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FOOD HABITS OF THE SOUTHWESTERN WILLOW FLYCATCHER DURING THE NESTING SEASON

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Abstract. The food habits and prey base of the endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*) are not well known. We analyzed prey remains in 59 fecal samples from an intensively-studied population of this flycatcher at the Kern River Preserve in southern California. These samples were collected during the nesting season in 1996 and 1997 from adults caught in mist nets, and from nestlings temporarily removed from the nest for banding. A total of 379 prey individuals were identified in the samples. Dominant prey taxa, both in total numbers and in percent occurrence, were true bugs (Hemiptera), flies (Diptera), and beetles (Coleoptera). Leafhoppers (Homoptera: Cicadellidae), spiders (Araneae), bees and wasps (Hymenoptera), and dragonflies and damselflies (Odonata) were also common items. Diet composition was significantly different between years, due to a large difference in the numbers of spiders between 1996 and 1997. There was also a significant difference between the diet of young and adults, with the diet of young birds having significantly higher numbers of odonates and beetles. There was a trend toward diet differences between males and females, but this was not significant at the $P = 0.05$ level.

Key Words: diet; *Empidonax traillii extimus;* fecal sacs; invertebrates; nestlings; Southwestern Willow Flycatcher.

One aspect of the ecology of the Southwestern Willow Flycatcher (*Empidonax traillii extimus*) that has received relatively little study is diet and feeding ecology. Earlier studies (e.g., Beal 1912, Bent 1942, McCabe 1991) provide information on the diet of Willow Flycatchers across their entire North American range, but do not present specific data on the southwestern subspecies. In addition, these sources present diet information in general terms, such as percentage of prey by different insect orders. We analyzed the contents of fecal samples collected from an intensively-studied Southwestern Willow Flycatcher population along the Kern River in southern California in order to (1) provide a detailed analysis of food habits and prey species during the nesting season; (2) compare food habits between years, at different times of the nesting season, and between adults and nestlings; and (3) relate patterns at the Kern River to published flycatcher diet data from outside of the Southwest. By identifying important categories of prey and the breadth of the diet, we can better understand this part of the flycatcher's ecological requirements, and evaluate potential threats to Willow Flycatchers and their prey base.

STUDY AREA

One of the largest and best-studied populations of the Southwestern Willow Flycatcher is at the Kern River Preserve in Kern County, southern California (Whitfield et al. 1999a). The Preserve is managed by the National Audubon Society and is comprised of approximately 500 ha of native cottonwood–willow riparian habitat along the South Fork of the Kern River near Lake Isabella. Elevation at the site is approximately 750 m. The breeding flycatcher population is spread out over several areas in the preserve, with vegetative cover in these areas consisting of a diverse mosaic of predominantly native vegetation, including mature red willow (*Salix laevigata*) and Fremont cottonwood (*Populus fremontii*), interspersed with small marshes dominated by cattail (*Typha* sp.), tule (*Scirpus* sp.), and bur-reed (*Sparganium eurycarpum*). One large portion of the site is dominated by young Gooding's willows (*Salix gooddingii*) established between 1983 and 1986, after the removal of cattle from the site. This part of the site is periodically inundated by Lake Isabella.

METHODS

COLLECTION AND HANDLING OF SAMPLES

Fecal samples were collected by field crew members during the 1996 and 1997 nesting seasons (June–August), when birds ''voluntarily'' provided them. Samples were obtained both from adult birds caught in mist-nets, and from nestlings that were handled during weighing and banding. Fecal samples were collected into plastic vials containing 70% ethanol, and the vials were then labeled with area name, date, and identifying reference to the bird that provided the sample (usually the number from the Federal bird band). Blood samples were also taken from birds during handling by means of a toenail clip. All samples (blood and fecal) were sent to the Colorado Plateau Field Station (CPFS) at Northern Arizona University for analysis.

