

## DIETS OF BREEDING SOUTHWESTERN WILLOW FLYCATCHERS IN DIFFERENT HABITATS

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**ABSTRACT.**—We identified arthropods in fecal samples from 56 Southwestern Willow Flycatchers (*Empidonax traillii extimus*) at three localities in Nevada and Arizona with different plant communities during the 2004 breeding season. We concurrently collected arthropods in flight with Malaise traps and on different plant species by sweep net. These potential prey were identified to Order and counted. Fecal samples contained 57 taxa of spiders and insects including 32 families in 8 Orders. Flycatchers consumed similar diversities (numbers of taxa), but different taxonomic compositions (abundances in Orders) of arthropods among localities. Diets of *E. t. extimus* more closely resembled compositions of arthropods swept from plants than those trapped in flight with Malaise traps. Fecal samples at Upper Pahranaagat Lake in southern Nevada contained arthropod compositions most related to those swept from *Salix gooddingii*. Fecal samples at the Virgin River near Mesquite in southern Nevada, where *Salix exigua* and naturalized *Tamarix ramosissima* grow, contained arthropod compositions most related to those swept from *S. exigua*. Fecal samples at Topock Marsh in western Arizona contained arthropod compositions most related to those swept from *T. ramosissima*, the dominant vegetation. The relation between flycatcher diet and arthropod composition on plants was least at Topock Marsh, suggesting prey from other communities are important in supplementing the fauna that develop on introduced *Tamarix*. The diverse diet of Southwestern Willow Flycatchers may take advantage of the increased nitrogen and sulfur contents of spiders and predaceous insects. Received 26 July 2006. Accepted 13 January 2007.

The Willow Flycatcher (*Empidonax traillii*) is a migratory passerine that breeds in northern and western United States and southern Canada, and winters in coastal areas from central Mexico to Panama (Sedgwick 2000). The Southwestern Willow Flycatcher (*Empidonax traillii extimus*) is one of 4–5 subspecies distinguished primarily by plumage coloration and wing morphology (Phillips 1948, Unitt 1987, Browning 1993, Sedgwick 2000). It breeds from southern California east to western Texas and north to southern Utah (Browning 1993). *E. t. extimus* typically arrives in early May, begins nesting in early June, and lays 2–4 eggs/clutch (Unitt 1987). Willow Flycatchers produce several clutches each season, incubate eggs 13–15 days, and fledge young 11–16 days after hatch (Sedgwick 2000). Fall migration of Southwestern Willow Flycatchers occurs from early August to mid-September (Wang and Finch 1997).

Breeding Southwestern Willow Flycatchers require riparian habitat; willow trees (*Salix* spp.) predominate most breeding areas (Sogge

et al. 2003) and are the most common nest site (Unitt 1987). Areas dominated by tamarisk (*Tamarix* spp.) also support breeding *E. t. extimus* (Sogge et al. 2003). Tamarisk is a shrubby tree native to Eurasia that has naturalized in the U.S. mostly as hybrids of *Tamarix ramosissima* and *T. chinensis* (Gaskin and Schaal 2002, 2003). Declining numbers of native riparian trees, concurrent with the spread of tamarisk, is a contributing factor in the decline in abundance of the Southwestern Willow Flycatcher and its resultant listing as endangered (USDI 1995).

Breeding Willow Flycatchers are generalist feeders that primarily consume arthropods, especially insects. Stomachs of Willow Flycatchers collected from across the species' range contained by volume mostly (41%) Hymenoptera followed by Coleoptera, Diptera, Lepidoptera, Hemiptera, fruits and seeds, Orthoptera, Odonata and Ephemeroptera, Araneae and Diplopoda, and Acari and Mollusca (Beal 1912). Most (73%) invertebrates delivered to nestlings in Ontario, Canada, were Hemiptera and Diptera but also included Mollusca, Arachnida, Isopoda, Orthoptera, Coleoptera, Hymenoptera, and Lepidoptera (Prescott and Middleton 1988). Prey in fecal samples from Southwestern Willow Flycatchers in southern California were mostly (78%)

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Araneae, Odonata, Hemiptera, Coleoptera, Hymenoptera, and Diptera (Drost et al. 2003).

Diets of *E. t. extimus* in separate breeding populations inhabiting different plant communities with dissimilar arthropod compositions have not been compared. Our objective was to quantify arthropod prey in fecal samples to compare diets at several localities with different plant species, including tamarisk, and to relate diets to abundances of arthropods trapped in flight or collected on plants. Specifically we were interested in four questions. (1) Does the diversity or taxonomic composition of arthropods eaten by flycatchers vary among different, geographically separated breeding populations? (2) Does the diversity or taxonomic composition of prey differ between adults (males and females) and young? (3) Are taxonomic compositions of arthropods eaten more related to those of arthropods collected on plants or trapped in flight? (4) Is flycatcher diet more related to arthropod compositions on native willows and poplars (*Populus* spp.) or on introduced tamarisk?

#### METHODS

Arthropods in flight and on plants, and fecal samples from *E. t. extimus* were collected at three localities. The Pahrnagat Lake site (37° 19' N, 115° 8' W; elevation 1,010 m) was at the north shore of Upper Pahrnagat Lake within Pahrnagat National Wildlife Refuge in south-central Lincoln County, Nevada. The lake is an impoundment that receives water from springs. Riparian plants primarily are mature *Populus fremontii* and *Salix gooddingii* whose canopies extend over soil that is partially flooded during spring. The Virgin River site (36° 47' N, 114° 6' W; 460 m) was along the north edge of the Virgin River near Mesquite in northeastern Clark County, Nevada. Vegetation predominantly is *Salix exigua* and *Tamarix ramosissima* growing between the river and a shallow channel of flowing water. The Topock Marsh site (34° 49' N, 114° 31' W; 130 m) is a tamarisk-dominated area along the west shore of Topock Marsh, an impoundment next to the Colorado River, within Havasu National Wildlife Refuge in western Mohave County, Arizona. Vegetation surrounding riparian habitats at all three localities is mostly crops or pasture within the floodplain and Mohave desert scrub outside of

the floodplain. Maximum temperature during July and minimum temperature during December average 36.8° and -3.5° C at Pahrnagat Lake, 41.1° and -1.6° C at Virgin River (Bunkerville, NV), and 42.6° and 5.6° C at Topock Marsh (Needles, CA) (NOAA 2006).

