

**SOUTHWESTERN WILLOW FLYCATCHER POTENTIAL PREY BASE
AND DIET IN NATIVE AND EXOTIC HABITATS**

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Abstract

Southwestern Willow Flycatcher Potential Prey Base and Diet in Native and Exotic Habitats

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I studied the potential arthropod prey base and diet of endangered, riparian obligate Southwestern Willow Flycatchers (*Empidonax traillii extimus*) breeding at Roosevelt Lake, Arizona, in 2002 and 2003. Much of the riparian habitat in the arid Southwest has been lost to development, agriculture, urbanization, and water management due to a rapidly growing human population. Remaining riparian vegetation has been dramatically altered due to the naturalization of exotic saltcedar (*Tamarix* spp.). Because the arthropod resource base associated with different vegetation may influence Southwestern Willow Flycatchers abundance, distribution, and behavior, potential resource differences should be investigated to enhance the management of this endangered species. However, little is known of the arthropod communities and their potential impact to flycatcher populations in Southwestern riparian habitats.

I used Malaise traps to quantify the arthropod abundance and community composition in three habitats utilized by breeding Willow Flycatchers: (1) native Goodding's willow (*Salix gooddingii*), (2) exotic saltcedar, and (3) a mixture of these two locally dominant riparian tree species. In addition to sampling the potential prey

base of the flycatchers, I characterized flycatcher diets by collecting Willow Flycatcher fecal samples during routine banding activities and identifying the arthropod fragments within them.

There was a significant and striking increase in arthropod abundance in 2003 compared to 2002, possibly due to the impact of a severe drought in 2002. Arthropod community composition varied by sampling period and habitat type, but total arthropod abundance did not differ statistically between native and exotic habitats in either year. Although, mixed habitats had significantly lower arthropod abundance than native habitat in 2002, they were statistically indistinguishable from both native and exotic habitats in 2003.

I found significant differences in the diet of flycatchers between years possibly associated with differences in the relative abundance of arthropod prey items. Flycatcher diet also varied in native, mixed and exotic habitats consistent across both years, with an exotic Homopteran (*Opsius stactogalus*) associated with saltcedar one of the important drivers.

Although I documented differences in the arthropod community of riparian habitats utilized by Southwestern Willow Flycatchers, and differences in the diets of flycatchers in these habitats, flycatcher diet does not appear to be linked to the dominant vegetation of a habitat. Many of the flycatchers' major prey items are not herbivores dependent on specific plant species. Based on Southwestern Willow Flycatchers' ability to exploit a diverse array of prey taxa, there is little indication that changes in the potential prey base associated with saltcedar has negatively impacted the arthropod food resources of riparian habitats at my study site. However, the same

may not hold true for other bird species with more restricted diets. Also these conclusions may not hold at sites lacking a mosaic of native and exotic riparian habitats patches.

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Table of Contents

LIST OF TABLES.....	ix
LIST OF FIGURES.....	x
CHAPTER 1. Changes to Southwestern Riparian Systems: Implications for Endangered Southwestern Willow Flycatchers.....	1
<u>Literature Cited</u>	8
CHAPTER 2. Southwestern Willow Flycatcher Potential Prey Base and Diet in Native and Exotic Habitats.....	13
<u>Introduction</u>	13
<u>Methods</u>	15
Study Site.....	15
Arthropod Sampling.....	16
Arthropod Sampling Design 2002.....	16
Arthropod Sampling Design 2003.....	17
Replicate Site Arthropod Sampling.....	18
Diet Sampling.....	19
<u>Data Analysis</u>	20
Total Arthropod Biomass.....	20
Arthropod Biomass by Taxonomic Group.....	21
Arthropod Community Composition.....	22
Replicate Site Arthropod Biomass.....	23

Southwestern Willow Flycatcher Diet.....	24
Weighted Abundance Index.....	24
<u>Results</u>	25
Total Arthropod Biomass.....	25
Arthropod Biomass by Taxonomic Group.....	27
Arthropod Community Composition.....	28
Replicate Sites.....	30
Southwestern Willow Flycatcher Diet.....	31
Weighted Abundance Index.....	32
<u>Discussion</u>	32
Arthropod Biomass and Community Composition.....	32
Southwestern Willow Flycatcher Diet.....	35
Relative Food Resource Base.....	38
Drought Effects.....	40
<u>Conservation Implications and management Recommendations</u>	41
<u>Literature Cited</u>	43

CHAPTER 3. Comparison of Arthropod Sampling Techniques to Assess

Southwestern Willow Flycatcher Diets	61
<u>Introduction</u>	61
<u>Methods</u>	61
Branch Clipping.....	62
Sticky Traps.....	63

Malaise Traps.....	63
<u>Results</u>	64
<u>Discussion</u>	64
<u>Literature Cited</u>	66
CHAPTER 4. Southwestern Willow Flycatcher Foraging Behavior at Roosevelt	
Lake	68
<u>Introduction</u>	68
<u>Methods</u>	69
<u>Results</u>	71
<u>Discussion</u>	73
<u>Literature Cited</u>	75
CHAPTER 5. Comparison of Arthropod Abundance and Community	
Composition Along a Vertical Gradient: Malaise Traps on the Ground Versus in	
the Tree Canopy	82
<u>Introduction</u>	82
<u>Methods</u>	83
<u>Results</u>	84
<u>Discussion</u>	85
<u>Literature Cited</u>	87

List of Tables

Table 2.1. Vegetation and canopy cover composition of Malaise trap sampling locations.....49

Table 2.2. Arthropod taxa captured in Malaise traps.....50

Table 2.3. Community analyses summary.....51

Table 2.4. Arthropod morpho-species with significant indicator species values (INDVAL) by sampling period.....52

Table 2.5. Summary of Southwestern Willow Flycatcher diets based on fecal analysis at Roosevelt Lake, AZ in 2002 and 2003.....53

Table 2.6. Summary statistics for comparison of weighted abundance index.....54

Table 4.1. Distribution of Southwestern Willow Flycatcher foraging observations..77

List of Figures

Figure 2.1. Total arthropod biomass by year and habitat.....	55
Figure 2.2. Biomass of the most abundant arthropod taxa by year and habitat.....	56
Figure 2.3. Biomass of important arthropod taxa by year and season.....	57
Figure 2.4. NMS ordination by sampling period.....	58
Figure 2.5. Proportion of <i>Opsius stactogalus</i> by habitat type and year as sampled using Malaise traps.....	59
Figure 2.6. Mean proportion of the eight major prey groups found in Willow Flycatcher diet samples.....	60
Figure 3.1. Mean arthropod captured by three sampling methods 2002.....	67
Figure 4.1. Distribution of flycatcher foraging maneuvers by habitat type.....	78
Figure 4.2. Flycatcher foraging height by habitat.....	79
Figure 4.3. Flycatcher foraging maneuver by sex.....	80
Figure 4.4. Flycatcher foraging height by sex.....	81

Chapter 1

Changes to Southwestern Riparian Systems: Implications for Endangered Southwestern Willow Flycatchers

Riparian ecosystems, especially those in the arid southwest, are of value as wildlife habitat far exceeding the spatial extent of riparian vegetation on the landscape (Knopf et al. 1988). While the value of these riparian areas has been documented for a variety of vertebrate taxa (Brode and Bury 1984, Cross 1985, Bury 1988, Knopf et al. 1988, Szaro 1991, Ellis et al. 1997), the literature examining the value of riparian habitats to avian communities is especially rich (Johnson et al. 1977, Ohmart and Anderson 1982, Knopf 1985, Knopf et al. 1988). Riparian vegetation comprises less than 1% of western landscapes (Knopf et al. 1988), but provides habitat for over 50% of bird species (Johnson et al. 1985).

Riparian systems in the Southwest have undergone rapid change in the last 100 years partly due to invasion by the exotic saltcedar (*Tamarix* spp.) introduced to the western United States in the late 1800s (Horton 1964). In the first half of the 20th century, some riparian areas experienced more than a 50% increase in saltcedar ground cover with a corresponding loss in areas suitable for native cottonwood (*Populus* spp.) and willow (*Salix* spp.) establishment (Busby and Schuster 1973). Currently, dense monocultures of saltcedar cover between 500,000 ha and 650,000 ha in 23 states, in drainages ranging from sea level to over 2000 m (Zavaleta 2000). The concomitant factors of exotic invasion and altered flow regimes may lead to the

demise of native riparian systems within the next 50 years (Rood and Mahoney 1990, Howe and Knopf 1991).

Many birds inhabiting the Southwest are at least partly dependent on riparian vegetation (Carothers et al. 1974, Ohmart and Anderson 1982, Hunter et al. 1988) but the invasion of saltcedar has altered the composition and structure of these forests (Ohmart and Anderson 1982, Loope et al. 1988, Vitousek 1990, Howe and Knopf 1991, Brock 1994, Bush and Smith 1995, Crawford et al. 1996). Habitats dominated by exotic saltcedar and native cottonwood-willow forests are distinct in terms of foliage density and diversity (Anderson et al. 1983). Because birds exhibit differential use of habitats with different structural components, these differences between saltcedar and cottonwood-willow habitats may play a role determining the bird community that inhabits them (Anderson et al. 1983). In addition to the structure of vegetation, the spatial distribution of vegetation and floristics influence habitat selection by birds (Holmes and Robinson 1981, Rotenberry 1985, Wiens et al. 1987, Knopf et al. 1990, Sedgwick and Knopf 1992).

There is no consistent impact of saltcedar-dominated habitats on southwestern riparian bird communities. The expansion of exotic saltcedar at the expense of native riparian vegetation has been shown to have negative effects on many riparian bird species on the lower Colorado River (Anderson et al. 1977) and lower Rio Grande (Engel-Wilson and Ohmart 1978); both studies reported lower bird density and species diversity in saltcedar habitats compared to cottonwood-willow habitats. Other authors indicate native and exotic habitats support similar bird communities. Ellis (1995) found no difference in bird species richness between saltcedar and

cottonwood habitats in the middle Rio Grande. Likewise, Brown and Trosset (1989) suggested that saltcedar was ecologically equivalent to native habitats for some bird species in the Grand Canyon, and that the presence of saltcedar improved the breeding habitat of all 11 species studied; American coot (*Fulica americana*), Bell's vireo (*Vireo bellii*), blue grosbeak (*Guiraca caerulea*), Bullock's oriole (*Icterus bullockii*), common yellowthroat (*Geothlypis trichas*), great-tailed grackle (*Quiscalus mexicanus*), hooded oriole (*Icterus cucullatus*), indigo bunting (*Passerina cyanea*), willow flycatcher (*Empidonax traillii*), yellow warbler (*Dendroica petechia*), and yellow-breasted chat (*Icteria virens*). Additionally, Thompson et al. (1994) suggested saltcedar and Russian olive (*Elaeagnus angustifolia*) combined with native vegetation provided vegetation structure similar to that historically found in the Rio Grande cottonwood-willow system. In some cases, the impact of saltcedar has been positive for riparian bird communities. Livingston and Schemnitz (1996) showed increased bird diversity and abundance in saltcedar compared to native habitats on the Pecos River.

Environmental factors, associated with elevation, offer a possible explanation for the diverse effects of saltcedar on birds. Hunter et al. (1985, 1988) documented that avian communities, particularly mid-summer breeding species, were most negatively affected by saltcedar in riparian systems at low elevations like those on the lower Colorado River, due to the lack of multi-layered foliage characteristic of cottonwood-willow forests that ameliorates the extreme thermal stress on eggs and nestlings. Likewise, in those riparian systems where the thermal environment is moderated by higher elevations, the impact of saltcedar on the bird community is

neutral or positive, like the middle Rio Grande and Pecos River respectively (Hunter et al. 1985, 1988).

Resource availability may also affect the habitat suitability of exotic compared to native riparian vegetation. Kleintjes and Dahlsten (1994) suggested that differences in arthropod resource base associated with different vegetation influenced bird abundance, distribution, and behavior. Food resource limitation could result in reduced reproduction and changes in spatial distribution including the complete exclusion of selected species from certain habitats (Newton 1977, Watson and Moss 1972, Newton 1980). Differences in bird numbers may be influenced by food in concert with environmental factors, such that food is limiting in some areas but not others (Newton 1980). For insectivorous bird species, a measure of potential arthropod food resources may explain differences in habitat use between native and exotic riparian habitats.

The impact of saltcedar on arthropod communities is not as well documented as its impact on vertebrate groups (Hunter et al. 1988, Brown and Trosset 1989, Ellis 1995, Ellis et al. 1997), but because food resources are often argued to limit bird populations (Lack 1954), measuring arthropod abundance and diversity may act as a surrogate for habitat quality for insectivorous birds. While Cohan et al. (1978) found fewer insects in saltcedar dominated habitats on the lower Colorado River, saltcedar had a higher ratio of insect to insectivore biomass compared to native habitats, suggesting exotic habitats were not food limited. On the middle Rio Grande, Mund-Meyerson (1998) found no difference in Order and Family richness or average size of arthropods inhabiting native cottonwood and exotic Russian olive or saltcedar. Also,

she noted greater arthropod abundance in saltcedar in August but no difference at other time periods, suggesting exotic riparian vegetation may have sufficient food resources for breeding birds (Mund-Meyerson 1998). Ellis et al. (2000) found that different taxa of ground-dwelling arthropods exhibited variable responses to native and exotic habitats. Although arthropod abundance may suggest differences in habitat quality, ultimately habitat quality is best measured by relative differences in fitness and productivity among habitats (Van Horne 1983).

From a management perspective, one species important to consider when exploring issues of riparian habitat quality is the riparian obligate Southwestern Willow Flycatcher (*Empidonax traillii extimus*). While the breeding distribution of Willow Flycatchers (*Empidonax traillii*) is widespread across much of North America, the southwestern subspecies is restricted to riparian habitats in the arid southwest (Sedgwick 2000). The Southwestern Willow Flycatcher was listed as endangered in 1995 (U.S. Fish and Wildlife Service 1995), with habitat loss and fragmentation considered as the primary threats to the survival of the subspecies (Marshall and Stoleson 2000). Southwestern Willow Flycatchers have declined over the past 100 years (Unitt 1987, U.S. Fish and Wildlife Service 1995) and this decline has been attributed to many factors, including loss of riparian habitat, water management practices, livestock grazing, brown-headed cowbird (*Molothrus ater*) brood parasitism, and the invasion of riparian habitats by saltcedar (U.S. Fish and Wildlife Service 1995). The largest impact on Southwestern Willow Flycatchers is believed to have come from the widespread loss of riparian habitat crucial for Southwestern Willow Flycatchers' nesting and foraging activities (Unitt 1987).

In addition to habitat loss and fragmentation due to water management and land use practices, the spread of exotic saltcedar has been implicated as a cause for the flycatchers decline (DeLoach et al. 2000, Marshall and Stoleson 2000). The Southwestern Willow Flycatcher readily breeds in saltcedar dominated habitats, especially at lower elevations across its range (Sogge et al. 2003). Some authors suggest saltcedar has negative impacts on the Southwestern Willow Flycatcher due to insufficient arthropod prey base (DeLoach et al. 2000). Others suggest migrating Willow Flycatchers utilize native willow habitats more than exotic habitats to exploit the higher arthropod densities in native habitats (Yong and Finch 1995).

However, many of the studies suggesting differences in habitat quality based on food resources among saltcedar and native habitats either did not quantify flycatcher diet or did not distinguish among those arthropod taxa important and not important in the diet. Early studies by Beal (1912) and Bent (1942) examined the diet of Willow Flycatchers in general, but did not specifically focus on the southwestern subspecies. Studies by Drost et al. (1998, 2001, 2003) identified important prey taxa for the subspecies, and found that diets vary by habitat type. However these habitats were geographically separate native habitats at high elevation sites in Arizona and Colorado (dominated by Geyer's willow (*Salix geyeriana*)), exotic (saltcedar) and mixed (saltcedar and Goodding's willow) habitats in central Arizona, and a native (with an overstory dominated by red willow (*Salix laevigata*), Goodding's willow (*Salix gooddingii*), and Fremont cottonwood (*Populus fremontii*)) site in southern California. Additionally, one study (DeLay et al. 2002) examined Southwestern Willow Flycatcher diet in relation to the composition of arthropods captured via

sticky trap sampling and found diet composition differed from the arthropod community sampled with sticky traps. The sites in this study, along the Gila River in New Mexico, were composed of exclusively native vegetation, with a component of box elder (*Acer negundo*), a tree species not found in breeding habitat at any other Southwestern Willow Flycatcher site. Moreover, Delay et al. (2002) found Southwestern Willow Flycatcher diets at their sites were more similar to diets in other parts of its range (Drost et al. 1998, 2001) than to the arthropod community in those sites, suggesting the subspecies is a diet specialist rather than a generalist as previously thought.