Sex of birds was determined by molecular genetic analysis of the blood samples (Griffiths et al. 1996), conducted at the genetics lab of Dr. Paul Keim at Northern Arizona University. Fecal samples were sorted and organized at CPFS, and alcohol levels topped off as needed. Each sample was assigned a unique, sequential number, and sample number, date, site, band number, age and sex of bird, and any explanatory notes were entered into a database.

SORTING, IDENTIFICATION, AND QUANTIFICATION

Individual samples were transferred to microscope dishes containing 70% ethanol, then teased apart under a variable-power (7–40x) dissecting microscope. Body fragments, wings or wing fragments, legs, head capsules, and sometimes whole invertebrates were separated out of the fecal sample and identified to the lowest taxonomic level possible (generally order or family) with the aid of standard invertebrate taxonomy literature. Important general references used were Borror et al. (1976), Kaston (1978), Thorp and Covich (1991), and Arnett (1993). Specialized references for particular groups included: Merritt and Cummins (1996) for aquatic invertebrates; Osborn (1912) for leafhoppers; Arnett (1973) for beetles; Cole (1969) and McAlpine et al. (1981) for flies; and Stephen et al. (1969), Goulet and Huber (1993), and Michener et al. (1994) for bees, wasps and other hymenopterans. Brodsky (1994) and Grodnitsky (1999) were useful for wings and wing venation. In addition to literature sources, we also compared food sample fragments with reference invertebrate collections at the Colorado Plateau Museum of Arthropod Biodiversity at Northern Arizona University.

Fragments from each sample were sorted into groups that were recognizably from the same invertebrate taxon. This aided in the identification process, and also facilitated counting the number of each prey taxon. For each group of fragments, we tabulated the minimum number of individuals required to account for the fragments present in the sample. The count was generally based either on head capsules, wings, terminal abdominal segments/genitalia (for homopterans) or chelicerae (for spiders). For example, when counting flies, one head capsule and three wings would be counted as two individuals (based on the wings); however, three head capsules and three wings would be counted as three individuals (based on the head capsules). Photographs or sketches were made of characteristic remains for future reference to other samples or identification manuals.

We entered the following information into a database for each prey taxon identified in each sample: sample number; identification of prey (including order, family, and lower level identification, where applicable); number of individuals of that taxon; percent of total sample volume represented by the taxon; and description of remains, including notes on identification (e.g., ''exoskeleton, partial head capsule—metallic green,'' or ''Calyptrate muscoid fly—leg, abdomen, calypter, antennae''). All samples were returned to alcohol vials after identification and saved, both for future reference and for further study or more precise identification of problematic fragments. Wings were generally permanently mounted on microscope slides for careful examination. All such slides were labeled with the sample number, and saved for future reference.

We examined most of the samples a second time, after we had gone through the entire series of samples. This reexamination included all samples where question marks were noted by the identification, and all samples containing invertebrate taxa that were generally difficult to identify. Any questions on identification were resolved during this reexamination, either confirming the original identification or correcting it. We were conservative on all final identifications; if we could not positively identify fragments as belonging to a particular taxon, they were recorded at the level of which we could be certain (e.g., ''unidentified insect'').

Statistical Analysis

We identified prey in the food samples to different taxonomic levels, depending on the amount and completeness of prey remains, and available references on particular taxonomic groups. Identification was generally to order or family level, but in a few cases prey were identified to genus level. Since many small categories at different taxonomic levels are confusing to present and interpret, we assigned each prey taxon to an ''analysis'' category for purposes of summary statistics and comparative statistical tests. These ''analysis'' categories (hereafter referred to as ''prey taxa'') were generally order or family taxonomic level, based on the level to which the majority of prey items in that group could be assigned (e.g., some spiders were identified to family or genus, but most could only be identified as far as the spider order, Araneae; hence we used Araneae as the prey taxon in the ''analysis'' field). Insofar as possible, the analysis categories were chosen to correspond to prey functional groups relative to flycatcher foraging (see Cooper et al. 1990). For example, wingless ants were placed in a separate category from other, flying forms of Hymenoptera, and the active, jumping/flying leafhoppers were analyzed separately from other, more sedentary groups of Homoptera (= Hemiptera, suborder Auchenorrhyncha).

