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AGE, HABITAT, AND YEARLY VARIATION IN THE DIET OF A GENERALIST INSECTIVORE, THE SOUTHWESTERN WILLOW FLYCATCHER

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Abstract. Characterizing avian diet is complex, especially for generalist insectivores, as food resources can vary over space and time, and individuals of different sexes and ages may consume different food. We examined diet of a generalist insectivore, the Southwestern Willow Flycatcher (*Empidonax traillii extimus*), at Roosevelt Lake in central Arizona from 2000 to 2004, determined from 344 fecal samples. We found that five prey categories accounted for 70% of the proportional abundance in flycatcher diet: Hymenoptera, Diptera, Cicadellidae, Coleoptera, and Formicidae, although the relative amounts of these and other taxa differed significantly among years. We detected no differences in diet between sexes of adults, but adults and nestlings differed, with higher proportions of Hymenoptera in adult samples and more Diptera in nestling samples. Using a subset of samples, we compared flycatcher diet in habitat patches dominated by native cottonwood (*Populus fremontii*) and willow (*Salix gooddingii*), exotic salt cedar (*Tamarix ramosissima*), or a mix of these tree species. We found that prey groups varied significantly among habitats in only one year, 2002, with Araneae, Lepidoptera, and Odonata significant indicators of native habitat, Cicadellidae and Hymenoptera significant indicators of exotic habitats, and Homoptera a significant indicator of mixed habitat. In 2002, a severe drought resulted in reduced prey base and near total reproductive failure, but we detected no major shift in the composition of adult diet during that year, suggesting that for generalists like the Southwestern Willow Flycatcher, overall insect abundance may be a more important driver of productivity than abundance of specific prey taxa.

Key words: *annual variation*, Empidonax traillii extimus, *endangered species*, *food resources*, *riparian*, Tamarix.

Edad, Hábitat y Variación Anual en la Dieta del Insectívoro Generalista *Empidonax traillii extimus*

Resumen. La caracterización de la dieta de las aves es compleja, especialmente para aves insectívoras generalistas, debido a que los recursos alimenticios pueden variar en el tiempo y en el espacio, y a que los individuos de diferente sexo o edad pueden consumir diferentes tipos de alimento. Examinamos la dieta de un insectívoro generalista*, Empidonax traillii extimus*, mediante el análisis de 344 muestras fecales en el Lago Roosevelt en Arizona central, desde el año 2000 al 2004. Encontramos que cinco de nuestras doce categorías de presa dieron cuenta del 70% de la abundancia proporcional en la dieta de *E. t. extimus*: Hymenoptera, Diptera, Cicadellidae, Coleoptera y Formicidae. Sin embargo, las cantidades relativas de estos y otros taxones difirieron significativamente entre años. No detectamos diferencias en la dieta de los adultos de diferente sexo, aunque la dieta de los adultos y polluelos fue diferente, con una mayor proporción de Hymenoptera en las muestras de los adultos y más Diptera en las de los polluelos. Utilizando un subgrupo de muestras, comparamos la dieta de *E. t. extimus* en parches de hábitat dominados por las especies arbóreas nativas *Populus* spp. y *Salix* spp., la especie exótica *Tamarix* spp., o en parches compuestos por una mezcla de estas tres especies. Encontramos que los grupos de presas variaron significativamente entre los hábitats sólo en el 2002, con Araneae, Lepidoptera y Odonata como indicadores significativos de hábitats nativos, Cicadellidae e Hymenoptera como indicadores significativos de hábitats exóticos y Homoptera como indicador significativo del hábitat mixto. En 2002, hubo una sequía severa que resultó en una reducción de la disponibilidad de presas y en un fracaso reproductivo casi total, pero no detectamos cambios mayores en la composición de la dieta de los adultos durante ese año. Esto sugiere que para una especie generalista como *E. t. extimus*, la abundancia general de insectos puede ser un promotor más importante de la productividad que la abundancia de algunos taxones de presa específicos.

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INTRODUCTION

Diet can influence many aspects of a species' life history, including habitat use, physiology, survivorship, breeding success, and migration. Although critical for understanding the habitat requirements for any species, we know relatively little about the foraging ecology and diet of many birds (Rosenberg and Cooper 1990). Variation in how birds acquire food resources can be influenced by both abiotic and biotic factors including age (Wunderle 1991), sex (Selander 1966, Petit et al. 1990), and habitat structure (Robinson and Holmes 1982, Whelan 2001).

What we do know of bird diet is often based on studies with only one or a few years of data, often with data combined across years (Lockwood et al. 1997, Burger et al. 1999, Deloria-Sheffield et al. 2001, Wiesenborn and Heydon 2007), even though foraging behavior and diet can vary significantly among years (Holmes 1966, Root 1967, Busby and Sealy 1979, Rotenberry 1980, Miles 1990) or even seasonally within years (Hejl and Verner 1990, Sakai and Noon 1990). Although studies of foraging behavior and prey selection are often highlighted as a research need for effectively managing endangered species (Burger et al. 1999, Hanula et al. 2000, Deloria-Sheffield et al. 2001), these species have relatively small populations, and obtaining sufficient sample sizes to control for effects such as age, sex, and year is often difficult.

For instance, several recent studies have used fecal samples to characterize the diet of the insectivorous Southwestern Willow Flycatcher (*Empidonax traillii extimus*; DeLay et al 2002, Drost et al. 2003, Wiesenborn and Heydon 2007), a Neotropical migratory passerine restricted to breeding in riparian habitats in the southwestern United States (Sedgwick 2000) and listed as endangered in 1995 (U.S. Fish and Wildlife Service 1995). These studies confirmed that the diet of the southwestern subspecies includes an array of arthropod taxa, as had been described earlier for the species based on stomach contents collected across the entire species' range (Beal 1912, Bent 1942). However, it is not clear whether differences in flycatcher diet highlighted among these studies could be due to annual variation, differences among sites, or a combination of both factors.