Even with the studies previously mentioned, the diet and arthropod community of habitats utilized by the Southwestern Willow Flycatcher remain poorly documented. To address the potential difference between habitats dominated by native, exotic, and mixed vegetation in relation to the arthropod prey base and diet of Southwestern Willow Flycatchers, I undertook the project described in Chapter 2. In Chapter 3, I detail a pilot study conducted to determine the relative effectiveness of three arthropod sampling techniques (Malaise trap, sticky-trap, and branch bag-and clip) to estimate arthropod prey availability for Southwestern Willow Flycatchers. In Chapter 4, I describe a study in which I documented the foraging behavior of Southwestern Willow Flycatchers in exotic, native and mixed habitats. In Chapter 5, I explain a one-time assessment of whether lifting Malaise traps into the canopy at heights where flycatchers actually forage results in difference in estimates of arthropod abundance and richness compared to traps left on the ground.

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Chapter 2 – Southwestern Willow Flycatcher Potential Prey Base and Diet in Native and Exotic Habitats

Introduction

The Southwestern Willow Flycatcher (*Empidonax traillii extimus*) was listed as endangered in 1995 (USFWS 1995), with habitat loss and fragmentation identified as primary threats to the survival of the subspecies (Marshall and Stoleson 2000). In addition to habitat loss and modification due to water management and land use practices, the replacement of native riparian vegetation (particularly cottonwoods (*Populus* spp.) and willows (*Salix* spp.)) by exotic saltcedar (*Tamarix* spp.) has considerably altered southwestern river systems in the past 100 years (Marshall and Stoleson 2000), with saltcedar now covering 500,000 – 650,000 ha (Hunter 1987, Zavaleta 2000).

The Southwestern Willow Flycatcher breeds in some saltcedar dominated habitats, especially at lower elevations across its range (Sogge et al. 2003a), but the value of this habitat for flycatchers has remained controversial. Some authors have suggested that saltcedar dominated habitats have insufficient arthropod prey base to sustain populations of Southwestern Willow Flycatchers (DeLoach et al. 2000), while others have indicated that these habitats are not food-limited (Cohan et al. 1978). Additionally, nearly 50% of Southwestern Willow Flycatcher territories are in habitats classified as mixed, containing both native and exotic vegetation (Sogge et al. 2003b), and the potential prey base in mixed habitats is unknown. Because mixed habitats are intermediate (in terms of vegetation composition) between native and

exotic sites, one may hypothesize one of two conclusions regarding the arthropod community composition and abundance: (1) mixed sites will have intermediate abundance and community composition compared to native and exotic sites, or (2) mixed sites will have higher abundances and more diverse community composition compared to native and exotic sites owing to the increased vegetation diversity of a habitat with co-dominant vegetation compared to those that are essentially monotypic (Haddad et al. 2001).

To assess habitat quality in terms of prey availability for Southwestern Willow Flycatchers requires knowledge of the range of prey taken. Early studies by Beal (1912) and Bent (1942) examined the diet of Willow Flycatchers in general, but did not specifically focus on the southwestern subspecies. Studies by Drost et al. (1998, 2001, 2003) identified important prey taxa for the Southwestern Willow Flycatcher and found that diets varied among native, mixed, and saltcedar habitats. However, comparison across habitats was confounded by wide geographic separation of study sites and differences in dominant native vegetation, with exotic (saltcedar), and mixed (saltcedar and Goodding's willow (*Salix gooddingii*)) habitats represented by sites in central Arizona, while native sites were located in Arizona, Colorado (both dominated by Geyer's willow (*Salix geyeriana*)), and southern California (with an overstory dominated by Fremont cottonwood (*Populus fremontii*), red willow (*Salix laevigata*), and Goodding's willow). Additionally, these studies lacked any measure of the relative prey base in the different habitats.

Only one study (DeLay et al. 2002) has compared Southwestern Willow Flycatcher diets to the arthropod community of the breeding habitat, and found that

diet composition differed from the arthropod community sampled. However, this study sampled relative arthropod abundance using sticky traps, a technique that may not adequately represent the arthropod community (Cooper and Whitmore 1990). In addition, the sites in this study were all dominated by box elder (*Acer negundo*), a native tree species not found in breeding habitat at other Southwestern Willow Flycatcher sites.

The Southwestern Willow Flycatcher (hereafter, the terms Willow Flycatcher and flycatcher also refer to the southwestern subspecies) has been intensively studied over the last 10 years in Arizona and many aspects of its biology including, productivity, habitat associations, breeding site characteristics, and demography are well understood. However, the association between flycatcher diet and the potential prey base remains poorly understood. In this study, I documented the potential prey base and Southwestern Willow Flycatcher diet as a means to assess the relative habitat quality of exotic saltcedar, native Goodding's willow, and mixed riparian habitats composed of both tree species. Specifically, I addressed the following questions: (1) Does arthropod abundance and community composition differ across native, mixed and exotic habitats? (2) Does Southwestern Willow Flycatcher diet vary across those habitats?

Methods

Study Site – This study was conducted at the Salt River Inflow to Roosevelt Lake in central Arizona, approximately 90 km northeast of Phoenix. The Salt River Inflow rests in a broad floodplain dominated by riparian forest patches of Gooding's

willow, saltcedar, or a mosaic of these two dominant tree species. Throughout the understory of the riparian forest there are patchily distributed saltcedar, mesquite (*Prosopis* spp.), grasses, and herbaceous cover. Surrounding uplands are characterized as Sonoran Desert Arizona Upland indicated by vegetation including saguaro (*Carnegiea gigantea*), palo verde (*Parkinsonia* spp.), mesquite, and creosote (*Larrea tridentata*). Elevation of the riparian floodplain is approximately 640m.

Arthropod Sampling – All arthropod sampling techniques have inherent biases and the choice of sampling technique may have profound effects on the interpretation of prey availability for an insectivore (Cooper and Whitmore 1990). In 2002, I used Malaise traps (model 2875AG, BioQuip Corporation, Gardena, CA), branch bag-and-clip techniques (Johnson 2000), and sticky traps (15.2cm x 30.5cm, model 2873, BioQuip Corporation, Gardena, CA) to determine the method(s) that most closely matched the diet of Southwestern Willow Flycatchers as reported in previous studies (Drost 1999, 2001, DeLay 2002). Malaise traps captured as many or more taxonomic groups found in flycatchers' diet and also captured relatively more total arthropods compared to the other two techniques (Chapter 3). Based on those results, I present only the results of Malaise traps.

Arthropod Sampling Design 2002 – A total of 50 Malaise trap sampling days were used to characterize the insect community of one native, one mixed, and one exotic habitat patch at Roosevelt Lake in 2002. Patches ranged from 85ha (native) to 181ha (mixed) to 283ha (exotic) in size and were separated from each other by at least 1.5 km. Depending on availability of Malaise traps, one or two traps were randomly placed in each habitat every two weeks from 24 April to 9 August. I

used an overlay of each discreet habitat patch in ArcView 3.2 to generate random UTM locations to determine sampling locations. In the field, if a random location was difficult to access due to the density of the vegetation or was in a place unlikely to represent a flycatcher foraging location (open field with no nearby tree perches), I selected the nearest suitable location. By the end of the season, 17 Malaise trap samples were collected from the native, 17 from the exotic, and 16 from the mixed sites.

Traps were operated for roughly 12-hour periods, opened at approximately 0500 and closed at approximately 1700. Arthropods were frozen in zip-loc bags for later sorting and identification at the Colorado Plateau Research Station. After initial sorting to the level of Order using standard references (Borror et al. 1976, Bland 1978), samples were stored in 70% ethanol for later sorting to the morpho-species level (Wolda 1990). A morpho-species reference collection was completed with the assistance of the Northern Arizona University Colorado Plateau Museum of Arthropod Biodiversity. I recorded length to the nearest mm of a subset of each morpho-species. I estimated biomass of morpho-species using regression equations relating length to biomass for the lowest taxonomic group possible (Rogers et al. 1977, Hodar 1996).

Arthropod Sampling Design 2003 – In 2003, 36 Malaise traps were used to sample the arthropod community at the same native, mixed, and exotic sites used in 2002, but several changes in the sampling protocol were made. First, four malaise traps were placed in each habitat type during each sampling period instead of the one or two used in 2002. Second, instead of sampling one day every two weeks as in

2002, I sampled each habitat simultaneously for one day on 17 May, 26 June, and 24 July, corresponding approximately to Southwestern Willow Flycatcher territory establishment, nesting, and post-nesting/dispersal respectively. Third, in 2003, Malaise traps were placed only in randomly selected locations that met minimum criteria for total canopy cover and percent composition in each habitat. All sampling locations had to have total canopy cover $\geq 75\%$ and canopy cover composition had to fall within specific ranges for each habitat type. At the native site, only locations that had $\leq 10\%$ saltcedar canopy cover and a minimum of 70% willow canopy cover were selected. In the mixed site, only locations with willow and saltcedar each representing a minimum of 15% of the canopy and mesquite making up no more than 15% of the canopy cover were used. Finally, in exotic habitat, only locations composed of 100% exotic vegetation were used (**Table 2.1**). I estimated canopy cover using a hand-held densiometer in each sampling location. These sampling locations, once identified at the start of the season, were repeatedly sampled at subsequent sampling periods. These changes in sampling protocol were made to reduce within-habitat variation and more accurately test differences among habitats.

Replicate Site Arthropod Sampling – Because only one site of each habitat type was repeatedly sampled, site differences could potentially confound any differences observed among habitat types. Therefore, on 27 June 2003, the day after I sampled the original sites, I simultaneously sampled two different replicate sites of each habitat type by placing two Malaise traps at randomly selected locations within each site that met the criteria outlined above for canopy cover and composition by habitat type. The replicate sites were also located on the Salt River Inflow to

Roosevelt Lake and had breeding populations of Southwestern Willow Flycatchers, but were distinct habitat patches, separated by 560 m – 2500 m from other occupied patches. Native replicate sites ranged in size from 127 ha – 152 ha, mixed replicates from 53 ha – 147 ha, and exotic replicates from 56 ha – 214 ha.

Diet Sampling – The use of fecal analysis has been shown to be an effective means to sample bird diet (Ralph et al. 1985, Rosenberg and Cooper 1990, Van Horne and Bader 1990, Burger et al. 1999, Deloria-Sheffield et al. 2001). Ralph et al (1985) showed close correspondence between fecal and gut samples of seven insectivorous Hawaiian forest birds (akepa (*Loxops coccineus*), akiapolaau (*Hemignathus munroi*), Hawaii creeper (*Oreomystis mana*), common amakihi (*Hemignathus virens*), elepaio (*Chasiempis sandwichensis*), Japanese white-eye (*Zosterops japonicus*), and red-billed leiothrix (*Leiothrix lutea*)), suggesting that differential digestion rates may not be an issue of great concern. In 2002 and 2003, a total of 149 fecal samples were opportunistically collected from Southwestern Willow Flycatchers during routine bird-banding activities as part of a long-term demographic study on the breeding population at Roosevelt Lake (the terms diet sample and fecal sample are used interchangeably). In 2002, 25 fecal samples were collected in native habitats, 19 in mixed, and 12 in exotic habitats. In 2003, 7 fecal samples were collected in native, 67 in mixed, and 19 in exotic habitats. Fecal samples were stored in 70% ethanol for later analysis at the USGS Colorado Plateau Research Station, Northern Arizona University.

A Leica Stereo Zoom 6 dissecting microscope was used to assist in the identification and quantification of the arthropod diet items teased apart in fecal

samples. Various reference sources were used to identify and quantify arthropod fragments present in fecal samples (Borror et al. 1976, Bland 1978, Calver and Wooller 1982, Ralph et al. 1985, Burger et al. 1999). Slides produced from Drost et al. (1998, 2001) were available as a reference and identification was also aided by the comparison of macerated arthropods captured in Malaise traps at Roosevelt Lake. Due to the difficulty identifying highly fragmented arthropod parts present in fecal samples, prey items were typically identified only to the taxonomic level of Order, and in some cases Family. The minimum number of individuals of each taxonomic group was estimated by using distinct features such as pairs of wings, paired spider fangs, mouthparts or head capsules. Digital photographs were taken of representative arthropod body parts and archived for future reference. After sorting and quantifying, fecal samples were returned to 70% ethanol vials for storage and future reference. Because chi-square analysis showed no significant difference in the diet of flycatchers by sex (2002: $\chi^2 = 13.059$, $df = 9$, $p = 0.1600$; 2003: $\chi^2 = 10.819$, $df = 9$, $p = 0.2883$) or age (2002: $\chi^2 = 2.224$, $df = 9$, $p = 0.9874$; 2003: $\chi^2 = 16.167$, $df = 9$, $p = 0.0635$), I lumped samples across these categories and categorized all fecal samples according to the dominant vegetation of the site where the sample was collected (native, mixed, exotic) and the year collected (2002 or 2003).

Data Analysis

Total Arthropod Biomass – I tested differences in arthropod biomass by year and habitat after converting number of individuals of each morpho-species to total biomass of each morpho-species (Rogers et al. 1977, Hodar 1996). To account for

different numbers of Malaise traps and slightly different sampling periods at each site, all biomass comparisons are made on a per trap per hour basis. I used a non-parametric Mann-Whitney U test to test for differences in total arthropod biomass per trap between the 2002 and 2003, and for differences between years within each habitat type.

I tested for differences in total arthropod biomass by habitat, season, and habitat x season interaction within each year using a two-way analysis of variance (ANOVA). I categorized all Malaise sampling events into three periods of approximately equal sampling effort (early, mid, and late season). To account for deviations from assumptions of normality and homogeneity of variance, I applied two techniques; first I log transformed all biomass data (Sokal and Rohlf 1995) and second, I rank transformed biomass data (Conover and Iman 1981) prior to running two-way ANOVAs. Rank transformation with parametric tests controlled for non-normality and heterogeneity of variance (Lehman 1975, Potvin and Roff 1993). In both years the analyses with both transformations agreed. Potential differences were tested with post-hoc Tukey's HSD test.

Arthropod Biomass by Taxonomic Group – I used multivariate analysis of variance (MANOVA) to test for differences in the arthropod biomass of major taxonomic groups (at the level of Order except in the case of Formicidae) of the three habitats, across the three sampling periods in both 2002 and 2003. I utilized a log transformation (Sokal and Rohlf 1995) and a rank transformation procedure (Conover and Iman 1981) followed by two-way MANOVA to test for differences in the

arthropod biomass composition by habitat, season, and a habitat x season interaction. There was strong agreement between the two transformation procedures.

Arthropod Community Composition – I used multi-response permutation procedure (MRPP) available through PC-ORD (McCune and Grace 2002) to test for differences in arthropod community (incorporating both abundance and composition) among each habitat. I tested for pair-wise differences in community composition (at the level of morpho-species) by habitat within each year and sampling period to control for changes in the arthropod community through time (six total MRPP tests, one for each year-season combination, 2002 and 2003; early, mid, and late sampling periods). In this procedure I used a Bray-Curtis distance measure to calculate the average weighted distance within each habitat grouping (Faith et al. 1987). The number of individuals of each morpho-species was log transformed to account for the high degree of variability among samples and to compress the impact of those samples with large abundances (McCune and Grace 2002). The weighted within-group dissimilarity (δ) was then compared to a random distribution of points, giving a probability of obtaining an expected value as extreme as the observed value.

Additionally, PC-ORD calculates a chance corrected within-group agreement (A) as an indication of the biological significance of potential statistical significance such that, when $A = 1$, all within group samples are identical, when $A = 0$, the within-group heterogeneity equals that expected by chance, and when $A < 0$, there is less within group homogeneity than expected by chance (Zimmerman et al. 1985).

PC-ORD indicator species analysis was used to determine the taxonomic groups driving patterns observed in the MRPP analysis. An indicator species value

(INDVAL) is based on its specificity (the relative abundance of each morpho-species in each habitat grouping) and its fidelity (the relative frequency of each morpho-species in each habitat grouping) (Dufrene and Legendre 1997). A probability value for each INDVAL is calculated in PC-ORD by randomly assigning each sample to one of the six groups 1000 times, recalculating an INDVAL for each randomized run, and comparing the proportion of times the randomized INDVAL exceeded the observed INDVAL (McCune and Grace 2002).

