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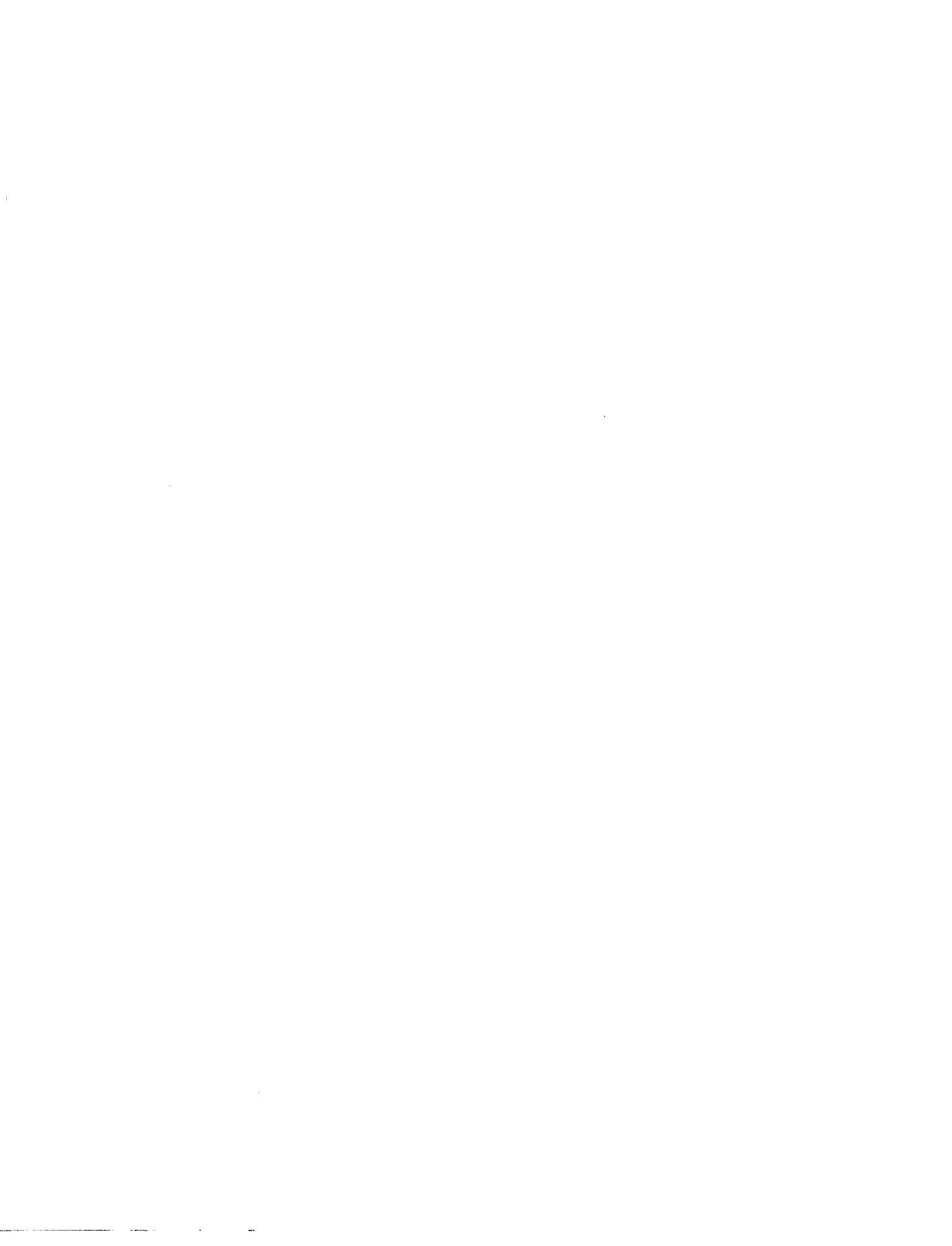
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**The foraging behavior of a guild of insectivorous birds in three
structurally different communities**

Hibbard, Perry Richard, M.S.

The University of Arizona, 1991

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**THE FORAGING BEHAVIOR OF A GUILD
OF INSECTIVOROUS BIRDS
IN THREE STRUCTURALLY DIFFERENT COMMUNITIES**

by

Perry Richard Hibbard

**A Thesis Submitted to the Faculty of the
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY
In Partial Fulfillment of the Requirements
For the Degree of
MASTERS OF SCIENCE
In the Graduate College
THE UNIVERSITY OF ARIZONA**

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Acknowledgment

I thank J.H. Brown and S.M. Russell for serving as thesis directors and for providing guidance and encouragement, especially during the early stages of this thesis. D. Vleck and J. Bronstein served on my thesis committee and provided additional assistance and direction.

I am thankful to S.M. Russell, D. Vleck, and J. Bronstein for critical reviews and comments on earlier drafts of this thesis. Their comments and criticisms greatly improved the content.

B. A. Maurer provided much needed assistance with the statistical design of this study. I am very grateful to him for his patience, advice, and comments.

J.B. Dunning, S. Goldwasser, N. Mays, T. Huels, J.S. Brown, L. Venable, A. Bammann, and R.L. Peck provided valuable discussion at various stages of this study.

J.S. Brown provided encouragement and helpful discussion of the potential importance of foraging rate.

R.L. Peck provided assistance in the field with vegetation samples.

R. Ogden Russell provided a tape recorder and parabolic arc for use in recording the vocalizations of *Camptostoma imberbe*.

R. D. Ohmart, D. Gabaldon, and colleagues contributed unpublished data from their massive and valuable catalogue of the diets of birds of the lower Colorado River, and R.D. Ohmart provided useful discussion of my results and his dietary catalogue data.

This study was conducted in Catalina State Park. I am grateful to Park Superintendent Neil Donkersley and his staff at the Park for the assistance provided during my work.

This study is dedicated to:

Perry Norman and Dorothy Lee Hibbard

for a lifetime of encouragement

Emily Lucia

and **Annaliese Noel**

"The woods are lovely, dark, and deep
But I have promises to keep
and miles to go before I sleep
and miles to go before I sleep"

Rebecca L. Peck

whose tolerance, criticism, and deep appreciation
of life underlie every page

- I have something to tell you -

and to **the birds**

who made all the long hot and cold days worth while

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ABSTRACT

The foraging behavior of six species of insectivorous foliage-gleaning birds was studied in three different communities in Arizona to examine the role of resource partitioning in coexistence. I recorded data during winter and spring, the harshest seasons. Two to four species coexisted in each community.

I recorded plant species, plant life-form, foraging height, plant portion, perch size, capture size, capture technique, and foraging rate. Foraging behavior was compared to the plant distribution profile, interspecifically among sympatric guild members within a season, intraspecifically between seasons, and intraspecifically between communities within a season.

Species differed most in plant species selected, foraging height, and capture technique, and varied the least in plant portion, perch site, and capture site. All species overlapped in most behaviors, but differed from other guild members in at least two foraging variables. Permanent residents showed the greatest differences. These findings are consistent with niche complementarity and the idea that competition has led to partitioning of the resources. However, other hypotheses cannot be ruled out.

CHAPTER 1

INTRODUCTION

Insectivorous foliage-gleaning birds are a conspicuous component of avian faunas of scrub and forested areas throughout North America. In the southwestern United States, several species of small foliage-gleaning birds are common in several structurally different communities. Some species in this guild are common in a variety of communities, while others are common in only one or two (Phillips et al. 1964; Root 1988). These species have in common small size, drab colors, and a propensity for inhabiting dense vegetation and moving quickly as they forage. An overview of these species would suggest that they are more similar than different in size, shape, and foraging behavior. This similarity has prompted many questions concerning the organization of this guild. That these species coexist in relatively stable, predictable assemblages (Cody 1974; Monson and Phillips 1981) leads to questions concerning the forces that structure this guild.

The coexistence of ecologically similar species has long been of interest to community ecologists interested in the forces, both biotic and abiotic, that have influenced the number and densities of species comprising a community. Although several factors, including competition, predation, climate, disturbance, and the physical structure of the habitat, have long been recognized as important, the relative importance

of these factors is debated (Connell 1983; Schoener 1983; Wiens 1977, 1989). Much of the debate has revolved around the role of competition. The predominant view in ecology until recently has been that vertebrate communities are relatively stable, and competition is the single most important factor in shaping species assemblages. That ecologically similar species coexist is an enigma inviting detailed study (MacArthur 1958; Cody 1974). The competitive exclusion principle (Hardin 1960; May 1973) predicts that ecologically similar species cannot coexist on a limiting resource unless there is niche differentiation. If competition is important in structuring the avian components of various communities, foliage-gleaning species must partition resources in some significant way.

How much overlap of utilization curves along a particular niche axis is compatible with stable coexistence of two or more species is among the most crucial questions of community ecology (Begon et al. 1986). A variety of factors affect the impact of competition, and separation may involve the partitioning along one major axis or involve the cumulative effects of partitioning along several axes. Where several species are competing for more than one resource, the latter pattern of separation might be expected (MacArthur 1972).

Since the late 1950s, many studies focusing on ecologically similar species have been conducted with varying results (for reviews, see Connell 1983; Schoener 1983). Several studies have found that similarities among similar species are superficial and have suggested that the differences between coexisting species (mostly congeners) are sufficient to allow for partitioning of resources and reduced competition (for example, MacArthur 1958; Cody 1974; Emmons 1980; Rusterholz 1981; Pyke 1982; Brown 1989). Other observers have questioned whether differences in foraging behavior between species are sufficient to account for resource partitioning, and have concluded

that factors other than competition appear to be the major influence in shaping coexistence. (Wiens and Rotenberry 1980, 1981; Strong et al. 1984).

Competition among coexisting species can be alleviated by partitioning resources in several ways (Cody 1974; Schoener 1983), such as by food size, food type, foraging habits, spatial segregation (horizontal or vertical), or temporal segregation. Measurement of overlap along various resource axes can provide insight into the mechanisms promoting coexistence. If differences between species are significant, competition may be central to the organization of the community. If, however, differences are minimal, factors other than competition may be more important in structuring these assemblages. Knowledge of the foraging strategies employed by ecologically similar species can be used to direct further studies. For instance, if species overlap significantly, further investigations into the circumstances of their coexistence should be directed towards factors influential in structuring non-equilibrium communities (Wiens 1977). If, however, species appear to overlap relatively little, then further studies might best investigate resource depletion by foraging birds as well as the diets of the coexisting species.

Although the interaction of several species in a food guild is likely to be complex and influenced by several factors, in this study I focus on the foraging behavior of ecologically and morphologically similar foliage-gleaning bird species inhabiting three structurally different communities in close proximity to one another. I recorded observations during the two seasons in which food resources were expected to be at their lowest densities and diversity. Interspecific and intraspecific (including inter-community) comparisons of foraging behavior were made to address the following questions:

1) How similar is the foraging behavior of guild members occupying the same community? Is there evidence for resource partitioning based on differences in foraging behavior?

2) How similar is the foraging behavior of a species between seasons within a community? Can changes be attributed to different features of the community, different microenvironmental effects, or to interspecific competition?

3) How similar is the foraging behavior of a species in structurally different communities? Does the basic foraging pattern of a species differ between communities? Can differences be attributed to different features of the communities, or to interspecific competition?

In addition, I will discuss other factors that may affect community structure leading to coexistence of these species, such as predation, weather disasters, parasitism, competition from non-guild members, distribution of arthropods, and diet, relying on the available literature and qualitative observations at the study site.

CHAPTER 2

STUDY SITES AND METHODS

Study Site Selection

I located three study plots representing structurally different vegetative communities within 1.5 km of each other in Catalina State Park, 19 km north of Tucson, Pima County, Arizona ($110^{\circ} 54' W$, $32^{\circ} 25' N$). All three study sites, denoted hereafter as palo verde - cactus, mesquite woodland, and mixed broadleaf, are located in the foothills of the Santa Catalina Mountains north of Pusch Ridge. Study plots varied in size depending on the size of the uninterrupted expanses of the community. I selected study communities based on close proximity to one another, structural differences between communities, internal homogeneity, and the size and continuousness of distribution.

I sampled only the core of each community type, leaving a buffer area between the study site and adjacent community types. Landmarks were used to delineate the study plots within each community.

Sample Seasons

I sampled from January through early March in winter of 1984, and from May through June in springs of 1984 and 1985. These five months represent the harshest

abiotic conditions in this region. The winter months of January through March are mild to cold with frequent intense freezes. Cold-deciduous tree species are leafless during this season. Spring months of May through June are hot, dry, and sunny. Drought-deciduous trees and shrubs are leafless during this season.

There are no weather records available from Catalina State Park. However, weather data reported in Sellers and Hill (1974) for the community of Winkelman most closely approximate conditions at the study site, taking into consideration elevation, aspect, and orographics. These data provide a general picture of weather conditions at Catalina State Park.

Temperatures are coldest in December and January (daily mean maximum 18.7° and 18.5° C respectively) with the mean number of days with minimum temperature below 0° C at 23 and 22. February temperatures are only slightly warmer. Due to cold air drainage patterns at the study sites, and due to exposure (considering aspect, slope, and vegetation), the mesquite woodland and mixed broadleaf communities I studied are probably colder than the Winkelman station, with more frequent freezing temperatures and lower mean maximums.

The mean maximum temperature for May is 33.6° C with 21 days above 32° C, while mean minima are 9.7° C with no lows below 0° C. June is the second hottest month with the mean maximum and minimum temperatures of 38.7° and 15.2° C, and an average of 29 days greater than 32° C. July is slightly hotter (39.5° and 20.8° C) but is much wetter due to the onset of summer rainfall. Temperatures above 40° C occur yearly; the highest temperature recorded (48.3° C) occurred during June.

Winter and summer are the wettest months, with 24% and 49% of the annual precipitation of 327 mm falling during these seasons. Mean precipitation for January through early March is 61 mm while a mean of 10 mm falls during May and June.

Vegetation Sampling

In all communities, I sampled the vegetation of the entire study site using a point-intercept technique (Mueller-Dombois and Ellenberg 1974). Within each homogeneous community, I established transects and, using a compass, laid out a meter tape in 100 m segments. I took samples at 2-5 m intervals depending on the size of the community and the number of points needed to characterize the community. The number of points taken in each community depended on community homogeneity. A running mean (Mueller-Dombois and Ellenberg 1974) was used for various vegetation factors (percent of dominant species, total canopy cover, and mean height) to determine sample size. Point intervals within each community were constant.

At each point I recorded the following information: 1) bare ground, basal cover, or canopy cover, 2) basal and canopy cover by each plant species and life-form (tree, shrub, half-shrub, grass, herb, vine, and stem succulent), and 3) presence of vegetation along a vertical line above each point, sampled at 0.5 meter intervals. I recorded both annual and perennial vegetation.

For this study, I defined the life-form categories as follows. A tree is a woody plant with a central main trunk. A shrub is defined as a woody plant without a main central trunk, generally less than 2 m in height, while a half-shrub is a perennial plant generally less than 0.5 m in height, predominantly herbaceous, but with a woody base. Grass is defined as any herbaceous monocot with basal buds, including sedges and rushes, and an herb is any free-standing, non-woody, herbaceous plant with apical buds. A vine is any plant that receives its support primarily by clinging to other plants. A stem-succulent is a predominantly leafless perennial plant with enlarged stems for storage of water (all were cacti on this study site). Forbs, defined as small (mostly annual)

herbaceous plants with apical meristems, were rare during the two sample seasons of this study. These definitions are modified from Shreve (1964). Plant species were not assigned to one life-form category; individuals were placed into categories based on the above definitions, such that a species may be represented in more than one life-form, though this was infrequent.

I used a telescoping pole delineated in 0.5 meter intervals to determine the presence or absence of each species for each height interval above a sample point. A species was considered present in a vertical cell (0.5 meter by 2.54 cm) if it contacted the pole at any point within the interval. The pole was equipped with horizontal and vertical levels.

I estimated relative plant volume by species and life-form using both vertical and horizontal transect information. Relative volume was estimated for plant species and life-forms using the number of cells occupied by the species or life-form divided by the total number of cells occupied by all vegetation.

In all communities, I sampled vegetation during a one-week period in spring. I took a winter sample in the mesquite woodland due to significant seasonal changes in that community. I conducted winter "test samples" in the palo verde - cactus and mixed broadleaf communities to determine whether significant changes in vegetation existed between study seasons, and found no differences.

Vegetation at the Study Sites

Each community contained significantly different vegetation as measured by species present, relative frequency of each species, and the height profile. The vegetation at each site is described below.

Palo Verde - Cactus Community. Within the palo verde - cactus community, I sampled an approximately 11.5 hectare study site located 0.8 - 2.5 km north of Sutherland Wash. Elevation is 830 m. This area is dominated by low rolling hills dissected by several small intermittent washes. The majority of the area has a southern aspect. Soils are predominantly alluvial with a few granitic ridges and outcrops dispersed throughout.

Species and life-form composition by relative volume are presented in Table 1. All plant names follow Lehr (1978). I took a total of 1003 points along transects throughout the study area. Total plant canopy cover was 46.6%. *Cercidium microphyllum* was the dominant plant species comprising 46.2% of the relative volume. *Calliandra eriophylla* (13.4%), *Encelia farinosa* (5.5%), *Heteropogon contortus* (6.0%), *Prosopis velutina* (4.7%), and *Aristida ternipes* (3.2%) were the other major components by relative volume. Several minor species were present at low densities, but were not recorded along the transects.

Trees, represented by four species, were the dominant life-form and occupied 52.3% of the relative volume. Half shrubs (9 species; 23.7%), perennial grasses (10 species; 13.4%), shrubs (5 species; 4.7%), vines (1 species; 3.2%), and cacti (5 species; 2.8%) are also present. Plants encountered along the transect did not exceed 4.0 m in height.

All four tree species within the study area are deciduous and were leafless during the winter study periods. The dominant species, *Cercidium microphyllum* and *Acacia greggii*, are drought- and cold-deciduous and were leafless during both study seasons. *Prosopis velutina* produced leaves in April and was leafed-out during the spring season. The majority of the other plant species show little change in foliage from the winter to spring study seasons.

Table 1. Vegetation of the Palo Verde - Cactus community. Relative plant volume (%) is provided by major species and by life forms. All names follow Lehr, 1986.

PALO VERDE - CACTUS COMMUNITY		
SPECIES/LIFE FORM	LIFE FORM	RELATIVE VOLUME
<i>Cercidium microphyllum</i>	Tree	46.2
<i>Calliandra eriophylla</i>	Half Shrub	13.4
Grasses (10 spp.)	Grass/Sedge	13.4
<i>Encelia fairnosa</i>	Half Shrub	05.5
Shrubs (5 spp.)	Shrub	04.7
Other Half Shrubs (3 spp.)	Half Shrub	04.7
<i>Prosopis velutina</i>	Tree	04.7
<i>Janusia gracilis</i>	Vine	03.2
Cacti (5 Spp.)	Cactus	02.8
Other Trees (2 spp.)	Tree	01.4
TOTAL		100.0
Tree (4 spp.)		52.3
Half Shrub (9 spp.)		23.7
Grass (10 spp.)		13.4
Shrub (5 spp.)		04.7
Vine (1 sp.)		03.2
Cacti (5 spp.)		02.8
Other		00.0
TOTAL		100.1

Mesquite Woodland Community. The mesquite woodland study site is represented by a 4.0 hectare stand located at the confluence of Montrose Canyon and Sutherland Wash (an intermittent stream). This site is located on a flat bench 4 m above the latter drainage. The soils are sandy alluvials with a well developed organic layer. The elevation is 830 m. This community is scattered over much of the elevated flats above the major drainages within the park and in the general area. Most of these areas show some degree of human disturbance and the study site represents the most undisturbed and best defined representation of this community. It is bordered by palo verde - cactus and mesquite scrub communities. The latter is composed of many of the same species as the mesquite woodland, but the plants are smaller, are shrubby, and form very dense thickets.

Species and life-form composition by relative volume is presented in Table 2. I took a total of 350 points in this highly homogeneous community. This woodland is dominated by tall trees (generally 5-10 m) and varies in appearance from winter to spring. All of the tree species in this woodland are winter-deciduous with leaves dropping in November and returning in mid-April, except for *Acacia gregii* which produces leaves in late May. In winter, the woodland has a bright, open appearance due to the lack of leaves and to the green winter grass, while in spring it appears dense due to the presence of leaves on the trees.

During winter, plant cover was 93.6%. A winter annual grass (*Hordeum* sp.) covers 88.8% of the ground. Vegetation by volume is dominated by *Prosopis velutina* (88.2% of perennial volume, 79.9% overall), *Hordeum* sp. (16.2% overall), *Acacia greggii* (5.2%, 1.3%), and *Celtis reticulata* (2.6%, 0.6%).