Summary statistics included the number of prey individuals per sample, the number of different, identified prey taxa per sample (i.e., the prey diversity per sample), the total number of each prey taxon aggregated across all samples, and the percent occurrence of each prey taxon in the samples. Percent occurrence was calculated as the number of samples in which a prey taxon was found, divided by the total number of samples.

For comparative purposes, we categorized samples by age of bird (adult or nestling), year, and month. We restricted comparisons between males and females to adult birds, assuming that any differences between the sexes would arise from birds foraging on their own, as opposed to nestlings being fed by their parents. We used non-parametric median tests (Daniel 1990) for comparisons of total prey numbers per sample and number of prey taxa per sample between adults and nestlings. For comparisons of prey composition (numbers of each prey taxon per sample), we used multivariate analysis of variance (MANOVA) on rank-transformed data (Conover and Iman 1981). In rank transformation, the data are ranked across the entire data set, with the rank values then substituted for the raw data values, and the analysis of variance model fit to the scored ranks. This approach controls for non-normality and heterogeneity of variances in the original data (Lehman 1975, Potvin and Roff 1993).

RESULTS

Overall Diet Composition

We analyzed a total of 59 samples collected from adult birds and nestlings in June, July, and August of 1996 and 1997 (Table 1). Comparison of diet between males and females was limited

TABLE 1. FOOD SAMPLES FROM WILLOW FLYCATCHERS AT THE KERN RIVER PRESERVE IN SOUTHERN CALIFORNIA, BY YEAR, MONTH, AGE, AND SEX OF BIRD

Factor		N[a]
Year	1996	18
	1997	40
Month	June	8
	July	43
	August	1
Age	Adult	16
	Nestling	34
Sex[b]	Female	11
	Male	5

[a] Number of samples for each category. Limited data were recorded for some samples, so the totals for the different classification factors (Year, Month, Age) range from 50 to 58.
[b] Includes adult birds only.

to birds foraging on their own (i.e., not including nestlings), so Table 1 only reflects totals by sex for adult birds. In the results and discussion that follow, we first present data for all samples combined, to provide a general picture of Southwestern Willow Flycatcher food habits during the breeding season at the Kern River site. Following this, the samples are broken down according to variables that may affect diet composition (year, age, etc.), for tests of differences among subgroups of the samples.

The most numerous food items (total numbers of prey individuals, combined across samples) at the Kern River site were true bugs (order Hemiptera), followed by flies (Diptera) and beetles (Coleoptera; Table 2). Most bugs were small species (seed bugs, family Lygaeidae, or similar). The largest numbers of flies identified were medium-sized muscoid flies (family Anthomyiidae and similar). Two medium-sized soldier flies (Stratiomyidae) were also identified, along with two gnats (Nematocera). Most beetles were very small species, but a few medium-sized species were also found (including flat-headed wood-boring beetles, family Buprestidae, and scarab beetles, family Scarabaeidae).

Next in order of abundance were termites (order Isoptera), leafhoppers (Homoptera: Cicadellidae), spiders (Araneae), bees and wasps (Hymenoptera), and dragonflies and damselflies (Odonata). The majority of spiders were small individuals. Families identified included lynx spiders (Family Oxyopidae, genus *Oxyopes*), jumping spiders (Salticidae), and crab spiders (Thomisidae). Hymenoptera in the diet were particularly diverse. Ants (Formicidae) were the only non-flying species (wings were not present in the samples). Various bees were the most numerous hymenopterans in the samples, with both medium- to large-sized species (Apoidea) and small species (Halictidae). Other hymenopterans included digger and thread-waisted wasps (Sphecidae) and parasitic forms ranging in size from tiny (Chalcididae) to medium-sized (Ichneumonidae, Leucospidae). Most termites were in the family Kalotermitidae. Cicadellids and odonates could not be identified to a finer level. Taken together with bugs, flies, and beetles, these groups comprised 85% of the prey numbers recorded in the samples.