Non-metric multi-dimensional scaling (NMS) was used to graphically represent the degree of dissimilarity between each sample. PC-ORD was used to create a dissimilarity matrix based on the distribution of different morpho-species in the various Malaise samples. Multiple iterations of the dissimilarity matrix are run to obtain a configuration of points in space that best represent the actual degree of dissimilarity present between the individual samples.

Replicate Site Arthropod Biomass – To test for the effect of a single site confounding potential differences by habitat type, I compared the two replicate sites to each originally sampled site. I used non-parametric Kruskal-Wallis to test for differences in total arthropod biomass among the two replicates and original sites. I also tested for differences in the arthropod biomass of major taxonomic groups (at the level of Order except in the case of Formicidae) among the two replicate sites and the original site using one-way MANOVA. I again used both log (Sokal and Rohlf 1995) and rank (Conover and Iman 1981) transformations to meet parametric assumptions required for the MANOVA.

Southwestern Willow Flycatcher Diet – I tested for differences in the prey composition of Southwestern Willow Flycatcher diet by habitat and year using a two-way MANOVA. To give equal weight to each fecal sample, I converted numbers of individual prey items to percent composition of each prey item in a given fecal sample by dividing the number of individual prey items by the total number of prey items in each fecal sample for each prey group. However, the diet data deviated from parametric assumptions of normality and homogeneity of variance. I utilized two approaches to control for these deviations from parametric assumptions prior to testing for differences in the prey composition of flycatcher diets by year, habitat, and the year x habitat interaction using two-way MANOVA. I first arcsin square-root transformed all percentage data (Sokal and Rohlf 1995). Secondly, I rank transformed the percentage data for each prey group and substituted the ranks for the original percentages in the parametric MANOVA (Conover and Iman 1981). The results of the two techniques were similar and any variation was due to differences in rarely consumed prey groups. Any differences revealed by the MANOVA were investigated using post-hoc Tukey's HSD tests.

Weighted Abundance Index – To obtain a more robust measure of habitat quality, I combined arthropod abundance and flycatcher diet by habitat using a weighting procedure developed by Poulin and Lefebvre (1997). The potential prey abundance was weighted by the relative importance of the prey item in the birds' diet using:

$$\text{Weighted abundance index} = \sum p_i(x_{ji}/y_i)$$

where p_i is the proportion of arthropods from prey item i in the birds diet, x_{ij} is the number of arthropods from prey taxa i sampled in Malaise trap j , and y_i is the number of prey items of prey taxa i collected over the all sampling periods and locations (Poulin and Lefebvre 1997). Due to the difference in taxonomic resolution between the arthropod and diet samples, I used the more coarse diet samples to determine prey taxa i . I calculated the mean weighted abundance index of each habitat six times by using the weighting factor (p_i) from each year-habitat combination (i.e., I calculated the mean weighted abundance index of native, mixed, and exotic habitats using p_i from the 2002 diet in native habitat, then recalculated the index for each habitat using the 2002 diet in mixed habitat, then again for the 2002 diet in exotic habitat, and the same for the diet in all three habitats in 2003). I tested for differences in the mean weighted abundance index by habitat using a series of six one-way ANOVAs for each diet by year-habitat combination.

Data for all tests were checked for normality and homogeneity of variance. I conducted univariate tests in JMP-IN 5.1, multivariate tests in SPSS 12.0, and community analyses in PC-ORD. I evaluated statistical significance at $\alpha = 0.05$, except for Bonferroni corrections (Sokal and Rohlf 1995) used in pair-wise comparisons. Results of statistical tests for rank-transformations and standard transformations were identical unless otherwise indicated.

Results

Total Arthropod Biomass – Over the two years of the study, 26,681 individual arthropods were captured via Malaise traps representing 14 different

Orders and 128 distinct morpho-species (**Table 2.2**). Members of Araneae, Coleoptera, Diptera, Formicidae, Hemiptera, Homoptera, flying Hymenoptera, Lepidoptera, Orthoptera, and Trichoptera represented 100% of the arthropod biomass collected in Malaise traps in 2002 and 98.99% in 2003. Four other arthropod groups (Neuroptera, Psocoptera, Pseudoscorpionida, and Thysanoptera) were excluded from analysis because they each accounted for than 1% of the total arthropod biomass.

The total arthropod biomass across all three habitats in 2003 was five times greater than arthropod biomass in 2002 ($U_{36,50} = 6.587$, $p < 0.0001$) (**Figure 2.1**). Additionally, the pattern of significantly greater in total arthropod biomass in 2003 compared to 2002 was consistent within each habitat type. Total biomass was almost two times greater in the native habitat ($U_{12,17} = 2.590$, $p = 0.0096$), more than 12 times greater in mixed habitat ($U_{12,16} = 4.016$, $p < 0.0001$), and almost four times greater in exotic habitat ($U_{12,17} = 4.273$, $p < 0.0001$) (**Figure 2.1**).

In 2002, I found significant differences in arthropod biomass by habitat type ($F_{2,41} = 3.9752$, $p = 0.0264$) (**Figure 2.1**). Subsequent post-hoc Tukey HSD tests revealed that the total arthropod biomass in native habitat was nearly twice as great as mixed habitat, but total biomass in exotic habitat was not statistically different from either of the other two habitat types. There were no differences in total arthropod abundance by season ($F_{2,41} = 2.1578$, $p = 0.1285$) or the habitat x season interaction ($F_{4,41} = 1.1844$, $p = 0.3320$).

In 2003, I found that there were no statistical differences in total arthropod biomass by habitat type ($F_{2,27} = 0.8302$, $p = 0.4468$), season ($F_{2,27} = 1.8498$, $p = 0.1766$), or the interaction of the two factors ($F_{4,27} = 0.8448$, $p = 0.5092$) (**Figure 2.1**).

In the figure, mean arthropod biomass of the mixed habitat appears much larger than mean arthropod biomass of both native and exotic habitats; however, there were no statistical differences due to the high within habitat variation in the mixed habitat. I captured an insect irruption in the mixed habitat during the middle sampling period with a biomass of 637.5 mg h^{-1} , over eight times the mean total arthropod biomass per hour collected in the other Malaise traps in the mixed habitat. When I removed this irruption from the analysis, there was still be no difference in the total arthropod biomass by habitat.

Arthropod Biomass by Taxonomic Group – In 2002, I found differences by habitat (Wilk's $\Lambda = 0.270$, $F_{18,66} = 3.344$, $p < 0.001$) in the biomass of Homoptera ($F_{2,41} = 3.343$, $p = 0.045$), Orthoptera ($F_{2,41} = 6.538$, $p = 0.003$), Formicidae ($F_{2,41} = 15.026$, $p < 0.001$), and Diptera ($F_{2,41} = 4.669$, $p = 0.015$). Subsequent Tukey's HSD post-hoc tests revealed that: (1) biomass of Homoptera in native habitat was greater than exotic habitat, but Homoptera biomass in the mixed habitat was equal to the other two habitats, (2) biomass of Orthoptera was greater in native habitat compared to mixed and exotic habitats, (3) Formicidae biomass was greatest in mixed habitat, and (4) Diptera biomass was greater in native habitats compared to mixed, with biomass in exotic habitat statistically indistinguishable from either of the other two (**Figure 2.2**).

In 2002, I found differences by season (Wilk's $\Lambda = 0.404$, $F_{18,66} = 2.100$, $p = 0.015$) in the biomass of Lepidoptera ($F_{2,41} = 6.707$, $p = 0.003$) and Diptera ($F_{2,41} = 4.715$, $p = 0.014$). Tukey's HSD post-hoc test indicated higher Lepidoptera biomass in early sampling periods and no difference in the Lepidoptera biomass of middle or

late sampling periods. Diptera biomass was higher in the early period compared to the late sampling period, but Diptera biomass in the middle period was not different from either the early or late time periods (**Figure 2.3**).

While I found no interaction between habitat and season in the arthropod biomass of any taxonomic group in 2002 (Wilk's $\Lambda = 0.264$, $F_{36,125} = 1.486$, $p = 0.057$), there was a significant interaction between habitat and season in 2003 (Wilk's $\Lambda = 0.024$, $F_{40,70} = 2.943$, $p < 0.001$) for three taxonomic groups: Hemiptera ($F_{4,27} = 13.621$, $p < 0.001$), Formicidae ($F_{4,27} = 4.174$, $p = 0.009$), and Trichoptera ($F_{4,27} = 5.385$, $p = 0.003$). During each sampling period, the habitat with the greatest Hemiptera biomass varied (early = native, mid = mixed, and late = exotic). Formicidae biomass was greatest in native habitats in all time periods, but biomass in exotic habitats declined after the early sampling period while the biomass in the mixed increased after the early period. In the early- and mid-sampling periods Trichoptera biomass was greatest in mixed habitat, but by the late sampling period the native site had the greatest Trichoptera biomass (**Figures 2.2 and 2.3**).

Arthropod Community Composition – In 2002, I found significantly different arthropod communities by habitat during each sampling period (Early: $A = 0.0688$, $p = 0.0076$; Mid: $A = 0.1011$, $p < 0.0001$; Late: $A = 0.0618$, $p = 0.0004$). During the early sampling period, pair-wise comparisons (Bonferroni corrected $\alpha = 0.05/3 = 0.0167$ for all pair-wise habitat comparisons) revealed significant differences in arthropod community composition between only native and exotic habitats ($A = 0.0779$, $p = 0.0058$). In the middle sampling period, all three pair-wise comparisons had significantly different arthropod communities (Native-Mixed: $A = 0.1001$, $p <$

0.0001; Native-Exotic: $A = 0.0674$, $p = 0.0031$; Mixed-Exotic: $A = 0.0699$, $p = 0.0048$). During the late sampling period, the arthropod communities between mixed and exotic habitats were statistically indistinguishable ($A = 0.0325$, $p = 0.0272$), but the communities of the other two pair-wise comparisons were significantly different (**Table 2.3** and **Figure 2.4**).

In 2003, I again found significant differences in the arthropod community by habitat in each sampling period (Early: $A = 0.1581$, $p = 0.0011$; Mixed: $A = 0.3005$, $p < 0.0001$; Exotic: $A = 0.1804$, $p = 0.0005$). During the early sampling period, the arthropod communities of the native and mixed habitats were indistinguishable ($A = 0.0628$, $p = 0.0709$), but the arthropod community of the exotic habitat was significantly different from the other two habitats. In the middle sampling period the arthropod community of all three pair-wise comparisons were significantly different (Native-Mixed: $A = 0.2326$, $p = 0.0052$; Native-Exotic: $A = 0.3050$, $p = 0.0053$; Mixed-Exotic: $A = 0.2125$, $p = 0.0053$). During the late sampling period, mixed and exotic habitats had statistically indistinguishable arthropod communities ($A = 0.0689$, $p = 0.0189$), but the arthropod community of native habitat was significantly different from both mixed and exotic habitats (**Table 2.3** and **Figure 2.4**).

I could not identify a suite of morpho-species between year or among the different sampling periods that consistently drove patterns of differences in the arthropod community by habitat. Apart from a few exceptions, the indicator species analysis (INDVAL) revealed that different morpho-species drove difference among the habitats at different times (**Table 2.4**). Some morpho-species significantly indicated the same habitat during more than one sampling period, but never during all

three sampling periods in both years, yet other morpho-species significantly indicated different habitats during different sampling periods (**Table 2.4**).

One insect species, *Opsius stactogalus*, the tamarisk leafhopper (morpho-species: Homo-3), is exclusively associated with saltcedar (Carothers and Brown 1991). I detected *Opsius* in all three habitats in both 2002 and 2003. *Opsius* made up 30-55% of the Homopteran community in native habitats and dominated the Homopteran community of the mixed and exotic habitats (67-100%), likely due to the greater preponderance of saltcedar at these two sites (**Figure 2.5**). During the middle sampling period in 2002 (INDVAL = 58.2, $p = 0.038$) and the late period in 2003 (INDVAL = 55.4, $p = 0.023$), *Opsius* significantly indicated exotic habitat (**Table 2.4**).

Replicate Sites – There were no differences in the total arthropod biomass among the two replicate sites and the originally sampled site for each habitat (Native: $H_{2,2,4} = 2.5417$, $p = 0.6372$; Mixed: $H_{2,2,4} = 3.500$, $p = 0.4779$; Exotic: $H_{2,2,4} = 6.1667$, $p = 0.1870$). Likewise, there were no differences in the arthropod biomass of major taxonomic groups among the two replicates and originally sampled sites (Native: Wilk's $\Lambda = 0.032$, $F_{10,2} = 0.922$, $p = 0.625$; Mixed: Wilk's $\Lambda = 0.028$, $F_{10,2} = 0.991$, $p = 0.601$; Exotic: Wilk's $\Lambda = 0.005$, $F_{10,2} = 2.682$, $p = 0.302$). Taken together, these results indicated that both the total arthropod biomass and the arthropod biomass of each taxonomic group were similar across different sites composed of the same vegetation along the Salt River Inflow to Roosevelt Lake. This result supports the hypothesis that the more extensive data from the original three sites were not

confounded by site effects and were in fact driven by differences in the dominant vegetation type.

Southwestern Willow Flycatcher Diet – Fecal sample analysis yielded a total of 1316 individual prey items. Eight taxonomic groups were used for analysis (Araneae, Coleoptera, Diptera, Formicidae, Hemiptera, Homoptera, flying Hymenoptera, and Lepidoptera). In 2002 and 2003, these eight groups represented 95.9% and 94.5% of prey items respectively. I excluded those arthropod taxonomic groups that were either extremely rare items in the diet (Blattaria, Neuroptera, Odonata, and Orthoptera) or were relatively rare in the diet and totally absent in the arthropod sampling (Isopoda) (**Table 2.5**). Because I detected no year by habitat interaction in flycatcher diet (Wilk's $\Lambda = 0.868$, $F_{16,272} = 1.246$, $p = 0.233$), I examined the effects of year and habitat on Southwestern Willow Flycatcher individually.

I found significant differences in Southwestern Willow Flycatcher diet by year (Wilk's $\Lambda = 0.810$, $F_{8,136} = 3.987$, $p < 0.001$). Subsequent post-hoc tests (Tukey's HSD) revealed flycatchers consumed a greater proportion of Diptera ($F_{1,143} = 10.485$, $p = 0.001$) and Hemiptera ($F_{1,143} = 11.276$, $p = 0.001$) in 2003 and more flying Hymenoptera ($F_{1,143} = 5.599$, $p = 0.019$) in 2002. Additionally, the rank-transformation analysis indicated the consumption of a higher proportion of Formicidae ($F_{1,143} = 4.815$, $p = 0.030$) in 2002 (**Figure 2.6**).

I found significant differences in flycatcher diet by habitat (Wilk's $\Lambda = 0.652$, $F_{16,272} = 4.048$, $p < 0.001$). Post-hoc tests indicated that differences in flycatcher diet by habitat were driven by: (1) more Homoptera ($F_{2,143} = 19.715$, $p < 0.001$) consumed

in exotic than in mixed, with the smallest percentage in native habitats, (2) more Lepidoptera ($F_{2,143} = 8.666$, $p < 0.001$) consumed in native habitat compared to mixed and exotic habitats, and (3) the rank-transformation analysis revealed greater consumption of Araneae ($F_{2,143} = 3.083$, $p = 0.049$) in native compared to exotic habitats, with the proportion of Araneae in mixed habitats indistinguishable from both native and exotic habitats (**Figure 2.6**). While flycatcher diet may vary through the course of the breeding season, separating fecal samples by both habitat and season resulted in sample sizes too small for reliable analyses.

Weighted Abundance Index – I found no differences in the relative abundance of food resources important to flycatchers' diet in native, mixed, or exotic habitats using the weighted abundance index (**Table 2.6**). Because flycatcher diet varied by habitat type, I compared the weighted abundance index of native, mixed, and exotic habitats based on the diet from each habitat in both years. All six one-way ANOVAs indicated that there were no significant differences in the weighted abundance index by habitat type.

Discussion

Arthropod Biomass and Community Composition – As indicated by Ellis et al. (2000), the arthropod community of native riparian habitats in the arid Southwest is not well documented and even less is known of the habitats dominated by exotic plants such as saltcedar. However, with a growing body of studies, including this one, it appears that although the arthropod communities of native and exotic riparian habitats are distinct, there are abundant arthropod resources available

to insectivore predators in saltcedar dominated habitats (Cohan et al. 1978, Mund-Meyerson 1998, Ellis et al. 2000, Yard et al. 2004).