Table 2. Vegetation of the Mesquite Woodland community. Relative plant volume (%) is provided for major species and for life forms. All names follow Lehr 1986.

MESQUITE WOODLAND COMMUNITY			
SPECIES/LIFE FORM	LIFE FORM	RELATIVE VOLUME	
		PERENNIAL VEGETATION ONLY	ALL VEGETATION
<i>Prosopis velutina</i>	Tree	88.2	73.9
<i>Hordeum</i> sp. (annual)	Grass	0.0	16.2
<i>Acacia greggii</i>	Tree/shrub	6.2	5.2
<i>Celtis reticulata</i>	Tree	3.1	2.6
<i>Hymenoclea</i> sp.	Shrub	0.9	0.8
<i>Lycium</i> sp.	Shrub	0.7	0.6
<i>Condalia globosa</i>	Shrub	0.6	0.5
<i>Opuntia</i> spp.	Cactus	0.2	0.2
TOTAL		99.9	100.0
Tree (3 spp.)		97.5	81.8
Grass/Sedge(1 spp.)		0.0	16.2
Shrub (3 spp.)		2.2	1.9
Half Shrub		0.0	0.0
Cacti (2 spp.)		0.2	0.2
Vine (1 spp.)		0.0	0.0
TOTAL		99.9	100.1

In winter four life-forms were present. Trees accounted for 81.8% of the relative volume, grass (1 species) accounted for 16.2%, shrubs for 1.9%, and stem succulents for 0.2%.

During spring the woodland was a dense forest with a closed canopy. Perennial vegetation (annuals are essentially absent until the advent of summer rains) provided a canopy cover of 79.6%. *Prosopis velutina* was the dominant species with a relative volume of 88.2%. *Acacia greggii* (6.2%), *Celtis reticulata* (3.1%) and shrubs (2.5%) provided the remaining cover.

In spring, only three life-forms were present. Trees (3 species) accounted for 97.5% of the relative volume. Shrubs (3 species; 2.2%) and stem succulents (2 species; 0.2%) were the only other life-forms represented.

Mixed Broadleaf Community. The mixed broadleaf community was represented in this study by a 1.4 hectare site located in lower Romero Canyon approximately 0.5 km east of the confluence of Romero Canyon with Sutherland Wash. The elevation is 850 m. The study site is located in a narrow, shallow canyon and is approximately 350 m in length. Similar vegetation is continuous with the study area for approximately 100 m up canyon and 800 m down canyon. Surrounding vegetation includes palo verde - cactus to the north on south facing slopes and mixed shrub grassland on the dry elevated slopes to the south. The Romero Canyon stream has surface water most of the year, though segments dry up in June, leaving only a few large pools. This community type is well represented throughout the southwest mountains and south into Sonora, Mexico (Minckley and Brown 1982).

Species and life-form composition by relative volume is presented in Table 3. I used five hundred points to characterize vegetation in this community. Vegetation was dominated by large (10-16 m) evergreen and winter-deciduous trees, with a variety of

Table 3. Vegetation of the Mixed Broadleaf community. Relative plant volume (%) is provided for major species and life forms. All species names follow Lehr 1986.

MIXED BROADLEAF COMMUNITY		
SPECIES/LIFE FORM	LIFE FORM	RELATIVE VOLUME
<i>Fraxinus pennsylvanica</i>	Tree	55.8
<i>Quercus grisea</i>	Tree	11.7
<i>Platanus wrightii</i>	Tree	10.6
<i>Mimosa biuncifera</i>	Shrub	5.3
<i>Dodonaea viscosa</i>	Shrub	3.6
<i>Baccharis sarothroides</i>	Shrub	3.0
<i>Muhlenbergia</i> sp.	Grass	3.0
<i>Quercus emoryi</i>	Tree	1.9
<i>Dasyllirion wheeleri</i>	Other	1.3
<i>Quercus arizonica</i>	Tree	0.9
Other Trees (2 spp.)	Tree	0.8
Other Grasses/Sedges (2 spp.)	Grass	0.7
Other Shrubs (2 spp.)	Shrub	0.7
Other species (4 spp.)	Other, Vine	0.8
TOTAL		100.1
Tree (7 SPP.)		81.6
Shrub (5 SPP.)		12.6
Grasses and Sedges		3.7
Other (3 SPP.)		2.2
Vine (1 SPP)		+
Half Shrub		0.0
Cacti		0.0
TOTAL		100.1

shrubs and small drought-tolerant trees on the fringes. Leaf abscission among deciduous species occurred in October to November, and new leaf growth appears in March. Perennial canopy cover was 22.7%.

Dominant species by relative volume were *Fraxinus pennsylvanica* (55.8%), *Quercus grisea* (11.7%), *Platanus wrightii* (10.6%), *Mimosa biuncifera* (5.3%), *Dodonea viscosa* (3.6%), *Baccharis sarothroides* (3.0%), *Muhlenbergia* sp. (3.0%), and *Quercus emoryi* (1.9%). Sparse stands of *Carex* sp. and *Eleocharis* sp. occur along the stream edge at various locations.

Five life-forms were represented in this community. Trees (7 species) accounted for 81.6% of the relative volume. Shrubs (5 species) accounted for 12.6% of the volume. Other life-forms represented were grasses (including sedges; 4+ species; 3.7%) and others (vines and leaf succulents; 4 species, 2.2%).

Bird Species

Once I established study sites, all resident insectivorous foliage-gleaning birds were sampled. I considered a species a resident if it was present within the study site on a daily basis during the seasons sampled. For the spring season, species were considered resident in a community only if several pairs were nesting within that community within Catalina State Park. Non-resident foliage-gleaning birds (mostly transient or from adjacent non-sampled communities) were occasionally observed within the three communities under study, but such occurrences were uncommon.

Six species of foliage-gleaning insectivorous birds met the definition of resident used in this study, and all are conspicuous components of the avian fauna in the communities in which they occurred. Three species, *Auriparus flaviceps* (verdin), *Camptostoma imberbe* (northern beardless-tyrannulet), and *Polioptila melanura*

(black-tailed gnatcatcher), were year-long permanent residents at Catalina State Park. Two species, *Vermivora luciae* (Lucy's warbler) and *Vireo bellii* (Bell's vireo), were present only during the spring season, and one species, *Regulus calendula* (ruby-crowned kinglet), was present only during the winter season. All spring residents nested in the communities in which they were resident.

All six of these species belong to the passerine order Passeriformes. *C. imberbe* is a sub-oscine tyrant flycatcher in the family Tyrannidae. *A. flaviceps* belongs to the family Remizidae, most closely related to tits in the family Paridae, while *P. melanura* and *R. calendula* belong to the subfamily Sylviinae in the family Muscicapidae. *V. bellii* belongs to the family Vireonidae, and *V. luciae* is a wood-warbler belonging to the subfamily Parulinae in the family Emberizidae. Names and classification used in this study follow the sixth edition of the A.O.U. check-list (AOU 1984).

All six species are morphologically similar. Average body weight (Dunning 1984) ranges from 8.5 g (*V. bellii*) to 5.0 g (*P. melanura*). Laudenslayer (1981) measured eight morphological characteristics of *A. flaviceps*, *P. melanura*, and *V. luciae* along the lower Colorado River. He found that these three species did not differ in weight (5.18-6.60 g), total length (98.41-104.72 mm), tail length (45.88-51.00 mm), exposed culmen length (7.01-8.84 mm) and exposed culmen length anterior to the nares (5.57-6.30 mm). *A. flaviceps* differed from *P. melanura* and *V. luciae* in two measures: bill depth (3.84, 2.25, 2.92 mm respectively), and bill width (3.69, 3.04, 3.33 mm). *P. melanura* differed from *A. flaviceps* and *V. luciae* in wingspan (140.12, 160.00, 161.70 mm). Overall, these species are similar and can be arranged along a continuum of size with most measurements. Although the species at either extreme may differ significantly, species pairs along morphological continua do not differ, and there are no distinct size categories.

These species are not sexually dimorphic, except in a few minor characteristics. Only *P. melanura* (spring only) males can be regularly distinguished from females by plumage.

Because nesting patterns are influenced by predation (Collias and Collias 1984) and because predation may influence guild structure (Root 1967; Cody 1974), I will provide a short description of the nests of these species. *Vireo bellii* constructs a cup-nest of grass and twigs. Nests are generally located in dense vegetation. In the mesquite woodland, nests were located at the ends of drooping mesquite branches, usually less than 2 m above the ground. *Polioptila melanura* builds a small cup-nest of grass, located on small branches (usually < 5 cm diameter) in trees (usually palo verde) with densely packed twigs. *Vermivora luciae* is one of only two cavity-nesting parulids (Morse 1989). It builds a small, loosely arranged cup-nest in a woodpecker hole or, more frequently, in a shallow natural cavity in the trunks of trees created by branch falls or rotted branches. This species is very secretive around its nest (Harrison 1979; personal observation) and nests are difficult to find. *Auriparus flaviceps* builds a relatively large domed nest constructed of dense aggregations of usually thorny twigs. Nests have one small side entrance and are usually conspicuously located at the ends of stout branches in trees. *Camptostoma imberbe* builds a loosely domed cup-nest high above the ground (5+ m) in trees and often on the ends of branches (living or dead) or in mistletoe clumps.

Bird Censusing

Two techniques were used to census birds depending on the size of, and visibility within, each community. In the palo verde - cactus and mixed broadleaf communities I used a variable strip transect (Emlen 1971). Data was limited to a perpendicular width

of 126 m either side of the transect line in the former community and to approximately 50 m either side of the transect line in the latter community. The narrow width of the transect in the mixed broadleaf community was due to the narrow width of the community which is limited to Romero Canyon. Distances along the transect in each census depended on the number of sightings, n_i , defined as the number of adult birds of the i th species. Because it is recommended that n_i be approximately 25-30 for a robust estimate (Burnham et al. 1980), I used several non-overlapping transect segments in each of these communities. I combined the total number of transects to obtain n_i for each community. The coefficient of detectability (C.D.) was estimated for each species in each community by plotting the sightings in 5 m intervals perpendicular to the transect line as described by Emlen (1971). The density, D , for each species was then estimated by the following equation:

$$D = (n_i/l)/C.D. \quad (1)$$

where l is the total length of the transect measured in units of 1.6 km (length in m divided by 1600). The resulting density is number of adult birds per 40 hectares. I used a compass and rangefinder to estimate sighting angle and distance with respect to the transect line to calculate perpendicular distance from the transect line.

Due to the small size of the mesquite woodland study site, I could not obtain large enough sample sizes without summing transects from widely dispersed and vegetatively dissimilar areas. As a result, I used the spot-mapping technique (International Bird Census Committee 1970). The regular territories of all adult birds occurring within the sample area were mapped (including territory outside of the sample area), and the number of birds utilizing the study area was estimated. This technique was aided by color leg-bands that allowed identification of some individuals.

I conducted censuses from January 4 to February 14, 1985 and June 1 - 21, 1984 and May 11 through June 30, 1985. Transects were flagged so that census routes did not vary. All censuses were conducted between 0730 and 0930 in winter and 0530 and 0930 in spring. A census consisted of identifying every adult bird observed or heard (call or song) along the transects.

Foraging Behavior

I quantified foraging behavior using the metronome technique of Wiens et al. (1970). I collected data every fifteen seconds (timed on a stopwatch) to mitigate the problem of independence of consecutively recorded behaviors. Due to a potential bias of independence from the technique used (see Landres and MacMahon 1980), the significance level was set at $p < .01$ and the highly significant level set at $p < .001$ (Brian Maurer, personal communication). This procedure, along with greater statistical probability required to reject the null hypothesis sufficiently minimizes the problem of independence (Brian Maurer, personal communication; see Landres and MacMahon 1980 and Maurer 1985 for brief discussions).

Birds were observed at close range as I followed them through the field. Only actively foraging birds were monitored, with observations of an individual bird limited to 3 consecutive minutes (12 points) to reduce sampling bias. Most sample periods ranged from 30 seconds to 120 seconds (2-8 data points). The presence of a single observer, myself, on a regular basis appears to have had little effect on the behavior of the birds. The birds appeared to become used my presence and paid little attention. I made and recorded all observations used in this study.

Two sets of data were gathered, requiring separate observation periods. These two sets will be referred to as foraging location and foraging rate data and are described

below. Communities were sampled on alternate days or on one day in the morning and the next day in the afternoon. The total amount of time spent in each community varied depending on area covered, ease of observations (including density of birds), and total observations recorded. I spent more observation hours in the palo verde - cactus community than in other communities since birds were more difficult to locate and observe, requiring more observation time to obtain adequate sample sizes.

Foraging Location Data. I collected foraging location data between June 1 and 25, 1984, between the hours of 0530 - 1300; between January 4 and February 24, 1985, between the hours of 0730 - 1800; and between May 4 - July 1, 1985, between the hours of 0530 - 1800, excluding 1200 - 1500. I recorded the following components of foraging behavior: 1) plant species and life-form searched or gleaned by a bird; 2) vertical height of perch site above ground: 0 - 0.5 m, >0.5 - 1.0 m, >1 - 2 m, >2 - 4 m, >4 - 8 m, >8 - 16 m, >16 m; 3) plant portion being used as a perch, defined as outer (the portion of a plant dominated by foliage and twigs), middle (the portion between the canopy and the main axis dominated by branches with relatively little foliage), inner (the inner axis of a plant extending from the ground to the top of the tree dominated by trunk and branches), or ground; 4) perch size, estimated as twig (<1.5 cm diameter), branch (>1.5 cm and <15 cm), trunk (> 15 cm), or ground; 5) capture site defined as foliage (including leaves and flowers), twig, branch, trunk, ground, or air; and 6) capture technique, defined as perch glean (perched while capture is made from vegetation), hover glean (hovering to capture food from vegetation), aerial hawk (leaving a perch to capture a flying insect), or hang-glean (hanging upside down while capture is made from vegetation).

The plant species selected, foraging height, plant portion, and perch site were recorded every 15 seconds of observation. I recorded food capture site and capture

technique when captures occurred. Most quantified observations of these two latter variables were recorded during foraging rate observations.

Foraging Rate Data. I collected foraging rate data between January 29 and February 24, 1985, between the hours of 0730 - 1800; and between May 4 and July 1, 1985, between the hours of 0530 - 1800 (excluding 1200 - 1500). This technique was modified from Cody (1974, pp 39-40; see also Landres and MacMahon 1980). For these observations, I used two stopwatches and a click counter, and recorded the following data: 1) continuous foraging time; 2) the number of perch changes during the recorded time sequence; 3) number of times the bird changed plants during the foraging sequence; 4) number of prey captures, 5) capture technique (as in foraging location above); and 6) capture site (as in foraging location above). The time interval between perch changes (i.e., time on perch) was not measured since this represented a short time period (<1 - 3 seconds) and is difficult to clock, leading to a relatively large measuring error. I estimated the average time between perch changes by dividing total time by the number of perch changes.

Analysis

I used a log-linear G test (Zar 1984) based on the number of foraging observations to test for differences in foraging behavior among species. I used pairwise comparisons to test species' use of vegetation by comparing the number of data observations each species spent on a particular plant species to plant volume as estimated by the number of cells occupied by each plant species or life-form. I made intraspecific comparisons between communities and seasons, and interspecific comparisons within a community by comparing data observations in each category tested from one species to its counterpart in another community, and one species to another species within a community.

CHAPTER 3

RESULTS

Bird Census

The densities (adults per 40 hectares) of the resident foliage-gleaning birds in each of the three communities for all seasons are provided in Table 4.

Foliage-gleaning birds were found in all three communities in all seasons except for the winter season in the mixed broadleaf community. *Auriparus flaviceps* was found in all communities and seasons in which foliage-gleaning birds were found. It occurred in higher densities in spring than in winter and reached its highest density (83.3) in the mixed broadleaf community. *Regulus calendula* was observed in the palo verde - mixed cactus and mesquite woodland during the winter season only, reaching its highest density (70.3) in the mesquite woodland. *Vermivora luciae* and *Vireo bellii* nested in the mesquite woodland and mixed broadleaf communities in spring. Both were present in high densities, reaching their highest densities (133.3 and 177.7 respectively) in the mixed broadleaf community during the spring of 1984. Densities were much lower (83.3 and 100.0) during the spring of 1985 in the same community, possibly a result of the unusually cold winter which may have reduced the number and density of arthropod prey. Two species were found in just one community each. *Poliophtila melanura* was common in the palo verde - cactus community all year, reaching its

Table 4. Density of resident foliage-gleaning birds in three communities at Catalina State Park. Density is expressed as number of adults per 40 hectares. S84 = Spring of 1984, S85 = Spring of 1985, W = Winter

SPECIES	COMMUNITY								
	Palo Verde-Cactus			Mesquite Woodland			Mixed Broadleaf		
	S84	W	S85	S84	W ¹	S85	S84	W ²	S85
<i>Auriparus flaviceps</i>	51.9	44.4	57.8	56.5	41.3	54.7	66.7	0	83.3
<i>Camptostoma imberbe</i>	0	0	0	+ ³	5.8	39.8	0	0	+ ⁴
<i>Polioptila melanura</i>	44.4	27.8	35.6	0	0	+ ⁵	+ ⁶	0	+ ⁷
<i>Regulus calendula</i>	0	22.2	0	0	70.3	0	0	+ ⁸	0
<i>Vermivora luciae</i>	0	0	0	87.0	0	77.0	133.3	0	83.3
<i>Vireo bellii</i>	0	0	0	73.9	0	59.6	177.7	0	100.0

¹ Represents the density computed for 6 censuses spanning a cold weather spell. For a more detailed report of densities see Table 5.

² Due to a particularly cold winter, no birds (including species other than foliage-gleaning birds) regularly inhabited this community during the Winter of 1985

³ Males observed infrequently and occasionally heard singing; no nests located during the summer, 1984 season; therefore, considered irregular in this community during this summer.

⁴ One male heard singing on one occasion in this community just outside the study area.

⁵ One male observed within this habitat on one day (June 30, 1985); No others observed here despite their common occurrence in adjacent mesquite scrub communities.

⁶ Female observed foraging along periphery of this community on 2 days.

⁷ One nest observed in this community though both male and female foraged primarily (>90% of foraging time) in adjacent Palo Verde-Cactus community. Foraging in this community occurred only in the nest tree (*Quercus grisea*).

⁸ Observed in this community only briefly (one bird for 40 seconds) on one occasion.

highest density in spring (44.4 in 1984 and 35.6 in 1985). One pair of this species was observed nesting in the mixed broadleaf community during the spring of 1985, although foraging occurred mostly (>90%) outside of the community. This species is also common in the mesquite scrub (a transitional community) adjacent to the mesquite woodland, which was not sampled in this study. *Camptostoma imberbe* was found in both seasons in the mesquite woodland, reaching its highest density (39.8) in the spring of 1985.

An unusually cold winter, with colder than normal temperatures and prolonged periods of below freezing temperatures, in 1984-1985 noticeably affected animals in the mixed broadleaf and mesquite woodland communities. The mixed broadleaf community was particularly affected. Bird life was transient in this community throughout the winter season and no residents were observed. This community was repeatedly censused during the winter season, and the only birds (including those of other guilds) observed were transients from adjacent communities who appear to have used this community primarily for water, and an occasional individual passing through the area. Consequently, I will omit the mixed broadleaf community (winter season only) from subsequent discussion.

Animals in the mesquite woodland community were also affected by the cold winter, but the effects did not last all winter. A prolonged freeze occurred between February 2-6, during which time high temperatures rarely reached above freezing. During this period, I searched intensively for arthropods using sweep netting, foliage-beating, and close inspection of trunks, branches, and twigs, but turned up few individuals. Nearly all birds (not just foliage-gleaners) vacated the woodland during much of this period, and several individual birds died.

To assess the impact of this cold-weather disaster, densities from censuses spanning the entire winter season are presented in Table 5. During this freeze, and for about 6 days after (February 2-12), the interior of this community was rarely visited by birds, and most activity was on the periphery (especially at sap trees which provided a supplementary food source; Hibbard and Mays, ms). Densities dropped dramatically.

R. calendula maintained the highest density in the mesquite woodland during the period of the freeze. Flying insects were the first arthropods to reappear after the freeze. *R. calendula*, the only regular aerial hawk among the foliage-gleaning birds, moved in before other bird species and took advantage of the flying insect resource, relying almost exclusively on hawking for prey capture during this period. The other foliage-gleaning birds did not appear regularly until after February 12, and they resumed foraging with little or no increase in aerial hawking.