Considered in terms of percent occurrence, flies were the most common prey taxon, with one or more flies present in nearly 75% of the

TABLE 2. DIET COMPOSITION OF SOUTHWESTERN WILLOW FLYCATCHERS AT THE KERN RIVER PRESERVE, BASED ON FECAL SAMPLES COLLECTED IN 1996 AND 1997 (N = 59). (TOTAL NUMBER OF PREY INDIVIDUALS AND PERCENT OCCURRENCE OF PREY TAXA)

Taxon	Number of prey individuals	Taxon	% occurrence in samples[a]
Hemiptera	69	Diptera	74.6
Diptera	63	Hemiptera	64.4
Coleoptera	43	Coleoptera	52.5
Isoptera	38	Odonata	40.7
Cicadellidae	35	Hymenoptera/flying	35.6
Araneae	27	Cicadellidae	35.6
Hymenoptera/flying	25	Araneae	30.5
Odonata	24	Plant	13.6
Plant	15	Lepidoptera larva	11.9
Unidentified insect	10	Isopoda	11.9
Lepidoptera larva	9	Unidentified insect	10.2
Isopoda	7	Homoptera/other	8.5
Homoptera/other	6	Lepidoptera adult	6.8
Lepidoptera adult	4	Isoptera	6.8
Formicidae	3	Formicidae	3.4

[a] Number of samples containing prey item *x*, divided by the total number of samples.

TABLE 3. COMPARISON BY YEAR (1996 VS. 1997) OF MAJOR PREY TAXA IN DIET SAMPLES FROM SOUTHWESTERN WILLOW FLYCATCHERS AT THE KERN RIVER PRESERVE

Taxon	Mean proportion in sample 1996	1997	$F_{1,33}$	P[a]
Diptera	0.15	0.19	0.03	0.875
Hymenoptera	0.08	0.05	0.75	0.393
Hemiptera	0.17	0.16	2.39	0.132
Cicadellidae	0.07	0.09	0.32	0.578
Odonata	0.05	0.09	0.32	0.574
Coleoptera	0.11	0.07	0.33	0.571
Araneae	0.09	0.01	13.75	0.001
Other taxa	0.28	0.35	0.06	0.804

[a] P values are from a MANOVA on transformed rank data (see text).

samples (Table 2). True bugs and beetles were both present in over half of the samples. These prey taxa were followed (in order) by dragonflies and damselflies, bees and wasps, leafhoppers, and spiders. All other diet components were present in fewer than 20% of the samples. Contributions of different prey taxa show some differences when measured by total numbers, compared to percent occurrence (Table 2). Noteworthy in this regard are the relatively higher placement of Isoptera in total numbers, and the higher placement of odonates in percent occurrence.

COMPARISONS BY YEAR, AGE, AND SEX

We compared prey composition (numbers of food items within major prey taxa, with rank transformation) of the samples between years (1996 vs. 1997). For this analysis (and those of age and sex, following), we used the seven most common invertebrate taxa in the samples (Diptera, Hymenoptera, Hemiptera, Cicadellidae, Odonata, Coleoptera, and Araneae), with remaining food items grouped in an ''other'' category. There was a significant difference in composition of major prey taxa between 1996 and 1997 (MANOVA: Wilks' $\Lambda = 0.5476$, $F_{8,26} = 2.68$, $P = 0.027$). Individual comparisons by prey taxon (Table 3) revealed that the difference between years was driven by a large difference in the numbers of spiders (Araneae) in the diet ($F_{1,33} = 13.75$, $P < 0.001$). Other prey groups did not differ significantly between years. Because of the small sample sizes for June (eight) and August (one), we did not statistically compare diet by month. Visual inspection of data summaries, however, suggests that there may be differences. For example, mean numbers of leafhoppers per diet sample were 1.38 in June vs. 0.49 in July, while spiders had mean numbers of 0.51 in July, but were not found at all in the limited number of June samples.