In both years of this study, I found no difference in the total arthropod biomass between habitats dominated by native versus exotic vegetation. While native habitats had greater total arthropod biomass than mixed habitats in 2002, this pattern was not consistent in 2003. Additionally, there was no difference in the total arthropod biomass through the course of the breeding season in both 2002 and 2003. Because not all arthropods are preyed upon equally (Wolda 1990), it is important to examine the community of arthropods that composed the total arthropod biomass.

Although there were no consistent differences in total arthropod biomass among native, mixed and exotic habitats, the arthropod community composition did differ among habitats. While the arthropod communities were statistically distinct by habitat within both years, the degree of graphical separation observed in the ordinations in 2002 was not as clear as the ordinations from 2003. The early, mid, and late sampling periods in 2002 represented combined samples that were collected over several weeks, while in 2003, samples were collected on a single day (**Figure 2.4**). Arthropod communities appear to be temporally dynamic, therefore collections made over several weeks are likely to capture these changes through time, resulting in a more heterogeneous community than that collected on a single day. Some of this temporal change could be driven by phenological changes in the plant community of these different habitat types (Root 1973, Thompson 1978, McGrath 2003). However, by comparing communities collected at different times in the three different habitats, I found no evidence that differences in phenology alone drove habitat differences (the

arthropod communities of the three habitats were not simply the same community offset in time). Instead, along with the lack of a suite of morpho-species (or even a single morpho-species) consistently associated with a particular habitat type, the arthropod community of each of these riparian habitats was unique at each time.

Nevertheless, there were cases where irruptions of single morpho-species dominated individual sampling events. The case of apparent greater total arthropod biomass in the mixed habitat in 2003 (**Figure 2.1**) was driven by a single Hemipteran morpho-species (Hemi-1) representing nearly 90% of the arthropods captured in one Malaise trap. This one Malaise trap collected more than eight times the total arthropod biomass than the mean of the other Malaise traps in mixed habitats. These irruptive events were not unique to mixed habitats. During the replicate sampling event, a single Malaise traps in the exotic habitat collected over 5.5 times the mean arthropod biomass of the other Malaise traps in exotic habitat during that experiment. This trap in the exotic habitat was dominated by the same Hemipteran morpho-species (Hemi-1), and represented almost 75% of arthropods captured in the Malaise trap. Also, one Malaise trap from the native habitat during another experiment (Durst 2004 unpublished data) had over three times the mean arthropod biomass of other Malaise traps operated in the native habitat on the same day. Again, a single morpho-species (Hyme-44) made up a large proportion (over 80%) of all arthropods in the irruptive event. Thus, a high degree of within habitat variation in arthropod populations seems to be inherent in the riparian habitats of Roosevelt Lake. However, the significance of these arthropod irruptions to Southwestern Willow Flycatchers remains to be tested. In several cases flycatchers and other insectivorous

bird species have been observed taking advantage of Ephemeroptera emergences from the Salt River (Cardinal and Paxton 2004). These flycatchers were not territory holders in the riparian habitat adjacent to the outbreaks, thus it is likely that willow flycatchers could respond to localized irruptions of terrestrial arthropods occurring within the riparian habitat. Because I observed these irruptive events in all three habitat types, arthropod irruptions do not appear to have a role in distinguishing among the quality of native, mixed, and exotic riparian habitats.

The value of mixed habitat is important to understand because nearly half of Southwestern Willow Flycatcher territories are found in habitats characterized as a varying mixture between native and exotic vegetation (Sogge et al. 2003b). While mixed habitats have more flycatcher territories than native or exotic habitats, there is no indication that differences in potential food resources among native, exotic, and mixed would drive such patterns. Mixed habitat did not have greater abundance of arthropods; in fact, the total arthropod biomass of mixed habitat was lower than native habitats in 2002. Also, the arthropod community of mixed habitats did not appear to be distinct. At various sampling periods in both 2002 and 2003, the arthropod community of mixed habitats was statistically indistinguishable from native habitats, exotic habitats, or both habitats.

Southwestern Willow Flycatcher Diet – This study is one in a series (Drost et al. 1998, 2001, 2003, DeLay et al. 2002) that explores the details of Southwestern Willow Flycatcher food habits, an aspect of flycatcher biology that remains relatively under-studied (Stoleson et al. 2000). In general it appears that similar arthropod prey items are important to Southwestern Willow Flycatchers across much of their range,

however the relative importance of different prey items appears variable, possibly reflecting the flycatchers' ability to exploit a diverse array of prey groups (this study, Drost et al. 1998, 2001, 2003; DeLay et al. 2002).

Differences in Southwestern Willow Flycatchers' diet between years appeared to be driven by differences in relative insect abundances (**Figures 2.2** and **2.6**). In 2003, both Diptera and Hemiptera were consumed in higher proportion than in 2002, while flying Hymenoptera and Formicidae, were consumed in higher proportion in 2002. Some differences were consistent with the differences in the relative abundance of these groups between the two years. However, flying Hymenoptera were consumed more readily in 2002, while the relative abundance of flying Hymenoptera was greater in 2003. The relative proportion of Hymenoptera that made up the entire arthropod community sampled in Malaise traps was greater in 2002 (2002: 19-24%; 2003: 8-15%). Thus, it seems likely that flycatchers may have been more likely to encounter and consume flying Hymenoptera in 2002 compared to 2003.

There were consistent differences in Southwestern Willow Flycatchers' diet by habitat between both 2002 and 2003 in only three taxonomic groups: Araneae, Homoptera, and Lepidoptera (**Figure 2.6**). Araneae and Lepidoptera, both consumed in greater proportion in native habitats, were not well represented in Malaise samples. These traps are designed to capture flying insects, and therefore may have under-represented Araneae. Likewise, while adult Lepidoptera are generally well represented in Malaise traps (Cooper and Whitmore 1990), they were found in relatively small abundance in the Malaise sampling at Roosevelt Lake. Lepidoptera

may have been better represented in Malaise traps had sampling occurred at night to capture nocturnal groups (Durst unpublished data), but since flycatchers are diurnal foragers Malaise traps were only operated during the day. However, flycatchers may have gleaned resting nocturnal Lepidoptera during their diurnal foraging bouts, but I could not distinguish between diurnal or nocturnal Lepidoptera in the fecal samples. Larval Lepidoptera were also not sampled in Malaise traps, but I was able to distinguish between adult (represented predominately by wing scales) and larval (represented by various larval features: crochets, hooks, and mouthparts) forms in the diet. Larval Lepidoptera were relatively unimportant in the diet making up only 11% of total Lepidoptera found in the diet. Using sampling methodologies that better sample Araneae and Lepidoptera in future studies may provide a clearer explanation of dietary differences in native habitats driven by these two groups.

Flycatchers consumed significantly more Homoptera in exotic habitats, less in mixed habitats, and the least in native habitats (**Figure 2.6**). Homoptera were well represented in Malaise samples. Although native habitat in 2002 had higher Homoptera biomass than exotic habitat, overall abundance of Homoptera was low. The large proportion of Homoptera in flycatcher diets in 2002, particularly in exotic habitats, may therefore reflect the superior ability of flycatchers to find and consume rare resources compared to the ability of Malaise sampling to detect these arthropods when they are relatively rare. In 2003, greater Homopteran abundance in mixed and exotic habitats was reflected in the diet.

The Homopteran community of Roosevelt Lake includes the saltcedar obligate tamarisk leafhopper (**Figure 2.5**). The proportion of *Opsioides* in the

Homopteran community is lowest in native habitats (30-55%) and highest in mixed and exotic habitats (67-100%) (**Figure 2.5**). While the dietary resolution was frequently sufficient to distinguish between Cicadellidae and other Homoptera, the distinction between *Opsius* and other Cicadellidae was not as clear. However, in some cases *Opsius* were clearly identified in dietary samples. Considering that, at a minimum, 60% of all Homoptera in the diet were Cicadellidae and over 90% of all Homopterans captured in the two years of the study were *Opsius*, it is highly likely that Southwestern Willow Flycatchers regularly preyed on this exotic leafhopper. If the Homopterans consumed more frequently in the mixed and exotic habitats, were in fact *Opsius*, then the relatively higher proportion of *Opsius* found in mixed and exotic habitats corresponded with the higher proportion of Homoptera appearing in the diet of birds in these same habitats. Because this insect species was introduced with the arrival of saltcedar, the flycatcher had no historic exposure to this prey item, yet it appears that they have been able to exploit this novel resource where it is available. In exotic habitats, where Homopterans made up 40% of the diet, flycatchers also consumed a diverse array of other arthropod prey taxa. Still, the importance of Homopterans in the diet in exotic habitats may well be linked to *Opsius*, making fluctuations in its abundance a potentially important driver of exotic habitat quality.

Relative Food Resource Base – Large differences in the abundance of some arthropod groups may reveal little about habitat quality for Southwestern Willow Flycatchers if those groups are not an important part of the diet. As a result, I used the weighted abundance index of Poulin and Lefebvre (1997) to combine flycatcher diet with arthropod abundance into a measure of the relative resource base in each

habitat. I expected that different diets would disproportionately increase the weighted abundance index of habitat where the diet data were obtained (e.g., using the diet from native habitats would reveal that the native habitat had the highest weighted abundance index, while using mixed diet would result in the mixed habitat having the highest abundance index, etc.), but this was not the case. Instead, I detected no difference in weighted abundance across habitats regardless of which diet was used to determine relative weightings (**Table 2.6**). The index indicated that there were no differences in the relative quality, in terms of food resources, among native, mixed, and exotic habitats for Southwestern Willow Flycatchers.

The diversity of prey in the flycatcher diet may have been an important factor contributing to the lack of difference in food resource quality among riparian habitats. The impact of saltcedar on avian taxa with more specialized dietary requirements may be contrary to that observed for the more generalist flycatcher. For example, the lack of soft-bodied larval Lepidoptera in saltcedar-dominated habitats could have negative consequences for the nestling development of many bird species with nestlings dependent on these items (Greenberg 1995). In contrast, both adults and young of more generalist insectivores, such as the Southwestern Willow Flycatcher, may be less dependent on the herbivorous arthropod community associated with any one particular plant species because they are able to exploit many “tourist” species not necessarily residing in exotic habitats. Of particular importance in this regard are the Diptera and Hymenoptera that may respond to the profuse flowering resources characteristic of saltcedar. Additionally, flycatchers and other riparian birds species (ash-throated flycatcher (*Myiarchus cinerascens*), Bewick’s wren (*Thryomanes*

bewickii), Bell's vireo (*Vireo bellii*), Lucy's warbler (*Vermivora luciae*), yellow warbler (*Dendroica petechia*), and yellow-breasted chat (*Icteria virens*) may compensate for the loss of native herbivorous arthropods by modifying their diets to include *Opsius* (this study, Yard et al. 2004). Any potential changes to the arthropod community associated with the invasion of saltcedar may have weaker effects on avian species with diverse diets and foraging tactics that allow them to exploit the abundant arthropod food resources in these exotic riparian habitats.

Drought Effects – Because resources are not always limiting in variable environments, the distinction between habitats of differing qualities is not always apparent. However, there can be critical periods when resources are in short supply and selective pressures between habitat types may become intense (Wiens 1977, 1985). The five-fold difference in total arthropod biomass between 2002 and 2003 is consistent with the impact of a millennial drought event (NOAA 2003) that occurred in 2002 and was concomitant with the near total reproductive failure of the Willow Flycatcher population (Smith et al. 2003). While this drought event could have served as a major selective event, clearly demarking differences among habitats, the event was so severe or the differences among habitats were so minor, that differential selection did not occur and all habitats were equally impacted. However, it seems clear that the adequacy of arthropod food resources to Southwestern Willow Flycatcher is clearly important. It is difficult to ascertain the normal arthropod abundance of these riparian habitats with only data representing two dramatically different years, but the lack of reproductive output in 2002 suggests that the impact of

the drought sufficiently depressed arthropod abundance such that the effect cascaded through multiple trophic levels.

Conservation Implications and Management Recommendations

I documented significant differences among both the arthropod communities of native, mixed and exotic riparian habitats utilized by Southwestern Willow Flycatchers, and in the diets of flycatchers in these habitats. Differences in flycatchers' diet were possibly driven by differences in the relative abundance of some arthropod prey taxa, suggesting flycatchers utilized native, mixed, and exotic habitats differently. Whether the differences that do exist in arthropod composition and flycatchers' diet among different riparian habitats translate into differing habitat quality may best be determined by measures of productivity and survival (Van Horne 1983). Other studies have failed to find differences between native- and saltcedar-dominated habitats in either physiological measures (Owen and Sogge 2000) or breeding productivity of flycatchers (Sogge et al. in press), parameters that rely on the adequacy of food resources (Newton 1980, Glick et al. 1983, Rands 1985, Rodenhouse and Holmes 1992, Lochmiller et al. 1993, Jenni-Eiermann and Jenni 1994, Martin et al. 1998, Howe et al 2000, Owen and Sogge 2000). Based on this evidence, and the ability of these birds to exploit a diverse array of arthropod taxa, there is little indication that changes in the potential prey base associated with saltcedar have an impact on riparian habitat quality for Southwestern Willow Flycatchers.

Considering the riparian habitat of Roosevelt Lake as a mosaic of native, mixed, and exotic patches, at a larger scale this riparian habitat could be coarsely classified as mixed. While I documented differences in the arthropod community of native and exotic dominated habitats, the broader mixed matrix surrounding these habitats may have influenced the arthropod community of each patch. In addition to the proximity of exotic, native and mixed riparian habitats, the surrounding Sonoran Desert Upland vegetation of Roosevelt Lake likely interacted to determine the arthropod community of the riparian floodplain. Thus, the potential impact of the invasion of saltcedar on arthropod food resources in other drainages across the range of the Southwestern Willow Flycatcher must consider the riparian habitat at a broader scale. There are two particular cases where the results of this study may not readily translate. First is that of riparian systems made up of saltcedar monocultures and second, those riparian systems nested within a matrix of agricultural or developed land. In both of these cases, inputs that possibly enhance the arthropod food resources of saltcedar-dominated habitats may be limited and may adversely impact the arthropod food base to flycatchers and other insectivores. Finally, riparian habitat loss remains the gravest threat to the Southwestern Willow Flycatchers (Marshall and Stoleson 2000) and management practices that preserve this endangered habitat (Noss et al. 1995) and the natural processes associated with it will remain the most important actions necessary to preserve this endangered species.

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Tables and Figures

Table 2.1. Vegetation and canopy cover composition of Malaise trap sampling locations. In 2002, Malaise traps were randomly placed each sampling period within the three habitats (17 Malaise traps in native and exotic habitats and 16 traps in mixed habitat). Due to the random placement of Malaise traps in 2002 there was a high degree of vegetation variability in the area surrounding the traps. In 2003, Malaise traps (12 in each habitat) were placed in random locations that met minimum requirements of vegetation composition by habitat type (see text). Once identified, these same locations were sampled through the remainder of the season. The vegetation criterion was established to reduce the within habitat variability experienced during the 2002 sampling.

Year	Habitat	Goodding's willow		Saltcedar		Mesquite		Total	
		Mean %	SE	Mean %	SE	Mean %	SE	Mean %	SE
2002	Native	70	6	3	2			73	5
	Mixed	10	2	21	4	2	1	33	4
	Exotic			69	3			69	3
2003	Native	82	3	2	2			84	1
	Mixed	23	4	53	3	4	3	80	2
	Exotic			85	1			85	1

Table 2.2. Arthropod taxa captured in Malaise traps. Diptera, Hemiptera, flying Hymenoptera, Homoptera, and Formicidae represented 98.2% of the total arthropods captured. Hemiptera were absent in 2002, but represented the second most numerous arthropod in 2003. Diptera and Hymenoptera had the greatest morphological diversity.

Taxa	Number of Individuals			Number of Morpho-species
	2002	2003	Total	
Diptera	2537	12189	14726	31
Hemiptera	0	5533	5533	6
Hymenoptera - flying	624	2160	2784	54
Homoptera	219	2425	2644	6
Formicidae	275	242	517	3
Lepidoptera	126	40	166	3
Coleoptera	15	85	100	12
Thysanoptera	0	77	77	1
Araneae	5	32	37	2
Orthoptera	26	11	37	2
Trichoptera	20	7	27	1
Psocoptera	0	17	17	1
Neuroptera	0	8	8	4
Pseudoscorpionida	0	6	6	1
Plecoptera	0	2	2	1

Table 2.3. Community analyses summary. The overall comparison is among all three habitats within each time period. Significance of pair-wise comparisons was evaluated using a Bonferonni correction ($\alpha = 0.05/3 = 0.0167$).