For generalist insectivores like Southwestern Willow Flycatchers, the distribution and abundance of food resources likely influences foraging behavior and diet (Holmes and Schultz 1988). Annual variation in arthropod abundance could influence diet by altering the relative abundance of preferred prey items (Hejl and Verner 1990, Miles 1990, Petit et al. 1990, Szaro et al. 1990, Miller and McEwen 1995). Several studies have described arthropod abundance in Southwestern riparian habitats (Stevens 1985, Ellis et al. 2000, Wiesenborn 2005, Wiesenborn and Heydon 2007, Durst et al. 2008), and some of these have documented significant annual variation in relative arthropod abundances (Stevens 1985, Wiesenborn 2005, Durst et al. 2008). However, it remains unclear how potential temporal variation in the arthropod prey base may affect flycatcher diet or if variation in diet would have an impact on adult breeding or nestling flycatchers.

In addition to temporal variation, habitat-based differences could potentially alter the diet of Southwestern Willow Flycatchers. Throughout the southwestern United States, riparian woodlands formerly dominated by native cottonwood (*Populus* spp.) and willow (*Salix* spp.) have been replaced by exotic salt cedar (*Tamarix* spp.). Although the flycatcher breeds primarily in riparian habitats dominated by native vegetation, approximately 28% of territories are in patches dominated by exotic salt cedar (Durst et al. 2007). The loss of riparian habitat in the southwestern United States, combined with the rapid spread of exotic salt cedar into many of these riparian areas, has led to interest in how habitats dominated by exotic vegetation may affect the arthropod prey base for riparian-obligate insectivorous birds (DeLoach et al. 2000, Yard et al. 2004, Durst et al. 2008). Southwestern riparian habitats dominated by native and exotic vegetation appear to support different arthropod communities (Yard et al. 2004, Wiesenborn and Heydon 2007, Durst et al. 2008). How flycatchers may respond to any differences in the prey base in different habitats is unclear; however, some authors have suggested that salt cedar habitats have insufficient arthropod prey base for these birds (DeLoach et al. 2000).

In this paper, we examine the diet of Southwestern Willow Flycatchers by taking advantage of five years of opportunistically collected fecal samples from both adult and nestling flycatchers. We collected samples from a single breeding site made up of a mosaic of riparian habitats between 2000 and 2004 to control for spatial variation and to allow us to isolate the effects of habitat and year. We were primarily interested in testing how diet varied: (1) between adult females and males, (2) between adults and nestlings, (3) among adult samples in different habitats, and (4) across years for both adult and nestling samples.

METHODS

STUDY SITE

We conducted this study at the Salt River and Tonto Creek inflows to Roosevelt Lake in central Arizona (33°40′N, 111°58′W) during the flycatcher breeding season (May–August) from 2000 to 2004. Riparian habitat at Roosevelt Lake covered a 242 ha mosaic of patchy woodlands made up of native Goodding's willow (*Salix gooddingii*) and Fremont cottonwood (*Populus fremontii*), and exotic salt cedar (*Tamarix ramosissima*) in a broad floodplain between 632 m and 678 m in elevation. We classified riparian forest patches composed of >90% willow or cottonwood cover as native, patches with >90% salt cedar cover as exotic, and those patches with intermediate levels of willow or cottonwood and salt cedar cover as mixed. Patch boundaries were delimited by nonriparian vegetation or by patches of different riparian vegetation. The understory vegetation of all patches consisted of a variety of grasses, forbs, and shrubs (mesquite [*Prosopis* spp.], coyote willow [*S. exigua*], salt cedar, seep willow [*Baccharis salicifolia*], and cocklebur [*Xanthium strumarium*]). Uplands surrounding the riparian floodplain were classified as Sonoran Desert Arizona Upland (Brown 1994).

DIET SAMPLING

We opportunistically collected fecal samples from Southwestern Willow Flycatchers that defecated during routine bird banding activities conducted during a long-term demographic study on the breeding population at Roosevelt Lake (Paxton et al. 2007). We collected these samples from any individual that provided one at any stage of the banding process, but we did not hold birds any longer than necessary to band them in order to obtain samples. All methods of estimating diet have limitations, but fecal analysis has been used to sample avian diets in many other studies (Ralph et al. 1985, Rosenberg and Cooper 1990, Van Horne and Bader 1990, Burger et al. 1999, Deloria-Sheffield et al. 2001) and is the least intrusive direct method, an important consideration given the endangered status of this subspecies. Adult birds were captured via passive (Ralph et al. 1993) or target mist-netting (Sogge et al. 2001) and sexed based on physical characteristics, behavioral cues, or genetic analysis (Paxton et al. 2002). We obtained fecal samples from nestlings when they were banded at 7–10 days of age (Paxton and Owen 2002). We collected adult and nestling flycatcher fecal samples from the same locations within our study area in each year.

We stored fecal samples in 70% ethanol and used a Leica (Wetzlar, Germany) Stereo Zoom 6 dissecting microscope to identify and quantify arthropod fragments present in fecal samples using references by Borror et al. (1976), Bland (1978), Calver and Wooller (1982), Ralph et al. (1985), and Burger et al. (1999); as well as slides produced by Drost et al. (2003); and comparisons with macerated arthropods captured in Malaise traps at Roosevelt Lake. Because many arthropod parts detected in fecal samples were highly fragmented and difficult to identify, we generally conducted our analyses at the level of order. However, we distinguished ants (Formicidae) from other Hymenoptera (hereafter strictly referring to bees and wasps); we were also able to distinguish among Hemiptera (true bugs), Homoptera (planthoppers), and Cicadellidae (leafhoppers). We considered all juvenile arthropods (mostly caterpillars) as a single prey type, larvae. We identified 12 total types of prey types for summary and analysis: Araneae (spiders), Cicadellidae, Coloeoptera (beetles), Diptera (true flies), Formicidae, Hemiptera, Homoptera, Hymenoptera, Isopoda (pillbugs), larvae, Lepidoptera (only adult butterflies and moths), and Odonata (dragon and damsel flies). We excluded individuals identified from orders that accounted for <0.5% of the total number of individuals from analysis, as well as unidentifiable arthropod fragments. The minimum number of individuals of each taxonomic group per sample was estimated by using distinct features such as pairs of wings, paired spider fangs, mouthparts, or head capsules. To control for observer bias, a single person sorted and identified items in all fecal samples randomly across years and habitats, and scored each sample blindly.