Foraging Behavior: Plant Selection

Foliage-gleaning birds select plants and then search the plant for arthropods or other food items. Most of the food items selected by foliage-gleaning birds are too small or too cryptic to be seen without close inspection (Laudenslayer 1981, Ohmart and Gabaldon, unpubl. ms). Birds may randomly "select" plants on which to search for food, or they may select plants non-randomly, perhaps based on expectation of food resources from experience. If selection is random, then birds would be expected to forage on plant species and life-forms proportionally to the relative volume of plants in the community. If selection is non-random, birds may identify individual plant species or life-forms and forage on plant species or life-forms disproportionate to plant volume.

Plant selection by bird species was tabulated by plant species and by plant life-form for both seasons. Tables 6-8 show plant distributions and selection by all foliage-

Table 5. Density of resident foliage-gleaning birds in the Mesquite Woodland community during the winter of 1985. Density is given as number of adults per 40 hectares.

SPECIES	JAN 25 ¹	FEB 2-12 ² (Cold Spell)	FEB 17-30 ³
<i>Auriparus flaviceps</i>	60.9	8.7 ⁴	56.5
<i>Camptostoma imberbe</i>	8.7	0	8.7
<i>Regulus calendula</i>	121.8	13.0	91.3

¹ Based on one transect

² Based on two transects

³ Based on three transects

⁴ Most individuals were observed on the periphery of the community, especially at sap holes (a supplementary food source; see Hibbard and Mays, ms).

Table 6. Plant selection (%) by foraging birds of plants by plant species and by plant life forms in the Palo Verde - Cactus community. W = Winter; S = spring.

PLANT RELATIVE ABUNDANCE	BIRD SPECIES					
	<i>Auriparus flaviceps</i>		<i>Polioptila melanura</i>		<i>Regulus calendula</i>	
	W (242)	S (359)	W (395)	S (249)	W (255)	
PLANT SPECIES:						
<i>Cercidium microphyllum</i>	46.2	47.1	75.5	78.2	84.6	70.9
<i>Calliandra eriophylla</i>	13.4	0.0	0.0	0.0	0.0	0.0
Grasses	13.4	15.5	0.0	0.0	0.0	0.0
<i>Encelia farinosa</i>	5.5	4.8	0.0	3.1	0.0	3.4
Shrubs	4.7	3.8	2.0	2.3	1.3	7.1
Other Half Shrubs	4.7	18.2	0.0	6.6	1.8	7.4
<i>Prosopis velutina</i>	4.7	7.0	16.2	5.6	10.7	8.0
<i>Janusia gracilis</i>	3.2	0.0	0.0	0.0	0.0	0.0
Cacti	2.8	1.4	3.4	0.6	0.3	0.0
Other Trees	1.4	2.3	2.9	0.7	1.3	0.2
G Statistic ¹		100.96	283.69	201.33	210.59	129.83
Significance		p<<.001	p<<.001	p<<.001	p<<.001	p<<.001
LIFE FORMS:						
Tree	52.3	56.4	94.6	84.5	96.6	79.1
Shrub	4.7	3.8	2.0	2.3	1.3	7.1
Half Shrub	23.7	23.0	0.0	9.7	1.8	10.8
Grass	13.4	15.5	0.0	2.9	0.0	3.0
Cacti	2.8	1.4	3.4	0.6	0.3	0.0
Vines	3.2	0.0	0.0	0.0	0.0	0.0
G Statistic ²		15.83	276.72	109.64	196.34	85.09
Significance		p<.01	p<<.001	p<<.001	p<<.001	p<<.001
G Statistic ³		4.20	276.72	115.26	193.36	78.75
Significance		NS	p<<.001	p<<.001	p<<.001	p<<.001

¹ Pairwise comparisons of bird species with vegetation; df = 9.

² Pairwise comparisons of bird species with vegetation; df = 5.

³ Pairwise comparisons of bird species with vegetation combining the vine and half shrub categories; df = 4.

Table 7. Plant selection (%) by foraging birds of plants by plant species and plant life forms in the Mesquite Woodland community. W = winter; S = spring.

	PLANT RELATIVE ABUNDANCE		BIRD SPECIES						
	W	S	<i>Auriparus flaviceps</i>		<i>Camptostoma imberbe</i>		<i>Regulus calendula</i>	<i>Vireo bellii</i>	<i>Vermivora luciae</i>
			W (244)	S (290)	W (192)	S (378)	W (255)	S (257)	S (190)
PLANT SPECIES									
<i>Prosopis velutina</i>	73.9	88.2	86.1	83.4	94.3	96.6	86.0	88.0	84.1
<i>Hordeum</i> sp. (annual)	16.2	0.0	0.4	0.0	0.0	0.0	0.9	0.0	0.0
<i>Acacia greggii</i>	5.2	6.2	1.6	6.4	3.3	1.5	2.3	5.7	12.1
<i>Celtis reticulata</i>	2.6	3.1	9.0	6.3	0.0	1.9	2.0	4.8	3.4
<i>Hymenoclea</i> sp.	0.8	0.9	1.2	0.0	0.0	0.0	0.8	0.0	0.0
<i>Lycium</i> sp.	0.6	0.7	1.6	0.3	2.6	0.0	6.7	0.8	0.5
<i>Condalia globosa</i>	0.5	0.6	0.0	3.5	0.0	0.0	0.8	0.8	0.0
<i>Opuntia</i> spp.	0.2	0.2	0.0	0.0	0.0	0.0	0.8	0.0	0.0
G Statistic ¹	326.63 ²		100.91	26.19	89.93	36.18	109.86	7.08	13.63
Significance	p<<.001		p<<0.01	p<.001	p<<.001	p<<.001	p<<.001	NS	NS
G Statistic ³			30.18		25.91		42.54		
Significance			p<.001		p<.001		p<.001		

Table 7. Continued.

	PLANT RELATIVE ABUNDANCE		BIRD SPECIES						
	W	S	<i>Auriparus flaviceps</i>		<i>Camptostoma imberbe</i>		<i>Regulus calendula</i>	<i>Vireo bellii</i>	<i>Vermivora luciae</i>
			W (244)	S (290)	W (192)	S (378)	W (255)	S (257)	S (190)
LIFE FORM									
Tree	81.8	97.5	96.9	96.1	97.6	100.0	90.3	98.5	99.6
Shrub	1.9	2.2	3.0	3.9	2.4	0.0	8.8	1.5	0.4
Half Shrub	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grass/Sedge	16.2	0.0	0.1	0.0	0.0	0.0	0.9	0.0	0.0
Cacti	0.2	0.2	0.0	0.0	0.0	0.0	0.8	0.0	0.0
Vine	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
G Statistic ⁴	347.82 ⁵		78.05	3.24	64.90	16.61	89.16	1.56	4.14
Significance	p<<.001		p<<.001	NS	p<<.01	p<.001	p<<.001	NS	NS
G Statistic ⁶			1.32		0.87		21.84		
Significance			NS		NS		p<.001		

1 Pairwise comparisons of bird species with vegetation; df = 7 in winter, 6 in summer.

2 Pairwise comparison of winter with summer vegetation; df = 7.

3 Pairwise comparisons of bird species with vegetation using perennial vegetation (= S); df = 6

4 Pairwise comparisons of bird species with vegetation; df = 3 in winter and 2 in summer.

5 Pairwise comparison of winter and summer vegetation (life forms); df = 3.

6 Pairwise comparisons of bird species with vegetation using perennial vegetation (= S); df = 2.

Table 8. Plant selection (%) by foraging birds of plants by plant species and plant life forms in the Mixed Broadleaf community.

	PLANT RELATIVE ABUNDANCE	BIRD SPECIES		
		<i>Auriparus flaviceps</i> (100)	<i>Vireo bellii</i> (271)	<i>Vermivora luciae</i> (102)
PLANT SPECIES				
<i>Fraxinus pennsylvanica</i>	55.8	58.0	53.2	64.6
<i>Quercus grisea</i>	11.7	29.0	11.8	7.1
Shrubs	12.6	1.0	15.4	5.3
<i>Platanus wrightii</i>	10.6	2.0	6.7	15.9
Grasses/Sedges	3.7	0.0	0.0	1.8
Other Trees	3.6	10.0	13.0	5.3
Other Plants	2.1	0.0	0.0	0.0
G Statistic ¹		60.65	60.37	14.92
Significance		p<<.001	p<<.001	NS
LIFE FORMS:				
Tree	81.6	99.0	84.7	92.8
Shrub	12.6	1.0	15.4	5.5
Half Shrub	0.0	0.0	0.0	0.0
Grass/Sedge	3.7	0.0	0.0	1.6
Cacti	0.0	0.0	0.0	0.0
Vine	0.0	0.0	0.0	0.0
Other	2.2	0.0	0.0	0.0
G Statistic ²		31.34	29.58	10.52
Significance		p<.001	p<.001	NS

¹ Pairwise comparisons of bird species with vegetation; df = 6.

² Pairwise comparisons of bird species with vegetation; df = 3.

gleaning birds in each community for each season by relative frequency, and results of comparisons. The following types of comparisons were made: 1) a bird species' selection of plants compared to the distribution of plants within a community; 2) interspecific pairwise comparisons of one species' selection of plants to another species' selection of plants within each community; and 3) intraspecific comparisons of one species' selection of plants from winter to spring within a community. All comparisons of plant selection compared both plant species and plant life-forms. In the following text, comparisons are stated as different only if they are significant or highly significant. The statistics are presented in the tables and are not repeated here.

First, I compared the selection of plants utilized for foraging by each bird species to the distribution of plants within the community. The null hypothesis was that selection of plants, both by plant species and life-forms, by a bird species does not vary from the distribution of plants within the community. Most pairwise comparisons in this test are significant, indicating that birds are selecting plants and life-forms non-randomly based on the distributions of plants by volume (Table 6-8). Only the non-significant comparisons are listed here.

In the palo verde - cactus community during the winter season, *Auriparus flaviceps* selected the vegetation in proportions expected based on volume of life-forms when the half-shrub and vine categories were combined. When these two categories are separated, *A. flaviceps* selected life-forms significantly differently from what is expected based on distribution. The justification for combining these two categories is that most individual vines (of one species, *Janusia gracilis*) are supported by half-shrubs, and it is often difficult to determine whether the forager is selecting prey while perched on a vine or a half-shrub. All other comparisons in this community for all bird species are significant (Table 6). In general, foliage-gleaning birds in this community

select plants for foraging differently from the volume of plants. In spring, *A. flaviceps* and *P. melanura* specialize on trees (94.6 and 96.6% respectively). In winter, both of these species decrease their use of trees; *A. flaviceps* uses a variety of life-forms, while *P. melanura* still selects mostly trees for foraging, but utilizes half-shrubs to a greater extent than in spring. *R. calendula*, present only in winter, forages mostly in trees, but uses other life-forms more than does *P. melanura*.

In the mesquite woodland, selection of vegetation used by foraging birds deviates from that expected by plant volume in 13 of 20 comparisons (Table 7). For the winter season, *Auriparus flaviceps* and *Camptostoma imberbe* utilized plant life-forms in the proportion expected by volume of life-forms when annuals are excepted from the comparison. However, when annuals are included in the comparisons, both species deviate significantly from the expected. The only annual present during the winter was a species of grass, *Hordeum* sp., which generally cannot support the weight of a bird, and therefore is not likely to be selected by a foraging bird. All other winter-season comparisons of bird plant selection to the distribution of plants deviate from that expected. In the same community in spring the two breeding season residents, *Vireo bellii* and *Vermivora luciae*, selected vegetation for foraging in the same proportions as predicted by plant distribution for both plant species and plant life-forms. Additionally, *Auriparus flaviceps* utilized life-forms in the proportions expected. The other three spring comparisons were significantly different (Table 7). In general, most bird species are selecting trees to the exclusion of other, albeit rare, life-forms, with the exception of *R. calendula*, which uses shrubs more than do the other birds. In winter, excepting the two cases described above, birds are selecting plants (both by species and life-forms) for foraging in a non-random manner. In spring, however, birds, more

often than not, are using the available vegetation for foraging identically to the distribution of vegetation.

Of the three bird species that used the mixed broadleaf community, two used plants significantly differently from that predicted by plant distribution by volume (Table 8). Only *Vermivora luciae* used vegetation (both plant species and plant life-forms) as expected. *A. flaviceps* foraged primarily on trees, *Vireo bellii* on trees and shrubs, and *Vermivora luciae* on trees and grasses/sedges.

In the other two types of comparisons of plant selection, I compared plant selection by one species with that of another within a community (interspecific), and one species' use of vegetation between seasons (intraspecific). If species select vegetation differently from the vegetative distribution by volume, they may not necessarily differ inter- or intraspecifically, and therefore, the difference may not reflect partitioning of resources, but perhaps the distribution of food resources on the plant among other things. In these pairwise tests, I tested the hypothesis that bird species pairs use vegetation identically. Interspecific and intraspecific pairwise comparisons for all communities are reported in Table 9.

In the palo verde - cactus community, the two year-long residents, *Auriparus flaviceps* and *Polioptila melanura*, selected plant species and plant life-forms differently from one another in both seasons. In spring, both species used trees, though selection of tree species varied. *P. melanura* also used half-shrubs more than did *A. flaviceps*. In winter, *A. flaviceps* selected shrubs and half-shrubs more, and trees less, than did *P. melanura*. The winter resident, *Regulus calendula*, selected plants differently than did *A. flaviceps*, but used plants in the same proportions as *P. melanura*.

Table 9. Plant selection summary of interspecific and intraspecific pairwise comparisons (G statistic) for all communities. S = spring; W = winter; * = $p < 0.01$ (G = 11.345, 15.086, 16.812, 18.475, and 21.666 for 3, 5, 6, 7 and 9 df); ** = $p < 0.001$ (G = 16.266, 20.515, 22.458, 24.322, and 27.877 for 3, 5, 6, 7 and 9 df).

SPECIES	SEASON	df	PALO VERDE - CACTUS			
			<i>A. flaviceps</i>		<i>P. melanura</i>	
			W	S	W	S
<i>A. flaviceps</i>	W		-	-	-	-
	S	Species 9	204.91**			
		Life Form 5	203.74**			
<i>P. melanura</i>	W	Species 9	80.23**	-	-	-
		Life Form 5	66.85**			
	S	Species 9	-	21.90*	39.50**	-
		Life Form 5		15.10*	33.64**	-
<i>R. calendula</i>	W	Species 9	58.79**		13.28	-
		Life Form 5	52.84**		11.14	-

Continued.

Table 9. Plant selection continued.

SPECIES	SEASON	df	MESQUITE WOODLAND				
			<i>A. flaviceps</i>		<i>C. imberbe</i>		<i>Vireo bellii</i>
			W	S	W	S	S
	W		-	-	-	-	-
<i>A. flaviceps</i>	S						
	Species	7	30.67**	-	-	-	-
	Life Form	3	1.91				
	W						
	Species	7	32.49**	-	-	-	-
	Life Form	3	1.19				
<i>C. imberbe</i>	S						
	Species	7	-	40.83**	18.05	-	-
	Life Form	3		18.60**	10.97		
	W						
	Species	7	26.24**	-	19.14*	-	-
	Life Form	3	8.71		11.25		
	S						
	Species	7	-	6.40	-	20.66*	-
	Life Form	3		2.68		7.27	
	W						
	Species	7	-	16.38	-	30.90**	8.11
	Life Form	3		6.18		2.19	1.15

Continued.

Table 9. Plant selection summary continued.

SPECIES	SEASON		df	MIXED BROADLEAF	
				<i>A. flaviceps</i> S	<i>Vireo bellii</i> S
<i>V. bellii</i>	S	Species	6	35.62**	-
		Life Form	3	21.20**	
<i>V. luciae</i>	S	Species	6	35.77**	26.17**
		Life Form	3	5.41	9.44

In intraspecific comparisons, *A. flaviceps* and *P. melanura* selected plant species and life-forms differently between seasons. Both species used plants other than trees more in winter than in spring.

Overall, concerning plant selection in the palo verde - cactus community, the two permanent residents differed in all comparisons, while *R. calendula* was most like *P. melanura*.

In the mesquite woodland, comparing the two year-long residents, *Auriparus flaviceps* selected a greater variety of plants and selected trees other than mesquite more than did *Camptostoma imberbe* in winter, but the two species did not vary in their use of life-forms. In spring, *A. flaviceps* selected a greater variety of tree species and shrubs than did *C. imberbe*, which used trees exclusive of other life-forms. The one winter resident, *Regulus calendula*, selected plant species, but not life-forms, differently from both *A. flaviceps* and *C. imberbe*. *R. calendula* also appears to have responded indirectly to the annual grass as will be discussed below. Spring residents, *Vireo bellii* and *Vermivora luciae*, selected plant species in different proportions than did *C. imberbe*, but used plants, both by species and by life-forms, the same as *A. flaviceps* and each other.

In intraspecific comparisons between seasons, *A. flaviceps* selected plant species differently between seasons, but used life-forms identically between seasons. Even though it used the same life-forms, it selected a different distribution of tree and shrub species between seasons. *C. imberbe* selected both plant species and life-forms similarly between seasons.

In the mixed broadleaf community, *A. flaviceps* differed from *Vireo bellii* in both plant species and life-forms selected, and from *Vermivora luciae* in plant species, but not life-forms. *A. flaviceps* used oak more and shrubs less than did *Vireo bellii*, and

selected oak and mesquite more and shrubs and grass/sedge less than did *Vermivora luciae*. *Vermivora luciae* selected tree species in different proportions and used shrubs less than did *Vireo bellii*.

Overall, for all communities, bird species frequently showed differences in the selection of plant species. These differences do not appear to be due to local variation in plant composition or to bird territories, but appear to reflect real differences in preference. The study sites are strongly homogeneous, and although interspecific aggressive interactions were common in spring, birds rarely totally excluded other species from their territories. In addition, I made every attempt to keep moving through the communities to sample different birds over the entire site. Birds often did use life-forms identically. In part, this is due to reduced plant variety, particularly in the mesquite woodland, and to a seemingly strong preference by most foliage-gleaning birds for trees.

Foraging Behavior: Foraging Height

Foraging birds may select foraging height based upon the height distribution profile of plants, or on some subset of the height distribution profile. In my analysis of foraging height, I made three types of comparisons: 1) foraging height compared to the plant height distribution profile, 2) interspecific comparisons of birds within a community in the same season, and 3) intraspecific comparisons within a community between seasons.

In the first type of comparison, bird foraging height preferences were compared to the plant height distribution profiles within each community. The null hypothesis in this test was that foraging birds select heights identical to available heights as measured by the plant height distribution profile. If birds select heights based on the distribution

of foraging sites, this suggests that available prey resources are distributed on vegetation uniformly with respect to vegetation height. If all species select a subset of available foraging heights, this alone does not suggest resource partitioning, but rather may reflect the distribution of suitable prey, the effects of predators, or the effects of competition with animals other than guild members. If foliage-gleaning birds tend to use the same foraging heights, this indicates that factors other than intra-guild competition are influencing their foraging behavior.

The second comparison directly addresses the question of resource partitioning. In this type of comparison, all pairwise combinations are tested by comparing the foraging height profile of one species with that of another guild member. The null hypothesis in this test is that foraging height profiles of any pair of species are identical. If two species select different foraging height profiles, then it is likely that they are partitioning resources, either by spatial separation or by prey species.

The third type of comparison focuses on year-long residents, and compares the effects of seasonal changes on foraging height. The null hypothesis in this test is that a species' foraging height profile is identical between seasons within a community. Differences between seasons may be due to distribution of suitable resources, effects of predators, effects of microenvironments, or the effects of competition from either guild or non-guild members. If a species forages over identical height profiles from one season to the next, it suggests that the influences listed above are constant, or that they have minimal affect on a bird's choice of foraging height. If a species forages at different heights between seasons, then one or more of these factors is implicated as influential in this behavior.