2002						
Comparison	Early		Mid		Late	
	A	p	A	p	A	p
Overall	0.0688	0.0076	0.1011	< 0.0001	0.0618	0.0004
Native-Mixed	0.0450	0.0547	0.1001	< 0.0001	0.0621	0.0020
Native-Exotic	0.0779	0.0058	0.0674	0.0031	0.0512	0.0072
Mixed-Exotic	0.0339	0.1387	0.0699	0.0048	0.0325	0.0272

2003						
Comparison	Early		Mid		Late	
	A	p	A	p	A	p
Overall	0.1581	0.0011	0.3005	< 0.0001	0.1804	0.0005
Native-Mixed	0.0628	0.0709	0.2326	0.0052	0.1246	0.0061
Native-Exotic	0.2192	0.0060	0.3050	0.0053	0.2410	0.0060
Mixed-Exotic	0.0964	0.0075	0.2125	0.0053	0.0689	0.0189

Table 2.4. Arthropod morpho-species with significant indicator species values (INDVAL) by sampling period. There were no morpho-species that consistently predicted native, mixed, or exotic habitats during the different sampling periods. While the arthropod community of each habitat changed through time, there were no morpho-species consistently driving these changes.

Sampling Period	Order	Family	Morpho-species	IndVal	p	Indicating Habitat	
2002	Early	Diptera	Lanxiniidae	dipt-26	66.9	0.027	Native
		Diptera	Pipunculidae	dipt-30	64.4	0.02	Native
		Homoptera	Cixiidae	homo-4	75.4	0.008	Native
		Hymenoptera	Sphecidae	hyme-6	65.7	0.024	Exotic
		Lepidoptera	Unidentified	lepi-4	66.3	0.017	Native
	Mid	Diptera	Sarcophagidae	dipt-1	54.6	0.003	Native
		Diptera	Bombyliidae	dipt-18	71	0.003	Exotic
		Homoptera	Cicadellidae	homo-3	58.2	0.038	Exotic
		Homoptera	Cixiidae	homo-4	53.2	0.046	Native
		Hymenoptera	Formicidae	hyme-45	82.6	0.001	Exotic
	Late	Diptera	Culicidae	dipt-62	54.4	0.033	Mixed
Hymenoptera		Sphecidae	hyme-9	60.8	0.016	Native	
2003	Early	Diptera	Lanxiniidae	dipt-26	71.8	0.02	Native
		Diptera	Acalyptera	dipt-60	44.4	0.014	Mixed
		Diptera	Culicidae	dipt-62	52	0.012	Native
		Lepidoptera	Unidentified	lepi-4	78.3	0.005	Native
	Mid	Diptera	Tephritidae	dipt-25	93.1	0.012	Mixed
		Diptera	Pipunculidae	dipt-30	79.8	0.009	Native
		Diptera	Tachinidae	dipt-44	86.4	0.004	Exotic
		Diptera	Dolichopodidae	dipt-59	44.8	0.004	Exotic
		Diptera	Acalyptera	dipt-60	41.8	0.009	Exotic
		Homoptera	Cixiidae	homo-4	92.2	0.013	Native
		Homoptera	Cicadellidae	homo-93	58.3	0.011	Exotic
		Hymenoptera	Vespidae	hyme-29	63	0.041	Mixed
		Hymenoptera	Apoidea	hyme-34	59.8	0.019	Mixed
		Hymenoptera	Apoidea	hyme-39	87.2	0.02	Mixed
		Hymenoptera	Formicidae	hyme-42	86.3	0.016	Native
		Hymenoptera	Formicidae	hyme-44	100	0.009	Native
		Hymenoptera	Formicidae	hyme-45	86.3	0.018	Mixed
		Hymenoptera	Eurytomidae	hyme-53	83.4	0.016	Native
		Hymenoptera	Unidentified	hyme-65	93.4	0.012	Mixed
	Hymenoptera	Sphecidae	hyme-9	55.6	0.039	Native	
	Late	Diptera	Dolichopodidae	dipt-28	72.2	0.014	Mixed
		Diptera	Tachinidae	dipt-44	75	0.04	Exotic
		Diptera	Dolichopodidae	dipt-59	48.5	0.018	Exotic
		Homoptera	Cicadellidae	homo-3	55.4	0.023	Exotic
		Homoptera	Cixiidae	homo-4	89.1	0.01	Native
		Hymenoptera	Formicidae	hyme-45	61.6	0.006	Mixed
		Trichoptera	Unidentified	tric-1	70.7	0.035	Native

Table 2.5. Summary of Southwestern Willow Flycatcher diets based on fecal analysis at Roosevelt Lake, AZ in 2002 and 2003. Panel A shows the number of individual prey items identified in each year and the total for both years. Panel B show the occurrence of each prey item expressed as a proportion (the number of samples with prey item ‘x’ divided by the total number of samples). The six most abundant groups, (in order of abundance) flying Hymenoptera, Cicadellidae, Diptera, Coleoptera, Formicidae, and other Homoptera, accounted for 80% of the total prey items.

A Prey Item	Number of Individual Prey Items			B Prey Item	Proportional Occurrence in Samples		
	2002	2003	Total		2002	2003	Average
Hymenoptera - flying	136	91	227	Hymenoptera - flying	0.66	0.70	0.68
Homoptera -Cicadellidae	49	153	202	Coleoptera	0.64	0.60	0.62
Diptera	51	130	181	Diptera	0.46	0.75	0.61
Coleoptera	80	75	155	Araneae	0.42	0.60	0.51
Hymenoptera -Formicidae	63	84	147	Homoptera - others	0.36	0.42	0.39
Homoptera - others	67	74	141	Homoptera -Cicadellidae	0.22	0.51	0.36
Araneae	40	64	104	Lepidoptera (adult)	0.37	0.28	0.32
Lepidoptera (adult)	32	25	57	Hymenoptera - Formicidae	0.34	0.22	0.28
Isopoda	17	29	46	Isopoda	0.18	0.33	0.26
Hemiptera	6	29	35	Hemiptera	0.07	0.28	0.18
Odonata	2	7	9	Odonata	0.02	0.07	0.04
Lepidoptera (larvae)	2	5	7	Lepidoptera (larvae)	0.02	0.04	0.03
Neuroptera	1	1	2	Neuroptera	0.01	0.01	0.01
Orthoptera	1	1	2	Orthoptera	0.01	0.01	0.01
Blattaria	0	1	1	Blattaria	0.00	0.01	0.01

Table 2.6. Summary statistics for comparison of weighted abundance index. Each row shows the statistics of a one-way ANOVA comparing the mean weighted abundance index of native, mixed, and exotic habitats. In each row the weighted abundance index was calculated with a different diet as a weighting factor (2002: df = 2, 47; 2003 df = 2, 33).

Comparison of Weighted Abundance Index by Native, Mixed, and Exotic Habitats			
Year	Diet Weighting Factor	F	p
2002	Native Diet	0.1749	0.8401
	Mixed Diet	1.2172	0.3052
	Exotic Diet	1.1301	0.3316
2003	Native Diet	2.2225	0.1243
	Mixed Diet	2.1463	0.1330
	Exotic Diet	1.7035	0.1977

Figure 2.1. Total arthropod biomass by year and habitat. Error bars represent one standard error and bars sharing the same letter are not significantly different.

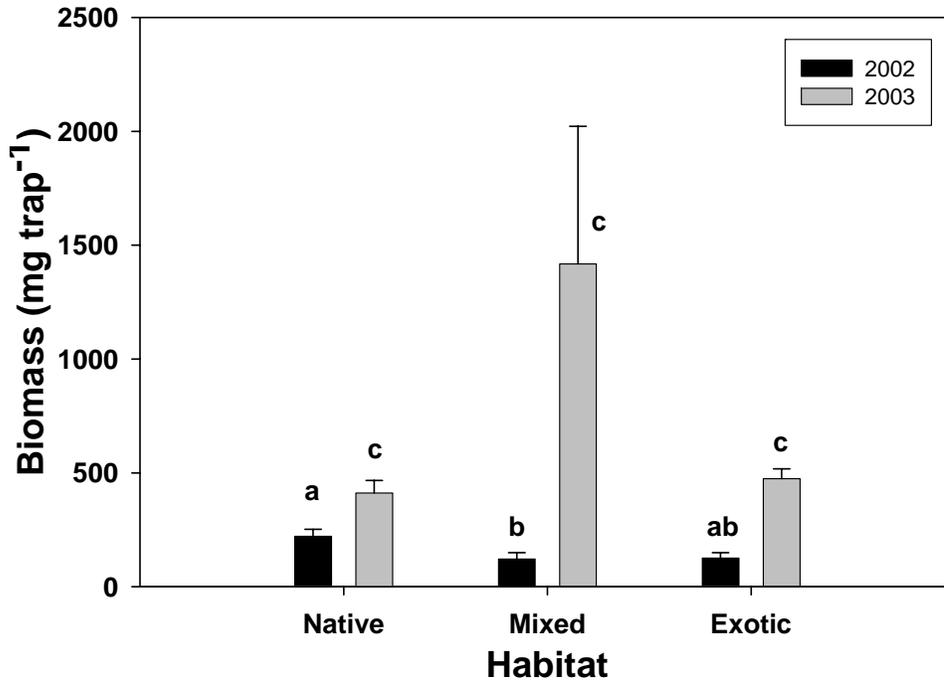


Figure 2.2. Biomass of the most abundant arthropod taxa by year and habitat. Error bars represent one standard error. In 2002, the biomass of Diptera, Formicidae, Homoptera, and Orthoptera varied by habitat. In 2003 there was a significant interaction between habitat and season in the biomass Formicidae, Hemiptera, and Trichoptera (see text).

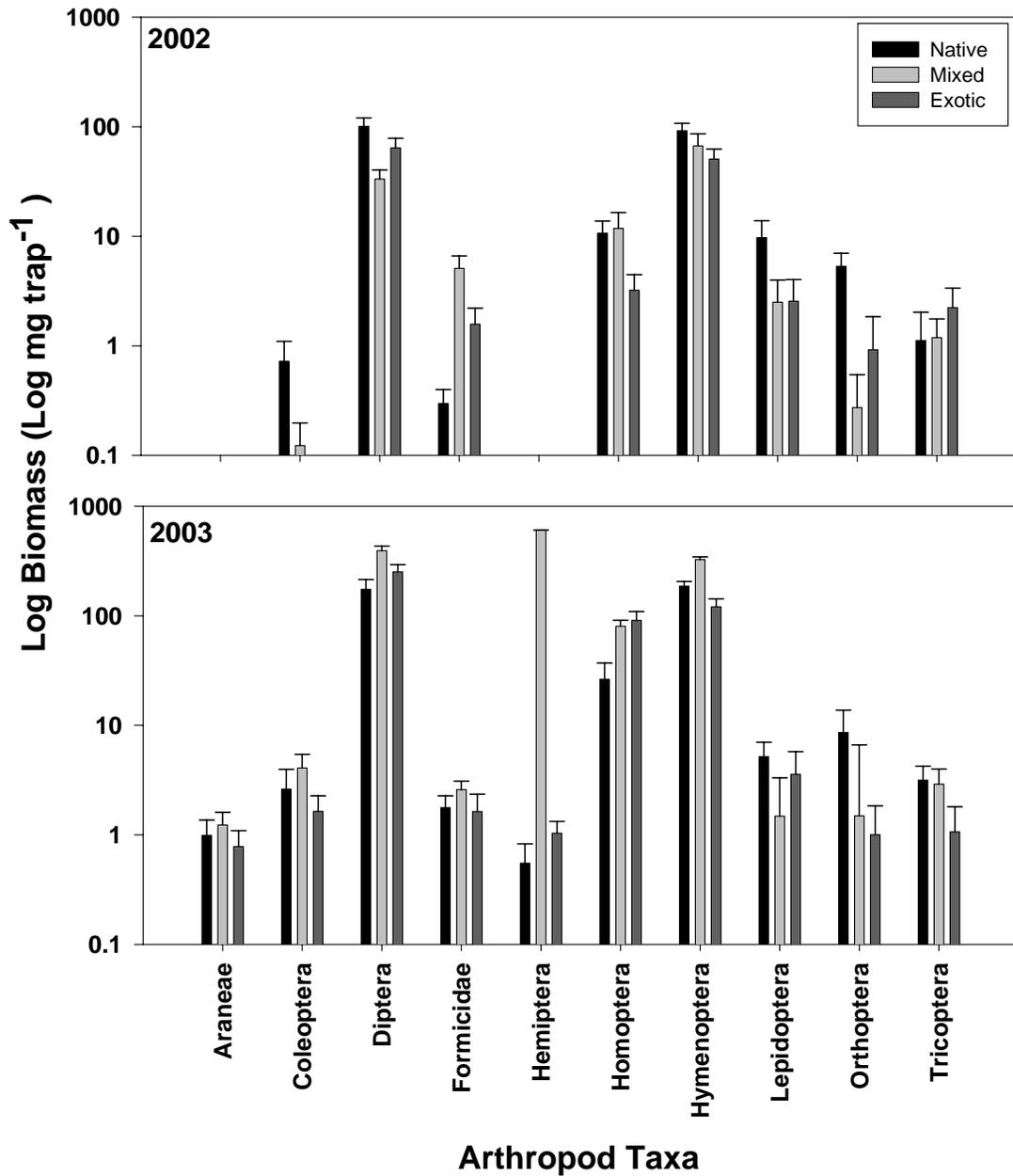


Figure 2.3. Biomass of important arthropod taxa by year and season. Error bars represent one standard error. In 2002, the biomass of Diptera and Lepidoptera varied by season. In 2003 there was a significant interaction between habitat and season in the biomass of Formicidae, Hemiptera, and Trichoptera (see text).

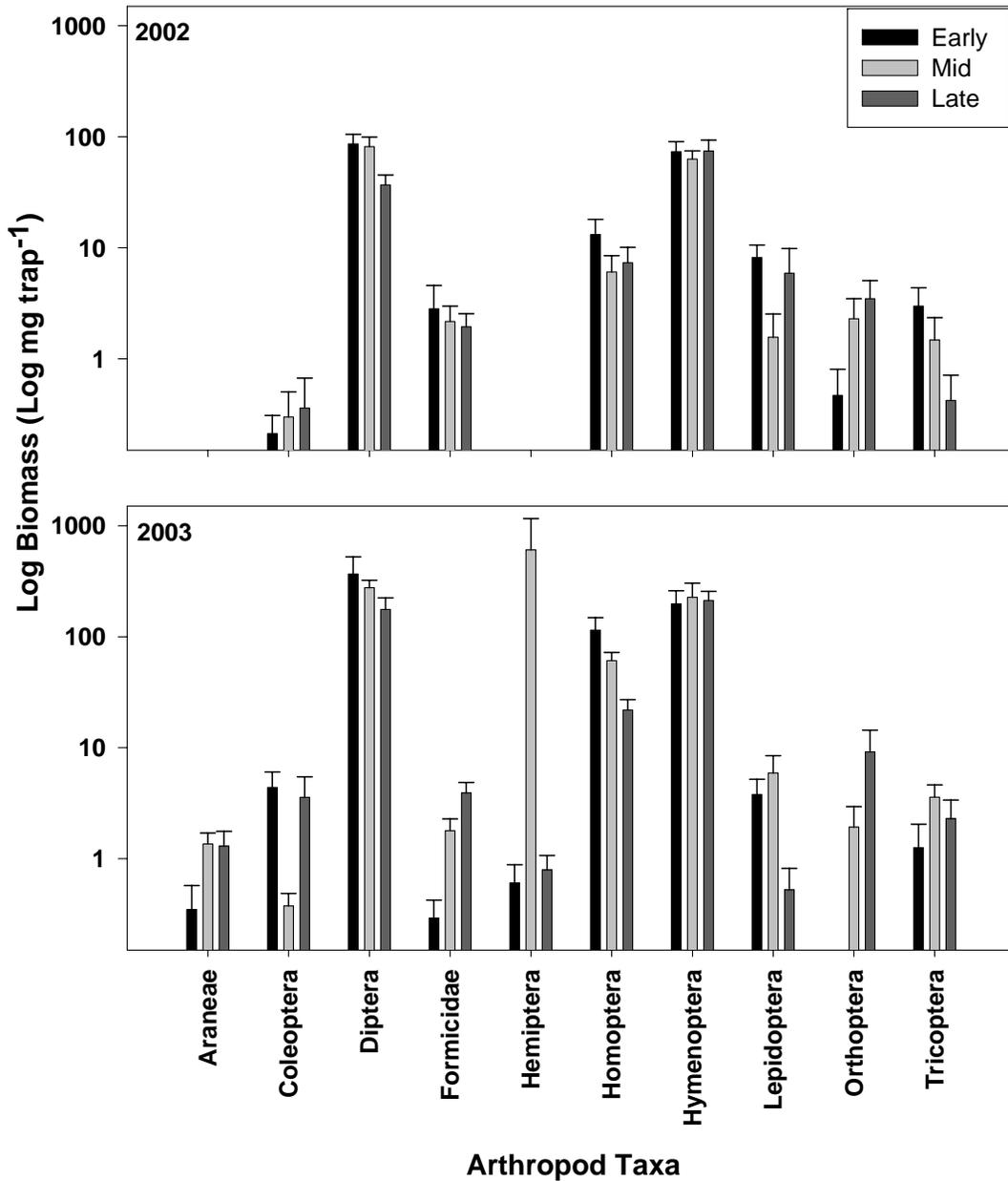


Figure 2.4. NMS ordination by sampling period. Each point represents a single Malaise trap. The distance between points represents the degree of similarity in the arthropod community (abundance and composition) of among Malaise traps. Note that the axes of each panel have no meaning and the relative position of points within each panel should only be compared within the same panel. It is not valid to compare points among different panels. Significant differences in pair-wise comparisons should be examined using **Table 2.3**.