There were also significant differences in diet composition between adults and nestlings (Fig. 1; Wilks' $\Lambda = 0.5236$, $F_{8,26} = 2.96$, $P = 0.017$). The contribution of odonates, beetles, and ''other taxa'' was significantly greater in the diet of nestlings as compared to adults (Table 4). Adults and nestlings were significantly different as well in the total numbers of prey individuals per fecal sample, as well as in the number of identifiable taxa per sample (Table 5). Diet samples from nestling birds contained significantly higher total numbers of prey than diet samples from adults (Median Test, $T = -3.62$, $P < 0.001$) and also contained more prey taxa per sample than samples from adults (Median Test, $T = -3.68$, $P < 0.001$). Some prey taxa were only found in samples from young birds, including termites, larval and adult Lepidoptera, isopods, and plant material.

Female and male Willow Flycatchers did not differ significantly in overall diet composition (Wilks' $\Lambda = 0.2398$, $F_{8,7} = 2.77$, $P = 0.098$). Individual comparisons by prey taxon were significantly different only for Diptera ($F_{1,14} = 4.76$, $P = 0.047$). The proportion of Diptera averaged 0.14 in the diet of females, roughly half that (0.26) in the diet of males.

DISCUSSION

OVERALL DIET COMPOSITION

The diet of breeding Southwestern Willow Flycatchers along the Kern River in southern California includes a broad range of flying, vegetation-dwelling, and ground-dwelling arthropods. Many prey items were identified to lower taxonomic levels than those used to summarize diet, and some of these more specific identifications provide additional insight into the foraging behavior of Southwestern Willow Flycatchers. Two of the flies identified were species in the suborder Nematocera (the group including midges and gnats), which are small, weakly-flying species. Most of the flies in the diet, however, were calyptrate muscoid flies (section Calyptratae, suborder Cyclorrhapha). These are medium-sized, strong-flying species. The largest number of Hymenoptera that were identified were bees (superfamily Apoidea), which are also strong fliers, and which typically feed from flowers. One whole food item brought by an adult to a nestling was collected, and identified as a medium-sized soldier fly (Diptera: Stratiomyidae), also a strong-flying, flower-visiting form.

Moderate numbers of spiders were also recorded in the diet. Some of these were small spiders that could have been caught while ''ballooning'' (being carried through the air on long

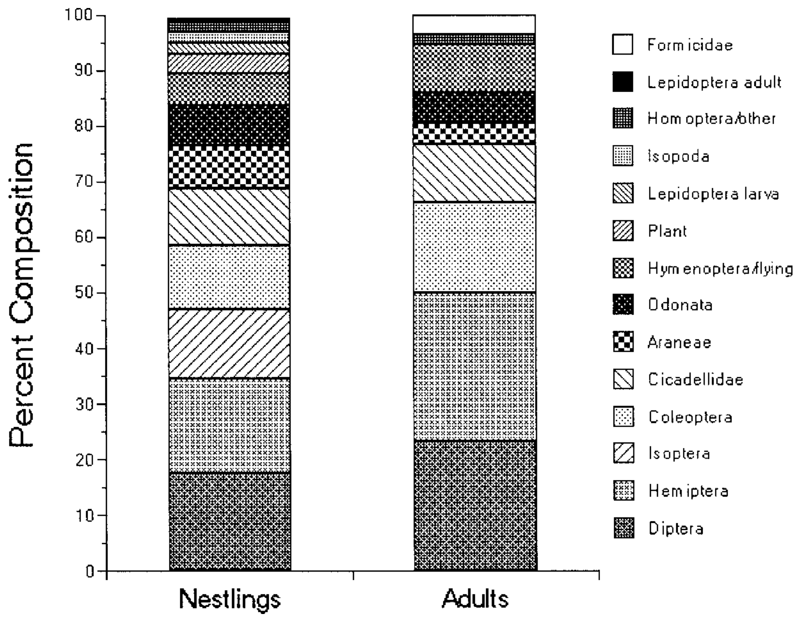

FIGURE 1. Diet composition (based on total number of prey individuals in major prey taxa) of nestling and adult Southwestern Willow Flycatchers, from the Kern River Preserve in southern California. N = 33 nestlings and 16 adults.

strands of their own silk). However, some of the remains were from spiders that were too large to be carried through the air. These must have been captured either from vegetation, from the ground, or out of their webs. In addition, some of the spiders were of groups—e.g., jumping spiders, family Salticidae—that do not build typical webs, and so must have been captured either on the ground or on vegetation. Leafhoppers, other homopterans, and small beetles are capable of flight, but spend most of their time on vegetation, and were probably taken primarily by hover-gleaning.