We collected a total of 344 fecal samples from adult and nestling Southwestern Willow Flycatchers between 2000 and 2004 (Table 1). There were 23 adults that were repeatedly

TABLE 1. The number of fecal samples opportunistically collected for diet analysis from adult and nestling Southwestern Willow Flycatchers captured at Roosevelt Lake, Arizona. Samples were collected from 2000–2004 across early (May and June) and late (July and August) seasonal sampling periods in native, mixed, and exotic riparian habitats. Note that we analyzed nestling samples from mixed habitat only and excluded 2002 data from nestling analysis. We analyzed adults by sex only in mixed habitats.

		Adult							
		Total		Female		Male		Nestling	
Year	Habitat	Early	Late	Early	Late	Early	Late	Early	Late
2000	Native	6	0						
	Mixed	15	1	4	1	11	0	2	17
	Exotic	6	0						
2001	Native	2	1						
	Mixed	16	2	8	0	8	2	13	6
	Exotic	13	4						
2002	Native	18	13						
	Mixed	20	18	9	8	11	10		
	Exotic	12	0						
2003	Native	3	0						
	Mixed	15	9	8	4	7	5	23	14
	Exotic	10	0						
2004	Native	12	1						
	Mixed	28	14	10	8	18	6	9	14
	Exotic	4	0						

sampled; all other samples represented unique individuals. In some cases, the multiple samples collected from the same adults were from different years and different habitats. To test the hypothesis that individuals may have stereotyped diet preferences, we classified each sample by individual and conducted a multiresponse permutation procedure (MRPP) analysis on frequency and occurrence data. If individuals exhibit stereotyped diets, samples from the same individual should cluster together; however, there was no evidence of this for either frequency ($A = -0.15$, $P = 0.96$) or occurrence ($A = -0.13$, $P = 0.99$) data. Thus, we considered the repeated samples and all samples collected from unique individuals as independent.

The opportunistic nature of sample collection prevented us from evenly replicating samples among all factors; therefore, we used different subsets of the 344 fecal samples to produce robust tests for specific dietary questions. For example, across all years, we consistently obtained fecal samples from only mixed habitats. Samples from mixed habitats were generally collected in territories that had native and exotic components in approximately equal proportions within the territory boundary. Likewise, because of severe drought conditions at Roosevelt Lake in 2002 (National Oceanic and Atmospheric Administration 2003), flycatcher-breeding productivity reached a 10-year low (1996–2005; Paxton et al. 2007), and we sampled only three nestlings in 2002. Therefore, to test the hypothesis that diet varied between the adult sexes, we limited analyses of sex to adult samples from only mixed habitats across all years ($n = 138$). To test whether adult diet differed from nestling diet, we used only samples from mixed habitats in all years except 2002 ($n = 198$). To test the hypothesis that diet varied across habitats, we used only adult samples collected in all habitats across all years ($n = 243$), even though fecal samples were not evenly distributed across native and exotic habitats in all years. We did not use nestling samples in our habitat analyses because there were no nestling samples collected in native and exotic habitats in some years. Finally, to test for the effect of annual variation in diet, we used adult and nestling samples from only mixed habitats ($n = 138$ and $n = 98$, respectively). Because arthropod sampling at our sites indicated that aerial arthropod community changed seasonally (Durst et al. 2008), we accounted for this variation by coding samples as either early season (May and June) or late season (July and August). We were limited to these two broad seasons instead of a finer temporal scale due to constraints of sample size.

STATISTICAL ANALYSIS

We characterized Southwestern Willow Flycatcher diet by calculating both the frequency and occurrence of each of the 12 prey types. We defined the frequency of a prey type in an individual diet sample as the total number of items of that type (number of individuals of that prey type) divided by the total number of items (total number of all prey individuals) in that sample (Rosenberg and Cooper 1990). Frequency therefore reflected the proportional abundance of prey types in each sample. For example, a fecal sample containing three Diptera and two Hymenoptera would have a frequency of 0.6 for Diptera and 0.4 for Hymenoptera. In the case of Lepidoptera, we frequently encountered wing scales as the only diagnostic feature. Because we could not deduce the number of Lepidoptera present in these samples, we counted them as a single prey item and thus may have underrepresented Lepidoptera in our frequency measures. We defined occurrence of a given prey type as proportion of samples that contained at least one individual of that prey type (Root 1967, Rosenberg and Cooper 1990). Occurrence can be thought of as a measure of the commonness of a prey type. For example, if we detected Diptera in 8 and Hymenoptera in 6 of 10 fecal samples, the occurrence of Diptera would be 0.8 and Hymenoptera 0.6. Frequency can be biased when a small percentage of samples have very large numbers of a particular prey type compared to others, potentially emphasizing differences among samples. Occurrence does not account for the differences in the relative number of individual prey types within a sample, potentially resulting in samples appearing more similar. Because of these contrasting biases, we analyzed both of these parameters.

Because the matrix of prey types in a diet sample represented the arthropod community as "sampled" by Southwestern Willow Flycatchers over some period of time before we collected a fecal sample, we adopted a community analysis approach based on both frequency and occurrence data to explore patterns and test hypotheses about Southwestern Willow Flycatcher diet. As a first layer of analysis, we used multiway multivariate analysis of variance (MANOVA) to test for the effects of: (1) adult sex, season, year, and their interaction using samples only from mixed habitats; (2) age, season, year, and their interaction using samples only from mixed habitats (excluding 2002); and (3) habitat, season, year, and their interaction using only adult samples. We used nonmetric multidimensional scaling (NMS; Kruskal 1964, Mather 1976) axis scores, representing the degree of dissimilarity among samples, as response variables in a MANOVA framework (DiMiceli 2006). We created a Bray-Curtis distance dissimilarity matrix based on the distribution of different prey types in all 344 diet samples for both the frequency and occurrence datasets. Multiple iterations of these dissimilarity matrices were run to obtain a configuration of points in ordination space with minimal stress that best represented the actual degree of dissimilarity between each diet sample based on each data matrix separately (frequency and occurrence). In an effort to normalize the community data matrices, improve homogeneity of variance, and reduce ordination stress, we used arcsin square root (Sokal and Rohlf 1995) and Beals smoothing (McCune 1994) to transform the frequency and occurrence datasets, respectively. Rather than use the axis scores to produce a graphical representation of the dissimilarity among diet samples coded by groups or factors of interest, we opted to use these axis scores from the ordination as response variables in the MANOVA to test the hypotheses detailed above. Although NMS axis scores were not always normally distributed with homogeneous variance, MANOVA is relatively robust to deviations in these assumptions (Rencher 1995).