Flying arthropods were collected with Malaise traps (Santee Traps, Lexington, KY, USA). Traps were placed in or at the edge of riparian stands inhabited by flycatchers. Two traps were placed at Pahrnagat Lake, one within a stand of *P. fremontii* and one within an adjacent stand of *S. gooddingii*. One trap was placed at Virgin River at the edge of a mixed stand of *S. exigua* and *T. ramosissima*. One trap was placed at Topock Marsh within *T. ramosissima*. We collected arthropods with Malaise traps during five, 7–8 day trapping periods beginning on 5–6 May, 1 June, 17 June, 9 July, and 21 July 2004 at Pahrnagat Lake and Virgin River, and 5 May, 2 June, 15 June, 6 July, and 20 July 2004 at Topock Marsh. Arthropods on plants near the Malaise traps were collected with a 38 cm-diameter, sailcloth sweep net on the last day of each trapping period. We sampled *P. fremontii* and *S. gooddingii* at Pahrnagat Lake, *S. exigua* and *T. ramosissima* at Virgin River, and *T. ramosissima* at Topock Marsh. Each plant species was sampled with 100 sweeps along a transect flagged at both ends. The same plants, therefore, were swept on each date and we swept plants without regard to presence of flowers. Collected arthropods were stored in 70% ethanol, sorted to Order following Triplehorn and Johnson (2005), and counted. Numbers of arthropods in abundant taxa (>1,000 individuals) were estimated by counting individuals in subsamples delineated in a grid-lined Petri dish. Minute (<1 mm long) Hymenoptera (Cynipoidea, Proctotruoidea, Ceraphoronoidea, and Chalcidoidea [except Chalcididae]) and nematoceros Diptera were not counted, because they were unlikely to be eaten by birds due to their size.

Fecal samples were collected into 70% ethanol during 15 May–9 August 2004 when birds, captured for banding or recaptured after previous banding, defecated. Birds were classified (nestling or adult) based on age and year when banded, and adults were classified to gender when possible (McLeod et al. 2005). Fecal samples came from different birds ex-

cept for two samples from an adult male on 18 May 2004 at Topock Marsh. Fecal samples were classified into five collection periods approximating trapping intervals at each locality. Each collection period started the day trapping began and each period ended (except for the last period) the day preceding the next trapping period. Fecal samples at Pahranaagat Lake were taken during only three of the collection periods (6–31 May, 17 Jun–8 Jul, and 21 Jul–6 Aug 2004).

Fecal pellets comprising samples were digested overnight in 10% KOH and neutralized with glacial acetic acid prior to examination through a stereo microscope. Small or medium-sized samples containing few arthropod parts were examined within a Petri dish. Identifiable arthropod parts in large samples, or abundant arthropod parts in small or medium-sized samples, were segregated into 5-ml scintillation vials to prevent repeatedly counting the same part. Arthropod parts were identified to the lowest taxon possible by comparing them with arthropods collected with Malaise traps and by sweeping plants, and with arthropods at the Bohart Museum of Entomology, University of California, Davis. The minimum number of individuals in each fecal sample was estimated by counting single body parts (e.g., head capsules, dorsal sclerites, ovipositors) and pairs of corresponding body parts (e.g., antennae, legs, wings). Arthropod parts from fecal samples and collected arthropods were deposited at the Bohart Museum. Images of identified arthropod parts are available at <http://bohart.ucdavis.edu>.

Diversity of arthropods in each fecal sample from *E. t. extimus* was measured by summing numbers of identified taxa and numbers of different, but unidentified, taxa. We averaged numbers of taxa in the two fecal samples from the same bird to enable all observations to be different birds. We compared numbers of taxa (transformed  $\log[Y + 1]$ ) among localities, among collection periods, and between nestlings and adults with ANOVA (version 10.2; SYSTAT, Richmond, CA, USA). Numbers of taxa ( $\log[Y + 1]$ ) were compared between adult males and females with an ANOVA that included locality and collection period as factors. Analyses weighted observations by the number of fecal samples.

Taxonomic compositions of arthropods in

*E. t. extimus* fecal samples were quantified as abundances in Orders. We averaged abundances in Orders across the two fecal samples from the same bird. We compared abundances in Orders ( $\log[Y + 1]$ ) among localities, among collection periods, and between nestlings and adults by testing the interactions between Order and locality, Order and collection period, and Order and age class in an ANOVA that included Order, locality, collection period, and age class as factors. Gender of adults was similarly compared by testing the interaction between Order and gender in an ANOVA that included Order, gender, locality, and collection period as factors. Abundances of arthropods ( $\log[Y + 1]$ ) were compared among localities within each Order with ANOVA. If localities differed, we compared abundances between localities with lsd tests. Analyses weighted observations by the number of fecal samples.

Relations between taxonomic compositions in fecal samples and those in Malaise-trap or sweep-net samples were calculated at each locality. Fecal samples were paired with each trap sample and sweep sample from the same collection period. We regressed arthropod abundances in Orders ( $\log[Y + 1]$ ) in fecal samples against abundances in the same Orders ( $\log[X + 1]$ ) in all combinations of trap and sweep samples. Transformed abundances in fecal samples simultaneously related to more than one set of trap or sweep samples were plotted by adjusting means within collection periods with regression (Sokal and Rohlf 1969). Analyses weighted observations by the number of fecal samples.