This range of prey corresponds relatively well with reports describing Willow Flycatcher feeding behavior. Willow Flycatchers primarily forage by hawking flying invertebrates from the air, and hover-gleaning prey from the surface of surrounding vegetation. The frequency of gleaning as a percentage of all foraging flights in Willow Flycatcher study populations ranges from 35% to 63% (Frakes and Johnson 1982, Barlow and McGillivray 1983). In Washington, feeding flycatchers generally made short (<3 m), horizontal flights from their foraging perches (Frakes and Johnson 1982). When foraging in open areas, or where understory vegetation is sparse or absent, Willow Flycatchers will also sally down to capture prey from on or near the ground (E. Paxton and M. Sogge, pers. observ.).

TABLE 4. Comparison of Diet Composition of Adult and Nestling Southwestern Willow Flycatchers at the Kern River Preserve

	Mean proportion in sample			
Taxon	Adults	Nestlings	$F_{1,33}$	P[a]
Diptera	0.18	0.16	2.18	0.149
Hymenoptera	0.05	0.07	2.55	0.120
Hemiptera	0.17	0.15	2.85	0.101
Cicadellidae	0.09	0.07	0.36	0.552
Odonata	0.05	0.10	6.21	0.018
Coleoptera	0.07	0.10	6.71	0.014
Araneae	0.04	0.04	1.51	0.228
Other taxa	0.35	0.31	5.34	0.027

[a] P values are from a MANOVA on transformed rank data (see text).

TABLE 5. Comparison of Total Number of Prey Individuals per Sample, and Number of Major Prey Taxa per Sample, in Diet Samples from Adult and Nestling Southwestern Willow Flycatchers at the Kern River Preserve

	Mean	Median	Range	N
Total prey per sample				
Adults	4.3	5	1–6	16
Nestlings	8.7	7	3–24	19
Prey taxa per sample				
Adults	3.1	3.5	1–4	16
Nestlings	5.4	5	2–10	19

Total numbers of prey

The total numbers of prey from all samples combined provides a general picture of the overall diet of the Kern River population, showing the numeric contribution of each prey taxon to the diet, averaged over any individual preferences. In the Kern River samples, three orders—true bugs, flies, and beetles—made up close to half of the total number of prey items (Table 2). Termites ranked fourth in terms of total numbers. Bees and wasps were relatively few in numbers, with dragonflies and damselflies recorded in just slightly lower numbers than bees and wasps. Given the large size of dragonflies and damselflies, and the relatively large size of many of the bees and wasps recorded (bees in the superfamily Apoidea, sphecid wasps, and other moderate-sized species), these groups are probably more important in the diet than simple rank order would indicate. Rare diet items include small seeds from unidentified fruit and a few tiny leaves, which were the only plant remains found. Given the small size and number of the leaves, they may have been ingested incidental to other feeding. Though infrequent and few in number, the plant remains are interesting for the additional breadth they indicate for the diet.

Percent occurrence of prey taxa

Percent occurrence is a measure of how prevalent a particular prey taxon is in the diet. The prey items that individuals in the population take most consistently should approach 100% in percent occurrence. At the other extreme, a prey taxon that is only rarely consumed will have a very low occurrence rate. Rosenberg and Cooper (1990) consider percent occurrence a relatively crude measure of diet. However, percent occurrence data avoid the bias that may be introduced into total prey numbers by one or a few individuals taking large numbers of a single prey taxon, either through individual preference, or due to a local or temporary abundance of the prey taxon. For example, the relatively large number of termites in the diet consisted of a total of 38 termites taken by only four birds (7% of the diet samples examined). By comparison, close to the same number of leafhoppers (35) were included in the diet, but these were distributed through 21 samples (37% of the samples examined). All of the termites examined in the samples were winged individuals, and probably represented chance occurrences of flycatchers feeding in the vicinity of termite mating flights, when large numbers of flying termites were in the air.