As a secondary analysis to explore patterns revealed in the MANOVA, we used nonparametric multiresponse permutation procedure (MRPP) to test for one-way, between group differences in: (1) age, (2) habitat within each year, and (3) year for adults and nestlings separately, using the frequency and occurrence community matrices rather than the axis scores produced from the NMS. We rank-transformed the Bray-Curtis dissimilarity matrices of arcsin square root–transformed frequency and Beals smoothing occurrence data. In addition to calculating a *P*-value for the MRPP analysis, we evaluated an effect size based on the chance corrected within-group agreement (A) for all comparisons within and across year, such that when $A = 1$, all within-group samples are identical; when $A = 0$, within-group heterogeneity equals that expected by chance; and when $A < 0$, there is less within-group heterogeneity than expected by chance (Zimmerman et al. 1985).

As a third layer of analysis to determine the types of prey items responsible for driving diet patterns observed in the MANOVA and MRPP analysis, we conducted an indicator species analysis. We used the arcsin square root– and Beals smoothing–transformed frequency and occurrence matrices, respectively, to obtain indicator species values (INDVAL). An INDVAL is based on specificity (the relative abundance of each morphospecies in each group or factor) and fidelity (the relative frequency of each morphospecies in each group or factor; Dufrêne and Legendre 1997), and thus incorporates both frequency and occurrence measures. A Monte Carlo randomization method was used to determine significant indicator species (for age, habitat, and year comparisons) by randomly assigning sampling units 1000 times, calculating an INDVAL and comparing the proportion of randomized INDVALs that were equal to or greater than the INDVAL from the transformed datasets to arrive at a *P*-value. We report only significant indicator species that had INDVAL > 25. Statistical significance for all tests was set at $\alpha = 0.05$. We conducted MANOVA using SPSS Version 15 (SPSS 2006), and MRPP and indicator species analysis using PC-ORD Version 4.41 (McCune and Mefford 1999). We present results of statistical analyses based on both frequency and occurrence data, but because these results generally agreed, we present graphs only for frequency-based data and note instances where the two measures differed.

RESULTS

In 344 diet samples we collected from Southwestern Willow Flycatchers, we identified 2713 total prey items. Hymenoptera (frequency = 0.19), Diptera (0.15), Cicadellidae (0.12), Coleoptera (0.12), and Formicidae (0.12) accounted for the greatest proportional abundance of prey types across all diet samples, and together represented 70% of identified prey items. Hymenoptera (occurrence = 0.71), Diptera (0.62), Coleoptera (0.61), Araneae (0.47), Homoptera (0.35), and Lepidoptera (0.33) were the six most commonly found prey types and occurred in at least one third of fecal samples. We were able to identify approximately 70% of fragments in fecal samples; the remainder was made up of unidentifiable arthropod parts and plant material.

We found that a three-dimensional solution was the most appropriate NMS ordination for both frequency (final stress = 22.7) and occurrence (final stress = 14.3) data for all 344 samples. The three-dimensional solution explained 75% and 88% of the total variation based on the distance between points in ordination space and the original data for frequency and occurrence matrices, respectively (frequency: axis 1 $r^2 = 0.33$, axis 2 $r^2 = 0.21$, axis 3 $r^2 = 0.21$; occurrence: axis 1 $r^2 = 0.32$, axis 2 $r^2 = 0.20$, axis 3 $r^2 = 0.36$).

ADULT SEX

We did not find differences in diet by sex for 138 samples (60 females and 78 males; Table 1) collected from adult flycatchers in mixed habitats, as indicated by the MANOVA, for either frequency or occurrence, although we did find a strong sex by season interaction and a weak effect of season (Table 2). We suspected that these seasonal effects were likely due to the uneven distribution of female and male samples by season within each year (Table 1). Because the MANOVA indicated that there was no difference in diet by sex, we did not conduct MRPP or indicator species analysis by sex, and we did not consider adult sex as a factor in subsequent analyses.

AGE

We tested for differences between adult and nestling diet using 198 samples (100 adult, 98 nestling) collected only in mixed habitats and excluded data from 2002 because of the limited number of nestling samples collected in that year (Table 1). We found no significant interactions but did detect a significant difference between adult and nestling diet based on both frequency and occurrence data in the MANOVA (Table 2). This difference was also apparent in the MRPP analysis (Table 3). Formicidae and Hymenoptera were significant indicators of adult diet, while Diptera, Hemiptera, and Lepidoptera were significant indicators of nestling diet (Table 4). The greatest difference in mean frequency of prey items between adult and nestling diet was in Diptera (adults = 0.15 vs. nestlings = 0.24; Fig. 1) and Hymenoptera (adults = 0.29 vs. nestlings = 0.14; Fig. 1). Formicidae had higher occurrence in adult compared to nestling samples (0.29 vs. 0.20). The occurrence of Hemiptera and Lepidoptera was higher in nestling compared to adult samples (0.43 vs. 0.22, and 0.46 vs. 0.21, respectively).

TABLE 2. We analyzed three nonmetric multidimensional scaling (NMS) axis scores based on 12 prey types in Southwestern Willow Flycatcher fecal samples at Roosevelt Lake, Arizona, from 2000 to 2004, with MANOVA. The analysis was on axis scores for both frequency and occurrence data, with frequency of a prey type in an individual fecal sample defined as the total number of items of a given prey type divided by the total number of all prey items in that sample. Occurrence of a given prey type was defined as the proportion of samples that contained at least one individual of that prey type. We tested for dietary differences: (1) between adult females and males ($n = 138$), (2) between adults and nestlings ($n = 198$), and (3) among native, mixed, and exotic habitats only for adult samples ($n = 243$). We considered year and season effects, and interactions with each of these main effects.