A profile of foraging heights compared to plant height distribution for all species in each community in each season is given in Figures 1-5. Foraging heights by

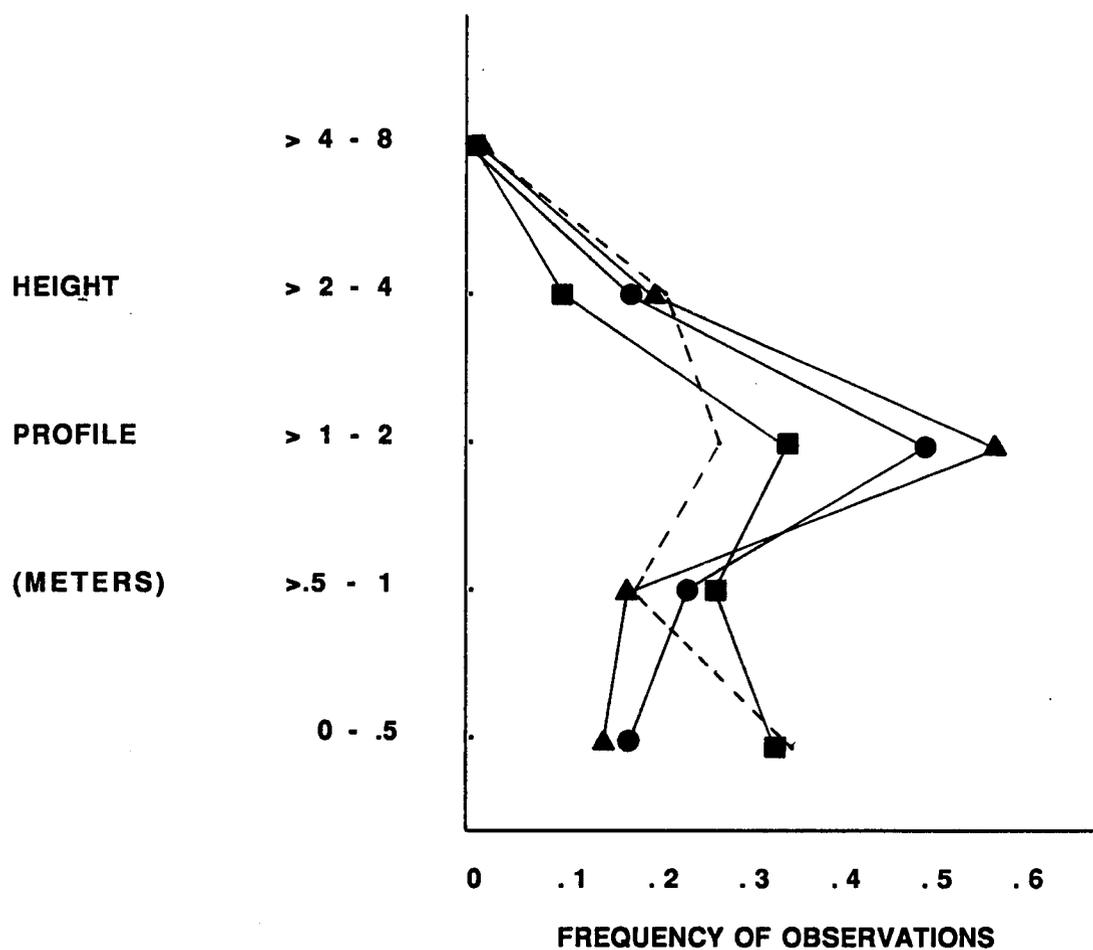


Figure 1. Vegetation and foraging height profiles for the Palo verde - cactus community for the winter season. The vegetation height profile is depicted by a dashed line. ■ = *Auriparus flaviceps*; ▲ = *Polioptila melanura*; ● = *Regulus calendula*.

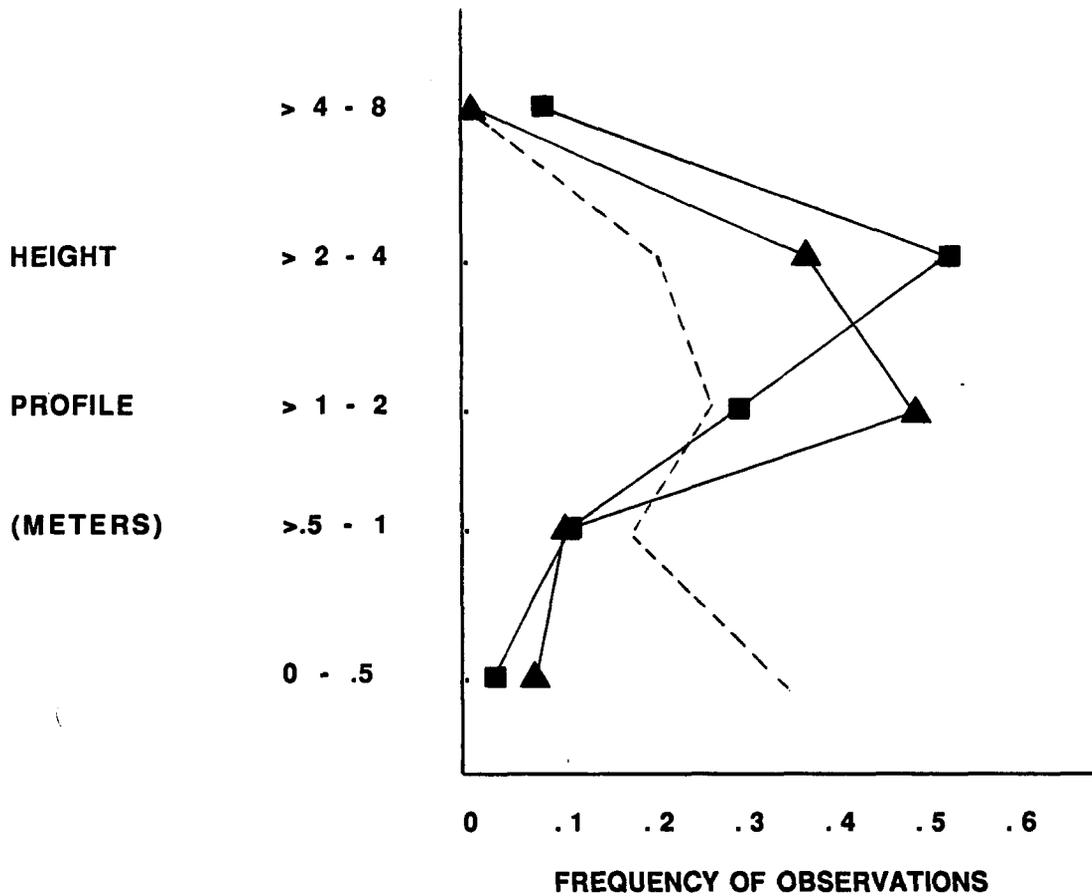


Figure 2. Vegetation and foraging height profiles for the palo verde - cactus community for the spring season. The vegetation height profile is depicted by a dashed line. ■ = *Auriparus flaviceps*; ▲ = *Polioptila melanura*.

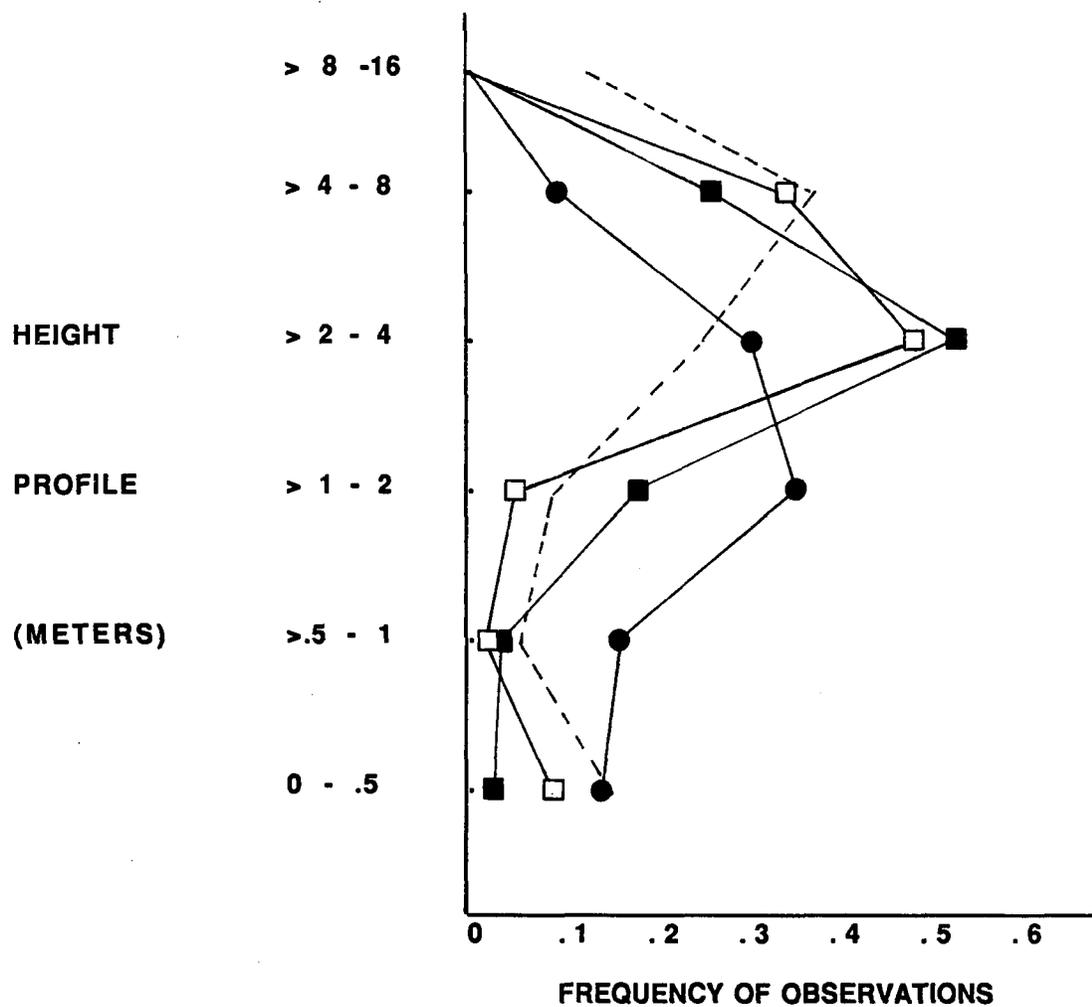


Figure 3. Vegetation and foraging height profiles for the mesquite woodland community for the winter season. The vegetation height profile is depicted by a dashed line. ■ = *Auriparus flaviceps*; □ = *Camptostoma imberbe*; ● = *Regulus calendula*.

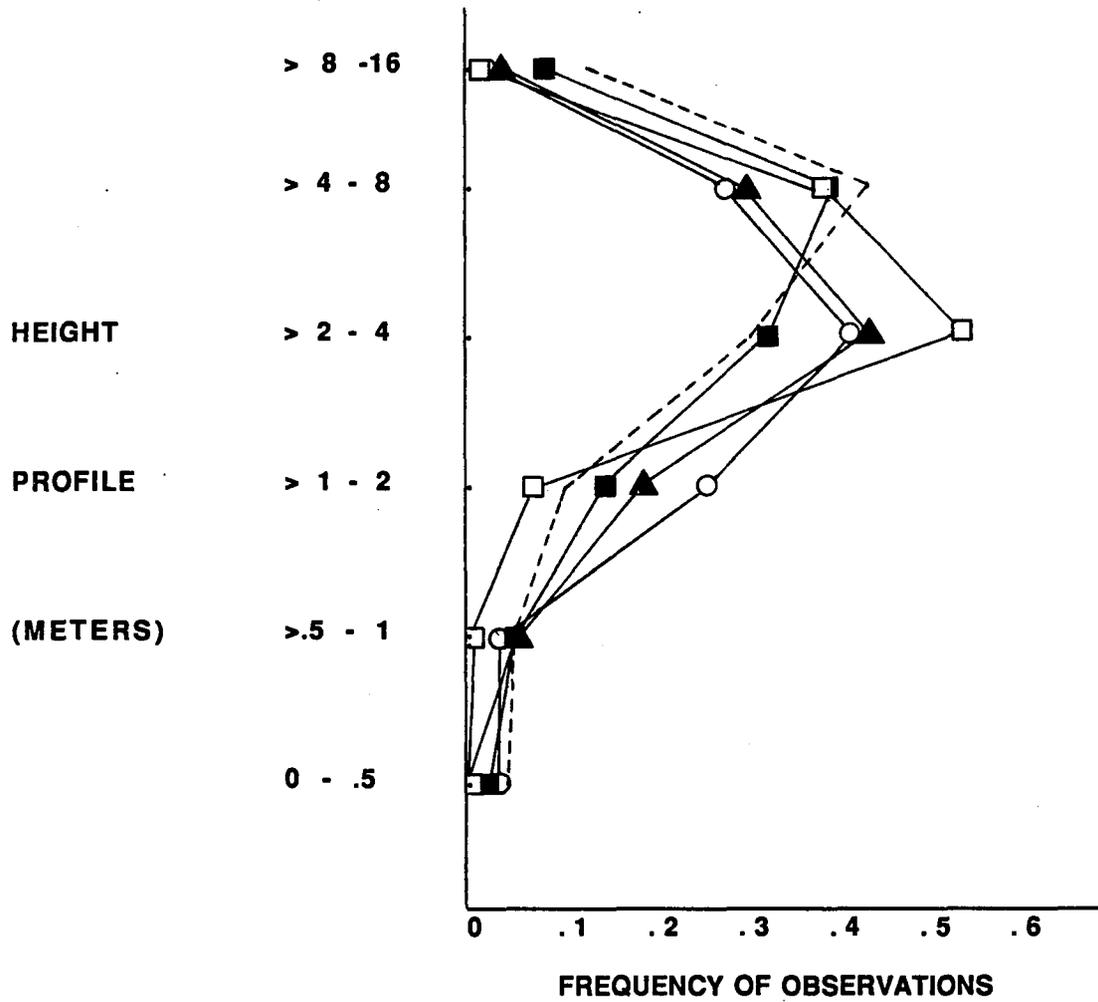


Figure 4. Vegetation and foraging height profiles for the mesquite woodland community for the spring season. The vegetation height profile is depicted by a dashed line. ■ = *Auriparus flaviceps*; □ = *Camptostoma imberbe*; ○ = *Vireo bellii*; ▲ = *Vermivora luciae*.

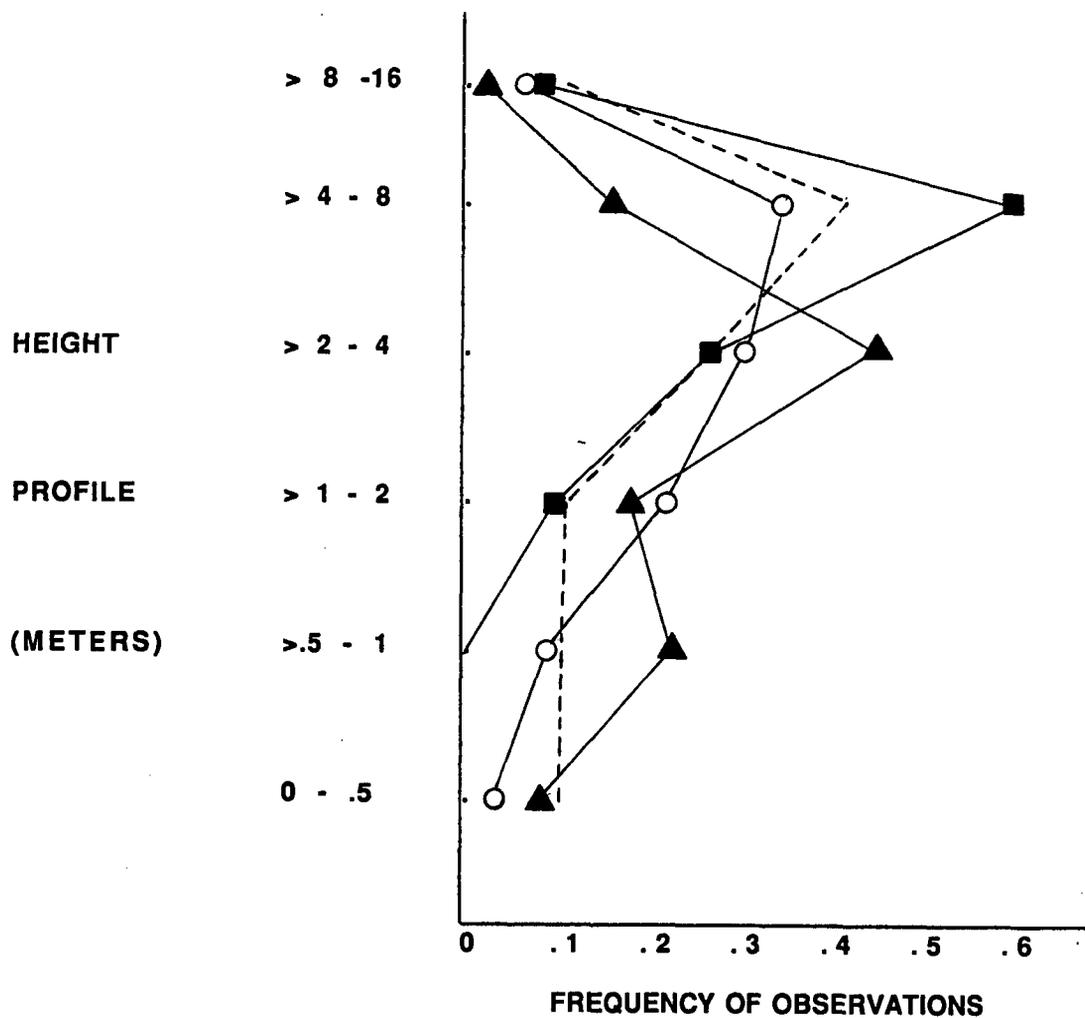


Figure 5. Vegetation and foraging height profiles for the mixed broadleaf community for the spring season. The vegetation height profile is depicted by a dashed line. ■ = *Auriparus flaviceps*; ○ = *Vireo bellii*; ▲ = *Vermivora luciae*.

frequency, along with sample sizes, are provided in Tables 10-12, which summarize all foraging behavior variables. A summary of interspecific and intraspecific pairwise comparisons of foraging height profiles is provided in Table 13.

In the palo verde - cactus community, all species foraged at heights proportionally different from the vegetation height distribution profile for both seasons. *Auriparus flaviceps* foraged proportionally lower than the plant height distribution in winter and proportionally higher in spring. *A. flaviceps* foraged significantly lower in winter than in spring. *Polioptila melanura* foraged proportionally higher than the vegetation distribution profile in both winter and spring, but foraged significantly lower in winter than in spring. In winter, *Regulus calendula* foraged proportionally higher than the distribution of vegetation.

Interspecifically, *A. flaviceps* foraged significantly lower than did *P. melanura* in winter and significantly higher in spring. *A. flaviceps* foraged significantly lower than *R. calendula* in winter, while *P. melanura* foraged over the same height distribution as *R. calendula*. Thus, in this community, only *P. melanura* and *R. calendula* foraged over identical height profiles. Figures 1-2 provide a visual summary of these differences.

In the mesquite woodland community, all species foraged at heights proportionally different from the distribution of the vegetation except in one case. *Auriparus flaviceps* foraged proportionally more in the 2-4 m height range in winter, but foraged at heights identical with the distribution of the vegetation in spring. *A. flaviceps* foraged significantly lower in winter than in spring. *Camptostoma imberbe* foraged proportionally lower than the vegetation height profile in winter, and proportionally more in the 2-4 m range in spring. *C. imberbe* foraged significantly lower in winter than in spring. *Regulus calendula* foraged proportionally lower than the

Table 10. Frequency (%) of five foraging variables for all seasons in the Palo Verde - Cactus community. See text for description of each foraging variable. W = winter; S = spring.

FORAGING VARIABLES	PALO VERDE - CACTUS				
	<i>A. flaviceps</i>		<i>P. melanura</i>		<i>R. calendula</i>
	W	S	W	S	W
Foraging Height (Meters)					
<i>N</i>	242	359	395	249	234
0 - 0.5	32.2	2.5	12.9	6.0	14.5
>0.5 - 1.0	25.2	9.5	17.2	9.2	22.2
>1.0 - 2.0	32.6	29.8	55.2	48.6	47.4
>2.0 - 4.0	8.7	51.0	19.9	35.3	15.8
>4.0 - 8.0	1.2	7.2	0.8	0.8	0
>8.0	-	-	-	-	-
Plant Portion					
<i>N</i>	242	359	395	249	234
Outer	91.2	93.3	89.6	92.0	82.9
Middle	7.0	4.2	9.1	6.4	17.1
Inner	1.2	2.5	1.3	1.6	0
Ground	0.4	0	0	0	0
Perch Site					
<i>N</i>	242	359	395	249	234
Twig	90.9	95.0	91.1	90.0	88.0
Branch	7.4	5.0	7.6	9.2	12.0
Trunk	1.2	0	1.3	0.8	0
Ground	0.4	0	0	0	0
Capture Site					
<i>N</i>	46	104	113	70	49
Flowers	0	21.2	0	4.3	0
Leaves	10.9	11.5	26.5	24.3	10.2
Twigs	23.9	9.6	60.2	0	34.7
Indistinguishable					
foliage	54.3	51.9	0	67.1	0
Branch	8.7	4.8	8.0	2.9	0
Trunk	2.2	0	0	0	0
Ground	0	0	0	0	0
Air	0	0	5.3	1.4	55.1
Unknown	0	0	0	0	0
Capture Technique					
<i>N</i>	46	104	113	70	49
Perch Glean	89.1	74.0	78.8	75.8	22.4
Hover Glean	2.2	1.9	15.0	18.6	22.4
Hang Glean	8.7	24.0	0.9	4.3	0
Hawk	0	0	5.3	1.4	55.1

Table 11. Frequency (%) of five foraging variables for all seasons for the Mesquite Woodland community. See text for a description of each foraging variable. AUFL = *Auriparus flaviceps*; CAIM = *Camptostoma imberbe*; RECA = *Regulus calendula*; VELU = *Vermivora luciae*; VIBE = *Vireo bellii*. W = winter; S = spring.

