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HABITAT AND SEX DIFFERENCES IN PHYSIOLOGICAL CONDITION OF BREEDING SOUTHWESTERN WILLOW FLYCATCHERS (*EMPIDONAX TRAILLII EXTIMUS*)

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Abstract.—The Southwestern Willow Flycatcher (*Empidonax traillii extimus*; hereafter "flycatcher") is a federally listed endangered species that breeds in densely vegetated riparian habitats dominated by native and exotic plants, including introduced monotypic saltcedar (*Tamarix ramosissima*). Some workers have theorized that saltcedar is unsuitable habitat for the flycatcher, primarily because it generally supports a smaller and less diverse invertebrate community (the flycatcher's food base) than native habitats (e.g. *Salix* spp.). However, differences in insect communities between native and saltcedar habitats are not proof that saltcedar habitats are inferior. The only way to evaluate whether the habitats differ in dietary or energetic quality is to document actual food limitation or its manifestations. Measurements of an individual's body condition and metabolic state can serve as indicators of environmental stressors, such as food limitation and environmental extremes. We captured 130 flycatchers breeding in native and saltcedar habitats in Arizona and New Mexico and measured 12 variables of physiological condition. These variables included body mass, fat level, body condition index, hematocrit, plasma triglycerides, plasma free fatty acids and glycerol, plasma glucose and beta-hydroxybutyrate, plasma uric acid, total leukocyte count, and heterophil-to-lymphocyte ratio. We found substantial sex-based differences in the condition of male and female flycatchers. Ten of the 12 measures of physiological condition differed significantly between the sexes. In all cases where male and female condition differed (except mass), the differences suggest that males were in poorer condition than females. We found few habitat-based differences in flycatcher condition. Only 3 of the 12 physiological condition indices differed significantly between habitats. Our data show that, at least in some parts of the flycatcher's range, there is no evidence that flycatchers breeding in saltcedar habitats exhibit poorer nutritional condition or are suffering negative physiological affects. *Received 8 April 2004, accepted 8 April 2005*.

Key words: diet, *Empidonax traillii extimus*, physiology, saltcedar, Southwestern Willow Flycatcher, tamarisk.

Diferencias entre Hábitats y Sexos en la Condición Fisiológica de Individuos Reproductivos en *Empidonax traillii extimus*

Resumen.—*Empidonax traillii extimus* es un atrapamoscas que está incluido en la lista federal de especies amenazadas y se reproduce en ambientes riparios con vegetación densa dominada por plantas nativas y exóticas, incluyendo la especie introducida *Tamarix ramosissima*. Algunos investigadores han propuesto que los ambientes

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dominados por *Tamarix* son inadecuados para este atrapamoscas, principalmente porque por lo general albergan comunidades más pequeñas y menos diversas de invertebrados (la base de su dieta) que los ambientes nativos (e.g. los dominados por *Salix* spp.). Sin embargo, las diferencias en las comunidades de insectos entre los distintos hábitats no demuestran que los ambientes dominados por *Tamarix* son de inferior calidad. El único modo de evaluar si los ambientes difieren en su calidad dietaria o energética es documentar la existencia de limitación de alimento o sus manifestaciones. Las medidas de la condición corporal de un individuo y su estado metabólico pueden servir como indicadoras de la presencia de agentes causantes de estrés en el ambiente, tales como limitación de alimento y condiciones ambientales extremas. En este estudio, capturamos 130 atrapamoscas que estaban criando en ambientes nativos y de *Tamarix* en Arizona y New Mexico, y medimos 12 variables relacionadas con su condición fisiológica. Estas variables incluyeron peso corporal, nivel de grasa, un índice de condición corporal, hematocrito, triglicéridos del plasma, ácidos grasos libres y glicerol en el plasma, glucosa e hidroxibutirato en el plasma, ácido úrico en el plasma, número total de leucocitos y el cociente entre heterófilos y linfocitos. Encontramos diferencias sustanciales con respecto al sexo: diez de las 12 medidas de la condición fisiológica difirieron entre machos y hembras. En todos los casos en que hubo diferencias entre sexos (excepto en el peso), éstas sugieren que los machos estaban en peores condiciones que las hembras. Encontramos pocas diferencias con respecto al hábitat en la condición de los atrapamoscas. Sólo tres de las 12 medidas de la condición fisiológica difirieron significativamente entre hábitats. Nuestros datos muestran que al menos en algunas partes del rango de distribución de *E. t. extimus,* no existe evidencia de que los individuos que se reproducen en ambientes dominados por *Tamarix* se encuentran en peores condiciones nutricionales o sufren de efectos fisiológicos negativos.