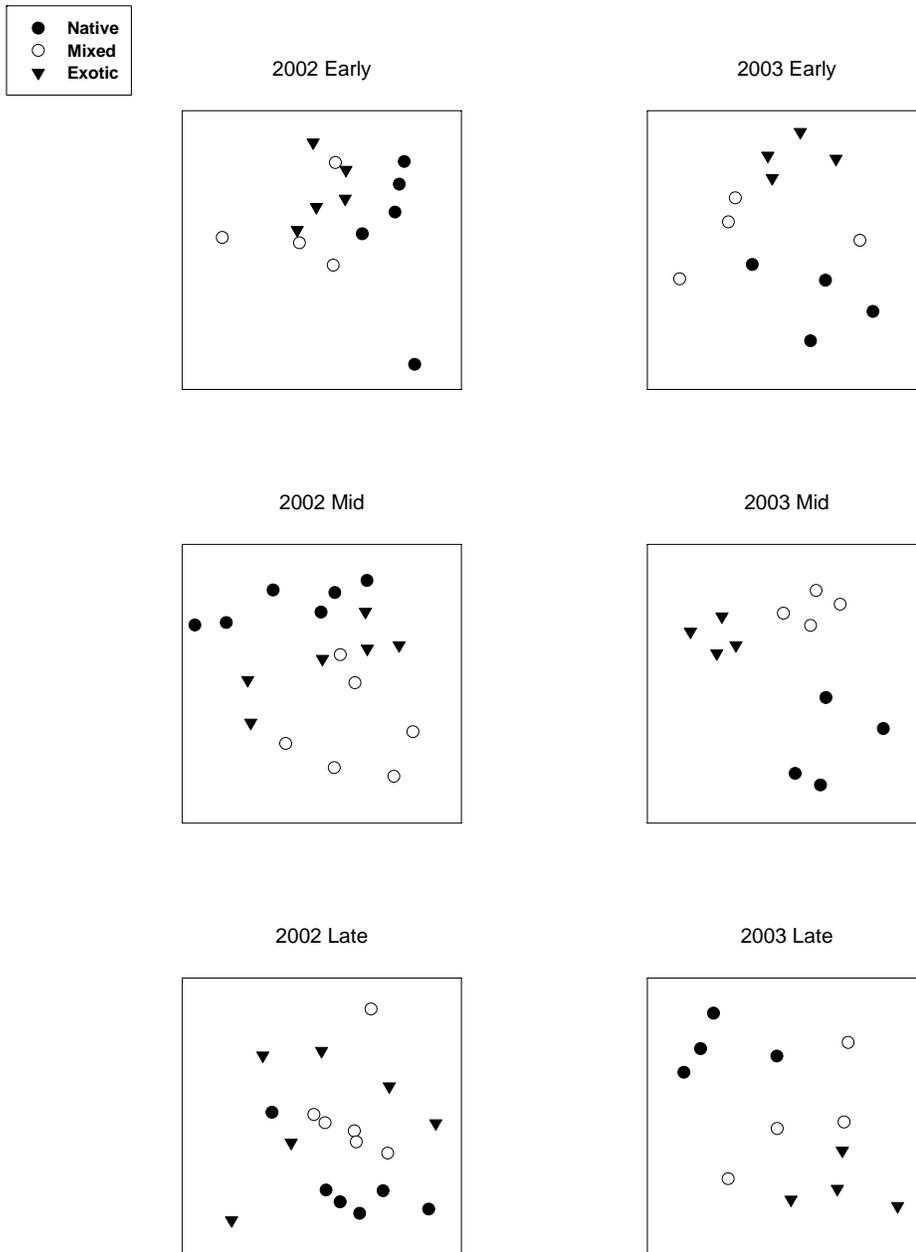


Figure 2.5. Proportion of *Opsius stactogalus* by habitat type and year as sampled using Malaise traps. Solid bars represent number of *Opsius* and hatched bars represent the number of all other Homoptera.

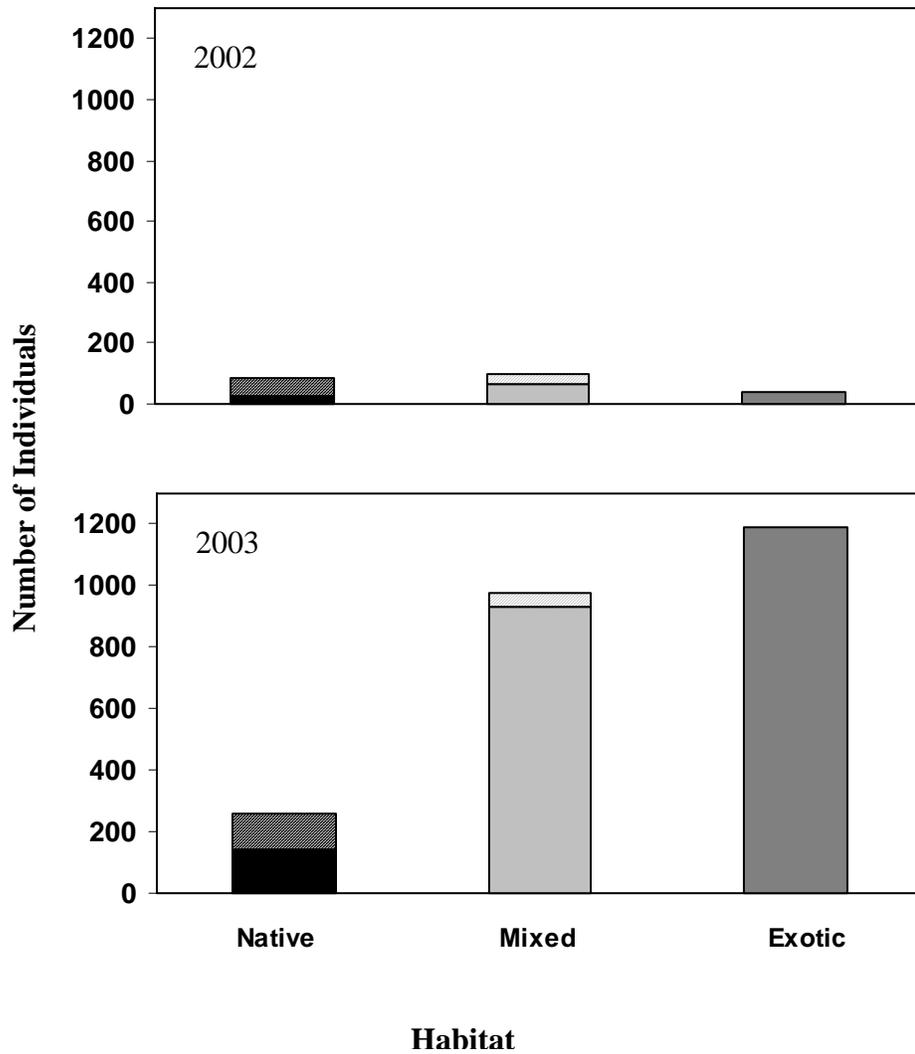
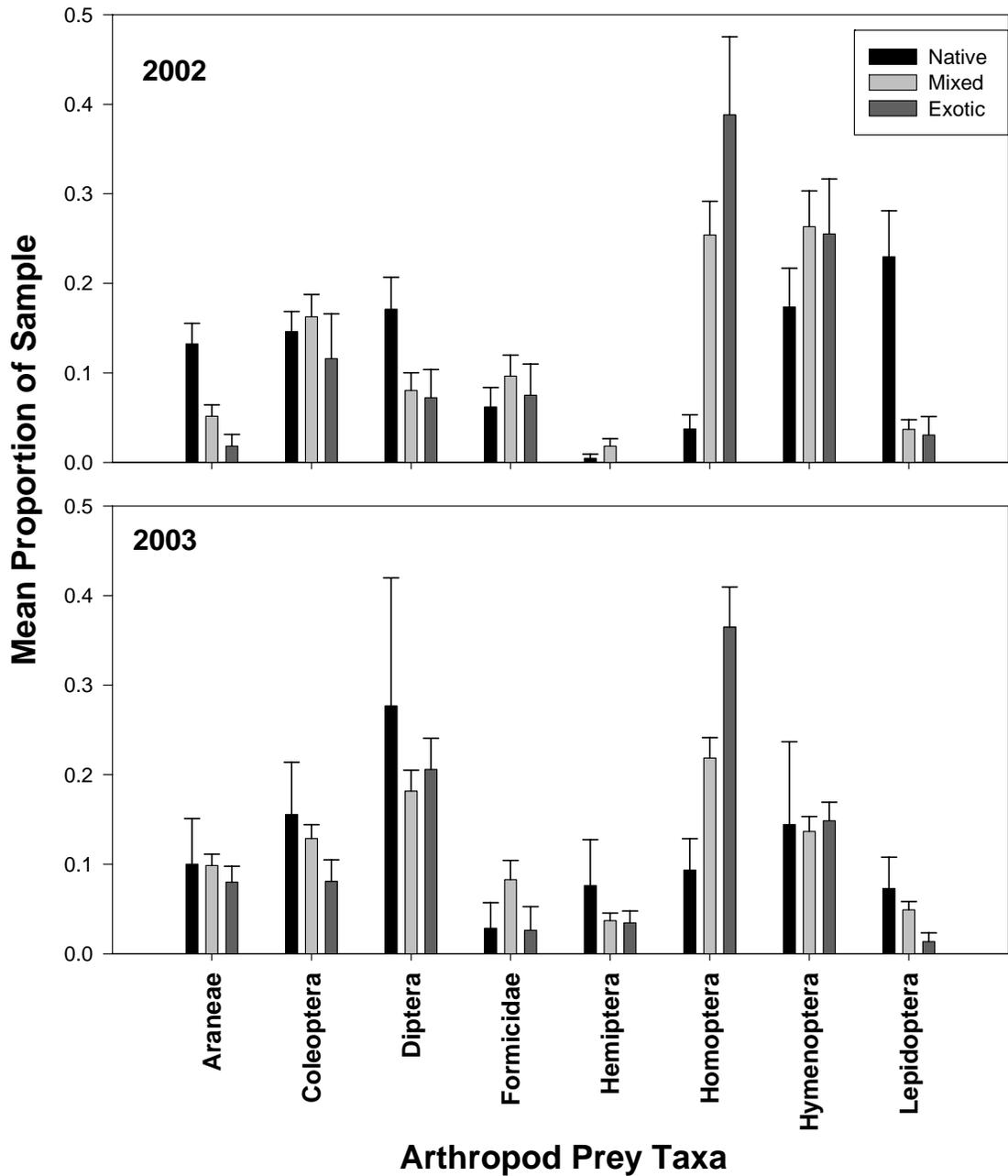


Figure 2.6. Mean proportion of the eight major prey groups found in Willow Flycatcher diet samples. Error bars represent one standard error. Flycatcher diet varied in proportion of Diptera, Formicidae, Hemiptera, and Hymenoptera consumed between 2002 and 2003. Flycatcher diet was significantly different by habitat across both years in the proportion of Araneae, Homoptera, and Lepidoptera identified in fecal samples.



Chapter 3 – Comparison of Arthropod Sampling Techniques to Assess Southwestern Willow Flycatcher Diets

Introduction

All arthropod sampling techniques have inherent biases and the choice of sampling technique may have profound effects on the interpretation of prey availability for an insectivore (Cooper and Whitmore 1990). To measure food availability for an insectivorous bird, the bird's foraging behavior should be used as the basis to identify an appropriate arthropod sampling methodology (Wolda 1990). Nearly all foraging events of Southwestern Willow Flycatchers on the Verde River in central Arizona were classified as aerial maneuvers (96.4%) directed at prey in mid-air (55.9%) or on foliage substrates (38.9%) (SWCA Inc. 2000). Thus, to document the arthropods present in the foraging micro-habitats used by Southwestern Willow Flycatchers, I used two passive flight-intercept sampling techniques (Malaise traps and sticky traps), and a branch bag-and-clip technique (Johnson 2000) in an attempt to capture the full range of arthropod prey potentially available to foraging flycatchers. My objective was to utilize multiple arthropod sampling techniques to determine the method(s) that best reflected the diet of Southwestern Willow Flycatchers (Drost 1999, 2001; DeLay 2002).

Methods

In 2002, I used a branch bag-and-clip technique, Malaise traps and sticky traps to sample the arthropod community of native (Goodding's willow), exotic (saltcedar),

and mixed (a mosaic of these two dominant tree species) habitats of the Salt River Inflow to Roosevelt Lake. I used the same native, exotic and mixed sites as described for the original arthropod sampling in Chapter 2.

Branch Clipping – I sampled the arthropod community inhabiting the foliage of the dominant tree species at native, mixed, and exotic sites using a branch clipping technique (Johnson 2000). Sampling events occurred at three different time periods: 2 June, 1 July, and 9 August. During each sampling event, all three sites were visited in the same order, starting at the exotic site and ending at the native site. Branch clipping commenced at approximately 0530 and ended around 1030 each day. At each site I established transects along trails. Sampling locations were determined by successively generating random numbers between 5 and 20, representing the distance in meters between sampling locations in each site. I used the same transects during each sampling period, but generated new random distances between sampling locations at each time period to sample different trees. At each sampling location, I selected branches from 3-6 m high in full foliage; most flycatcher foraging events take place from 4-5 m high (SWCA Inc 2000). I attempted to collect branches of similar volume and phenological state in each site. Branches were collected as described by Johnson (2000). After collection, branches were quickly transferred to labeled plastic bags and frozen as soon as possible. During each sampling period, I collected 20 willow branches from the native site, 20 saltcedar branches from the exotic site, and 15 of each species at the mixed site. In the fall of 2002, I sorted the arthropods collected from the branches to Order, and standardized arthropod abundance per gram of branch after all branches were air-dried and weighed. I

analyzed 122 branch samples evenly distributed among the three sampling periods; 40 were from the native site, 34 from the mixed (evenly split between saltcedar and willow branches), and 48 from the exotic site.

Sticky Traps – In 2002, I used sticky traps (15.2cm x 30.5cm, model 2873, BioQuip Corporation, Gardena, CA) in conjunction with Malaise trap sampling. Malaise traps served as a central location for sticky trap sampling. Four sticky traps were placed at the cardinal directions 5-10 m from the central Malaise trap; an additional sticky trap was placed adjacent to the Malaise trap. All sticky traps were hung in vegetation 1-2 m high. To prevent birds from interacting with sticky traps, I placed each sticky trap in a chicken-wire “cage” (1.5 inch diameter mesh). Sticky traps were active during the same period as the associated Malaise trap. To “close” and store the sticky traps, I coated both sides of the sticky trap with a layer of saran-wrap. Sorting and quantification of the arthropods captured with sticky traps was conducted at the USGS Colorado Plateau Research Station. Arthropods captured with sticky traps were sorted to Order; and the identification was necessarily conducted through the clear saran-wrap covering, as efforts to remove the coating destroyed the samples. I analyzed a total of 203 sticky traps, evenly distributed among all sampling periods, 67 from the native site, 66 from the mixed site, and 70 from the exotic site.