## RESULTS

More spiders and insects were caught by Malaise traps than by sweeping plants during collection periods when fecal samples were taken. Malaise traps ( $\bar{x} \pm \text{SD}$ , range) caught more ( $1,473 \pm 1,519$ , 32–3,060;  $n = 3$ ) arthropods within *P. fremontii* than within *S. gooddingii* ( $904 \pm 308$ , 549–1,089;  $n = 3$ ) at Pahranaagat Lake, and more ( $13,236 \pm 13,354$ , 6,661–37,089;  $n = 5$ ) arthropods at Virgin River than at Topock Marsh ( $2,748 \pm 968$ , 2,050–4,392;  $n = 5$ ) per collection period. We swept fewer ( $68 \pm 55$ , 14–124;  $n = 3$ ) arthropods from *P. fremontii* and more ( $340 \pm 414$ , 77–817;  $n = 3$ ) from *S. gooddingii* at Pahranaagat Lake, fewer ( $514 \pm 270$ , 338–988;

$n = 5$ ) arthropods from *S. exigua* than from *T. ramosissima* ( $1,253 \pm 948$ ,  $426-2,857$ ;  $n = 5$ ) at Virgin River, and fewer ( $138 \pm 50$ ,  $72-193$ ;  $n = 5$ ) arthropods from *T. ramosissima* at Topock Marsh per collection period.

Fecal samples were collected from 56 *E. t. extimus*, 17 at Pahranaagat Lake, 20 at Virgin River, and 19 birds at Topock Marsh. Fifty-seven taxa of spiders and insects, including 32 families, 15 genera, and 8 species, were identified in fecal samples (Appendix). Numbers of taxa in fecal samples from birds did not differ among localities ( $F = 1.5$ ;  $df = 2, 48$ ;  $P = 0.25$ ) or among collection periods ( $F = 0.48$ ;  $df = 4, 48$ ;  $P = 0.75$ ). Fecal samples ( $\bar{Y} \pm SD$ ) from Pahranaagat Lake contained  $4.8 \pm 1.9$  (range = 2–9,  $n = 17$ ) taxa, samples from Virgin River contained  $4.6 \pm 2.3$  (range = 1–11,  $n = 20$ ) taxa, and samples from Topock Marsh contained  $3.7 \pm 1.4$  (range = 2–6,  $n = 19$ ) taxa. Numbers of taxa in fecal samples did not differ between nestlings and adults ( $F = 0.05$ ;  $df = 1, 48$ ;  $P = 0.82$ ). Fecal samples from nestlings contained  $4.3 \pm 2.0$  (range = 1–8,  $n = 14$ ) taxa, and fecal samples from adults contained  $4.3 \pm 1.9$  (range = 2–11,  $n = 42$ ) taxa. Numbers of taxa in fecal samples from birds also did not differ ( $F = 0.46$ ;  $df = 1, 26$ ;  $P = 0.50$ ) between adult males and females. Fecal samples from males contained  $4.3 \pm 1.3$  (range = 2–6,  $n = 22$ ) taxa and fecal samples from females contained  $5.2 \pm 2.8$  (range = 2–11,  $n = 13$ ) taxa.

Two-hundred and ninety-six individual spiders and insects in eight Orders were found in fecal samples from *E. t. extimus* (Appendix). Taxonomic compositions of arthropods from fecal samples varied among localities ( $F = 4.2$ ;  $df = 14, 384$ ;  $P = 0.001$ ) but did not vary among collection periods ( $F = 0.82$ ;  $df = 28, 384$ ;  $P = 0.74$ ). We detected a weak, but non-significant, difference in taxonomic compositions between nestlings and adults ( $F = 1.8$ ;  $df = 7, 384$ ;  $P = 0.080$ ). Taxonomic compositions did not vary between adult males and females ( $F = 0.20$ ;  $df = 7, 250$ ;  $P = 0.98$ ).

Variation in taxonomic compositions of fecal samples among localities (Fig. 1) was evident when arthropod abundances were compared within each order. Arthropod abundances in fecal samples did not vary among localities in Araneae ( $F = 0.55$ ;  $df = 2, 53$ ;  $P = 0.58$ ), Blattodea ( $F = 0.42$ ;  $df = 2, 53$ ;  $P =$

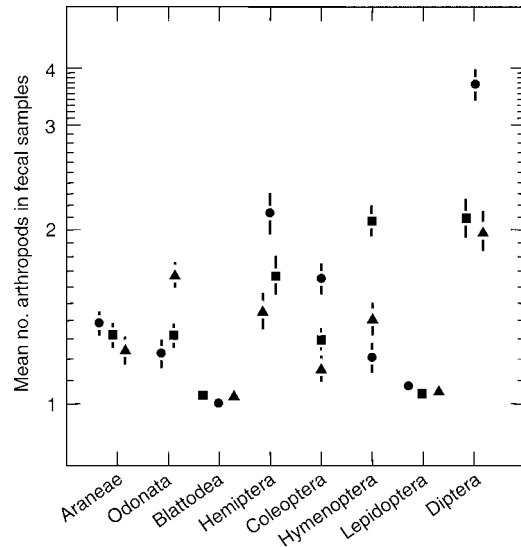


FIG. 1. Mean abundances (antilog  $\log[Y + 1]$ ) of arthropods by Orders in Southwestern Willow Flycatcher fecal samples. Circles = Pahranaagat Lake, Nevada; squares = Virgin River, Nevada; triangles = Topock Marsh, Arizona. Vertical bars are  $\pm$  SE's pooled within Orders. Overlapping symbols diagonally offset.