FORAGING VARIABLES	MESQUITE WOODLAND						
	AUFL		CAIM		RECA	VIBE	VELU
	W	S	W	S	W	S	S
Foraging Height (Meters)							
<i>N</i>	204	290	192	378	255	190	257
0 - 0.5	3.9	2.8	8.3	0.3	14.1	3.1	1.6
>0.5 - 1.0	3.9	3.8	3.6	0.8	15.7	3.5	5.8
>1.0 - 2.0	16.2	13.8	6.8	6.3	32.5	24.5	18.9
>2.0 - 4.0	52.0	31.4	47.4	52.4	29.8	40.9	43.2
>4.0 - 8.0	24.0	38.6	33.9	38.6	7.8	26.1	28.4
>8.0	0	9.7	0	1.6	0	1.9	2.1
Plant Portion							
<i>N</i>	204	290	192	378	255	190	257
Outer	93.1	94.1	85.4	95.8	82.0	92.1	75.1
Middle	6.4	5.2	14.6	3.2	14.1	7.9	23.7
Inner	0.5	0.7	0	1.0	3.9	0	1.2
Ground	0	0	0	0	0	0	0
Perch Site							
<i>N</i>	204	290	192	378	255	190	257
Twig	94.6	93.8	91.7	88.6	82.4	93.2	84.8
Branch	4.9	7.2	8.3	11.4	16.9	6.8	15.2
Trunk	0.5	0	0	0	0.4	0	0
Ground	0	0	0	0	0.4	0	0
Capture Site							
<i>N</i>	35	50	334	162	250	35	70
Flowers	0	32.0	1.2	11.7	0	2.9	2.9
Leaves	11.4	16.0	4.2	33.3	10.8	31.4	25.7
Twigs	51.4	10.0	76.9	24.1	50.4	11.4	11.4
Indistinguishable foliage	28.6	36.0	0	25.3	0	45.7	54.3
Branch	8.6	6.0	4.5	3.7	1.2	8.6	2.9
Trunk	0	0	0	0	0.4	0	0
Ground	0	0	0	0	0	0	0
Air	0	0	2.4	1.9	37.2	0	2.9
Unknown	0	0	10.8	0	0	0	0
Capture Technique							
<i>N</i>	35	50	334	162	250	35	70
Perch Glean	68.6	52.0	78.7	62.3	38.4	68.6	74.3
Hover Glean	2.9	2.0	13.8	22.2	23.6	11.4	14.3
Hang Glean	28.6	46.0	5.1	13.6	0.8	20.0	8.6
Hawk	0	0	2.4	1.9	37.2	0	2.9

Table 12. Frequency (%) of five foraging variables for all seasons in the Mixed Broadleaf community. See text for a description of each foraging variable. S = spring.

FORAGING VARIABLES	MIXED BROADLEAF		
	<i>A. flaviceps</i> S	<i>Vireo bellii</i> S	<i>Vermivora luciae</i> S
Foraging Height (Meters)			
<i>N</i>	100	271	102
0 - 0.5	0	2.6	5.9
>0.5 - 1.0	0	8.9	20.6
>1.0 - 2.0	9.0	20.2	15.7
>2.0 - 4.0	26.0	29.2	42.2
>4.0 - 8.0	59.0	34.7	13.7
>8.0	6.0	4.4	2.0
Plant Portion			
<i>N</i>	100	271	102
Outer	94.0	83.8	61.8
Middle	5.0	14.4	36.3
Inner	1.0	1.5	2.0
Ground	0	0.4	0
Perch Site			
<i>N</i>	100	271	102
Twig	93.0	91.1	91.2
Branch	7.0	8.1	7.8
Trunk	0	0.4	0
Ground	0	0.4	1.0
Capture Site			
<i>N</i>	32	50	25
Flowers	0	0	0
Leaves	0	14.0	20.0
Twigs	0	0	0
Indistinguishable foliage	87.5	72.0	76.0
Branch	12.5	6.0	0
Trunk	0	0	0
Ground	0	0	0
Air	0	8.0	4.0
Unknown	0	0	0
Capture Technique			
<i>N</i>	32	50	25
Perch Glean	78.1	70.0	76.0
Hover Glean	6.3	14.0	12.0
Hang Glean	15.6	8.0	8.0
Hawk	0	8.0	4.0

Table 13. Foraging height summary of interspecific and intraspecific pairwise comparisons [G statistic, df = 4 (Palo Verde Community) or 5] for all communities. W = winter; S = spring; * = $p < 0.01$ (G = 13.277, 15.086 for 4 and 5 df); ** = $p < 0.001$ (G = 18.467, 20.515 for 4 and 5 df). For a summary of intercommunity comparisons see Table 18.

SPECIES	SEASON	Vegetation	PALO VERDE - CACTUS			
			<i>A. flaviceps</i>		<i>P. melanura</i>	
			W	S	W	S
<i>A. flaviceps</i>	W	23.09**	-	-	-	-
	S	225.55**	47.84**	-	-	-
<i>P. melanura</i>	W	98.97**	52.39**	-	-	-
	S	114.88**	-	16.24**	46.66**	-
<i>R. calendula</i>	W	54.62**	32.39**	-	7.04	-

Continued.

Table 13. Continued (foraging height summary).

MESQUITE WOODLAND								
SPECIES	SEASON	Vegetation		<i>A. flaviceps</i>		<i>C. imberbe</i>		<i>Vireo bellii</i>
		W	S	W	S	W	S	S
<i>A. flaviceps</i>	W	131.61**	108.53**	-	-	-	-	-
	S	-	11.29	51.38**	-	-	-	-
<i>C. imberbe</i>	W	79.50**	89.31**	14.81**	-	-	-	-
	S	-	121.04**	-	63.99**	39.81**	-	-
<i>R. calendula</i>	W	250.67**	342.69**	76.70**	-	107.96**	-	-
<i>Vireo bellii</i>	S	-	63.88**	-	23.00**	-	38.80**	-
<i>Vermivora luciae</i>	S	-	102.11**	-	33.50**	-	63.37**	4.28

Continued.

Table 13. Continued (foraging height summary).

MIXED BROADLEAF				
SPECIES	SEASON	Vegetation S	<i>A. flaviceps</i> S	<i>Vireo bellii</i> S
<i>A. flaviceps</i>	S	34.60**	-	-
<i>Vireo bellii</i>	S	38.85**	39.58**	-
<i>Vermivora luciae</i>	S	60.04**	75.56**	28.62**

distribution of vegetation in winter. Both *Vireo bellii* and *Vermivora luciae* foraged proportionally lower than the vegetation distribution profile in spring.

In Interspecific comparisons, *A. flaviceps* foraged at approximately the same heights as *C. imberbe* in winter and significantly more in the lower and upper ranges (versus the middle) in spring. In winter, *A. flaviceps* foraged significantly lower than *R. calendula*, and in spring, foraged significantly higher than did *Vireo bellii* and *Vermivora luciae*. *C. imberbe* foraged significantly higher than did *R. calendula* in winter and significantly higher than *Vireo bellii* and *Vermivora luciae* in spring. *Vireo bellii* and *Vermivora luciae* foraged over the same height profiles. Thus, all species foraged over different height profiles except for two pairs: *A. flaviceps* and *C. imberbe* in winter and *Vireo bellii* and *Vermivora luciae* in spring. Figures 3-4 provide a visual summary of these differences.

In the mixed broadleaf community frequency distributions of foraging height of all species differed from the height distribution of vegetation. *Auriparus flaviceps* foraged proportionally higher, while *Vireo bellii* and *Vermivora luciae* foraged proportionally lower than the vegetation distribution profile. *A. flaviceps* foraged significantly higher than *Vireo bellii* and *Vermivora luciae*. *Vireo bellii* foraged significantly higher than did *Vermivora luciae*. Thus, *A. flaviceps* forages high in the canopy, *Vireo bellii* forages proportionally more in the middle range, and *Vermivora luciae* forages lower spending 26% of its foraging time at 1 m or less. Figure 5 provides a visual summary of these differences.

Foraging Behavior: Portion of Plant Used

The portion of the plant used by foraging foliage-gleaning birds is related to, but not the same as, perch size. A bird may select a foraging location within a plant for

predator avoidance or because of the distribution of arthropods on the plant, or both. This selection may be more or less independent of perch size. I did not quantify the structure of plants to determine the volume represented by each portion of plants; as a result I did not compare use of portions by birds with the frequency distributions of the portions. Qualitatively, the outer portion appears to be the most frequent portion by volume, accounting for at least 50% of the total volume, followed by middle, with the inner occupying the least volume. Differences and similarities in foraging portion profiles can be attributed to the same influences discussed for foraging height.

For this foraging behavior, I made interspecific and intraspecific pairwise comparisons of bird species' use of the portions of plants. In the interspecific comparisons, I tested the null hypothesis that species forage in plant portions identical to one another in the same community in the same season. In the intraspecific comparisons, I test the null hypothesis that year-long residents forage in the same plant portions in winter as in spring within a community.

The portion of the plant used by foragers is summarized by frequency in Tables 10-12 for all communities. Interspecific and intraspecific pairwise comparisons are summarized in Table 14. Across all sites, all foliage-gleaning birds used the outer portion of the plant for most of their foraging (82-94%), using the middle of the plants with the second highest frequency (4.2-17.1%). The inner portion of the plant is seldom used while foraging (0-2.5%) and the ground is utilized the least (0-1.0%).

In the palo verde - cactus community, interspecific comparisons show that the yearlong resident species used the portions of plants in the same manner in both winter and spring. Intraspecifically, these species also used the portions similarly between seasons. The winter resident, *Regulus calendula*, used the inner region of plants significantly more than either *A. flaviceps* or *P. melanura*.

Table 14. Plant portion summary of interspecific and intraspecific pairwise comparisons (G statistic; df = 3) for all communities. W = winter; S = spring; * = $p < 0.01$ (G = 11.345 for 3 df); ** = $p < 0.001$ (G = 16.266 for 3 df). For a summary of intercommunity comparisons see Table 18.

SPECIES	SEASON	PALO VERDE - CACTUS			
		<i>A. flaviceps</i>		<i>P. melanura</i>	
		W	S	W	S
<i>A. flaviceps</i>	W	-	-	-	-
	S	5.36	-	-	-
<i>P. melanura</i>	W	2.79	-	-	-
	S	-	2.04	1.63	-
<i>R. calendula</i>	W	16.72**	-	12.87**	-

Continued.

Table 14. Continued (foraging portion summary).

SPECIES	SEASON	MESQUITE WOODLAND					
		<i>A. flaviceps</i>		<i>C. imberbe</i>		<i>Vireo bellii</i>	
		W	S	W	S	S	S
<i>A. flaviceps</i>	W	-	-	-	-	-	-
	S	0.39	-	-	-	-	-
<i>C. imberbe</i>	W	8.55	-	-	-	-	-
	S	-	1.90	26.71**	-	-	-
<i>R. calendula</i>	W	15.01*	-	11.40*	-	-	-
<i>V. bellii</i>	S	-	3.40	-	8.97	-	-
<i>V. luciae</i>	S	-	41.87**	-	65.19**	24.81**	-

Continued.

Table 14. Continued (foraging portion summary).

SPECIES	SEASON	MIXED BROADLEAF	
		<i>A. flaviceps</i> S	<i>V. bellii</i> S
<i>A. flaviceps</i>	S	-	-
<i>V. bellii</i>	S	8.08	-
<i>V. luciae</i>	S	34.04**	21.14**

In the mesquite woodland, interspecific comparisons reveal that *A. flaviceps* and *C. imberbe* used portions of the plants in the same proportions for both winter and spring. In winter, *Regulus calendula* selected the middle and inner portions of plants more than did *A. flaviceps* and *C. imberbe*. In spring, all species used plant portions in the same manner except *Vermivora luciae*, who used the inner portion of the plants significantly more than all other guild members, *A. flaviceps*, *C. imberbe*, and *Vireo bellii*. Intraspecifically, *Auriparus flaviceps* used the portions of the plants in identical proportions for both seasons. However, *Camptostoma imberbe* used the middle portion of plants more in winter than in spring.

In the mixed broadleaf community, *A. flaviceps* and *Vireo bellii* used the plant portions in the same manner, but as in the mesquite woodland, *Vermivora luciae* used the middle portion to a greater extent than did the other species.

In all communities, foliage-gleaning birds specialized on the outer region of the plant, using the middle portion to a lesser extent. There were few differences between species selection of plant portions.

Foraging Behavior: Perch Site

Foliage-gleaning birds search for prey while perched in a plant, or rarely, on the ground. The size of available plant parts may influence the perch sites selected. I did not quantify the relative proportions of plants occupied by the various available perch sites, and did not compare bird perch selection to available perch sites. For this behavior, I compared species pairs interspecifically, testing the null hypothesis that one species used perch sites identically to another species in the same community in the same season. I also compared year-long resident species intraspecifically from winter

to spring season in each community, testing the null hypothesis that year-long residents use the same perch sites in both seasons.

The parts of plants used as perch site by foraging foliage-gleaning birds is summarized by frequency in Tables 10-12 for each community. Interspecific and intraspecific pairwise comparisons are summarized in Table 15. All foliage-gleaning birds studied used twigs most frequently (82.4 - 95.0%) and branches much less frequently (4.9 -16.9%). Trunk (0 - 1.3%) and the ground (0 - 0.4%) were used infrequently.

In the palo verde - cactus community, interspecific comparisons indicate that all species used perch sites in the same proportions in both seasons. Intraspecifically, *A. flaviceps* and *P. melanura* did not vary from winter to spring seasons (Table 15).

In the mesquite woodland, interspecific pairwise comparisons show that all species selected perch sites in the same proportions while foraging except *R. calendula*, which used branches more than did *A. flaviceps*. Intraspecifically, *A. flaviceps* and *C. imberbe* used the same perch sites for foraging in winter as in spring.

In the mixed broadleaf community, all species used perch sites in the same manner. All three species used twigs more than 90% of the time, and all selected branches approximately 7 to 8% of the time. Both *Vermivora luciae* (1.0%) and *Vireo bellii* (0.4%) perched on the ground on occasion. *Vermivora luciae* used the ground as a perch site to hover-glean and perch-glean prey from small rushes growing along the stream.

Table 15. Perch site summary of interspecific and intraspecific pairwise comparisons (G statistic; df = 3) for all communities. W = winter, S = spring; * = $p < 0.01$ ($G = 11.345$ for 3 df); ** = $p < 0.001$ ($G = 16.266$ for 3 df). For a summary of intercommunity comparisons see Table 18.

SPECIES	SEASON	PALO VERDE - CACTUS			
		<i>A. flaviceps</i>		<i>P. melanura</i>	
		W	S	W	S
<i>A. flaviceps</i>	W	-	-	-	-
	S	8.93	-	-	-
<i>P. melanura</i>	W	1.94	-	-	-
	S	-	7.78	0.83	-
<i>R. calendula</i>	W	8.06	-	7.76	-

Continued.

Table 15. Continued (perch site summary).

SPECIES	SEASON	MESQUITE WOODLAND				
		<i>A. flaviceps</i>		<i>C. imberbe</i>		<i>Vireo bellii</i>
		W	S	W	S	S
<i>A. flaviceps</i>	W	-	-	-	-	-
	S	2.89	-	-	-	-
<i>C. imberbe</i>	W	3.20	-	-	-	-
	S	-	3.32	1.31	-	-
<i>R. calendula</i>	W	18.56**	-	9.69	-	-
<i>V. bellii</i>	S	-	0.03	-	3.09	-
<i>V. luciae</i>	S	-	8.84	-	1.94	7.79

Continued.

Table 15. Continued (perch site summary)

SPECIES	SEASON	MIXED BROADLEAF RIPARIAN	
		<i>A. flaviceps</i> S	<i>V. bellii</i> S
<i>A. flaviceps</i>	S	-	-
<i>V. bellii</i>	S	1.40	-
<i>V. luciae</i>	S	1.43	1.11

Foraging Behavior: Capture Site

From perch sites, foliage-gleaning birds capture prey from plant parts while either stationary or hovering (flying insects were always captured by leaving the perch). Capture sites may be the same as perch sites, though the perch site and capture site are frequently different parts of the plant. Rarely, a bird will use a perch site on one plant to survey another plant. I recorded capture sites as foliage, branches, trunk, ground, and air. I subdivided foliage into flowers, leaves, and twigs, though I was frequently unable to make this distinction while observing foraging birds.

Data used in these comparisons represent the sites of observed captures. I compared capture sites interspecifically, testing the null hypothesis that one species captures prey from the same proportion of sites as do other species in the same community in the same season. I also compared capture sites intraspecifically between seasons, testing the null hypothesis that year-long residents capture prey from the same proportion of sites in spring and in winter.

The parts of plants from which prey were captured by foliage-gleaning birds is summarized by frequency in Tables 10 - 12. Interspecific and intraspecific pairwise comparisons of capture sites are summarized in Table 16 for each community. As indicated by their guild name, foliage-gleaning birds predominantly gleaned prey from foliage (44.9 - 96.7% of prey captured, but mostly > 85%). Prey were also gleaned from branches (1.2 - 8.7%), and hawked from the air (0 - 8%, but up to 55.1% in one species in one community).

In the palo verde - cactus community, Interspecific comparisons indicate that *A. flaviceps* and *P. melanura* captured prey from the same sites in both winter and spring. It should be noted that in spring, *A. flaviceps* took a high percentage of its prey from flowers (21%, mostly mesquite), while *P. melanura* did not capture any prey from

flowers. This difference is not reflected in the G-test because all foliage categories were grouped together because exact capture sites were frequently uncertain, and I wanted to avoid an artificial "either/or" category in addition to "flower" and "leaf". *Regulus calendula* captured a significant percentage of its prey from the air (55.1%) while *P. melanura* captured only 5.3% from the air, and *A. flaviceps* made no captures from the air. *R. calendula* differed from both *P. melanura* and *A. flaviceps* in prey capture sites. Intraspecific comparisons indicate that *Auriparus flaviceps* and *Poliioptila melanura* utilized the same capture locations from winter to spring.

In the mesquite woodland, interspecific comparisons indicate that *A. flaviceps* and *C. imberbe* used the same capture sites in both winter and spring. In spring, *A. flaviceps* used the same capture sites as *Vireo bellii* and *Vermivora luciae*. *A. flaviceps* made 32.0% of its captures from flowers while *C. imberbe* made only 11.7% of its captures from flowers, and *Vireo bellii* and *Vermivora luciae* only 2.9%. Again, for the statistical analysis, flowers were grouped with foliage; hence, these differences are not reflected in the G-test results. *Camptostoma imberbe* also used the same capture sites as *Vireo bellii* and *Vermivora luciae*, and *Vireo bellii* used the same capture sites as *Vermivora luciae*. Intraspecifically, both *A. flaviceps* and *C. imberbe* used the same capture sites in winter and spring. In winter, *R. calendula* made 37.2% of its captures from the air while *C. imberbe* (1.9%) and *A. flaviceps* (0%) used this site infrequently or not at all. Hence, there was a significant difference in the choice of capture sites between *R. calendula* and both *A. flaviceps* and *C. imberbe*.

In the mixed broadleaf community all three spring species utilized the same capture sites (Table 16).

In summary, all species (with one exception) in all three communities used the same capture sites, dominated by foliage (though there were some differences within the

Table 16. Food capture site summary of interspecific and intraspecific pairwise comparisons (G statistic) for all communities. W = winter; S = summer; * = $p < 0.01$ ($G = 13.277$ for 4 df); ** = $p < 0.001$ ($G = 118.467$ for 4 df). For a summary of intercommunity comparisons see Table 18.

SPECIES	SEASON	PALO VERDE - CACTUS			
		<i>A. flaviceps</i>		<i>P. melanura</i>	
		W	S	W	S
<i>A. flaviceps</i>	W	-	-	-	-
	S	3.24	-	-	-
<i>P. melanura</i>	W	6.62	-	-	-
	S	-	2.23	4.44	-
<i>R. calendula</i>	W	50.09**	-	52.96**	-

Continued.

Table 16. Continued (food capture site summary).