		Occurrence			Frequency		
Factors		*F*	df	*P*	*F*	df	*P*
Sex	Year∗sex∗season	1.2	6,236	0.33	1.4	6,236	0.23
	Sex∗season	4.9	3,118	0.003	5.1	3,118	0.002
	Year∗season	0.3	12,312	0.99	0.4	12,312	0.97
	Year∗sex	0.7	12,312	0.76	1.0	12,312	0.48
	Season	2.5	3,118	0.06	2.9	3,118	0.04
	Sex	0.7	3,118	0.56	0.4	3,118	0.74
	Year	1.2	12,312	0.31	1.3	12,312	0.21
Age	Year∗age∗season	0.3	9,438	0.97	0.5	9,438	0.90
	Age∗season	2.4	3,180	0.07	1.8	3,180	0.14
	Year∗season	0.7	9,438	0.75	0.8	9,438	0.58
	Year∗age	1.1	9,438	0.38	1.0	9,438	0.41
	Season	1.2	3,180	0.30	1.9	3,180	0.13
	Age	7.9	3,180	<0.001	5.9	3,180	0.001
	Year	1.8	9,438	0.07	2.1	9,438	0.03
Habitat	Year∗habitat∗season	0.9	6,434	0.47	1.4	6,434	0.20
	Habitat∗season	0.9	6,434	0.48	0.9	6,434	0.46
	Year∗season	0.8	12,574	0.66	0.7	12,574	0.70
	Year∗habitat	1.4	24,630	0.08	1.6	24,630	0.04
	Season	0.9	3,217	0.46	1.6	3,217	0.19
	Habitat	1.8	6,434	0.10	1.8	6,434	0.11
	Year	0.9	12,574	0.56	1.3	12,574	0.22

HABITAT

We tested for the effect of habitat on adult Southwestern Willow Flycatcher diet using 243 samples that we collected in native, mixed, and exotic habitats from 2000 to 2004 (Table 1). While all three habitats were not well represented in all years, we found a marginal interaction between year and habitat in frequency data but no differences by habitat, year, season, or the other interactions that included habitat measured with either metric in our MANOVA (Table 2). Because of the interaction between year and habitat, we conducted MRPP analysis by habitat within each year. We found differences in flycatcher diet among native, mixed, and exotic habitats only in 2002 (Table 3), the only year where all three habitats were well represented (Table 1). In 2002, Araneae, Lepidoptera, and Odonata were significant indicators of native habitat, Homoptera was a significant indicator for mixed habitat, and Cicadellidae and Hymenoptera were significant indicators of exotic habitats (Table 4). Araneae, Lepidoptera, and Odonata were more frequent in diets from native habitat compared to mixed and exotic habitats (Fig. 2). Cicadellidae were more frequent in samples from exotic habitats compared to native and mixed habitats (Fig. 2). Although they did not differ greatly in terms of frequency, Homoptera and Hymenoptera were most common in samples in mixed and exotic habitats, respectively. Occurrence of Homoptera was 0.58 in mixed habitats, but only 0.25 in exotic and 0.13 in native habitats. Occurrence of Hymenoptera in exotic habitats was 0.92, but only 0.68 and 0.52 in mixed and exotic habitats, respectively.

TEMPORAL

Because there was a significant effect of year in the age analysis and a marginal interaction between habitat and year using the frequency data in the MANOVA, we used MRPP analyses to investigate differences in diet by year for adults and nestlings separately, using only samples collected in mixed habitats (138 adults, 98 nestlings, excluding data from 2002; Table 1). We found significant differences in both adult and nestling diet by year (Table 3). For adults, Hymenoptera and Diptera were significant indicators of 2000 and 2001, respectively (Table 4), and were most frequent in adult diets in those years (Fig. 3). For nestlings, Lepidoptera, Hymenoptera, and Hemiptera were significant indicators of 2000, 2001, and, 2004 respectively (Table 4). Lepidoptera was most frequent in nestling samples in 2000 (Fig. 4). While there appeared to be little difference in the frequency of Hemiptera and Hymenoptera in nestling diet by year (Fig. 4), Hemiptera had the greatest occurrence in nestling diet

TABLE 3. We conducted multiresponse permutation procedure (MRPP) analysis based on 12 prey types in Southwestern Willow Flycatcher fecal samples at Roosevelt Lake, Arizona, from 2000 to 2004. Both frequency (the total number of items of a given prey type divided by the total number of all prey items in a fecal sample) and occurrence (the proportion of samples that contained at least one individual of that prey type) data were used to conduct the analysis. In addition to the *P*-value, the MRPP provided an effect size based on the chance corrected within-group agreement (*A*) for all comparisons within and across years, such that when $A = 1$, all within-group samples are identical; when $A = 0$, within-group heterogeneity equals that expected by chance; and when $A < 0$, there is less within-group heterogeneity than expected by chance. We tested for dietary differences: (1) between adult females and males across all years from samples only in mixed habitats ($n = 138$), (2) between adults and nesting across all years except 2002 in only mixed habitats ($n = 198$), (3) among native, mixed, and exotic habitats within each year for adult samples ($n = 243$), and (4) among year in mixed habitats for adults and nestlings separately ($n = 236$).

		Frequency		Occurrence	
Factor		*A*	*P*	*A*	*P*
Sex		0.005	0.13	0.013	0.02
Age		0.037	<0.001	0.027	<0.001
Habitat	2000	0.040	0.10	0.026	0.17
	2001	–0.010	0.60	–0.010	0.66
	2002	0.104	<0.001	0.107	<0.001
	2003	0.005	0.39	0.012	0.30
	2004	0.019	0.14	0.004	0.35
Year	Adult	0.060	<0.001	0.042	<0.001
	Nestling	0.083	<0.001	0.094	<0.001

in 2004 (0.70 compared to 0.53 in 2001, the next-highest year), and Hymenoptera had the greatest occurrence in nestling diet in 2001 (0.84, only slightly more than 0.78 in 2004).

DISCUSSION

Our study highlights important sources of variation in the diet of Southwestern Willow Flycatchers, but because our study covered five years, we are able to make generalizations about flycatcher diet. We found that only 5 of 12 prey categories accounted for 70% of the proportional abundance in flycatcher diet. The similar annual proportional abundance of these five prey types indicated that each group had approximately equal relative importance to Southwestern Willow Flycatchers breeding at Roosevelt Lake over these five years. Some prey types such as Cicadellidae and Formicidae were consumed in high proportional abundance but not in high occurrence in flycatcher diet, indicating that a few individuals consumed large numbers of these prey items. The high frequency and low occurrence of these prey types was likely due to their small size and aggregated distribution in the environment. For example, the tamarisk leafhopper (*Opsius stagtogalus*) is small and is patchily distributed but occurs in high abundance in salt cedar dominated habitats (Wiesenborn 2005).