$0.66$ ), Hemiptera ( $F = 2.4$ ;  $df = 2, 53$ ;  $P = 0.10$ ), or Lepidoptera ( $F = 0.33$ ;  $df = 2, 53$ ;  $P = 0.72$ ). Only one spider (Araneae) fragment was identifiable to family—a terminal leg segment with spatulate hairs characteristic of Anyphaenidae. The Blattodea collected were all specimens of the introduced cockroach *Blattella vaga* Hebard (Blattellidae). Leafhoppers (Cicadellidae) were the most abundant arthropod family in fecal samples (Appendix). Arthropod abundances in fecal samples varied among localities in Odonata ( $F = 4.3$ ;  $df = 2, 53$ ;  $P = 0.018$ ), Coleoptera ( $F = 4.3$ ;  $df = 2, 53$ ;  $P = 0.018$ ), Hymenoptera ( $F = 6.7$ ;  $df = 2, 53$ ;  $P = 0.003$ ), and Diptera ( $F = 6.9$ ;  $df = 2, 53$ ;  $P = 0.002$ ).

Odonata were more abundant in fecal samples at Topock Marsh than at Pahranaagat Lake ( $P = 0.008$ ) or Virgin River ( $P = 0.031$ ). Odonata comprised 20% of arthropods in fecal samples at Topock Marsh and included dragonflies (Anisoptera) and damselflies (Zygoptera), distinguished by their large or small tarsal segments. Coleoptera were more abundant in fecal samples at Pahranaagat Lake than at Topock Marsh ( $P = 0.005$ ). Taxa consumed included a medium sized scarab (Scar-

TABLE 1. Linear regressions of arthropod abundances, transformed  $\log(Y + 1)$ , in Orders in Southwestern Willow Flycatcher fecal samples against abundances in the same Orders in sweep-net and Malaise-trap collections at three localities in southern Nevada and western Arizona.

Predictor variable <sup>a</sup>	B ± SE	F <sup>b</sup>	P	R <sup>2</sup>
<b>Pahranaagat Lake</b>				
<i>Salix gooddingii</i> sweep	0.17 ± 0.02	80.0	0.001	0.37
<i>S. gooddingii</i> trap	0.12 ± 0.02	42.2	0.001	0.24
<i>Populus fremontii</i> sweep	0.18 ± 0.03	35.7	0.001	0.21
<i>P. fremontii</i> trap	0.034 ± 0.019	3.38	0.068	0.025
<b>Multiple regression<sup>c</sup></b>				
<i>S. gooddingii</i> sweep	0.17 ± 0.02	83.7	0.001	0.38
<i>P. fremontii</i> trap	0.036 ± 0.015	6.11	0.015	0.028
<b>Virgin River</b>				
<i>Salix exigua</i> sweep	0.11 ± 0.02	40.0	0.001	0.20
<i>Tamarix ramosissima</i> sweep	0.086 ± 0.016	27.3	0.001	0.15
<i>S. exigua</i> & <i>T. ramosissima</i> trap	0.073 ± 0.016	21.2	0.001	0.12
<b>Topock Marsh</b>				
<i>Tamarix ramosissima</i> sweep	0.085 ± 0.020	17.5	0.001	0.11
<i>T. ramosissima</i> trap	0.051 ± 0.014	13.6	0.001	0.083

<sup>a</sup> Transformed  $\log(X + 1)$ ; traps placed within, or at the edge of (Virgin River), plant species.

<sup>b</sup> Simple regression error df: Pahranaagat Lake, 134; Virgin River, 158; Topock Marsh, 150.

<sup>c</sup> Model with each predictor variable  $P = 0.05$  and highest total  $R^2$  (0.40); error df = 133.

abaeidae) resembling a June beetle, weevils (Curculionidae), a medium sized Cerambycidae (*Aneflomorpha* sp.), and at least two species of Coccinellidae (*Olla v-nigrum* [Mulsant] and *Psyllobora* sp.). The most commonly consumed beetles were in the family Chrysomelidae; several fecal samples contained remains of the common species *Crepidodera opulenta* LeConte.

Hymenoptera were more abundant in fecal samples at Virgin River than at Pahranaagat Lake ( $P = 0.001$ ) or Topock Marsh ( $P = 0.017$ ). Small bees (Halictidae) were the predominant Hymenoptera eaten, mostly at Virgin River, but ants also were found in several samples. Diptera were more abundant at Pahranaagat Lake than at Virgin River ( $P = 0.003$ ) or Topock Marsh ( $P = 0.001$ ). Chironomidae and Syrphidae were the most abundant Diptera identified in fecal samples. Chironomidae were mostly found at Pahranaagat Lake, while Syrphidae were mostly found at Topock Marsh. Syrphid flies consumed at Topock Marsh included *Copestylum pallens* (Weidemann), *Palpada alhambra* (Hull), and *Syrtrita pipiens* (Linnaeus). The most commonly eaten syrphid was *S. pipiens*. Species in two genera of Stratiomyiidae were consumed—*Myxosargus* sp. nr. *knowltoni* Curran and an uniden-

tified species of *Sargus*. Other flies identified in fecal samples included *Ravinia* sp. (Sarcophagidae), *Ceroxys laticulcus* (Loew) (Otitidae), and unidentified taxa of Chironomidae, Tachinidae, Scathophagidae, Tabanidae, and Dolichopodidae.