SPECIES	SEASON	MESQUITE WOODLAND					
		<i>A. flaviceps</i>		<i>C. imberbe</i>		<i>V. bellii</i>	
		W	S	W	S	S	
<i>A. flaviceps</i>	W	-	-	-	-	-	-
	S	0.20	-	-	-	-	-
<i>C. imberbe</i>	W	2.41	-	-	-	-	-
	S	-	2.05	0.79	-	-	-
<i>R. calendula</i>	W	33.59**	-	125.27**	-	-	-
<i>V. bellii</i>	S	-	0.20	-	2.49	-	-
<i>V. luciae</i>	S	-	2.83	-	0.32	3.13	-

Continued.

Table 16. Continued (food capture site summary).

SPECIES	SEASON	MIXED BROADLEAF	
		<i>A. flaviceps</i> S	<i>Vireo bellii</i> S
<i>A. flaviceps</i>	S	-	-
<i>Vireo bellii</i>	S	4.90	-
<i>Vermivora luciae</i>	S	6.38	3.05

foliage category). Only *Regulus calendula*, a regular aerial hawk during this study, differed from all other guild members.

Foraging Behavior: Capture Technique

In observed captures, foliage-gleaning birds were observed using four techniques: perch-glean, hover-glean, hang-glean, and aerial hawk (defined in Chapter 2). Most species used a combination of these techniques. I compared capture techniques between species and within a species between seasons. In the interspecific pairwise comparisons, the number of captures using each technique was compared between species pairs, testing the null hypothesis that the two species used the same techniques in the same proportions. In the intraspecific comparisons, I tested the null hypothesis that one species used the same techniques in the same proportion from winter to spring season in the same community.

The foraging techniques used for prey capture are summarized by frequency in Tables 10-12. Interspecific and Intraspecific pairwise comparisons are summarized in Table 17.

For all foliage-gleaning birds, the perch-glean was, with one exception (*R. calendula* in the palo verde-cactus community), the most frequent technique employed for prey capture, ranging from 38.4% of the captures (*Regulus calendula*) to 89.1% (*Auriparus flaviceps*). All four techniques were used by all species except that *A. flaviceps* was never observed to use the aerial hawk technique.

In the palo verde - cactus community, interspecific comparisons indicate that *A. flaviceps* and *P. melanura* differed significantly in prey capture techniques in both winter and spring. In both seasons, both species relied primarily on the perch-glean (>74%), though *A. flaviceps* used the hang-glean frequently, while *P. melanura* often

Table 17. Foraging technique summary of interspecific and intraspecific pairwise comparisons (G statistic, 3 df) for all communities. W = winter; S = summer; * = $p < 0.01$ ($G = 11.345$ for 3 df); ** = $p < 0.001$ ($G = 16.266$ for 3 df). For a summary of intercommunity comparisons see Table 18.

SPECIES	SEASON	PALO VERDE - CACTUS			
		<i>A. flaviceps</i>		<i>P. melanura</i>	
		W	S	W	S
<i>A. flaviceps</i>	W	-	-	-	-
	S	5.47	-	-	-
<i>P. melanura</i>	W	16.49**	-	-	-
	S	-	27.92**	4.57	-
<i>R. calendula</i>	W	71.06**	-	60.79**	-

Continued.

Table 17. Continued (foraging technique summary).

SPECIES	SEASON	MESQUITE WOODLAND				
		<i>A. flaviceps</i>		<i>C. imberbe</i>		<i>V. bellii</i>
		W	S	W	S	S
<i>A. flaviceps</i>	W	-	-	-	-	-
	S	2.68	-	-	-	-
<i>C. imberbe</i>	W	21.13**	-	-	-	-
	S	-	31.31**	18.01**	-	-
<i>R. calendula</i>	W	71.23**	-	167.90**	-	-
<i>V. bellii</i>	S	-	17.26**	-	0.93	-
<i>V. luciae</i>	S	-	27.44**	-	3.83	2.38

Continued.

Table 17. Continued (foraging technique summary).

SPECIES	SEASON	MIXED BROADLEAF	
		<i>A. flaviceps</i> S	<i>V. bellii</i> S
<i>A. flaviceps</i>	S	-	-
<i>V. bellii</i>	S	6.29	-
<i>V. luciae</i>	S	2.87	0.57

used hover-glean and aerial hawk techniques. In winter, *Regulus calendula* relied more on the aerial hawk technique (55.1%) than any other species, differing significantly in capture technique from both *A. flaviceps* and *P. melanura*. Intraspecific comparisons indicate that *A. flaviceps* and *P. melanura* did not vary in capture techniques from winter to spring.

In the mesquite woodland community, interspecific comparisons show that *A. flaviceps* and *C. imberbe* varied significantly in their use of the capture techniques in winter and in spring. In winter, *Regulus calendula* used the hover-glean and aerial hawk more frequently than did either *A. flaviceps* or *C. imberbe*. In spring, *A. flaviceps* used the hover-glean and aerial hawk less frequently and the hang-glean more frequently than did *Vireo bellii* and *Vermivora luciae*. *C. imberbe* used capture techniques in the same proportion as did *Vireo bellii* and *Vermivora luciae*. *Vireo bellii* and *Vermivora luciae* did not vary from one another in their use of capture techniques. Intraspecifically, *A. flaviceps* used the same proportion of techniques from winter to spring. By contrast, *Camptostoma imberbe* used the hover-glean (22.2 versus 13.8%) and hang-glean (13.6 versus 5.1%) more in spring than in winter and differed significantly between the two seasons.

In the mesquite woodland the two permanent residents used proportionally different capture techniques, and both differed from the winter seasonal species. In spring, the two seasonal species used the same proportion of capture techniques as did *C. imberbe*.

In the mixed broadleaf community, none of the pairwise comparisons showed any significant differences, indicating that all three spring species used the capture techniques in the same proportions.

In all communities, although the perch-glean was the most widely employed capture technique, most species varied from other species in their repertoires. *A. flaviceps* specialized in the hang-glean and did not use the hover-glean, and *R. calendula* utilized the aerial hawk much more than did other foliage-gleaning birds. The other species, although not showing particular specializations, used different proportions of capture techniques dominated by the perch-glean. The two spring seasonal species, *Vireo bellii* and *Vermivora luciae*, did not differ from one another in either community, and used the same proportion of techniques as one resident in each community.

Inter-community Comparisons

Inter-community pairwise comparisons were made for species occupying more than one community during the same season. The results of these comparisons are given in Table 18. All comparisons were made within season and all were tested against the null hypothesis that each foraging behavior was employed similarly between the communities being tested.

Comparisons of foraging height were significantly different in all but one case: *Vireo bellii* foraged at the same height in both the mesquite woodland and the mixed broadleaf communities. Comparisons of the portion of plants selected while foraging were not significant except in one case: *Regulus calendula* utilized the inner portion more in the mesquite woodland and the middle portion slightly more in the palo verde - cactus community. Perch site, capture site, and foraging technique did not vary between communities for the species involved.

Statistical comparisons of plant species used by foraging birds were not made since plant species varied substantially between communities and many plant species were found in only one community (Tables 1-3). However, I made comparisons of plant

Table 18. Inter-community pairwise comparisons (G statistic) for selected species. W = winter, S = spring; PVC = Palo Verde - Cactus; MW = Mesquite Woodland; MB = Mixed Broadleaf; * = $p < 0.01$ (G = 11.345, 13.277, and 15.086 for 3, 4 and 5 df); ** = $p < 0.001$ (G = 16.266, 18.467, and 20.515 for 3, 4 and 5 df). Community height profiles and life-form distributions are significantly different ($p < 0.001$) from one another in all community pairwise comparisons (see text for statistics).

SPECIES		INTER-COMMUNITY COMPARISONS			
FORAGING VARIABLE	df	PVC-MW W	PVC-MW S	PVC-MB S	MW-MB S
<i>Auriparus flaviceps</i>					
Foraging Height	5	122.01**	164.80**	156.23**	21.30**
Plant Portion	3	2.07	3.80	1.09	0.09
Perch Site	3	3.28	1.40	0.57	0.07
Capture Site	4	1.14	0.10	2.05	1.03
Capture Technique	3	7.48	5.66	2.22	8.92
Plant Life Form	5	153.25**	16.20*	6.51	2.42
<i>Regulus calendula</i>					
Foraging Height	5	46.25**			
Plant Portion	3	13.73**			
Perch Site	3	5.10			
Capture Site	4	5.99			
Capture Technique	3	7.01			
Plant Life Form	5	45.36**			
<i>Vireo bellii</i>					
Foraging Height	5				11.47
Plant Portion	3				10.42
Perch Site	3				2.42
Capture Site	4				4.50
Capture Technique	3				4.95
Plant Life Form	3				37.41**
<i>Vermivora luciae</i>					
Foraging Height	5				31.78**
Plant Portion	3				6.16
Perch Site	3				6.17
Capture Site	4				1.30
Capture Technique	3				0.16
Plant Life Form	3				10.12

life-forms used by foraging birds between communities. Although pairwise comparisons of life-forms proportions is significant ($p \ll .001$) between all communities (for palo verde - cactus/ mesquite woodland, $G=217.40$, $df=5$; for palo verde - cactus/mixed broadleaf, $G=272.58$, $df=5$; for mesquite woodland/mixed broadleaf, $G=55.77$, $df=5$), only 4 of the 7 pairwise intraspecific comparisons of life-forms utilized by bird species were significant, indicating some preference for particular life-forms despite the relative abundance of the plants. *A. flaviceps* used half-shrubs and shrubs proportionally more in the palo verde - cactus community than in the mesquite woodland in winter and spring. However, *A. flaviceps* used plant life-forms in approximately the same proportions in the palo verde - cactus/ mixed broadleaf communities and in the mesquite woodland/ mixed broadleaf communities. *Regulus calendula* used half shrub, shrub, and grass life-forms more in the palo verde - cactus community than in the mesquite woodland. *Vireo bellii* used shrubs more in the mixed broadleaf community than in the mesquite woodland. *Vermivora luciae* used plant life-forms in approximately the same proportions in the mesquite woodland and mixed broadleaf communities.

In general, individual bird species varied little in their foraging strategies between communities. The one parameter that varied the most was foraging height, which is not surprising given differences in height profiles between communities. Only *Vireo bellii* foraged over the same height profile between communities. The other parameter that accounts for most of the other significant inter-community differences within a species was the selection of plant life-forms for foraging substrate.

Of all foliage-gleaning species, *R. calendula* varied the most between communities; it differed in foraging height, portion of plant used, and plant life-forms selected. This species, present here only in winter and nesting elsewhere in a

community much different from those in this study, appears to be the most plastic forager in the foraging guild represented in this study.

Foraging Rate

The rate at which a species moved through a community while foraging may provide some insight into the density and abundance of food. Because foliage-gleaning birds changed perch rapidly as they moved through the community, stationary time on a perch was not measured and variance could not be calculated. As a result, the data were not treated statistically and I can only report qualitative estimations of foraging rate.

Foraging rates for all species in all communities are summarized in Table 19. The mean time on perch varied from as little as 1.34 seconds (*Polioptila melanura*, winter) to 5.70 seconds (*Camptostoma imberbe*, spring). The mean time between captures varied from 8.54 seconds (*P. melanura*, winter) to 43.10 seconds (*C. imberbe*, spring). The mean time spent on an individual plant (therefore, a reflection of the frequency with which birds moved from one plant to another) varied from 21.12 seconds (*Regulus calendula*, palo verde - cactus) to 150.60 seconds (*Auriparus flaviceps*, palo verde - cactus, spring).

One consistent trend across all communities is that birds changed perch and plants more frequently in winter than in spring, suggesting that foraging birds moved through the community faster and covered more territory in winter than in spring. Additionally, the time between captures was less in winter than in spring. This apparent anomaly may reflect greater selectivity of prey during spring when food resources are more abundant and energy requirements less.

In the palo verde - cactus community, *P. melanura* moved at a faster rate than does *A. flaviceps* and *R. calendula*. In the mesquite woodland, in winter, *A. flaviceps* and

Table 19. Foraging rates for all species for all communities.

BIRD SPECIES	SEASON	N	SEARCH TIME		CAPTURES		TIME ON PLANT	
			N	MEAN TIME ON PERCH	N	MEAN TIME BETWEEN CAPT.	N	MEAN TIME ON ONE PLANT
PALO VERDE - CACTUS								
<i>Auriparus flaviceps</i>	W	747	262	2.47	46	14.07	26	24.88
	S	2409	584	4.13	104	23.16	16	150.60
<i>Polioptila melanura</i>	W	956	714	1.34	112	8.54	30	31.87
	S	1533	719	2.13	69	22.2	25	61.3
<i>Regulus calendula</i>	W	718	275	2.61	49	14.65	34	21.12
MESQUITE WOODLAND								
<i>Auriparus flaviceps</i>	W	523	234	2.24	35	14.94	11	47.54
	S	1534	431	3.56	50	30.68	19	80.74
<i>Camptostoma imberbe</i>	W	2362	467	5.06	185	12.77	46	51.34
	S	6983	1225	5.70	162	43.10	51	136.92
<i>Regulus calendula</i>	W	3247	1387	2.34	250	11.99	137	23.70
<i>Vireo bellii</i>	S	1032	290	3.56	35	29.49	18	57.33
<i>Vermivora luciae</i>	S	1513	587	2.58	70	21.61	17	89.00
MIXED BROADLEAF								
<i>Auriparus flaviceps</i>	S	656	167	3.93	32	20.50	7	93.71
<i>Vireo bellii</i>	S	1446	373	3.88	50	28.92	31	46.65
<i>Vermivora luciae</i>	S	622	208	2.99	25	24.88	11	56.15

R. calendula moved at about the same rate while *C. imberbe* was much slower, spending nearly twice as much time between perch changes. In spring, *Vermivora luciae* moved the fastest, with *A. flaviceps* and *Vireo bellii* moving at approximately the same rate, while *C. imberbe* was the slowest foraging foliage-gleaning species. In the mixed broadleaf community, *Vermivora luciae* moved the fastest, while *A. flaviceps* and *Vireo bellii* moved at about the same rate. All three species inhabiting this community traveled slower in this community than in other communities in the same season.

CHAPTER 4

DISCUSSION

Studies of foraging behavior generally presume that arthropod faunas vary both between plant species and between substrates on a particular species of plant. Although this seems to make sense, arthropod distributions on plants are poorly understood (Morse 1989; Southwood 1978; Strong et al. 1984). If insectivorous birds overlap in their use of foraging substrates, but differ by preferring particular subsets of the substrate available, partitioning of the resource is not necessarily achieved, and this difference in behavior may not lead to coexistence. If, however, partitioning of the available substrates leads to partitioning of food resources due to specialization on arthropods, coexistence is potentially mediated by food partitioning. It is therefore important to have some sense of the degree of specialization among prey arthropods. Because this study presumes variation in arthropod distributions on plant parts involving both densities and species, a brief discussion of the known relevant distributions is warranted.

Several studies discuss the tendencies for arthropod faunas to vary among plant taxa including plant species, resulting in different insect associations on subgroups of plants within a community (see discussions in Hodkinson and Hughes 1982, Price 1984 especially chapters 3 and 16, and Strong et al. 1984). Strong et al. (1984) point out

that the majority of insects studied are monophagous or oligophagous (the authors do not cite overall percentages, but only those for specific taxa of insects), and Ehrlich and Raven (1967) point out that plant-herbivore interactions are so linked taxonomically that these interactions may be the major factor responsible for terrestrial organic diversity. In addition to differences in the number of arthropod species found on different plant species, the densities of arthropods may also vary among plant species. Holmes and Robinson (1979) found that although arthropod species were "generally similar" on the leaves and twigs of three deciduous hardwood tree species, average densities of arthropods between the tree species varied significantly.

A variety of studies examining microhabitat selection by arthropods is dispersed throughout the literature, though I am aware of few studies that have examined the diversity of arthropods on different plant parts (foliage, twigs, branches, trunk, etc.) of the same plant species. Price (1984, chapter 16) discusses the concept of the niche and cites several articles that indicate that different insects may be found on different plant organs, though most of these studies deal with habitat selection of one taxon of closely related arthropods. However, the thickness of the bark, epidermis, or other plant tissues, and the distance from the surface to tissues (especially phloem) have been shown in many studies to influence the plant organ or part of organ selected for feeding and ovipositing by various arthropods (see Price 1984 and Strong et al. 1984 for discussions).

One study (Schultz et al. 1977) examined the diversity of arthropods on various organs of an architecturally simple and chemically toxic shrub, creosote bush (*Larrea tridentata*), and recorded feeding, oviposition, and concealment sites used by 22 species of phytophagous insects. Only 6 species fed predominantly on more than one plant part, while 16 were specific to plant organs. Of these, 10 species fed only on leaves, and

there was a preference for old or new leaves with only one species regularly eating both. Similar preferences were observed in selection of concealment and oviposition sites.

Although specific studies involving the micro-distributions of arthropods on plants are few, the existing literature supports the premise that different faunas inhabit different plant parts. Thus, if a foliage-gleaning bird captures most of its prey from twigs, it is likely taking arthropods proportionally different from those taken by a bird concentrating on leaves.

In the following discussion, I will discuss my results, and then will directly address the questions set forth in the introduction. I will end this chapter by discussing some stomach content data relevant to the species in this study.

Density

The densities of foliage-gleaning bird species vary considerably from one community to the next throughout the Southwest. The species and densities of birds in all communities in this study are within the ranges reported for the same species in similar or same communities in southern Arizona. Foliage-gleaning birds were most abundant in the mixed broadleaf and mesquite woodland communities, where they were the most conspicuous guild of birds in the seasons studied. They were least abundant, but still common, in the palo verde - cactus community.

In the palo verde - cactus community, the three species of foliage-gleaning birds observed are common, as they are in similar Sonoran Desert communities throughout the southwest (Monson and Phillips, 1981). Tomoff (1974) surveyed breeding birds in desert shrub communities around Tucson, Arizona, and reported densities of 8-16 breeding birds per 40 hectares for *Polioptila melanura* and 16-36 breeding birds per 40 hectares for *Auriparus flaviceps* in the two communities (S1 and S2) most similar

to the present study site. Tomoff's densities are much lower than those found in this study for the former species but approximately equal for the latter species. Although Tomoff's communities are palo verde - cactus, his sites vary significantly in composition from my study site. Total cover and grass cover are much higher in my study area, suggesting a higher productivity and, presumably, a higher density of food species.

Information on the densities of bird species in mesquite woodlands is rarely published. This is due in part to the scarcity of this community and the relatively small area it covers, and to a great extent, to the lack of recognition that it is a distinct community. Bird densities in mesquite scrublands are frequently reported, but these rarely involve the mature mesquite woodland community. Because of their specific geographical requirements and a long history of human abuse, remaining woodlands are small and localized (Gavin 1973; Minckley and Brown 1982). Although small and very homogeneous in structure and composition, the mesquite woodland is very productive and supports high densities of birds and other animal species (Gavin 1973 and personal observation). Bird species that utilize this community occupy other communities as well, and I am not aware of a vertebrate species that is specific to this community (see species lists in Gavin 1973). Gavin (1973) reported bird densities from a partially restored mesquite woodland located 43 km NE of my study site. For all species but *Vermivora luciae*, Gavin reported densities well below those I recorded. He reported peak densities of 16.4 individuals per 40 hectares for *Vireo bellii*, 13.5 for *Auriparus flaviceps*, 27.2 for *Regulus calendula*, and 254.2 for *Vermivora luciae*. He did not observe *Camptostoma imberbe* (though subsequent reports verify nesting birds in the vicinity of his study site; personal observation; Chuck Hunter, personal communication). Personal observations suggest that densities vary greatly from one

woodland to another due to size and to the various conditions of the woodlands. Nearly all woodlands remaining in the Southwest are damaged by clearing, woodcutting, human occupation, lowering of the water table by water pumping, and cattle grazing. The site in this study, although small, represents one of the least disturbed woodlands known to me. Gavin's site, for instance, has few low mesquite branches that hang down nearly to the ground; these sites were regularly utilized by nesting *Vireo bellii* in my study site and may account for some of the differences in the densities reported by Gavin and myself.

Abiotic factors, especially severe and prolonged freezes, may be an important factor affecting the densities of small and insectivorous birds in mesquite woodlands. This community type is frequently found at the confluence of two drainages and is affected by cold air drainage. During particularly cold periods, cold air frequently flows through mesquite woodlands and may stay in these areas, making them much colder than surrounding communities (personal observation). One such cold period occurred during this study and its effects on the densities of birds are reported above. However, "recolonization" by many of the same and by new individuals was relatively rapid (within 2 weeks), and post-freeze densities were just slightly below pre-freeze densities (Table 2). Other factors such as precipitation and its effect on food resources (Dunning and Brown 1982) and the number of suitable nest sites may also be important. Although densities vary, essentially the same species, minus *C. imberbe*, are common and conspicuous components of the avian fauna in mature mesquite woodlands throughout the southwest (personal observation).