TABLE 4. We conducted indicator species analysis based on 12 prey types in Southwestern Willow Flycatcher fecal samples at Roosevelt Lake, Arizona, from 2000 to 2004. Indicator species analysis obtains indicator species values (INDVAL) based on the relative abundance of each morphospecies in each group or factor and the relative frequency of each morphospecies in each group or factor. Significant indicator species ($P < 0.05$) were determined from Monte Carlo randomization by randomly assigning sampling units 1000 times, recalculating an INDVAL, and comparing the proportion of randomized INDVALs that were equal to or greater than the original INDVAL. We report only significant indicator species that had INDVAL > 25. We conducted indicator species analysis using both (A) frequency (the total number of items of a given prey type divided by the total number of all prey items in that sample) and (B) occurrence (the proportion of samples that contained at least one individual of that prey type) data. We used indicator species analysis to determine significant prey groups for: (1) adult or nesting for age analysis, (2) native, mixed, or exotic for habitat analysis in 2002, and (3) and year for adults and nestlings separately.

Factor	Group	Prey type	INDVAL	*P*
(A)				
Age	Adult	Hymenoptera	49.8	0.007
	Nestling	Diptera	50.8	0.001
	Nestling	Hemiptera	25.2	0.02
	Nestling	Lepidoptera	30.1	0.002
2002 habitat	Native	Araneae	37.0	0.02
	Exotic	Cicadellidae	38.9	0.002
	Mixed	Homoptera	31.8	0.03
	Native	Lepidoptera	47.5	0.001
Year: adult	2001	Diptera	28.7	0.004
	2000	Hymenoptera	29.4	0.003
Year: nestling	2000	Lepidoptera	51.5	0.001
(B)				
Age	Adult	Formicidae	53.1	0.008
	Adult	Hymenoptera	51.0	0.001
	Nestling	Diptera	51.2	0.001
	Nestling	Hemiptera	51.4	0.03
	Nestling	Lepidoptera	52.3	0.001
2002 habitat	Native	Araneae	35.6	0.01
	Exotic	Cicadellidae	41.3	0.008
	Mixed	Homoptera	38.1	0.02
	Exotic	Hymenoptera	34.8	0.04
	Native	Lepidoptera	42.9	0.003
	Native	Odonata	46.8	0.21
Year: nestling	2004	Hemiptera	26.8	0.05
	2001	Hymenoptera	25.8	0.009
	2000	Lepidoptera	30.0	0.001

The diversity of arthropod prey in flycatcher diet that we observed at Roosevelt Lake is generally consistent with results of other studies (Beal 1912, Bent 1942, DeLay et al. 2002, Drost et al. 2003, Wiesenborn and Heydon 2007) although some site-specific differences were evident. Our study differs from these primarily in that we rarely encountered Odonata and larvae across five years of sampling, although both of these prey were important at similar habitats in central Arizona (U.S. Geological Survey, unpubl. data), and Odonata

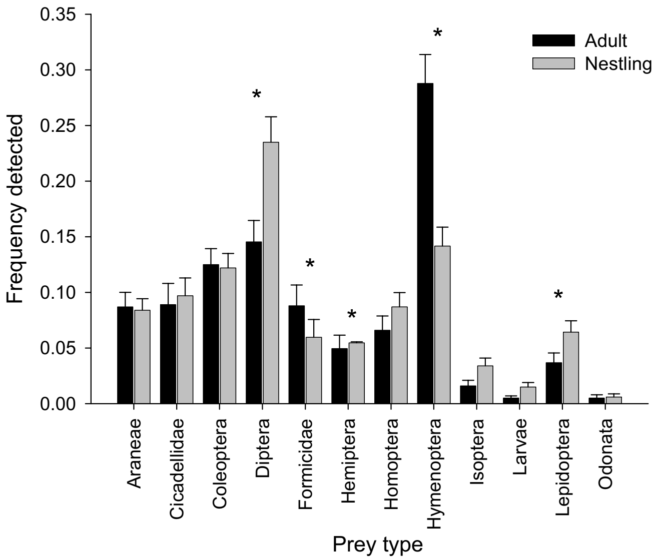

FIGURE 1. Mean diet frequency of 12 prey groups for adult (*n* = 100) and nestling (*n* = 98) Southwestern Willow Flycatchers at Roosevelt Lake, Arizona, from 2000 to 2004. We defined the frequency of a prey type in an individual fecal sample as the total number of items of that prey type divided by the total number of all prey items in that sample. We distinguished Formicidae from other Hymenoptera, and we considered all juvenile arthropods as a single prey type, larvae. Asterisks denote significant species by age based on indicator species analysis ($P < 0.05$). Error bars represent SE.

were frequently consumed along the Colorado River (Wiesenborn and Heydon 2007).

The lack of differences by sex in adult flycatcher diet is consistent with other recent flycatcher diet studies (DeLay et al. 2002, Drost et al. 2003, Wiesenborn and Heydon 2007). Previous studies specific to Southwestern Willow Flycatchers found no differences by sex in the proportion of different foraging maneuvers, although there was evidence that males forage higher in tree canopy than females (SWCA Inc., unpubl. data, Durst 2004). If these foraging differences result in differences in diet, they apparently do so at finer taxonomic levels of resolution than we were able to address. Given the slight sexual size dimorphism in this species (Sedgwick 2000), we may not expect strong differences between the diets of female and male Southwestern Willow Flycatchers, in contrast to species with more marked sexual size dimorphism (Selander 1966).