Relations between taxonomic compositions in fecal samples and those in Malaise-trap or sweep-net samples differed among localities. Taxonomic compositions of fecal samples at Pahranaagat Lake were related to those in sweep samples of *S. gooddingii* and *P. fremontii* and trap samples within the stand of *S. gooddingii* (Table 1). Most variation in compositions of fecal samples at Pahranaagat Lake (40%) was simultaneously related to compositions of arthropods swept from *S. gooddingii* and trapped within *P. fremontii* (Table 1, Figs. 2–3). Most of this variation (38%) was explained by arthropod compositions swept from *S. gooddingii*. Taxonomic compositions of fecal samples at Virgin River were related to those in sweep samples of *S. exigua* and *T. ramosissima*, and trap samples at the edge of both species (Table 1). Most variation in compositions of fecal samples at Virgin River (20%) was related to compositions of arthropods swept from *S. exigua* (Fig. 4). Taxonomic compositions of fecal samples at Topock

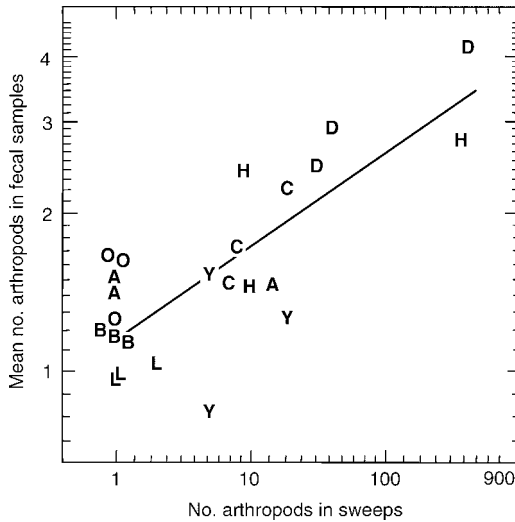


FIG. 2. Mean abundances (antilog  $\log[Y + 1]$ ) of arthropods in Southwestern Willow Flycatcher fecal samples during three collection periods, adjusted for arthropod abundances trapped within *Populus fremontii*, regressed against arthropod abundances ( $X + 1$ ) swept from *Salix gooddingii* at Upper Pahranaagat Lake, Nevada. A = Araneae; B = Blattodea; C = Coleoptera; D = Diptera; H = Hemiptera; L = Lepidoptera; O = Odonata; Y = Hymenoptera. Overlapping letters diagonally offset.

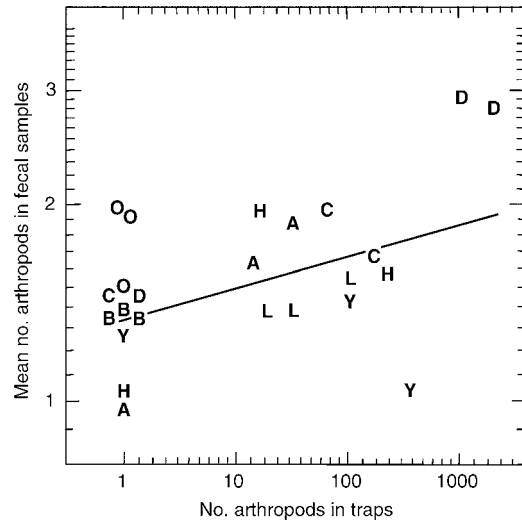


FIG. 3. Mean abundances (antilog  $\log[Y + 1]$ ) of arthropods in Southwestern Willow Flycatcher fecal samples during three collection periods, adjusted for arthropod abundances swept from *Salix gooddingii*, regressed against arthropod abundances ( $X + 1$ ) trapped within *Populus fremontii* at Upper Pahranaagat Lake, Nevada. A = Araneae; B = Blattodea; C = Coleoptera; D = Diptera; H = Hemiptera; L = Lepidoptera; O = Odonata; Y = Hymenoptera. Overlapping letters diagonally offset.

Marsh were related to those in sweep and trap samples of *T. ramosissima* (Table 1). Most variation in compositions of fecal samples at Topock Marsh (11%) was related to compositions of arthropods swept from *T. ramosissima* (Fig. 5). The low percentage of explained variation at Topock Marsh partly was due to Odonata. Dragonflies and damselflies were found in fecal samples and captured ( $n = 22$ ) in the Malaise trap but not caught by sweep net (Fig. 5). Compositions of fecal samples at Virgin River or Topock Marsh were not simultaneously related to more than one set of sweep or trap collections.

#### DISCUSSION

Breeding Southwestern Willow Flycatchers preyed upon a diverse variety of spiders and insects. Birds ate arthropods that were different in size, ranging from ladybird beetles (Coccinellidae) 2 mm in length to dragonflies (Zygoptera) 4 cm in length. Prey also differed in flight ability and included strong-flying dragonflies, and flower-visiting bees and non-flying ants

(Formicidae). Spiders and insects from a variety of habitats were eaten. Prey included aquatic water boatmen (Corixidae), terrestrial spiders, arboreal leafhoppers, and ground-dwelling cockroaches.

Fecal samples with similar arthropod diversities, but different arthropod compositions, among breeding populations in different habitats suggest *E. t. extimus* adapt their diets to spiders and insects that are available. Individual birds at all three localities ate an average of four different taxa per fecal sample. This constant diversity in diet may result from birds eating a mixture of herbivorous and predaceous arthropods. Reproduction by insectivorous birds has been found to be affected by diet protein. For example, Blue Tits (*Parus caeruleus*) laid larger eggs when fed a high-protein diet and had larger clutches when provided with particular amino acids, such as sulphur-containing methionine (Ramsey and Houston 1997, 1998). Predaceous insects contain nitrogen concentrations averaging 15% higher than herbivorous insects; nitrogen con-