Malaise Traps – The protocol for Malaise traps (model 2875AG, BioQuip Corporation, Gardena, CA) in 2002 is described in full in Chapter 2. I analyzed a total of 50 Malaise sample, 17 from both the native and exotic sites, and 16 from the mixed site.

Results

Malaise traps captured 4.5 times more arthropods than did sticky traps, and almost 20 times more than branch bag-and-clips (**Figure 3.1**). Branch bag-and-clips yielded a mean of 3.7 arthropods per branch, nearly all Homoptera. Sticky traps captured a mean of 14.8 arthropods per trap, with approximately equal proportions of Araneae, Diptera, Hymenoptera, and Thysanoptera. Mean arthropod captures from Malaise traps yielded 67.5 individuals, with Diptera and flying Hymenoptera accounting for over 80% of all individuals and Formicidae, Homoptera, and Lepidoptera dominating the remainder of each Malaise sample.

I compared the composition of arthropods captured via each sampling technique with the arthropod prey groups found in Southwestern Willow Flycatchers' diets (Drost et al. 1999, 2001, DeLay 2002). Excluding rare items found in both the various arthropod sampling techniques and flycatchers' diet, Malaise traps best represented prey items found in flycatchers' diet, with all five major components of Malaise captures being found in the diet. There were only three taxonomic groups found in flycatchers' diets that were well represented in sticky traps (Thysanoptera were rarely identified in the diet). Branch bag-and-clip captured only one taxonomic group (Homoptera) that was found in flycatchers' diet (**Figure 3.1**).

Discussion

Malaise traps sampled a broader spectrum of the arthropod community in the riparian habitats of Roosevelt Lake than either of the other two methods. All arthropods, except larval Lepidoptera, that were collected with branch clipping were

also represented in the other two sampling techniques. Additionally, branch clipping was completely ineffective in representing more active members of the arthropod community, such as Diptera, flying Hymenoptera, and Coleoptera, which were captured in sticky and Malaise traps. Sticky traps and Malaise traps captured essentially the same Orders of arthropods, but individuals over 5mm were rarely found on sticky traps, while Malaise traps captured individuals from much wider range of size classes (personal observation).

In addition, sorting and quantifying individuals was more accurate and took less time per sample with Malaise traps. Branch-clip samples usually entailed separating arthropods from leaf litter that accumulated in bags. Likewise, arthropods captured in sticky traps were fixed in position on the trap and frequently crushed, making identification more difficult.

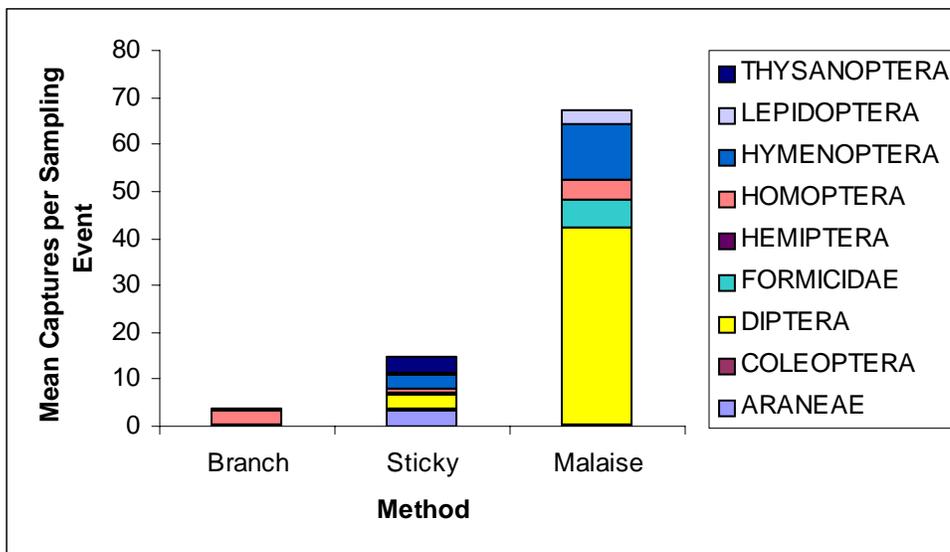
While Malaise traps provided the best representation of the Southwestern Willow Flycatcher diet compared to the other two techniques, there is no single arthropod sampling technique that provides an exact representation of avian diet. Due to the plasticity of foraging behaviors, birds are able to more effectively “sample” the arthropod community (Hutto 1990, Wolda 1990, Johnson 2000). However, based on the comparison of a variety of arthropod sampling techniques, Malaise traps were the best means to measure the arthropod prey base of Southwestern Willow Flycatchers and for this reason Malaise traps were the sole arthropod sampling method used in 2003 and the sole method reported for 2002 in Chapter 2.

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Figures

Figure 3.1. Mean arthropod captured by three sampling methods 2002. Malaise traps captured 4.5 times more arthropods as sticky traps, and almost 20 times more than branch bag-and-clips. Branch bag-and-clips yielded a mean of 3.7 arthropods per branch, nearly all Homoptera. Sticky traps captured a mean of 14.8 arthropods per trap, with approximately equal proportions of Araneae, Diptera, Hymenoptera, and Thysanoptera. Mean arthropod captures from Malaise traps yielded 67.5 individuals, with Diptera and flying Hymenoptera accounting for over 80% of all individuals and Formicidae, Homoptera, and Lepidoptera dominating the remainder of each Malaise sample.



Chapter 4 – Southwestern Willow Flycatcher Foraging Behavior at Roosevelt Lake

Introduction

To measure food availability for an insectivorous bird, the use of foraging behavior to assess resource availability has been argued to be an important tool (Hutto 1990, Wolda 1990). For an insectivore feeding in two or more habitats, differences in foraging behavior between habitats could reflect fundamental differences in the prey availability in those habitats. Additionally, differences in foliage structure may have significant influences on foraging efficiency and energetics in different habitats (Holmes and Robinson 1981). Robinson and Holmes (1982) indicated that the suite of foraging behaviors utilized by a bird will influence the prey items that could potentially be procured and consumed. The invasion of saltcedar into riparian habitats in the Southwest has altered these habitats with the potential to change the invertebrate community (Kleintjes and Dahlsten 1994); a change that could lead to differences in the foraging behaviors used by Southwestern Willow Flycatchers in these two habitats.

A previous study on Southwestern Willow Flycatchers (SWCA, Inc. 2000) indicated that over 96% of their foraging behaviors could be classified as aerial maneuvers (wing powered) with 55.9% being directed at aerial prey (hawking by my definition) and 38.9% directed at prey on foliage (gleaning and swiping by my definition). Males and females exhibited the same types of foraging maneuvers, but males foraged higher in the canopy than females. These observations were made at

two sites; both dominated by native riparian vegetation, so no comparisons of foraging behavior across habitat types (particularly native versus exotic) could be made.

I studied the foraging ecology of the same population of Southwestern Willow Flycatchers at Roosevelt Lake detailed in Chapter 2. My objectives were to: (1) compare differences in foraging behavior by habitat type, and (2) compare differences in foraging behavior by sex.

Methods

In 2003, foraging observations were opportunistically recorded during routine re-sighting activities as part of a long-term demography study on the population of Southwestern Willow Flycatchers at Roosevelt Lake. I used a focal animal approach (Altmann 1974) with delayed count before data was collected (Bradley 1985) to reduce loss bias and dependence of sequential observations. Once a flycatcher was detected in its territory, one minute was allowed to elapse before recording a single foraging maneuver to eliminate the possible bias of disproportionately recording more obvious foraging behaviors (Bell et al. 1990, Hejl et al. 1990). For each foraging observation I recorded: unique territory number associated with a flycatcher or pair of flycatchers, an overall assessment of the habitat type where the behavior occurred (in predominately native vegetation, exotic vegetation, or some co-dominant mixture), sex of the bird (if known), foraging maneuver (defined below), height at which the behavior occurred, the average canopy height in the vicinity of the maneuver, starting perch, foraging substrate, and ending perch.

Based on previous observation of Southwestern Willow Flycatchers, there were three foraging maneuvers that encompassed the breadth of foraging methods these birds used to obtain arthropod prey (modified from Remsen and Robinson 1990). All maneuvers were aerial wing-powered behaviors. I defined the first as “glean” and used the term synonymously with sally-hover, hover-glean, or sally-stall. All gleaning behaviors were directed at foliage substrates and entailed at least a temporary pause or stall in flight motion. The second behavior I defined was “hawk,” those foraging behaviors directed at aerial substrates for flying prey items, synonymous with sally. The final behavior I recorded was a “swipe” that most closely conforms to a sally-strike or sally-glide, where the bird procures a food item from a foliage substrate, while in flight, but without the temporary pause or stall characteristic of what I defined as “gleaning”. In a swipe maneuver, the bird remained in constant flight motion, quickly capturing a prey item from foliage and continuing on its original flight path.

I used contingency table chi-square analysis to test for differences in foraging behavior by habitat type and sex. One-way ANOVA and t-tests were used to test for differences in absolute foraging height by habitat and sex respectively. I tested for potential differences in multiple comparisons using Tukey’s HSD. To determine relative foraging height, I divided the height the foraging behavior by the average canopy height where the foraging event occurred. I tested for differences in relative foraging height in the same manner as described for absolute foraging height following an arcsin square root transformation (Sokal and Rohlf 1995). In all tests I considered $\alpha = 0.05$ as significant, except when modified for a Bonferroni correction

in the case of pair-wise comparisons when comparing chi-square results (Sokal and Rohlf 1995). All analyses were conducted using JMP-IN 5.1.

Results

I recorded a total of 193 foraging observations on Southwestern Willow Flycatchers during the 2003 breeding season. More foraging observations were made of male flycatchers (62.3%) due to the relative ease of spotting and tracking males compared to females (**Table 4.1**). Also, most foraging observations were from birds inhabiting mixed habitats (60.1%) due to the fact that more flycatcher territories were located in mixed riparian patches (**Table 4.1**).

Overall, hawking accounted for 63.7% of all foraging maneuvers, with the remainder split approximately equally between gleaning (18.6%) and swiping (17.6%). I found differences in foraging maneuver by habitat type ($\chi^2 = 10.47$, $df = 3$, $p = 0.033$). However, of the three subsequent pair-wise comparisons, there were marginal differences in foraging behavior between only the mixed versus exotic habitat (Bonferroni correction $\alpha = 0.017$, $\chi^2 = 8.6$, $df = 3$, $p = 0.015$). In the mixed habitat more foraging maneuvers were directed at aerial substrates (hawking), while in exotic habitat, there was more foraging on foliage (gleaning and swiping)(**Figure 4.1**).

There were differences between the heights of foraging maneuvers by habitat ($F_{2,158} = 6.78$, $p = 0.002$). Tukey's HSD post-hoc test indicated foraging maneuvers were highest in native habitats (7.4 m) compared to both exotic (5.2 m) and mixed habitats (5.6 m). However, it is important to note that there were differences in the

average canopy height where the foraging events occurred by habitat type ($F_{2,158} = 7.80$, $p = 0.001$), with canopy in native habitats (10.6 m) significantly higher than both exotic (7.6 m) and mixed habitats (8.0 m). Thus, a more reasonable test of differences in foraging height by habitat was to control for the canopy height by testing for differences in relative foraging height. There were no differences in the relative height of foraging maneuvers by habitat type ($F_{2,158} = 0.43$, $p = 0.653$). Flycatchers at Roosevelt Lake consistently foraged at a height between 70% and 75% of canopy height in each habitat (**Figure 4.2**).

I found no differences in foraging maneuvers between male and female Southwestern Willow Flycatchers at Roosevelt Lake ($\chi^2 = 0.10$, $df = 3$, $p = 0.950$) (**Figure 4.3**). Additionally, I recorded foraging behavior for 44 birds of unknown sex that were not considered in this analysis. If these 44 birds of unknown sex were not evenly divided between males and females, it is possible that this analysis could change due to the large proportion of swiping behavior observed in these unknown birds (~ 45%).

There were differences in both the absolute and relative height of foraging events by sex. Males foraged more than 25% higher than females in terms of absolute foraging height ($t_{70} = -3.23$, $p = 0.002$). Also, when taking the relative position in the canopy where foraging events occurred, males foraged nearly 29% higher than females ($t_{70} = -3.79$, $p < 0.001$) (**Figure 4.4**).

Discussion

Given the large differences in structural and vegetation components between exotic saltcedar and native willow dominated habitats (Anderson et al. 1983), the minor differences in Southwestern Willow Flycatcher foraging maneuvers were surprising (Holmes and Robinson 1981, Rotenberry 1985, Wiens et al. 1987, Knopf et al. 1990, Sedgwick and Knopf 1992). One would expect the vegetation structure of native and exotic habitats to be most distinct, yet the only differences in foraging behavior were between the mixed and exotic habitats, presumably habitats that are not as structurally different as native and exotic habitats.

While there were differences in Southwestern Willow Flycatchers' diet by habitat (Chapter 2), the prey taxa (Ananeae, Homoptera and Lepidoptera) that drove differences in diet most likely could be procured in similar fashion. If differences in Lepidoptera consumption were driven by nocturnal forms (as hypothesized in Chapter 2), all of these prey items would be primarily obtained through foliage-directed foraging maneuvers. The greatest differences observed in flycatcher foraging behavior were between mixed and exotic habitats. Flycatchers exhibited more gleaning and swiping behaviors in exotic habitat, precisely the types of foraging behaviors that could account for the increased consumption of Homoptera in exotic compared to mixed habitats.

The lack of difference in foraging maneuvers between male and female Willow Flycatchers agreed with the results observed by SWCA Inc. (2000) on the Verde River. Likewise, the difference in foraging height, with males foraging higher than females, was also documented (SWCA Inc. 2000). Given that there were no

differences in diets of flycatchers by sex (Chapter 2), the use of similar foraging maneuvers to obtain similar prey is to be expected. Willow Flycatchers are sexually monomorphic and are best distinguished in the field based on behavioral characteristics. These same behavioral characteristics may explain differences in foraging height by sex. Females typically spend more time lower in the canopy (personal observation). Male singing perches are frequently the highest point in a territory and may serve multiple functions, including feeding (SWCA Inc. 2000).

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Tables and Figures

Table 4.1. Distribution of Southwestern Willow Flycatcher foraging observations. More observations were recorded for males because of their relatively more conspicuous behavior. In 2003, most flycatcher territories were in habitats that were best categorized as mixed, thus more observations were recorded in mixed habitats.

		Number of Observations
Habitat	Naive	13
	Mixed	116
	Exotic	64
Sex	Male	120
	Female	29
	Unknown	44

Figure 4.1. Distribution of flycatcher foraging maneuvers by habitat type. There were differences in foraging maneuver by habitat type ($\chi^2 = 10.47$, $p = 0.033$). However, of the three subsequent pair-wise comparisons, there were marginal differences in foraging behavior only between the mixed versus exotic habitat (Bonfornii correction $\alpha = 0.017$, $\chi^2 = 8.58$, $p = 0.014$).