The three most prevalent (highest percent occurrence) diet items were the same three that ranked highest in terms of total prey numbers, except that the order of Diptera and Hemiptera was reversed (Table 2). Termites (Isoptera) were much lower (near the bottom) in percent occurrence compared to total numbers, and bees and wasps (Hymenoptera) and dragonflies and damselflies (Odonata) ranked higher in percent occurrence than in numbers. Presumably due to their size and relatively low availability, more than one odonate was never found per sample; hymenopterans were usually only one per sample as well (we recorded two individuals in only four samples). In contrast, individual samples often contained two or more leafhoppers or spiders (up to six per sample for leafhoppers). This accounts for the lower total numbers, but higher percent occurrence, of hymenopterans and odonates.

COMPARISONS

Temporal differences

Diet composition differed significantly between 1996 and 1997 (Table 3). This difference was primarily due to a much higher contribution of spiders to the diet in 1996 compared to 1997. Otherwise, the diet of the Kern River flycatchers was remarkably consistent between years. In particular, proportions of the two most numerous items in the diet (Hemiptera and Diptera) were very similar in 1996 and 1997 (Table 3). Small sample sizes did not permit statistical comparison of changes in prey composition over the course of the season, but this would be worth investigating. Given the marked seasonal changes that may occur in invertebrate communities, corresponding shifts in the diet of the flycatchers would not be surprising.

Age differences

There were significant differences in the food samples from adults and nestlings. These included differences in composition (relative numbers within different prey taxa; Table 4) and differences in quantity (total numbers of prey per sample, and numbers of identified taxa per sample; Table 5). Numbers of prey individuals and prey diversity were both significantly higher in samples from nestlings than in samples from adults (Table 5). For all of the samples taken together, the diet of nestlings was also substantially more diverse than that of adults (Fig. 1). The young birds from which we obtained samples were relatively advanced (7–10 days old) so we do not expect there to be differences based simply on differential ability to digest invertebrate prey (cf. Karasov 1990, for very young birds); nor did we observe evident differences in the fragments recovered that would suggest differential digestion between adults and young.

We do not know the reason for these differences between adults and young. They may be related to higher feeding rates for nestlings, a wider selection of prey by adult birds that are attempting to meet the demands of hungry nestlings, or a broader availability of different prey during the nesting period. Since both total prey numbers and number of prey taxa were higher in nestlings than adults, the higher prey diversity may simply be an artifact of higher prey numbers. Our analysis did not allow us to examine this possibility. Some food items were found only in samples from young birds (termites, lepidopterans, isopods, and plant matter). This could reflect differential food selection for the young or could be a sampling artifact (except for termites, total numbers for these items were 15 or less).

Males and females

There was not a significant overall difference in diet between males and females. However, our samples sizes were small, resulting in relatively low power to detect differences. Individual comparisons by prey taxon showed a significant difference between the sexes in the relative contribution of flies (higher in males). There are potential behavioral reasons for differences in diet between males and females during the nesting season (e.g., foraging in proximity to the nest vs. farther away, or differences in roles between the sexes in feeding the young); this comparison warrants further examination in future studies.

Comparisons with Other Published Studies

Other studies (Beal 1912, Bent 1942, McCabe 1991) have all reported bugs, various hymenopterans, and flies as prominent food items of Willow Flycatchers (these reports are based on data from Willow Flycatchers in various parts of their North American range, but not the Southwest). Species of flies (Diptera) made up a consistently high portion of the diet at the Kern River and in other areas. The Kern River samples had higher numbers of some taxa, notably beetles and spiders, than reported in previous works. The spiders (and probably some of the beetles and homopterans) are of interest because many of them are presumably taken by gleaning. Large numbers of termites (Isoptera) were found in samples from the Kern River, but were not reported for samples from other areas across the Willow Flycatcher's range (Beal 1912, McCabe 1991).