With water present all year and flowing above the surface most of the year, the mixed broadleaf community is a very productive community supporting high densities of birds and invertebrates. Foliage-gleaning birds are conspicuous members all year. Densities found at the study site are similar to those reported for similar communities,

including cottonwood-willow, in the southwest (Chuck Hunter, personal communication).

Other factors not quantified in this study may differentially affect foliage-gleaning bird species. I did not detect predation on any of the species studied here, though vertebrate predators, such as snakes, skunks, and large flycatcher birds, capable of preying on foliage-gleaning birds were common, especially in the mesquite woodland, and I observed evidence of predation on other species. Although solitary, the foraging habits and small size of foliage-gleaning birds may minimize predation during diurnal foraging. Nocturnal predators, especially snakes and mammals, may be important, and probably affect nest location and construction (Collias and Collias 1984), limiting suitable nesting sites.

Nest parasitism by the brown-headed cowbird (*Molothrus ater*) may also affect bird densities. Parasitism was common, but of the foliage-gleaning birds, only *P. melanura* and *V. bellii* were affected. Parasitism appeared to have had the greatest effect on the latter species. Of four nests observed in the mesquite woodland, all failed due to the cowbird; in all cases, nests with cowbird eggs were abandoned. However, at least one *V. bellii* nest in the mesquite woodland and four in the mixed broadleaf community were successful, as I observed one fledgling of this species in the former community and at least eight in the latter community. *P. melanura* nests were also parasitized, with the adults generally rearing one cowbird. One major difference observed at the study site was that the cowbirds did not arrive on the site until after *P. melanura* had fledged its first clutch. Observed parasitism only affected second brood in this species. By contrast, cowbirds were already present when *V. bellii* appeared at the study site. Thus, parasitism had an obvious asymmetric effect on foliage-gleaning birds and undoubtedly affected the densities of some species. It is not clear, however, how parasitism

influences the structure of avian communities and its effect on the coexistence of foliage-gleaning birds.

Overall, although the densities of foliage-gleaning birds in these three communities vary throughout the southwestern United States and northern Mexico, the species assemblages observed here are common throughout this area. The foliage-gleaning guild composed of these and other species is an important part of southwest avian faunas in these communities.

Utilization of Plant Species and Life-forms

In general, foliage-gleaning birds selected plant species differently from 1) the distribution of plants in the community, 2) other foliage-gleaning species, and 3) winter to spring in the same community. Exceptions to this pattern are few (8 of 35 pairwise comparisons; Tables 6-9) and involve seasonal species in all but one case. Seasonal species frequently spend other seasons in communities that are vegetatively very different from those occupied during these study seasons (Morse 1989; Fitzpatrick 1982; Franzreb 1984). As a result, they may be more flexible in the selection of plant species for foraging, and therefore perhaps more likely to use vegetation identically to its distribution (e.g., *Vermivora luciae* selected a greater variety of plant species than other foliage-gleaning birds and was involved in 4 of the 8 exceptions to the general pattern stated above). All permanent residents differed proportionally from one another in plants selected for foraging. Additionally, most of the deviation from these generalizations occurred in the mesquite woodland (6 of the 8 exceptions) which is vegetatively the most homogeneous community, dominated by one plant species, *Prosopis velutina*.

In general, foliage-gleaning birds select plant life-forms 1) differently from the distributions of life forms, but 2) similarly to other sympatric foliage-gleaning birds. In the palo verde - cactus community birds select different profiles of life-forms for foraging in winter than in spring, but show no change in preference between seasons in the mesquite woodland. Thirteen of the 17 non-significant comparisons, representing identical selection of life-forms for foraging, occurred in the mesquite woodland, which is dominated by one life-form (97% trees), and all but one non-significant comparison involves seasonal species. Again, seasonal species tend to show less preference for particular life-forms than do the permanent residents, and are therefore more likely to select life-forms in the proportions found within the community.

It is apparent that bird species do key in on specific plant species. This would suggest that birds seek plant species because the plant enhances predator avoidance, ease of harvesting of food resources, or the availability of specific food items. The first two may explain why foliage-gleaning birds prefer trees, especially palo verde, mesquite, and cat-claw acacia. Differences in preferences by different bird species, however, suggests that the availability of different food items might be important in plant selection. Any factors that limit the search time for suitable prey will enhance an individual's survival (Stephens and Krebs 1986); if a bird can recognize plant species, it can increase its foraging effectiveness if arthropods are specific to plants, or if the bird is more effective than its potential competitors in harvesting arthropods from particular plant species. Likewise, if a bird learns to find and handle specific prey items better than its potential competitors, then food partitioning can occur and coexistence of guild members is facilitated (Brown 1989; Cody 1974). The selection evident here suggests a means of resource partitioning that may be sufficient to allow for coexistence of guild members.

The results reported here are similar to those reported elsewhere. Holmes and Robinson (1981) found that temperate forest birds, especially foliage gleaners, departed significantly from random in their reliance on tree species even when some of the trees had the same growth form. They attributed this selection to the variation in arthropod abundances and diversity among plant species. Foliage-gleaning birds had a stronger preference for specific plant species than those of other guilds. Sherry and Holmes (1985) found that insectivorous birds keyed on plant species and that insectivorous birds often selected habitats based on the presence or absence of particular combinations of plant species. Maurer and Whitmore (1981) reported that foliage-gleaning birds selected tree species differently from random and some species changed plant species between young and mature forests. They attribute this to opportunistic foraging behavior such that some species will modify their foraging behavior when presented with altered resource distributions due to change in community structure. In this case it is clear that bird species are selecting specific plant species for reasons other than the plants themselves; this may reflect indirect selection of prey species. Morse (1989) summarizes several additional studies that indicate birds select plants from which to glean insects in a nonrandom way, and concludes that birds use specific plants to locate preferred prey.

Foraging Height

Avian foraging height has been analyzed in many studies because it is generally thought to be an important component in apportionment of resources within a community (MacArthur 1958, 1972; Cody, 1974; Fitzpatrick, 1978; Holmes et al, 1979; Landres and MacMahon, 1983). In all but one case (one season in one community) in this study, birds foraged at heights different from those predicted by the relative volume of plant

material (vegetation height profile; Table 13). In addition, interspecific pairwise comparisons show that most species (14 of 16 pairwise comparisons) select different distributions of foraging heights (Table 13). The exceptions involve seasonal species, one in winter compared to a permanent resident and a pair in spring. Intraspecific inter-community comparisons show that species occupying more than one community (4 of the 6 species in this study) foraged at different height profiles in 6 of 7 cases, the exception being that of *Vireo bellii* (Table 18). Such changes in foraging height profiles have been reported in other studies (Landres and MacMahon 1983; Laudenslayer 1981; Maurer and Whitmore 1981).

Landres and MacMahon (1983), citing high overlap in foraging height, conclude that foraging height alone does not appear to be an important aspect of resource allocation in the guilds in their study (which included foliage-gleaning birds). However, it appears that birds within the foliage-gleaning guild are highly selective along this axis within a given community, and it is clear that their selectiveness, although involving a great deal of overlap, distinguishes one species from another with only a few exceptions. Further, the differences in foraging height profiles are not due to differences in bird morphology as all of these birds are morphologically similar (Laudenslayer 1981; Dunning 1984). It may be that differences in foraging height profiles are due to differences in preferred food resources. This is discussed below.

Foraging: Plant Portion, Perch Site, Capture Site and Technique

Of the four other foraging variables measured in this study, perch size and capture site appear to be the most similar among foliage-gleaning birds, while portion and foraging technique are the least similar. Capture site and perch site are the same for all species except *Regulus calendula*. As their guild name implies, foliage-gleaning

birds, including *R. calendula*, spend most of their time searching foliage and make most of their captures of arthropods from foliage. Most foliage is supported by small twigs, and as a result, foliage-gleaning birds searching the foliage spend most of their time perched on twigs. Wintering *R. calendula* captured significant numbers of prey from the air by hawking, which accounts for its deviation from the typical foliage-gleaning repertoire.

Foliage-gleaning birds spent most of their foraging time in the outer portion of plants (Table 10; Laudenslayer 1981; Landres and MacMahon 1983). This is as expected, because foliage is much denser on the outer portions of most plants used by foliage-gleaning birds. Variation in the use of the portions among species was significant in more than half of the pairwise comparisons, and birds varied their use between the outer and middle portions. All of the significant pairwise comparisons involve either *R. calendula* or *Vermivora luciae*, both of which differ from all other species in their more frequent use of the middle portion of plants. These two species occur in different seasons, but the latter relies on the middle portion more than does the former (inter-seasonal comparison for the mesquite woodland, $G=11.12$, $df=2$, $p<.05$).

Foliage-gleaning birds rarely use the inner portion of plants, especially of trees. There are three apparent explanations for this. First, the inner portion is dominated by large branches and the trunk, most of which is vertical. Thus, to utilize this substrate a foraging bird must work vertically, which is perpendicular to its normal orientation (Morse 1989). Second, feet adapted to perching on twigs are often inadequate for efficient movement along larger substrates. The inner portion of trees is the region least utilized by small insectivorous birds, and rarely by foliage-gleaning birds (Morse 1989). Third, the microhabitat of the trunk and larger branches is often quite different from that of the small branches, twigs, and foliage. The bark is often rougher and

thicker, providing a different habitat for arthropods. Collectively, points two and three suggest a habitat quite different from that normally encountered by foliage-gleaning birds; relatively few species of birds specialize in this region, and these species are characterized by relatively large feet and long bills (for example, nuthatches and woodpeckers). Smooth-barked species, such as palo verde, provide relatively little suitable habitat for arthropods, and these prey are rare on the trunks of these trees (personal observation).

A fourth explanation is that species of other guilds may be more specialized at capturing prey from the inner portion and competitively exclude the less-adapted (for this substrate) foliage-gleaning birds. Bewick's wrens (*Thryomanes bewickii*), woodpeckers, and lizards (especially *Urosaurus ornatus* and *Sceloporus magister*) frequently forage in this portion of trees and are common to abundant in all three study communities (personal observation). Foliage-gleaning birds do not use the inner portion differently between seasons nor between communities (inter-seasonal comparison and inter-community comparisons, G-test, $p > .01$).

The ground was rarely used by foraging foliage-gleaning birds, either as a foraging perch or capture site. Differences in arthropod faunas, predation pressures, and competition from non-guild members may explain the avoidance of this substrate. The ground habitats support arthropod faunas that differ from arboreal and shrub faunas (personal observations). Foliage-gleaning birds are solitary foragers and are likely to be more vulnerable to predation than other species while foraging on the ground. Potential ground-foraging competitors possess various strategies, such as social foraging (wrens), quickness of foot and wing (all species), and foraging in dense vegetation (towhees and thrashers), that are suitable for ground foraging. Several species of birds (especially towhees, thrashers, and wrens) and lizards (especially

Cnemidophorus spp.) are common to abundant in all three communities in the study area. The presence of these species, as well as the different morphological requirements for foraging effectively on the ground, excludes foliage-gleaning birds from this substrate.

Foliage-gleaning birds employ a repertoire of 4 maneuvers to capture prey (except *A. flaviceps* which does not use the aerial hawk technique). All species except *R. calendula* (but see Laurenzi et al. 1982) use the perch-glean technique for most of their captures (> 62%), but considerable variation in the reliance on various techniques accounts for significant differences in 10 of the 16 pairwise comparisons. Use of hover-gleaning, hang-gleaning, and aerial hawking varies considerably between species. Intraspecific use of techniques, both between season and between communities, indicates that species (except *C. imberbe*) do not alter their relative use of the different techniques (1 of 11 intraspecific pairwise comparisons is significant). In this study, *R. calendula* was observed using the hawking technique much more often than may be typical (Laurenzi et al. 1982; Franzreb 1984). This technique may be used more in winter and especially in areas with frequent freezes, because flying insects appear to recover faster than sedentary species after cold weather, illustrating that this species is quite capable of varying its use of techniques to take advantage of fluctuations in the types and frequencies of arthropods, and is apparently more "willing" to do so. Observations during this study suggest that short, sudden freezes may affect the relatively less mobile arthropods that cling to foliage more than flying insects that may be able to seek more suitable shelter during short cold periods. After the freeze in the mesquite woodland, the first conspicuous arthropods (upon close inspection) were flying insects. *R. calendula* took advantage of this resource and moved back into the woodland, relying primarily on aerial hawking, while other guild members did not increase the

proportion of aerial hawking and did not reinhabit the woodland until foliage arthropods were again conspicuous.

Although reliance on various techniques may be influenced phylogenetically, environmental factors, such as type of prey and habitat of prey, may be equally important in the selection of capture techniques. Phylogenetic influence is suggested by various relationships. For example, parids and close relatives (including *A. flaviceps*) frequently use the hang-glean technique, while sylvids (*P. melanura* and *R. calendula*) frequently use the aerial hawking technique (Bent 1949; Root 1967). However, *C. imberbe*, a tyrant flycatcher, uses the aerial hawk technique - one closely associated with its family - less than do other foliage-gleaning birds. It appears that clades that tend to be characterized by a particular capture behavior (as well as other foraging behaviors), tend to occupy the same guild (Morse 1989). In fact aerial hawking is unobserved or rare in many tyrant flycatchers that occupy other guilds, such as fruit-eating and foliage-gleaning (Fitzpatrick 1978, 1980). Among the foliage-gleaning birds studied here, morphological characteristics appear to have converged in response to this way of existence, and there is no particular reason to suggest that capture techniques should be any more constrained than other features (Morse 1971; Fitzpatrick 1978). This is supported by the fact that most foliage-gleaning birds appear capable of employing all of these techniques. Specialization on various prey items may account for the variation in use of techniques. For instance, the hover-glean was the technique most frequently employed to capture lepidopteran larvae (personal observation) and the hang-glean allowed *A. flaviceps* access to nectar and insects on flowers. *R. calendula* frequently used the aerial hawk, somewhat opportunistically, to capture flying insects - which it does relatively infrequently on its breeding territories (Franzreb 1984) - while *P. melanura* spent little time searching the sky for insects

and seldom used this technique. It appears likely that the reliance on particular capture techniques is more a result of specialization on particular arthropod groups than due to phylogenetically constrained behaviors.

Foraging Rate

The rate of foraging may be important in partitioning available resources. It has been shown that the rate of foraging alone might be sufficient to allow coexistence of similar species based on the efficiency of harvesting a variable (size, types, and/or densities) resource. This can occur when each species has a greater foraging efficiency in a particular season (Brown 1989 and personal communication). Even if foliage-gleaning birds are feeding on the same food resources, coexistence may occur due to seasonal variation in foraging efficiency, which may be revealed by differences in foraging rates. The data presented here suggest variation in the rate of harvesting resources.

Mean time on a perch, mean time between captures, and mean time on one plant vary interspecifically within season, and intraspecifically between seasons. Mean time on a perch and on a plant provide an index of the rate at which a species moves through the community in search of prey. In general, the larger a species' territory, the faster it moves. For example, in the palo verde - cactus community, *Polioptila melanura* occupies territories 1.5 to 2.5 times larger than those of *Auriparus flaviceps* (personal observation; see Table 1 and Tomoff 1974) and travels approximately twice as fast, estimated by mean time on perch, as *A. flaviceps* (Table 19).

Mean time between captures is an index of the time spent searching for a prey item, and perhaps to some degree, selectivity in prey. For example, for all permanent residents, mean time between captures was greater in spring than in winter. In general,

prey densities on the study sites, though not measured, appeared to be much higher in spring than in winter. The increased time between captures probably reflects selectivity. Birds appeared to be searching out specific prey items, especially lepidopteran larvae. Birds may have been selecting larger items (hence the larvae) to feed to chicks (see Root 1963), although most items were consumed on site followed by continued foraging. Greater selectivity may have been possible in spring than in winter due to energetic constraints that require that small wintering birds consume more food (Morse 1989).

Among seed eating sparrows and finches, Benkman and Pulliam (1988) found that sparrows, which eat smaller seeds than finches, forage at a faster rate, make more captures, and are more sedentary in areas of relatively high food densities. The differences in suitable prey among these families affect their foraging behavior, tendencies to disperse, and the habitats in which they occur. These considerations may apply to some extent to *Auriparus flaviceps* and *Polioptila melanura*. The latter appears to eat smaller arthropods (Laudenslayer 1981; Gabaldon and Ohmart unpubl. ms) and does not eat plant material. Other than lepidopteran larvae, the food handled by *P. melanura* was usually small and unidentifiable, whereas *A. flaviceps* frequently fed on larger items, including grasshoppers and female mesquite scale insects, *Toumeyella mirabilis*, which greatly increased handling time. This suggests partitioning of food resources. Additionally, if *P. melanura* must consume more food items than *A. flaviceps*, the necessity of increased time spent foraging may place restrictions on the communities (including perhaps, the densities of potential competitors) that *P. melanura* can profitably occupy. This may provide some insight into why *P. melanura* is not present in some communities such as the mesquite woodland (even though they are common in adjacent mesquite scrub) and mixed broadleaf.

Differences in foraging rate among foliage-gleaning birds were qualitatively apparent, which fostered an attempt to measure the differences quantitatively. The latter data appears to uphold the qualitative observations. The observed differential foraging rates may be due to dietary differences, primarily involving size of food items. Food partitioning, however, is not required if, as Brown (1989) has demonstrated, cohabitants vary seasonally in their foraging effectiveness. Variation in foraging rates as observed in these species provides an opportunity for differential success in foraging efficiency, and thus a potential means of coexistence.

Foraging Behavior and Partitioning of Food Resources

In this section I will directly address the questions posed in Chapter 1. First, I asked: how similar is the foraging behavior of guild members occupying the same community, and is there evidence for resource partitioning based on differences in foraging behavior? Although convergent in morphology and showing overlap in nearly all foraging categories - attributes that group these species together in a foraging guild - each of the foliage-gleaning species utilizes a different array of foraging behaviors that makes it distinguishable by foraging strategy alone. The characteristic behavior of each species suggests that it specializes on various combinations of behaviors within the general repertoire characteristic of foliage-gleaning birds. The overlap of categories clearly demonstrates that each species is capable of most, if not all, of the basic behaviors studied here. That species differ significantly within these categories, and that these behaviors do not appear to be constrained by differences in morphology nor phylogenetic relationships, suggests a basis for resource partitioning sufficient to allow for coexistence. Other hypotheses, however, are not ruled out, and I will address this

more after examining the other questions. Table 20 summarizes the differences in foraging behavior for each community for each season.

Secondly, I asked: how similar is the foraging behavior of a species between seasons within a community, and to what factors can changes (if any) be attributed? Only three species of birds were found in the same community year-round, and all showed changes in foraging behavior from winter to spring season. The differences between seasons are discussed above and are summarized in Table 21. Most of the observed changes occurred among all permanent resident species between seasons. For example, all permanent species foraged at lower heights in winter than in spring. This would suggest that factors other than competition between guild members influenced these changes; however, these comparisons do not directly take into account the presence of seasonal residents that change in all communities each season. Although all species shifted downward, all permanent species still foraged over different profiles.

Microclimate, plant phenological changes, and arthropod distributional changes - all of which are interrelated - are likely to account for the observed changes in foraging behavior. There is no evidence that behavioral changes are due to competition. Likewise, competition from non-guild members is unlikely to have caused the observed changes. In the palo verde - cactus community, both *A. flaviceps* and *P. melanura* foraged significantly lower in the canopy in winter than in spring, and both used half-shrubs and shrubs more. Lizards, especially *Cnemidophorus* spp., are conspicuous ground foragers and frequently forage in half-shrubs in spring, but are absent in winter. Given few plant phenological changes in this community between these two seasons, it is possible that competition with lizards keeps birds in the trees during spring. However, non-foliage-gleaning birds are also ground and low-shrub foragers, and are equally conspicuous in both seasons. It seems more likely, though untested, that

Table 20. A summary of foraging differences between foliage-gleaning birds in each community for each season. Key differences listed indicate that species used that behavior proportionately more than the other species, but not necessarily greater than other behaviors. All differences shown are significant ($p < .01$).