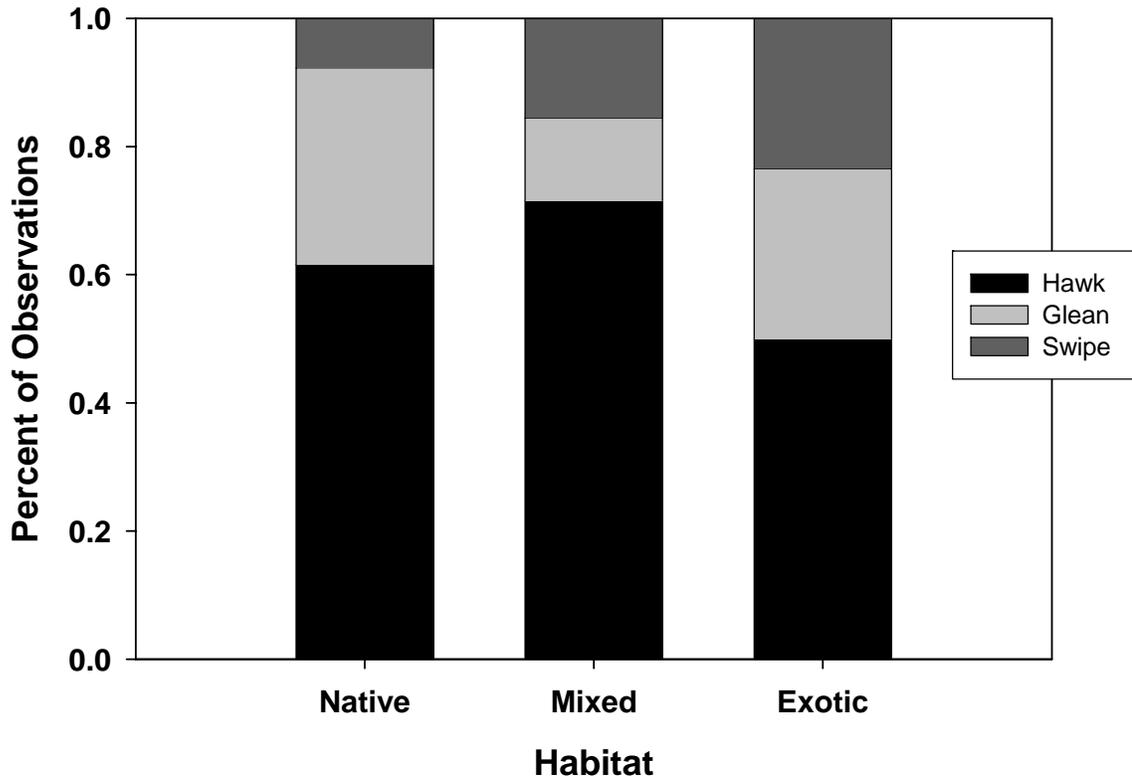


Figure 4.2. Flycatcher foraging height by habitat. The height of flycatcher foraging events is displayed in the dark bars and the estimated canopy height where foraging events occurred is shown with the addition of the gray bar. Relative foraging height is calculated by dividing the foraging height by the canopy height. There were differences between the heights of foraging maneuvers by habitat ($F = 6.78$, $p = 0.002$). Tukey's HSD post-hoc test indicated foraging maneuvers were highest in native habitats (7.4 m) compared to both exotic (5.2 m) and mixed habitats (5.6 m). There were no differences in the relative height of foraging maneuvers by habitat type ($F = 0.43$, $p = 0.653$).

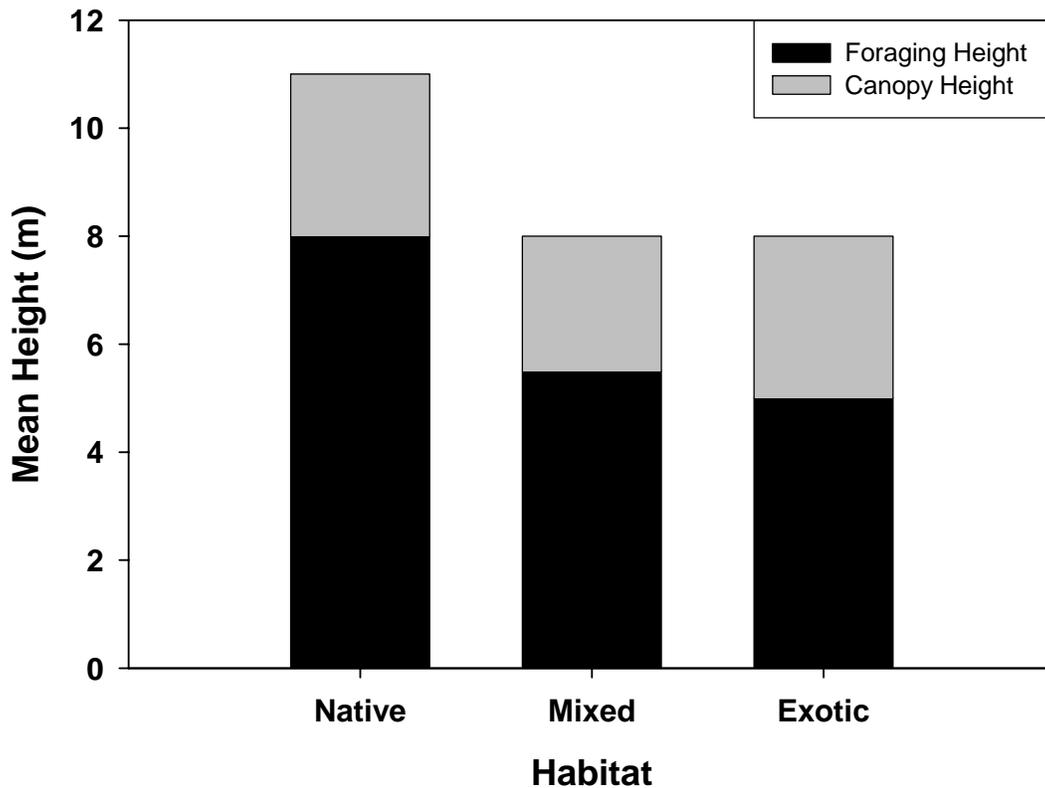


Figure 4.3. Flycatcher foraging maneuver by sex. Foraging maneuvers of male and female flycatchers did not differ ($\chi^2 = 0.10$, $p = 0.950$).

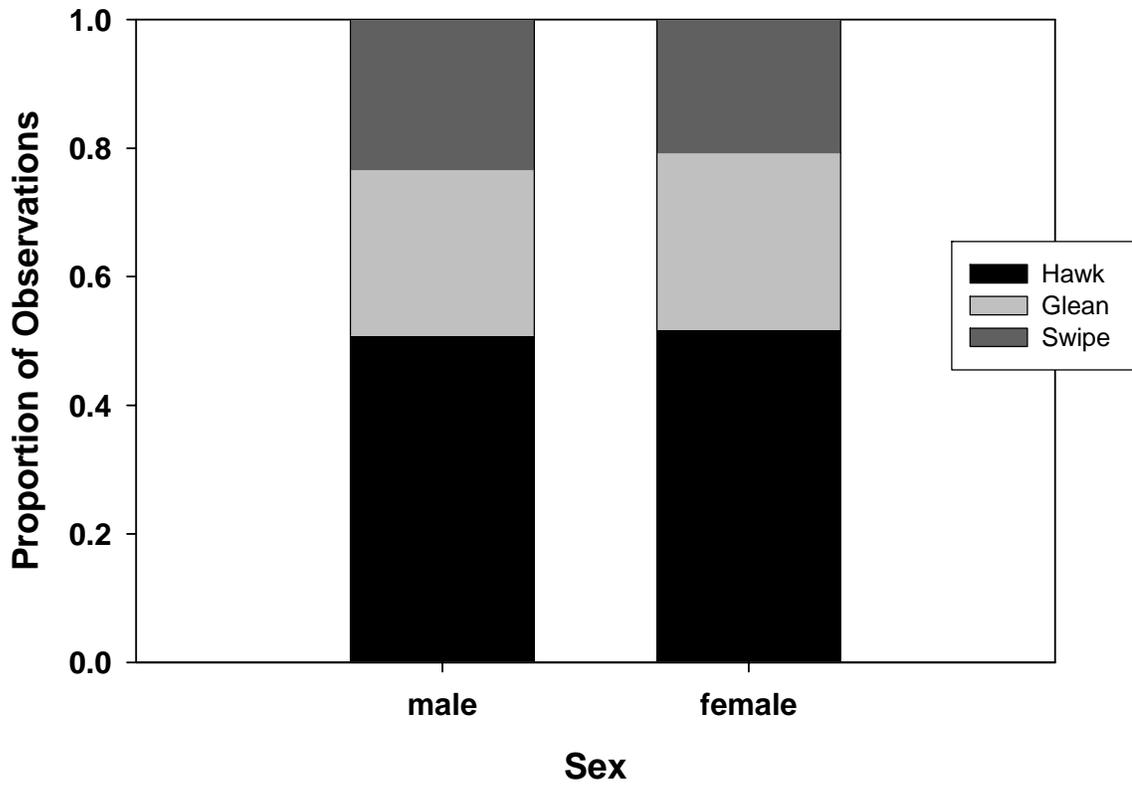
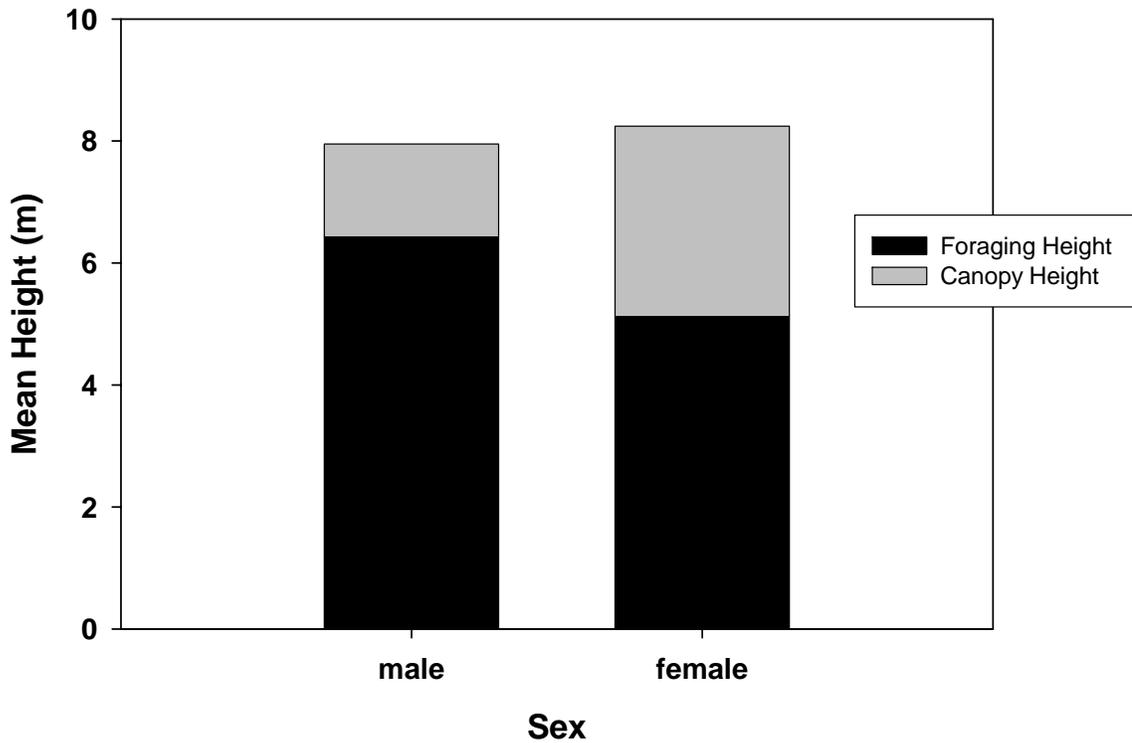


Figure 4.4. Flycatcher foraging height by sex. The height of male and female flycatcher foraging events is displayed in the dark bars and the estimated canopy height where foraging events occurred is shown with the addition of the gray bar. Relative foraging height is calculated by dividing the foraging height by the canopy height. Males foraged more than 25% higher than females in terms of absolute foraging height ($t = -3.23$, $p = 0.002$) and nearly 29% higher in relative foraging height ($t = -3.79$, $p < 0.001$).



**Chapter 5 – Comparison of Arthropod Abundance and Community
Along a Vertical Gradient: Malaise Traps on the Ground Versus in the Tree
Canopy**

Introduction

Arthropod abundance may not be correlated with arthropod prey available to a foraging insectivorous bird (Johnson 2000). All arthropods may not be considered prey items for a particular bird species (Wolda 1990), and all microhabitats may not be equally used by a particular bird species (Hutto 1990). To account for these potential discrepancies between sampled arthropod abundance and prey items taken by a particular bird species, steps should be taken to exclude items not considered prey (Cooper and Whitmore 1990). When measuring arthropod prey available to an avian insectivore, it is important to focus arthropod sampling in the microhabitats that are utilized by foraging birds (Wolda 1990). Due to variation in arthropod abundance and community composition along vertical gradients (Sutton and Hudson 1980, Sutton et al. 1983), Su and Woods (2001) have suggested that sampling along these gradients is necessary to represent the entire arthropod community. To address the potential discrepancy between arthropods found at Southwestern Willow Flycatchers foraging height (5-6m) and arthropods captured via Malaise sampling (0-1m above the ground), I conducted a one-time vertical sampling event in each of the sites originally sampled in Chapter 2.

Methods

I conducted these experiments following the final sampling period in 2003 at the same locations used for arthropod sampling described in Chapter 2. At each sampling location, I paired one Malaise trap on the ground with one hoisted 3-5m into the canopy on a telescoping pole. At all sampling locations, vertical pairs were within 5-10m of each other in areas of similar vegetation structure and composition. Due to the difficulty in accessing the canopy traps once they were in place, I sampled each site for approximately 24-hour periods. As a result, unlike the sampling protocol described in Chapter 2, these traps collected nocturnal as well as diurnal arthropods. Due to the limited number of Malaise traps available, I sampled each site on successive days. I sampled the native-dominated site on 25-26 July, mixed site on 26-27 July, and exotic site on 27-28 July. All other aspects of the vertical sampling event were identical to the protocol described in Chapter 2.

To test for the effect of sampling height on arthropod abundance, I lumped samples across the three habitats into those from canopy traps and those from ground traps. I then used a paired t-test to test for differences in morpho-species richness by sampling height. To test for differences in arthropod abundance between canopy and ground samples, I converted the total arthropod abundance to biomass (Rogers et al. 1977, Hodar 1996) as described in Chapter 2. I log-transformed total arthropod biomass to meet assumptions of homogeneity of variances and normality (Sokal and Rohlf 1995) and corrected for differential sampling times before testing for differences in total biomass by sampling height using a paired t-test. I used multivariate analysis of variance (MANOVA) to test for differences in the arthropod

abundance of major taxonomic groups (at the level of Order except in the case of Formicidae) between canopy and ground Malaise traps. I utilized a rank transformation procedure (Conover and Iman 1981) to control non-normality and heterogeneity of variances. Lastly, I compared the ranked order of the major taxonomic group captured between canopy and ground sampling (Johnson 2000). Univariate statistical tests were conducted in JMP-IN 5.1, multivariate tests were conducted in SPSS 12.0, and $\alpha = 0.05$ was used to evaluate statistical significance.

Results

Ground Malaise samples had 1.5 times greater morpho-species richness compared to the canopy Malaise traps ($t_{11} = 4.778$, $p = 0.0006$) and collected a mean of 26.8 morpho-species, versus 17.2 in canopy traps. Ground Malaise traps had over three times the total arthropod biomass per unit time compared to the canopy Malaise traps ($t_{11} = 3.1865$, $p = 0.0087$).

I found differences between canopy and ground Malaise traps ($\Lambda = 0.178$, $F_{10,13} = 5.993$, $p = 0.002$) in the abundance of three taxonomic groups: Diptera ($F_{1,22} = 29.852$, $p < 0.001$), flying Hymenoptera ($F_{1,22} = 8.373$, $p = 0.008$), and Orthoptera ($F_{1,22} = 10.812$, $p = 0.003$). In all three groups, the abundance was greater at ground level compared to the canopy. The four most commonly captured Orders were the same in both ground and canopy Malaise traps as was their rank abundance (from highest to lowest): Hymenoptera, Diptera, Homoptera, and Lepidoptera. These four Orders accounted for 95.2% and 96.0% of the total number of arthropod captured in canopy and ground vertical Malaise sampling, respectively.

Discussion

Southwestern Willow Flycatchers forage between 5-6m despite greater overall arthropod abundance, greater abundance of at least two taxonomic groups important in flycatchers' diet (Diptera and Hymenoptera) (Chapter 2), and higher morpho-species richness between ground level and 1m. While there were clearly morpho-species differences between canopy and ground Malaise traps, the degree of taxonomic resolution in the diet samples (Chapter 2) was not great enough to allow me to determine whether these differences would misrepresent habitat quality by basing sampling only on ground traps. Elevated canopy Malaise traps may provide a better representation of the abundance of arthropod prey available to Southwestern Willow Flycatchers, but of the taxonomic groups well represented in both Malaise traps and flycatchers' diet, the same Orders were found at the same rank abundance in both the canopy and ground samples.

The decision to examine the potential difference in arthropods sampled with ground level Malaise traps and at a height more representative of most flycatcher foraging events was undertaken at the very last sampling period in the last year of the study. While the study detailed in Chapter 2 may not have represented the microhabitat in which willow flycatchers most commonly forage, the vertical sampling study indicates that similar taxonomic groups in similar relative numbers were found at both 0-1 m and 3-5 m above the ground. Additionally, due to the similarity in coarse taxonomic groups captured and the similarity in the relative abundance of those groups, the benefits of extensive use of more labor-intensive

vertical sampling over the course of the season may not be worth the extra sampling effort.

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