detracted by the observer or simply shift their attention from foraging to being alert. That is why some workers skip a short period of time before they start to collect foraging data (Hejl et al. 1990). On the other hand, the post section of a sequence may be related to the giving-up time

Table 3.3. Advantage and disadvantage of five different foraging rates based on data from insectivorous migratory songbirds at Gulf coast stopover sites, 1993–1994.

Foraging rate	Advantage	Disadvantage
Original sequences, Sequential rate	<ol style="list-style-type: none"> <li>1. Easy to record.</li> <li>2. With variation measurement.</li> <li>3. Can be used to test the difference among sexes or other variables.</li> </ol>	<ol style="list-style-type: none"> <li>1. Number of attacks and duration are both variables. Thus the resulting rate may be affected by the distributions of number of attacks and duration of foraging sequences.</li> <li>2. Include uncertain sections before the first attack and after the last attack.</li> <li>3. May be underestimated from the inclusion of 0- and 1- attacks sequences.</li> </ol>
Original sequences, Overall rate	<ol style="list-style-type: none"> <li>1. Easy to record.</li> </ol>	<ol style="list-style-type: none"> <li>1. No variation measurements.</li> </ol>
Original sequences, Adjusted overall rate	<ol style="list-style-type: none"> <li>1. Easy to record.</li> </ol>	<ol style="list-style-type: none"> <li>1. No variation measurements.</li> <li>2. Have to know the property of pre and post sections first.</li> </ol>
Closed sequences or intervals, Overall rate	<ol style="list-style-type: none"> <li>1. More accurate because of deleting those portions of uncertainty.</li> <li>2. Interval length alone is enough to calculate foraging rate.</li> </ol>	<ol style="list-style-type: none"> <li>1. No variation measurement.</li> <li>2. Not easy to transcribe from the tape.</li> <li>3. May be overestimated from the exclusion of 0- and 1- attacks sequences.</li> </ol>
First three intervals, Overall rate	<ol style="list-style-type: none"> <li>1. Easy to record.</li> <li>2. More accurate because of deleting those portions of uncertainty.</li> <li>3. Number of attacks is fixed, duration alone is enough to calculate foraging rate.</li> </ol>	<ol style="list-style-type: none"> <li>1. No variation measurement.</li> <li>2. May be biased by using only the first three intervals because the first three intervals are shorter than the last three intervals for most species.</li> <li>3. Smaller sample size than other methods.</li> </ol>

for a patch based on the optimal foraging theory (Krebs et al. 1974) because the average foraging rate, or the mean interval is the giving-up threshold. If one stops recording when the bird is lost from sight, it is likely that one ends at the moment when the bird “gave up” the patch and moved out of it. Thus the post section will be equal to or longer than the mean interval. As a result, both the pre and post sections of a foraging sequence were longer than expected. Therefore, it seems reasonable to count both the pre and post sections as one attack. The resulting foraging rates (adjusted overall rate) fall between those foraging rates from the original sequences and that from the closed sequences. The adjusted overall rate turns out to be a reasonable estimate because foraging rates from the original sequences are too low and foraging rates from the closed sequences are too high. However, the adjusted overall rate may be overestimated if the post section is in fact longer than the mean interval and the pre section. An alternative way is to count the pre section as one attack and the post section as 1/2 attack.

The overall rate from the first three intervals was the highest among the five rates for most species. Two potential sampling errors might be responsible for its great departure (either negative or positive) from the overall rates of closed sequences: (1) foraging rate from the first three intervals were higher than that from the last three intervals and shorter sequences also tend to have higher rates than longer ones; (2) the first three intervals had the smallest sample size, and this resulted in high variation.

The type of prey along with the type of foraging behavior might influence foraging rates (Morse 1968, Benkman and Pulliam 1988). For instance, the Eastern

Wood-Pewee, the only flycatcher in this analysis, had the lowest foraging rate because of its “sit-and-wait” strategy and the resulting attacks on larger flying prey. On the other hand, perch-gleaners searched for prey constantly from perch to perch and thus had higher encounter and foraging rates. Among perch-gleaners, foraging rates might also depend on the distribution and abundance of prey. Yellow-rumped Warblers have been recorded to attack once per 2 seconds for over 40 attacks. The Worm-eating Warbler did not have as high an attack rate as did the Yellow-rumped Warbler because prey inside suspended dead leaves take more time to find, and thus the Worm-eating Warbler has less variable foraging rates from all methods than the Yellow-rumped Warbler. If the percent coefficient of variation,  $100 (\text{standard deviation}/\text{mean})$ , of the sequential rate is ranked by species, species that forage on surface prey have higher values than species that forage on subsurface prey or species that catch prey in the air (Table 3.2). This might imply that the dispersion of surface prey is more irregular and unpredictable than the dispersion of subsurface prey or flying insects. Therefore, the foraging rates of perch-surface-gleaners are more variable. On the other hand, foraging rates from different methods usually have more similar results for the Eastern Wood-Pewee and the Worm-eating Warbler.

Although I used the first three intervals as a unit to calculate foraging rate, it is possible to use any other number, e.g., five or 10, but some species were not followed long enough to reach five intervals; three intervals were used in this analysis to obtain a larger sample size. It would be interesting to find the optimal number of intervals needed to be recorded for a reliable foraging rate estimate. Obviously, three intervals



are not optimal for most species in this study because the foraging rate calculated from the first three intervals departed greatly from foraging rates from other methods.