The age-based differences in diet we documented were driven primarily by higher frequency and occurrence of Diptera and lower frequency and occurrence of Hymenoptera in nestling diet relative to that of adults. In addition, Hemiptera and Lepidoptera appeared more common in nestling diet, although they did not account for a large proportion of it. Differences between adult and nestling diet are often attributed to differing dietary requirements of rapidly growing nestlings (Newton 1967). Although reported as important in the diet of nestling insectivorous birds (Darveau et al. 1993, Greenberg 1995), larvae were consistently rare in both adult and nestling samples at our site. Araneae have been argued to be important for nestling growth in some passerine species (Ramsay and Houston 2003, Wiesenborn and Heydon 2007), presumably because of the high concentration of amino acids in Araneae compared to other arthropods (Ramsay and Houston 2003); however, we found no evidence that Araneae were more prevalent in flycatcher nestling diet. We did not have any way to assess the ecology of the Diptera that were more frequent in nestling diet to determine whether they were predatory and therefore more likely to be rich in protein content compared to herbivorous prey (Fagen et al. 2002). One caveat of our data is that they reflected nestling diet near the end of the nestling stage, and other diet items may have been important at earlier stages of development, as nestling diet may change as nestlings mature and dietary demands shift (Cowie and Hinsley 1988).

Although Malaise-trap sampling indicated that arthropod communities at our study site varied among riparian habitats in 2002, 2003, and 2004 (Durst 2004, Durst et al. 2008), we detected differences in Southwestern Willow Flycatcher diet among native, mixed, and exotic habitats in only one year, 2002. The greatest diet differences in both frequency and occurrence

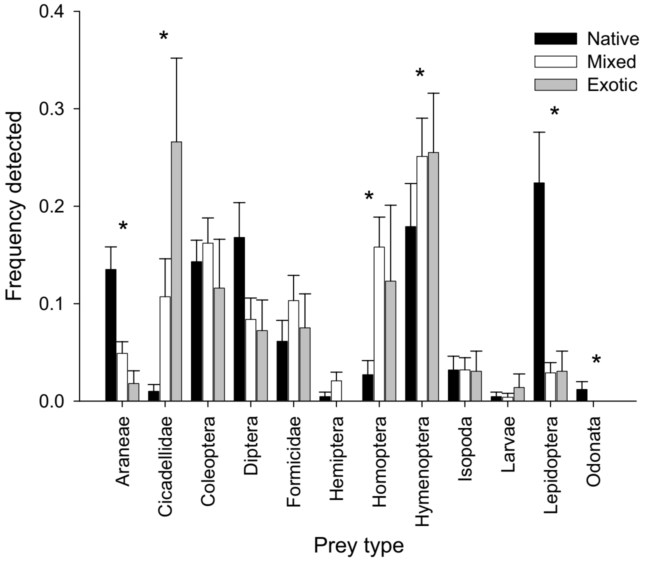

FIGURE 2. Mean diet frequency of 12 prey groups among native, mixed, and exotic habitats from adult Southwestern Willow Flycatchers at Roosevelt Lake, Arizona in 2002 (*n* = 81). We defined the frequency of a prey type in an individual fecal sample as the total number of items of that prey type divided by the total number of all prey items in that sample. We distinguished Formicidae from other Hymenoptera, and we considered all juvenile arthropods as a single prey type, larvae. Asterisks denote significant species by habitat based on indicator species analysis ($P < 0.05$). Error bars represent SE.

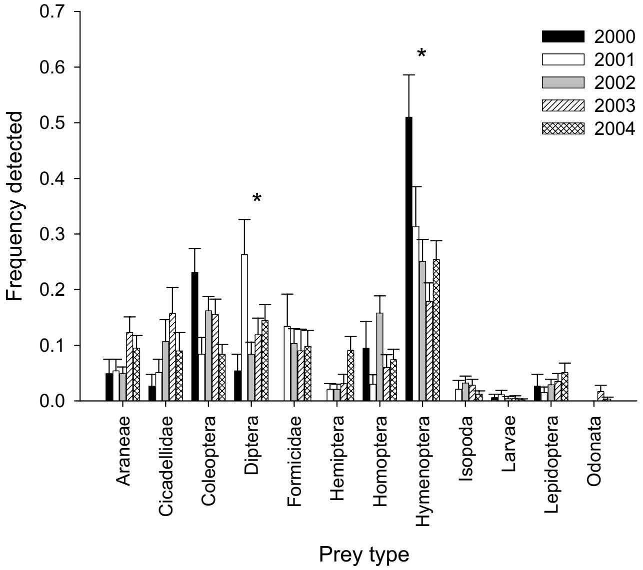

FIGURE 3. Mean diet frequency of 12 prey groups by year from adult Southwestern Willow Flycatchers in mixed habitat (*n* = 138) at Roosevelt Lake, Arizona, from 2000 to 2004. We defined the frequency of a prey type in an individual fecal sample as the total number of items of that prey type divided by the total number of all prey items in that sample. We distinguished Formicidae from other Hymenoptera, and we considered all juvenile arthropods as a single prey type, larvae. Asterisks denote significant species by year based on indicator species analysis ($P < 0.05$). Error bars represent SE.

by habitat in 2002 were that Araneae and Lepidoptera were more prevalent in native habitats and Cicadellidae in exotic habitats. These differences are consistent with other studies that found salt cedar-dominated habitats had higher levels of Cicadellidae in avian diet, apparently driven in part by the salt cedar-obligate tamarisk leafhopper (Yard et al. 2004, Weisenborn and Heydon 2007). Additionally, Weisenborn and Heydon (2007) found differences in flycatcher diet in a single year among three sites with varying proportion of salt cedar and suggested that arthropods in Southwestern Willow Flycatcher diet were more similar to those found on native vegetation compared to exotic salt cedar. This finding could indicate that the diet of birds in mixed habitats in our study should be intermediate to diets in purely native and exotic habitats; however, if there is any trend towards this, we detected differences in diet among these habitats in only one of five years. A caveat of our habitat comparisons was that we collected the largest number of samples across all three habitats in 2002; thus, 2002 was the year when we were most likely to be able to detect differences. However, even if there were differences in diet among habitats across multiple years, these potential differences do not appear to have consequences on the physiological condition (Owen et al. 2005) or breeding productivity (Paxton et al. 2007) of adult Southwestern Willow Flycatchers in native, mixed, or exotic habitats. While generalists like Southwestern Willow Flycatchers may tolerate substantial variation in relative prey abundance among different habitats, this may not be the case for avian species that have more restricted diets. Thus, differences in the arthropod community between native willow– and exotic salt cedar–dominated habitats could affect riparian obligate species differentially depending on their ability to exploit arthropod prey resources associated with salt cedar.