Palo Verde - Cactus: Winter

	<i>A. flaviceps</i>	<i>P. melanura</i>	<i>R. calendula</i>
Plant Species	<i>Cercidium</i>	<i>Cercidium</i>	<i>Cercidium</i>
	< 50%	> 70%	> 70%
Plant Life Form	Half-shrubs	Trees	Trees
Foraging Height	Low	High	High
Plant Portion	Outer	Outer	Inner
Perch Site	Twig	Twig	Twig
Capture Site	Foliage	Foliage	Air
Capture Technique	Hang-glean	Perch-Glean	Hawk

Palo Verde - Cactus: Spring

	<i>A. flaviceps</i>	<i>P. melanura</i>
Plant Species	<i>Prosopis</i>	<i>Cercidium</i>
Plant Life Form	Cacti	Half-shrubs
Foraging Height	High	Middle
Plant Portion	Outer	Outer
Perch Site	Twig	Twig
Capture Site	Foliage	Foliage
Capture Technique	Hang-glean	Perch-glean

Mesquite Woodland: Winter

	<i>A. flaviceps</i>	<i>C. imberbe</i>	<i>R. calendula</i>
Plant Species	<i>Celtis</i>	<i>Prosopis</i>	<i>Lycium</i>
Plant Life Form	Trees	Trees	Trees
Foraging Height	Higher	High	Middle/Low
Plant Portion	Outer	Outer	Inner
Perch Site	Twigs	Twigs	Branches ¹
Capture Site	Foliage	Foliage	Foliage
Capture Technique	Hang-glean No Hawk	Perch-glean	Hawk

Mesquite Woodland: Spring

	<i>A. flaviceps</i>	<i>C. imberbe</i>	<i>Vireo bellii</i>	<i>Vermivora luciae</i>
Plant Species	<i>Acacia</i> <i>Celtis</i>	<i>Prosopis</i> <i>Celtis</i>	<i>Acacia</i> <i>Celtis</i>	<i>Acacia</i>
Plant Life Form	Trees Only	Trees	Trees	Trees ¹
Foraging Height	High	Middle	Mid-low	Mid-low
Plant Portion	Outer	Outer	Outer	Middle
Perch Site	Twig	Twig	Twig	Twig
Capture Site	Foliage	Foliage	Foliage	Foliage
Capture Technique	Hang-gl. No Hawk	Others	Others	Others

Table 20. Continued

Mixed Broadleaf: Spring			
	<i>A. flaviceps</i>	<i>Vireo bellii</i>	<i>Vermivora luciae</i>
Plant Species	<i>Quercus</i>	<i>Dodonea</i>	<i>Fraxinus</i> <i>Platanus</i>
Plant Life Form	Trees	Shrubs ¹	Trees
Foraging Height	High	Middle	Low
Plant Portion	Outer	Outer	Middle
Perch Site	Twigs	Twigs	Twigs
Capture Site	Foliage	Foliage	Foliage
Capture Technique	Perch-glean	Perch-glean	Perch-glean

¹ Significantly different from *Auriparus flaviceps* only.

Table 21. Summary of seasonal changes in foraging behavior for all permanent residents. The behavior activity indicates the way in which the species differs most between seasons and does not necessarily represent the most frequent behavior. Differences are indicated only if they are significant ($p < .01$). ND = no difference, gl. = glean.

	Palo Verde - Cactus		Mesquite Woodland	
	Winter	Spring	Winter	Spring
<i>Auriparus flaviceps</i>				
Plant Species	Grass Shrubs Half-shrub	<i>Cercidium</i> <i>Prosopis</i>	Different proportion of trees and shrubs between seasons	
Plant Life Form	ND		ND	
Foraging Height	Low	High	Low	High
Plant Portion		ND	ND	
Perch Site		ND	ND	
Capture Site		ND	ND	
Capture Technique		ND	ND	
<i>Polioptila melanura</i>				
Plant Species	<i>Encelia</i> <i>Ericameria</i>	<i>Cercidium</i> <i>Prosopis</i>		
Plant Life Form	Half-shrub Grass	Trees		
Foraging Height	Low	High		
Plant Portion		ND		
Perch Site		ND		
Capture Site		ND		
Capture Technique		ND		
<i>Camptostoma imberbe</i>				
Plant Species			ND	
Plant Life Form			ND	
Foraging Height			Low	High
Plant Portion			Middle	Outer
Perch Site			ND	
Capture Site			ND	
Capture Technique			>Perch-gl. >Hawk	>Hover-gl. >Hang-gl.

birds forage lower in winter in response to the distributions of arthropods; more favorable microenvironments occur closer to the ground (due to differences in microtopography and to plant distribution), increasing the probability that arthropods can survive and remain active there during cold weather.

The third question asks: how similar is the foraging behavior of a species in structurally different communities, and to what can differences in foraging behavior (if any) be attributed? Between communities, foliage-gleaning birds maintained their same foraging strategies, varying only in foraging height (in all species except *V. luciae*) and in selection of plant life-forms (in 4 of 6 comparisons). Only *R. calendula* differed in selection of portion of the plant. Of these variables, foraging height is the one most expected to differ because plant heights vary significantly between communities. The proportions of life-forms also vary significantly between communities, but trees are the dominant life-form in all three, and in all communities, foliage-gleaning birds selectively utilize trees. The differences observed between communities appears to be due to structural differences in the communities and to the birds' response to these differences. There is no direct evidence that differences are due to competition, either within or between guilds. The differences in foraging behavior between communities are summarized in Table 22.

It is clear that the foliage-gleaning birds studied here have distinct foraging strategies. Despite overlap in most behaviors, each species specializes over a distinctive subset of the overall foraging repertoire. These similar, yet distinctive, foraging strategies are evidenced by the fact that an experienced observer can quickly identify all foraging members of the guild studied here without reference to field marks.

Although these results are consistent with the predictions of competition theory, other hypotheses have not been ruled out. In particular, these results might be

Table 22. Summary of changes in foraging behavior between communities within each season. The behavior activity indicates the way in which the species differs most between seasons and does not necessarily represent the most frequent behavior. Differences are indicated only if they are significant ($p < .01$). PV-C = Palo Verde - Cactus, MW = Mesquite Woodland; MB = Mixed Broadleaf, ND = no difference.

	PV-C	MW	PV-C	MW	PV-C	MB	MW	MB
	Winter		Spring		Spring		Spring	
<i>Auriparus flaviceps</i>								
Pt. Life Form	Half-sh.	Trees	Cacti	Trees	ND		ND	
Foraging Ht.	Low	Middle	High	Higher	High	Higher	High	Higher
Plant Portion	ND		ND		ND		ND	
Perch Site	ND		ND		ND		ND	
Capture Site	ND		ND		ND		ND	
Capt. Technique	ND		ND		ND		ND	
<i>Regulus calendula</i>								
Pt. Life Form	Half-sh.	Trees						
Foraging Ht.	Low	Middle						
Plant Portion	Middle	Inner						
Perch Site	ND							
Capture Site	ND							
Capt. Technique	ND							
<i>Vireo bellii</i>								
Pt. Life Form							Tree	Shrubs
Foraging Ht.							ND	
Plant Portion							ND	
Perch Site							ND	
Capture Site							ND	
Capt. Technique							ND	
<i>Vermivora luciea</i>								
Pt. Life Form							ND	
Foraging Ht.							High	Lower
Plant Portion							ND	
Perch Site							ND	
Capture Site							ND	
Capt. Technique							ND	

explained by the hypothesis that each species' foraging strategy is the result of optimal use of specific resources and represents a long evolutionary history independent of current competition with the present assemblage of species.

If ongoing competition is influencing current assemblages of cohabitants, then one would predict that the removal of a competitor would lead to changes in the foraging strategy of a remaining guild member. This crucial experiment was not performed in this study. However, I did attempt to address this by examining the changes in the foraging behavior of a particular species from one community to the next as guild members varied. If a species changes its foraging strategy little as its competitors change, current competition can be expected to have little effect on the current assemblage unless one competitor species is replaced by a very similar competitor species. Changes in the assemblage of species from one community to the next did not involve a one-to-one replacement of one species by another. As a result, it is difficult to address this issue directly. It is, however, interesting that species did not change their foraging behavior between communities despite the change in the number of species of potential competitors other than changes that can be explained by changes in community structure. These results tend to support the hypothesis that foraging strategies are not in direct response to current competition.

Stomach Contents and Diets

The question of whether subtle, yet significant, variation in foraging behavior is sufficient to allow for the partitioning of resources still remains. Demonstration of differences of foraging behavior does not necessarily imply either resource partitioning nor the existence of significant competition. Before the role of competition in structuring guilds can be adequately evaluated, one must demonstrate that foraging

species can (at least occasionally) reduce prey densities enough to cause stress to competitors and therefore reduce competitors' population growth rate (MacArthur 1959; Maurer 1983, 1984), and that variation in foraging behavior results in partitioning of limiting resources. Some data pertaining to bird species studied here is available and can help address this latter point.

Stomach contents have been used by some researchers to identify whether different foods are eaten by birds with different foraging strategies (Holmes et al. 1979; Laudenslayer 1981; Sherry 1984; Ohmart et al. Unpubl. ms). Some data from foliage-gleaning birds in Arizona can address the question of whether or not foliage-gleaning birds in the same community are eating the same food. In a limited sample of stomach contents (n=19-33), Laudenslayer (1981) found that three foliage-gleaning birds occupying mesquite scrub communities along the lower Colorado River in Arizona ate similar arthropods, dominated by eruciform larvae of lepidoperans and coleopterans. Despite overlap in food items, he found that all pairwise comparisons involving *Auriparus flaviceps*, *Polioptila melanura*, and *Vermivora luciae* (the only 3 foliage-gleaning birds common to his study area and mine) were significantly different ($.05 > p > .01$) for both prey types and prey size. Thus, foliage-gleaning birds utilizing similar foraging techniques in the same community used different proportions of food items.

The largest sample of stomachs of foliage-gleaning birds from the same and similar communities comes from Ohmart and his coworkers and students, who collected *Auriparus flaviceps*, *Polioptila melanura*, *Regulus calendula*, and *Vermivora luciae* along the lower Colorado River (Ohmart and Gabaldon, Unpubl. ms). Ohmart and Gabaldon grouped the data by season (5 recognized), and by communities (riparian and scrub). For the bird species in question, sample sizes ranged from as few as 68 gizzards

(*Vermivora luciae*) to as many as 209 (*Auriparus flaviceps*). In all but one pairwise comparison within and between seasons, different species fed on significantly different groupings of food items ($p < .01$; my calculations from "sum number", defined as the total number of individuals of a particular taxon found in the total stomach sample for a bird species, and from "weighted sum number," a number calculated by multiplying the sum of the number of food items of taxon_i / total number of items in stomach_i by the total number of prey/ number of stomachs in sample).

Because bird diets vary considerably from season to season (Laurenzi et al. 1982; Rosenberg et al. 1982; and personal observation on study sites), comparisons between seasons (ie, overall diet) are least reliable, though it is possible that in the same area and subject to the same food choices, species "average out" temporal changes in the prey availability. Within-season comparisons are most satisfying in terms of the likelihood that they represent real differences in food preferences. A few examples are useful to demonstrate within-season differences.

During the winter season in the lower Colorado River valley, the diets of *A. flaviceps*, *P. melanura*, and *R. calendula* showed a high degree of overlap (from 31.1-64.2% for pairwise comparisons). *P. melanura* and *R. calendula* showed the greatest overlap (64.2%); Homoptera (especially Cicadellidae; 30.3 and 26.8%) Diptera (14.2 and 19.3%), and Coleoptera (8.3 and 16.8%) were major components of their diets. Even though both utilized dipterans, *R. calendula* fed heavily on midges, a family not harvested by *P. melanura*. Additionally, lepidopteran larvae were important for *P. melanura* (12.0%), but contributed a minor portion (1.2%) to the diet of *R. calendula*. *A. flaviceps* and *R. calendula* shared the fewer proportion of food items (31.1%). The three main dietary groups for *A. flaviceps* (Coccoidea, 32.4; lepidopteran larvae, 14.9%; and spiders 10.2) accounted for 66.5% of its diet, but only for 9.3% of the diet

of *R. calendula*. Likewise, the three main groups for *R. calendula* (listed above), which accounted for 62.9% of its diet, accounted for only 7.8% of the diet of *A. flaviceps*. Lepidopteran larvae and spiders accounted for most of the overlap between *A. flaviceps* and *P. melanura* (40.5%).

In the early spring season, 4 main prey groups accounted for greater than 70% of the diets of *A. flaviceps*, *P. melanura*, and *Vermivora luciae*, resulting in high dietary overlap (47.2 to 72.0%). Lepidopteran larvae accounted for the greatest food group for all three species (53.0, 28.4, and 32.7%), and most of the overlap. Spiders were a major group for *A. flaviceps* (14.5%), but accounted for 9.4% for *P. melanura* and only 3.6% for *V. luciae*. Coleoptera were a major group in the diets of *P. melanura* (19.6%) and *V. luciae* (26.6%), but accounted for only 2.3% of the diet of *A. flaviceps*. All three species relied on Homoptera (5.9, 13.3, and 9.7%), though reliance on particular homopteran families varies. Additionally, hemipterans were important for *P. melanura* (8.5%) and *V. luciae* (6.9%), but not for *A. flaviceps* (1.8%). *A. flaviceps* fed on plant material (3.0%) which was not utilized by the other two species. Pairwise comparisons (G tests, $p < .01$) show that, despite the high dietary overlap, all three species utilize significantly different diets (using "sum number" data). However, when "weighted sum number" data is compared, regrouping the data into 5 total food groups (condensing, using an "other" category for most groups), *P. melanura* and *V. luciae*, the pair with the greatest dietary overlap, used the main food groups in approximately the same proportions ($G = 5.65$, $df = 4$, $p > .10$), while the other comparisons remain highly significant ($p < .001$).

Although the above data indicates that different bird species fed on different groups of arthropods, some procedural practices in the gathering and grouping of this data suggest caution in its interpretation. To gather a large sample, birds were collected

over a relatively large area, and specimens from similar communities (for example, mesquite communities) were grouped together (Robert D. Ohmart, personal communication). In such a combined sample, different bird species may have come from slightly different areas due to differences in local abundances. Because arthropod densities and faunas may vary substantially between similar communities, the observed differences could result from differences in prey availability rather than bird diet choice.

In my study, I attempted to quantify food used as prey, but the nature of the observations made such categories so broad that they were useless. My qualitative impression, however, is that despite overlap in many areas, most species appeared to be using different subsets of the available food resources. In particular, *A. flaviceps* fed on food items other than adult and immature arthropods. This species is known to feed on nectar (Bent 1946; Taylor 1971; personal observation of nectar feeding include use of penstemon, ocotillo, and saguaro), and insect eggs (Bent 1946; personal observation). Additionally, *A. flaviceps* uses mesquite sap as an important supplemental food source in winter, which it will defend from other birds including *R. calendula* and wintering warblers. During the freeze that occurred during this study, resident *A. flaviceps* from the mesquite woodland used sap resources on the fringes of the woodland as their primary food source for nearly 10 days. During this time, *R. calendula* also used the sap resource, but not to the extent that *A. flaviceps* did, perhaps in part due to behavioral dominance by *A. flaviceps* (Hibbard and Mays, ms). During both winter and spring seasons, *A. flaviceps* in the palo verde - cactus and mesquite woodland communities spend a significant, but highly variable, portion of their foraging time harvesting resources other than arthropods. My observations, both qualitative and quantitative, suggest that partitioning of food resources may occur.

Summary

Insectivorous foliage-gleaning birds are conspicuous and major components of the palo verde - cactus, mesquite woodland, and mixed broadleaf communities studied here. The six species found within the study area are morphologically similar and are grouped together by their reliance on a similar foraging strategy. Despite their overall similarity, each species is distinctive in its foraging repertoire, a subset of the generalized foliage-gleaning strategy.

Three foliage-gleaning species occurred in the palo verde - cactus community. *Auriparus flaviceps* and *Polioptila melanura* were common in winter and spring, and in winter *Regulus calendula* was a common addition. In winter *R. calendula* and *P. melanura* were most similar, but differed in the portion of plants in which they foraged and the techniques used to capture prey. *A. flaviceps* differed from the others in use of plant species and life forms, foraging height, and capture technique. In spring, the two permanent residents differed in plant selection by species and life forms, in foraging height and capture technique.

In the mesquite woodland, *Auriparus flaviceps* and *Camptostoma imberbe* were present in both seasons. *Regulus calendula* was present in winter, and *Vireo bellii* and *Vermivora luciae* were resident in spring. All five species were seasonally common. Despite the overall uniformity of this community, cohabitants differed in several behaviors. In winter, all three residents used different proportions of tree species, foraged at different levels, and used different capture techniques. *R. calendula* used the inner portion of plants significantly more than did the other species. In spring, there were fewer differences among the residents. *A. flaviceps* and *C. imberbe* differed in the same behaviors as in winter, as well as in proportion of plant life forms on which they foraged, with the former using all life forms and the later using only trees. *V. bellii* and

V. luciae differed only in the portion of the plant selected for foraging, with the latter also using the middle portion proportionally more. Both of these species differed from *C. imberbe* only in the proportion of plant species selected. It is worth noting that all four spring residents select markedly different nest sites.

In the mixed broadleaf community *Auriparus flaviceps*, *Vireo bellii*, and *Vermivora luciae* were common in the spring. The three differed in their relative selection of plant species and foraging heights. *A. flaviceps* foraged highest and *V. luciae* the lowest with *V. bellii* in between. *V. bellii* differed from *A. flaviceps* in its relative use of life forms, and *V. luciae* differed from the other two in using the middle portion of the plants more while foraging. As noted above, all three differ markedly in selection of nest locations.

Auriparus flaviceps is common in all three communities all year long. It tends to forage higher than other guild members except in the palo verde - cactus community in winter. It forages predominantly in the outer portions of plants. In the palo verde - cactus community it selects half shrubs and other low vegetation more than other guild members in winter, and it selects mesquite more than other guild members. *A. flaviceps* uses mostly the perch glean and hang glean, and does not hawk. It feeds more at flowers than other species, and uses a greater variety of foods, including nectar, tree sap, and insect eggs, than do other guild members.

Polioptila melanura is common in the palo verde - cactus community, rare in the mixed broadleaf community, and absent from the mesquite woodland community, though it is common in mesquite scrub communities adjacent to the woodlands. More than other guild members, it prefers trees, and forages primarily at middle levels in the outer portion of plants. It uses all foraging capture techniques. *P. melanura* is more similar to *Regulus calendula* than *A. flaviceps* in its winter foraging behavior. *P. melanura* was

never observed using non-arthropod food items. It was a conspicuous victim of *Molothrus ater*, the brown-headed cowbird, but mostly on second and later clutches.

Regulus calendula is a common winter resident in the palo verde - cactus and mesquite woodland communities. It varied more in plant selection and foraging height from community to community than other guild members. It did not use the hang glean capture behavior, but used the other three behaviors, especially the hawk, in high proportions, relying, relatively, the least on perch gleans. In the mesquite woodland in winter it was observed feeding on mesquite sap though it was frequently driven off by *A. flaviceps*.

Camptostoma imberbe was uncommon in winter and common in spring in the mesquite woodland. In terms of its distribution and abundance, it is the most variable species in the foliage-gleaning guild represented here. It was also found in cottonwood and ash areas, but was not found in the mixed broadleaf study site. It foraged in high to middle heights in trees, moved slower, and used the outer portion more than other guild members. It used all four capture techniques, but used the hawk the least.

Vireo bellii was a common spring resident in the mesquite woodland and mixed broadleaf communities. It foraged more on shrubs (in the mixed broadleaf community only) and at middle heights (both communities) than other guild members. It used all four capture techniques. It was a conspicuous victim of *Molothrus ater*, the brown-headed cowbird.

Vermivora luciae was a common spring resident of the mesquite woodland and mixed broadleaf communities. It foraged lower and more in the middle portion of plants than did other guild members. It used all four capture techniques. *V. luciae* is very secretive around its nests, and nests are difficult to find. It appeared to be unaffected by *Molothrus ater*.

Seasonal changes in foraging behavior occurred in all three permanent residents. Changes mostly involved selection of plants by species, generally involving proportional shifts in species used. All residents foraged lower in winter than in spring. These changes appear to be in response to changes in the distribution of arthropods.

Changes in foraging behavior between communities involved only plant species selected (all cases), plant life forms selected (in half the cases), and foraging height (all cases). These differences are attributed to the difference in vegetation, both by species and structure, between the three communities.

Despite the similarities in foraging behavior, all foliage-gleaning species studied here differed in some respect, and all were identifiable based on their foraging "profiles." The results of this study are consistent with the idea that competition for food resources is important in structuring these assemblages, though these results are not conclusive. Other hypotheses, not requiring competition in ecological time, can also account for these results. In particular, it is possible that these behaviors represent optimal use of specific resources that are the result of long evolutionary histories of individual bird species. The species in this particular set of foliage-gleaning birds appear to be the most different in the biologically most plastic trait, behavior. This suggests that, although other factors, both biotic and abiotic, are undoubtedly important, competition for food resources may play a major role in the within-guild structuring of this fauna.

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