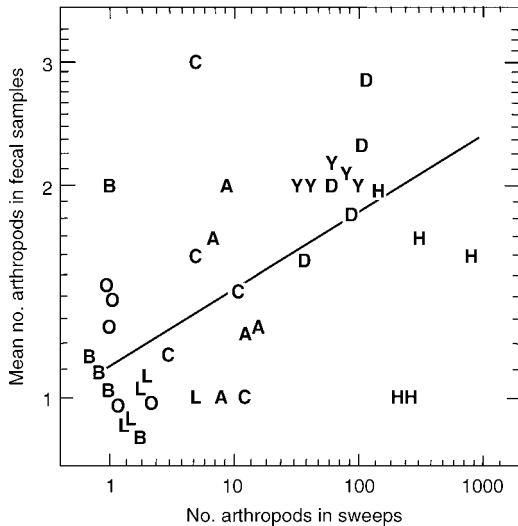


FIG. 4. Mean abundances (antilog  $\overline{\log[Y + 1]}$ ) of arthropods in Southwestern Willow Flycatcher fecal samples during five collection periods regressed against arthropod abundances ( $X + 1$ ) swept from *Salix exigua* along the Virgin River, Nevada. A = Araneae; B = Blattodea; C = Coleoptera; D = Diptera; H = Hemiptera; L = Lepidoptera; O = Odonata; Y = Hymenoptera. Overlapping letters diagonally offset.

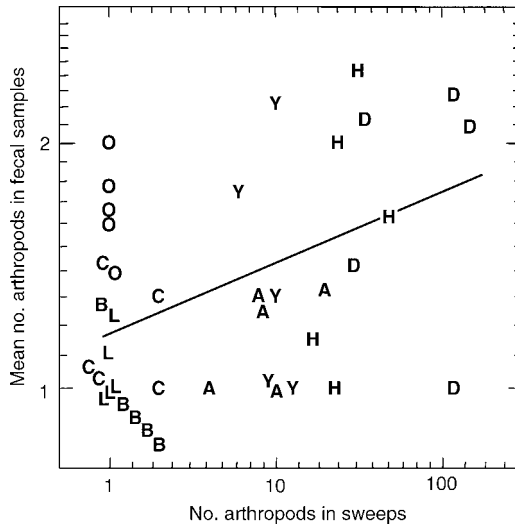


FIG. 5. Mean abundances (antilog  $\overline{\log[Y + 1]}$ ) of arthropods in Southwestern Willow Flycatcher fecal samples during five collection periods regressed against arthropod abundances ( $X + 1$ ) swept from *Tamarix ramosissima* at Topock Marsh, Arizona. A = Araneae; B = Blattodea; C = Coleoptera; D = Diptera; H = Hemiptera; L = Lepidoptera; O = Odonata; Y = Hymenoptera. Overlapping letters diagonally offset.

centrations are similar in predaceous insects and spiders (Fagan et al. 2002). Many arthropods eaten by Southwestern Willow Flycatchers were predaceous, including spiders, dragonflies, damselflies, ladybird beetles, and wasps (e.g., Vespidae and Sphecidae). Spiders also are rich in specific amino acids such as those containing sulphur (Ramsay and Houston 2003). Equivalent predation on spiders, comprising 7.4% of prey, at all three localities suggest they may have been eaten independent of abundance. More study and careful experimentation would be needed to demonstrate that flycatchers are augmenting their diets by preferentially selecting predaceous arthropods. If they do not, one must assume a random selection of a variety of arthropods supplies the required amounts of nutrients including nitrogen.

Our finding that similar diets are eaten by male and female adults concurs with the analyses by Drost et al. (2003) of fecal samples from breeding *E. t. extimus* in southern California. However, in contrast to our results, Drost et al. (2003) found nestlings ate a greater diversity of prey than did adults. These au-

thors also found that diet compositions eaten by nestlings and adults differed with nestlings eating more Coleoptera and Odonata. Our data also suggests that nestlings and adults consume different compositions of spiders and insects, but this difference was small and difficult to detect. Diet shift during nestling development has been observed in Blue Tits and Great Tits (*Parus major*), with young (3–9 days of age) nestlings provided with more spiders (Cowie and Hinsley 1988). These authors suggest adults preferentially select spiders as food for young nestlings. Young nestlings may require specific amino acids provided by spiders (Ramsey and Houston 2003).

Compositions of arthropods in fecal samples show greater similarity to those collected by sweep net than to those collected by Malaise trap. This suggests that *E. t. extimus* forages more upon arthropods on plants than upon insects in flight. Willow Flycatchers glean, or fly and take prey from a substrate, and hawk, or fly and take prey that is in flight. Frequencies of these behaviors have been observed to vary by locality. Gleaning com-

prised 35 and 46% of foraging behaviors at two localities in Washington (Frakes and Johnson 1982) and 37 and 63% of foraging behaviors at two localities in Ontario, Canada (Barlow and McGillivray 1983). Frequencies of foraging behaviors may not equal frequencies of predation, because some foraging attempts likely are not successful. Insects in Orders we swept from plants may have been hawked. Hymenoptera and Diptera, common consumers of pollen and nectar, could have been hawked while flying between flowers. Conversely, insects in Orders caught in traps may have been gleaned. Dragonflies and damselflies land on plants but usually evade capture by sweep net.

The similarity between arthropod compositions in diets and what could be collected by sweeps or Malaise traps varied inversely with tamarisk's prevalence at each locality. The similarity was greatest at Pahrnagat Lake, where native riparian trees are predominant, intermediate at Virgin River, where native *S. exigua* is mixed with naturalized *T. ramosissima*, and least at Topock Marsh, where *T. ramosissima* predominates. Greater prevalence of tamarisk appeared to result in lesser correspondence between predation by flycatchers and prey abundance. This suggests tamarisk provided a small proportion of arthropods eaten by flycatchers. Less predation on tamarisk arthropods is supported by the finding that arthropod composition in fecal samples at Virgin River resembled those on *S. exigua* more than *T. ramosissima*. However, abundances of these plants may have differed and influenced flycatcher diet.