Intuitively, the selection of the optimal number of intervals may depend on the detectability of the species, ease of following, study sites, season, and the memory ability of the observers. Visibility (Wagner 1981, Bradley 1985) can be another important factor affecting the choice of the optimal number of intervals because birds vary in their secretiveness and in vegetation density where they forage.

In short, it is important to study the properties of foraging sequences before one can select a reliable method to calculate foraging rates. The overall rate is more realistic than the sequential rate if one is interested in a long-term foraging rate. Overall rates from the original sequences tend to be biased through inclusion of pre and post sections much longer than expected for most species. Overall rates from closed sequences are clearly a more reliable estimator than those from the original sequences because pre and post sections have been deleted. However, exclusion of 0- and 1-attack sequences from calculation of the overall rate may be a problem too. The adjusted overall rate from the original sequences seems to be a compromise that solves the problem from the pre and post sections and keeps those 0- and 1-attack sequences in the calculation at the same time. Due to the non-normal distribution of foraging data, logarithmical transformation may be an alternative solution. However, they operate on the sequential rate rather than the overall rate. A computer simulation program should be useful to clarify some of the confusing points that arose from this analysis.

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# **APPENDIX** **COMPARISON OF FORAGING ECOLOGY OF INSECTIVOROUS** **MIGRATORY SONGBIRDS**

Species	Attack behavior <sup>a</sup>	Habitat strata <sup>b</sup>	Substrate <sup>c</sup>	Foraging rate <sup>d</sup>
Yellow-billed Cuckoo	leg/wing	canopy	foliage	slow
Acadian Flycatcher	wing	canopy/subcanopy	foliage	slow
Eastern Wood-Pewee	wing	subcanopy/canopy	air/foliage	slow
Ruby-crowned Kinglet	leg	canopy/subcanopy	bark/foliage	medium
Blue-gray Gnatcatcher	leg/wing	canopy	foliage/bark	medium
Gray-cheeked Thrush	leg	ground	leaf litter/ground	medium
Swainson's Thrush	leg	ground/canopy	leaf litter/bark	fast
Wood Thrush	leg	ground	leaf litter	fast
Gray Catbird	leg	ground/canopy	leaf litter/foliage	fast
White-eyed Vireo	leg	canopy/subcanopy	bark/foliage	medium
Philadelphia Vireo	leg/wing	canopy	foliage	medium
Red-eyed Vireo	leg/wing	canopy	foliage	medium
Blue-winged Warbler	leg	subcanopy/canopy	foliage	medium
Golden-winged Warbler	leg	canopy	foliage/bark	fast
Tennessee Warbler	leg	canopy	foliage	fast
Northern Parula	leg	canopy	foliage/bark	fast
Yellow Warbler	leg	canopy	foliage	medium
Chestnut-sided Warbler	leg	canopy	foliage/bark	medium
Magnolia Warbler	leg	canopy/subcanopy	foliage/bark	medium
Yellow-rumped Warbler	leg	canopy	foliage/bark	medium
Black-throated Green Warbler	leg	canopy	foliage/bark	medium
Blackburnian Warbler	leg	canopy	foliage/bark	medium
Bay-breasted Warbler	leg	canopy	bark/foliage	medium
Black-and-white Warbler	leg	canopy	bark	medium
American Redstart	wing/leg	canopy/subcanopy	foliage/bark	medium
Prothonotary Warbler	leg	subcanopy/canopy	foliage	medium
Worm-eating Warbler	leg	subcanopy/canopy	foliage	fast
Ovenbird	leg	ground	leaf litter/foliage	medium
Northern Waterthrush	leg	ground	mud/ground	fast
Common Yellowthroat	leg	understory/subcanopy	bark/foliage	medium
Hooded Warbler	wing/leg	subcanopy/understory	foliage/bark	medium
Summer Tanager	wing	canopy/subcanopy	foliage	slow
Scarlet Tanager	wing/leg	canopy	foliage	slow

<sup>a</sup> Attack behaviors are divided into leg-powered maneuvers and wing-powered maneuvers. Leg/wing indicates that either categories of attack behavior is used less than 70% of total observations, and leg-powered maneuvers are used more frequently than wing-powered maneuvers. The same rule is applied to habitat strata and substrate.

<sup>b</sup> Only the first one or two predominant categories of habitat strata are listed.

<sup>c</sup> Only the first one or two predominant categories of substrate are listed.

<sup>d</sup> Foraging rates are divided into three categories: slow, under two attacks per minute, medium, between two and six attacks per minute, and fast, larger than six attacks per minute.

## VITA

Chao-Chieh Chen was born on 18 January 1964 in Yunlin, Taiwan. He attended National Cheng Kung University in 1983 and graduated with a degree of Bachelor of Science in Biology in 1987. He graduated from National Normal University as a Master of Science in Biology in 1989. He served in the Army for two years. Then, he worked for the Institute of Biology at National Normal University as a research assistant for a year.

Chao-Chieh Chen was an enthusiastic bird-watcher as an undergraduate. When he was a Master student, he started to study birds. To pursue further knowledge and skill, he came to the United States in August 1992. He began his doctorate study in the School of Forestry, Wildlife, and Fisheries at Louisiana State University, Baton Rouge, and he is currently a candidate for the degree of Doctor of Philosophy.

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**Major Field:** Wildlife and Fisheries Science

**Title of Dissertation:** Foraging Behavior and Habitat Selection of  
Insectivorous Migratory Songbirds at Gulf Coast  
Stopover Sites in Spring

**Approved:**

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**Date of Examination:**

20 Sept. 1996