At Roosevelt Lake, Malaise trapping from 2002 to 2004 revealed a five-fold difference in arthropod biomass between a severe drought year in 2002 and 2003, and a halving of arthropod species richness from 2003 to another, milder drought year in 2004 (Durst 2004, Durst et al. 2008). This variation in the relative abundance of preferred prey items across years has often been argued to result in annual variation in the diet of insectivorous birds (Hejl and Verner 1990, Miles 1990, Szaro et al. 1990, Petit et al. 1990, Miller and McEwen 1995). However, in spite of these significant differences in both arthropod abundance and diversity, overall diet composition from 2002 and 2004 was within the range of variation documented in other years. Thus, we did not see dramatic changes in flycatcher diet patterns, at least at the taxonomic level of resolution we were able to assess, that corresponded to what were evidently major environmental perturbations leading to the two lowest breeding success rates (2002 and 2004) over a 10-year period from 1996

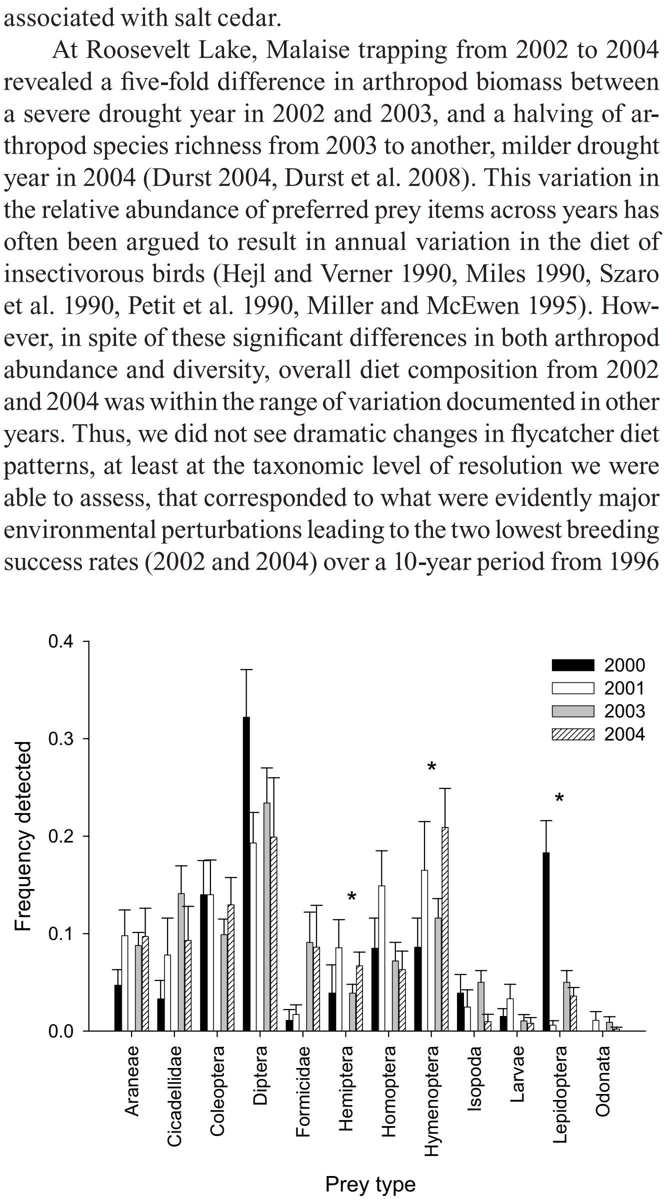

FIGURE 4. Mean frequency of 12 prey groups by year from nestling Southwestern Willow Flycatchers in mixed habitat (*n* = 98) at Roosevelt Lake, Arizona, from 2000 to 2004 (excluding 2002). We defined the frequency of a prey type in an individual fecal sample as the total number of items of that prey type divided by the total number of all prey items in that sample. We distinguished Formicidae from other Hymenoptera, and we considered all juvenile arthropods as a single prey type, larvae. Asterisks denote significant species by year based on indicator species analysis ($P < 0.05$). Error bars represent SE.

to 2005 (Paxton et al. 2007). This discrepancy could be due to failure of estimates of arthropod abundance to accurately reflect the potential prey base for avian insectivores (Hutto 1990, Wolda 1990) and highlights the challenges of linking prey availability to the diet composition of generalist insectivores that use a variety of foraging methods and exploit arthropods inhabiting various microsites. Alternatively, it could reflect the relative plasticity in diet of a generalist insectivore like the Southwestern Willow Flycatcher that has evolved to exploit the variable arthropod resources typical of dynamic riparian systems. If so, it underscores that events that influence the overall abundance of arthropods, such as regional droughts or the conversion of riparian habitat to agricultural or urban landscapes, may be critical drivers of productivity for generalists such as Willow Flycatchers.

Our study highlights the challenges of describing diet for generalist insectivores, especially those with small population sizes that inhabit habitats where food resources are likely to vary significantly among years. One challenge of such studies is obtaining sufficient samples to make valid inferences, and though the sample sizes used in our study for each year are often small, they are comparable, or considerably larger in some years, to those used in several other published studies of diet (Burger et al 1999, Deloria-Sheffield et al. 2001, Drost et al. 2003, Wiesenborn and Heydon 2007). Based on our findings, we make several recommendations for future studies. First, given the potential for annual variation in diet at even a single site, long-term data should be used in evaluating diet whenever possible. Most avian conservation management decisions are frequently based on data from a single year or multiple years pooled together (Marzluff and Sallabanks 1998), and our data demonstrate that this could be misleading for generalist species like Southwestern Willow Flycatchers. Second, sample sizes of each age and sex category should be clearly stated in the results, especially if samples are pooled, so that the potential for one age or sex category to drive the pattern in any one year can be assessed. Third, assessments of habitat quality based on dietary analyses, either within or across locations, should be tempered with an appreciation of how annual variation can confound these comparisons. Overall, our study concurs with several others that have cautioned about the potential for oversimplification or misrepresentation of general patterns in habitat use (Schooley 1994, Morrison et al. 1998, Lõhmus 2003) and in avian foraging and diet patterns (Hejl and Verner 1990, Miles 1990, Petit et al. 1990, Szaro et al. 1990) when annual variation is not considered.

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