Most arthropod biomass on *T. ramosissima* branches (98%) is comprised of only 2–3 herbivorous species, the armored scales *Chionaspis* spp. (Diaspididae) and the tamarisk leafhopper *Opsius stactogalus* Fieber (Cicadellidae) (Wiesenborn 2005). Armored scales are attached to plants and were not found in fecal samples from flycatchers. Tamarisk leafhoppers have been found in diets of several passerine species along the Colorado River in the Grand Canyon, Arizona (Yard et al. 2004). Populations of *O. stactogalus* are highly variable, spatially and temporally (Wiesenborn 2005) and likely provide an inconsistent food supply. *O. stactogalus* also would provide a relatively low source of nitrogen, consistent

with other herbivorous Hemiptera (Fagan et al. 2002), because it appears to feed on phloem (Wiesenborn 2004). Predation by *E. t. extimus* on Hemiptera did not differ among localities despite different abundances of *T. ramosissima* and, expectedly, *O. stactogalus*.

Birds at Topock Marsh ate mainly Odonata and Diptera. The large size of Odonata, especially dragonflies, compared to other arthropods in fecal samples suggests they comprised a large proportion of arthropod biomass eaten by flycatchers at Topock Marsh. Dragonflies and damselflies are predaceous as aquatic nymphs and as terrestrial adults, and contain high nitrogen concentrations compared with other insects (Fagan et al. 2002). Most Diptera eaten by flycatchers at Topock Marsh were Syrphidae and may have been visiting tamarisk flowers. Immature syrphids are aquatic or terrestrial and typically predaceous or saprophagous (Vockeroth and Thompson 1987). Adult insects that immigrate into tamarisk after developing as immatures elsewhere, such as in the adjacent marshland or at its nutrient-rich edge, contribute significantly to the diet of breeding flycatchers at Topock Marsh. Immigrant predaceous insects seem to supplement *Tamarix*'s minimal arthropod food web and provide birds with nitrogen-rich food. Spiders and insects developing within or immigrating into *T. ramosissima* appear to supply adequate nutrition, because *E. t. extimus* breeding in tamarisk are not physiologically stressed (Owen et al. 2005).

#### CONSERVATION IMPLICATIONS

Preserving or restoring habitat for Southwestern Willow Flycatchers should strive to maintain or maximize overall arthropod abundance and diversity. Food availability in native habitats may be more effectively monitored by sweeping arthropods from plants than by capturing them with Malaise traps. However, an alternative method of sampling plant arthropods would be helpful, because sweeping can cause significant plant damage and disturbance. *Salix* spp., especially *S. gooddingii* and *S. exigua*, appear to be most effective in providing breeding *E. t. extimus* with arthropod food. Not all arthropods captured by flycatchers on or near *S. gooddingii* or *S. exigua* may have developed on these plants as immatures. Flying insects landing on *Salix*



spp. may have been eating or gathering pollen or nectar, consuming honeydew, capturing prey, thermoregulating, or resting. An inadequate food supply produced by riparian habitats preserved or restored for *E. t. extimus* may need to be supplemented by immigrant insects, such as Odonata. Aquatic or other non-riparian habitats may be required to produce the abundance and diversity of arthropods needed to sustain populations of breeding Southwestern Willow Flycatchers.