On the other hand, the observed diet at the Kern River included quite low numbers of flying Hymenoptera (bees and wasps) compared to reports from elsewhere in the flycatcher's range. This paucity of Hymenoptera in the diet may be due to the relative scarcity of flowering shrubs at the Kern River site. Willows at the Kern River site flower by early May, so insects attracted to flowering willows are not represented in our samples. Malaise trap samples for flying insects at the Kern River site support this idea, being heavily dominated by flies, with few Hymenoptera (M. Whitfield, unpubl. data). The Kern River diet samples also contained relatively few Lepidoptera larvae (caterpillars), which make up a moderate proportion of the diet in other studies.

Management Implications and Research Needs

Southwestern Willow Flycatchers take a wide range of invertebrate prey, including flying, and ground- and vegetation-dwelling species. This diverse prey base, in conjunction with the variety of foraging techniques used by the birds (and suggested by the food data), indicates significant flexibility in the diet. Such flexibility and range in the diet should be advantageous in the face of variable conditions (e.g., from site to site, or year to year).

The dual issues of exposure to chemical toxins and effects of adjacent land use are important to Southwestern Willow Flycatcher conservation efforts. Of 209 breeding sites known in the year 2000, at least 37 (18%) were associated with runoff and other water inputs (e.g., irrigation canals, sewage treatment outflows) from agricultural and urban sources (Table 6 in U.S. Fish and Wildlife Service 2001). Chemical toxins are one possible explanation for deformities observed in Southwestern Willow Flycatchers (Sogge and Paxton 2000; cf. Mora et al. *this volume*), and exposure to pesticides and other harmful chemicals is particularly a threat at sites surrounded by intensive agriculture and along lowland riparian sites downstream from pollution sources. The wide variety of invertebrate prey taken by Willow Flycatchers provides many potential avenues for accumulating environmental toxins. The prey base includes species of terrestrial and aquatic origins, so harmful chemicals may be accumulated from either of these sources. Because flycatchers feed on many strong-flying prey species (such as bees, wasps, flies, and dragonflies), toxins could be introduced into the diet even from sources relatively distant from breeding sites. In light of this, additional research is needed on the level of harmful compounds present in the food base, and potential impacts to Southwestern Willow Flycatchers (Stoleson et al. 2000a, Mora et al. *this volume*).

Willow Flycatcher prey base may be strongly influenced by habitats and land uses adjacent to riparian breeding sites. Adjacent invertebrate-rich habitats such as mesquite or wetlands may provide good source areas for strong-flying ''tourist'' species that can travel to the flycatcher's breeding patch. Adjacent areas with intensive agriculture likely provide fewer (or at least different) prey taxa, especially if the area is treated with pesticides to control insects. On the other hand, some agricultural activities or crops may attract pollinators and other potential prey taxa. Finally, conversion of surrounding habitats to urban use is likely to dramatically alter the local distribution and abundance of the flycatcher's invertebrate prey, especially where insect control measures are aggressively pursued.

This study documents the diet composition and diversity only at the Kern River, a native-dominated riparian site. It is unknown whether the same patterns hold true at flycatcher breeding sites dominated by non-native saltcedar (*Tamarix ramosissima*). This is an important consideration in that almost half of all known Southwestern Willow Flycatchers territories are in sites dominated by saltcedar or by mixtures of native vegetation and saltcedar (Sogge et al. *this volume*). Although Tracy and DeLoach (1999) suggest that saltcedar habitats do not support an adequate prey base for nesting flycatchers, the relative quality of saltcedar habitats is not clearly known (Stoleson et al. 2000a). Specific data on flycatcher diet composition in saltcedar habitats are needed to help address these questions.

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