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#### LITERATURE CITED

- BARLOW, J. C. AND W. B. MCGILLIVRAY. 1983. Foraging and habitat relationships of the sibling species Willow Flycatcher (*Empidonax traillii*) and Alder Flycatcher (*E. alnorum*) in southern Ontario. *Canadian Journal of Zoology* 61:1510–1516.
- BEAL, F. E. L. 1912. Food of our more important flycatchers. USDA, Biological Survey Bulletin 44:1–67.
- BROWNING, M. R. 1993. Comments on the taxonomy of *Empidonax traillii* (Willow Flycatcher). *Western Birds* 24:241–257.
- COWIE, R. J. AND S. A. HINSLEY. 1988. Feeding ecology of Great Tits (*Parus major*) and Blue Tits (*Parus caeruleus*), breeding in suburban gardens. *Journal of Animal Ecology* 57:611–626.
- DROST, C. A., E. H. PAXTON, M. K. SOGGE, AND M. J. WHITFIELD. 2003. Food habits of the Southwestern Willow Flycatcher during the nesting season. *Studies in Avian Biology* 26:96–103.
- FAGAN, W. F., E. SIEMANN, C. MITTER, R. F. DENNO, A. F. HUBERTY, H. A. WOODS, AND J. J. ELSER. 2002. Nitrogen in insects: implications for trophic complexity and species diversification. *American Naturalist* 160:784–802.
- FRAKES, R. A. AND R. E. JOHNSON. 1982. Niche convergence in *Empidonax* flycatchers. *Condor* 84:286–291.
- GASKIN, J. F. AND B. A. SCHAAL. 2002. Hybrid *Tamarix* widespread in U.S. invasion and undetected in native Asian range. *Proceedings of the National Academy of Sciences USA* 99:11256–11259.
- GASKIN, J. F. AND B. A. SCHAAL. 2003. Molecular phylogenetic investigation of U.S. invasive *Tamarix*. *Systematic Botany* 28:86–95.
- MCLEOD, M. A., T. J. KORONKIEWICZ, B. T. BROWN, AND S. W. CAROTHERS. 2005. Southwestern Willow Flycatcher surveys, demography, and ecology along the lower Colorado River and tributaries, 2004. Annual report submitted to USDI, Bureau of Reclamation, Boulder City, Nevada, by SWCA Environmental Consultants, Flagstaff, Arizona, USA.
- NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION (NOAA). 2006. Western U.S. climate historical summaries. Western Regional Climate Center, Reno, Nevada, USA. [www.wrcc.dri.edu/Climsum.html](http://www.wrcc.dri.edu/Climsum.html) (accessed 30 March 2006).
- OWEN, J. C., M. K. SOGGE, AND M. D. KERN. 2005. Habitat and sex differences in physiological condition of breeding Southwestern Willow Flycatchers (*Empidonax traillii extimus*). *Auk* 122:1261–1270.
- PHILLIPS, A. R. 1948. Geographic variation in *Empidonax traillii*. *Auk* 65:507–514.
- PRESCOTT, D. R. C. AND A. L. A. MIDDLETON. 1988. Feeding-time minimization and the territorial behavior of the Willow Flycatcher (*Empidonax traillii*). *Auk* 105:17–28.
- RAMSAY, S. L. AND D. C. HOUSTON. 1997. Nutritional constraints on egg production in the Blue Tit: a supplementary feeding study. *Journal of Animal Ecology* 66:649–657.
- RAMSAY, S. L. AND D. C. HOUSTON. 1998. The effect of dietary amino acid composition on egg production in Blue Tits. *Proceedings of the Royal Society of London, Series B* 265:1401–1405.
- RAMSAY, S. L. AND D. C. HOUSTON. 2003. Amino acid composition of some woodland arthropods and its implications for breeding tits and other passerines. *Ibis* 145:227–232.
- SEDGWICK, J. A. 2000. Willow Flycatcher (*Empidonax traillii*). *The birds of North America*. Number 533.
- SOGGE, M. K., S. J. SFERRA, T. D. MCCARTHEY, S. O. WILLIAMS, AND B. E. KUS. 2003. Distribution and characteristics of Southwestern Willow Flycatcher breeding sites and territories: 1993–2001. *Studies in Avian Biology* 26:5–11.
- SOKAL, R. R. AND F. J. ROHLF. 1969. *Biometry*. W. H. Freeman and Co., New York, USA.
- TRIPLEHORN, C. A. AND N. F. JOHNSON. 2005. Borror and DeLong's introduction to the study of insects. Seventh Edition. Thomson Brooks/Cole, Belmont, California, USA.
- UNITT, P. 1987. *Empidonax traillii extimus*: an endangered subspecies. *Western Birds* 18:137–162.
- U.S. DEPARTMENT OF INTERIOR (USDI). 1995. Endangered and threatened species—Southwestern Willow Flycatcher final rule. *Federal Register* 60:10694–10715.
- VOCKEROTH, J. R. AND F. C. THOMPSON. 1987. Syrphidae. Pages 713–743 in *Manual of Nearctic Diptera*. Volume 2 (J. F. McAlpine, Editor). Monograph 28. Agriculture Canada, Biosystematics Research Centre, Ottawa, Ontario, Canada.
- WANG, Y. AND D. M. FINCH. 1997. Migration of the

- Willow Flycatcher along the middle Rio Grande. Wilson Bulletin 109:253–268.
- WIESENBORN, W. D. 2004. Mouth parts and alimentary canal of *Opsius stactogalus* Fieber (Homoptera: Cicadellidae). Journal of the Kansas Entomological Society 77:152–155.
- WIESENBORN, W. D. 2005. Biomass of arthropod trophic levels on *Tamarix ramosissima* (Tamaricaceae) branches. Environmental Entomology 34: 656–663.
- YARD, H. K., C. VAN RIPER III, B. T. BROWN, AND M. J. KEARSLEY. 2004. Diets of insectivorous birds along the Colorado River in Grand Canyon, Arizona. Condor 106:106–115.

APPENDIX. Abundances of Arthropoda in fecal samples from Southwestern Willow Flycatchers in southern Nevada and western Arizona.

Order	Taxon below Order	n <sup>a</sup>
Araneae		19
	Tetragnathidae	2
	Anyphaenidae	1
Odonata		21
	Anisoptera	4
	Zygoptera	4
Blattodea	Blatellidae	2
Hemiptera		6
	Heteroptera	2
	Corixidae	4
	Miridae	3
	Cicadellidae	43
	Derbidae	1
Coleoptera		12
	Scarabaeidae	1
	Coccinellidae	4
		1
	<i>Olla v-nigrum</i> (Mulsant)	1
	<i>Aneflomorpha</i> sp.	1
	Chrysomelidae	5
		1
	<i>Pachybrachis</i> sp.	1
	<i>Crepidodera opulenta</i> LeConte	2
	Curculionidae	1
Hymenoptera		15
	Ichneumonoidea	2
	Braconidae	3
	Chrysididae	1
	Formicidae	5
		1
	<i>Pseudomyrmex</i> sp.	1
	Pompilidae	1
	Vespidae	1
	Sphecidae	1
	Apoidea	5
	Halictidae	7
		2
	<i>Agapostemon</i> sp.	2
Lepidoptera		4
	moths	1
Diptera		24
	Nematocera	7
	Chironomidae	31
	Stratiomyidae	1
		1
	<i>Sargus</i> sp.	1
	<i>Myxosargus</i> sp. nr. <i>knowltoni</i> Curran	1
	Tabanidae	1
	Dolichopodidae	1
	Syrphidae	5
		4
	<i>Copestylum pallens</i> (Weidemann)	4
	<i>Palpada alhambra</i> (Hull)	2
	<i>Syritta pipiens</i> (Linnaeus)	13

APPENDIX. Continued.

Order	Taxon below Order	n <sup>a</sup>
	Acalyptratae	2
	Otitidae	2
	<i>Ceroxys latiusculus</i> (Loew)	1
	<i>Ochthera mantis</i> (DeGeer)	2
	Ephydriidae	1
	Drosophilidae	1
	Scathophagidae	1
	Calyptratae	4
	Calliphoridae	1
	Sarcophagidae	2
	<i>Ravinia</i> sp.	1
	Tachinidae	1

<sup>a</sup> Abundances of higher taxa do not include those of lower taxa.