The Southwestern Willow Flycatcher (*Empidonax traillii extimus*; hereafter "flycatcher") is a federally listed endangered species (U.S. Fish and Wildlife Service 1995) that breeds in dense riparian habitats along rivers, streams, lakes, and other wetlands. Flycatchers breed in a diverse array of riparian habitats (Sogge and Marshall 2000), including those dominated by introduced species such as saltcedar (*Tamarix ramosissima*) and Russian olive (*Elaeagnus angustifolia*). Use of saltcedar is extensive; rangewide, 25% of flycatcher territories are found in habitats dominated by saltcedar (Sogge et al. 2003).

Saltcedar has been implicated as a causative factor in the decline of some southwestern bird species and communities (e.g. Hunter et al. 1987). Furthermore, DeLoach et al. (2000) proposed that saltcedar habitats are unsuitable for breeding flycatchers because saltcedar plants generally host fewer invertebrates than native willows (*Salix* spp.) and thus do not provide adequate food resources. In the first study of flycatcher diet, Drost et al. (1998) found significant differences among native and saltcedar habitats, with trends toward lower prey diversity and reliance on smaller prey items in the saltcedar habitat. However, differences in insect communities and flycatcher diet between native and saltcedar habitats are not, in themselves, evidence that saltcedar habitats are inferior or detrimental. The only way to determine whether the habitats differ in terms of dietary or energetic quality is to document actual food limitation or its manifestations.

One way to investigate manifestations of food limitation is by measuring variables that reflect the physiological state of an individual. Plasma metabolite levels depend strongly on food intake, so differences in daily pattern of food intake and changes in body mass (e.g. from differences in diet) may be reflected in concentrations of the different metabolites in an individual bird (Jenni-Eiermann and Jenni 1994, 1998). In addition, plasma metabolites may reflect differences in the overall fattening rate of the population and, hence, the quality of a particular habitat (Guglielmo et al. 2002). Hematological variables, such as hematocrit and leukocyte count, may provide additional information on the nutritional and immunological

health of an individual bird (Gross and Siegel 1983, Gershwin et al. 1985, Amand 1986). Other traditional measures of condition, which do not require collecting blood, include body mass and visual assessment of subcutaneous fat stores. Fat is the primary form of energy storage in birds, and energy stores fluctuate in relation to dietary intake and metabolic demands (Blem 1990).

We measured plasma concentrations of triglycerides, beta-hydroxybutyrate (BOHB), nonesterified fatty acids (NEFA), glycerol, glucose, and uric acid to characterize individual physiological condition of flycatchers breeding in saltcedar and native habitats in Arizona and New Mexico. In addition, we measured hematocrit (packed red blood cell volume), total and differential leukocyte (WBC) counts, and energetic condition. Few studies have investigated the link between habitat quality and a bird's physiology (but see Mazerolle and Hobson 2002). If saltcedar habitats present greater physiological challenges (e.g. food or water limitations, disease) than native habitats, birds breeding in exotic habitats will have lower values for fat level, body condition index, hematocrit, uric acid, and triglycerides. By contrast, WBC count, heterophil-to-lymphocyte [H:L] ratio, NEFA, glycerol, and BOHB should be higher in poor-quality patches. In addition, because sex-related differences have been documented for several of the indicators of physiological condition listed above (Gavett and Wakeley 1986, Hõrak et al. 1998, Kern et al. 2001), we examined differences between breeding males and females.

Methods

The study was conducted during the summers of 1999 and 2000 in south-central Arizona and southwestern New Mexico (Table 1). We captured, measured, and took blood samples from flycatchers breeding in both native and exotic habitats. The dominant plant species within the native breeding sites were willow, cottonwood (*Populus* spp.), and boxelder (*Acer negundo*). Native sites had ≤10% saltcedar. The exotic sites were dominated by saltcedar, with <10% native vegetation. Native sites were located at the Salt River inflow to Roosevelt Lake, the Lower San Pedro River, and the middle Gila River in Arizona, and in the Cliff–Gila valley in New Mexico. Exotic-dominated patches were found at the Tonto Creek and Salt River inflows to Roosevelt Lake, the Lower San Pedro River, the Gila River near the San Pedro River confluence, and the middle Gila River in Arizona.

The blood chemistry of a bird can vary with season and time of day. In females, a 10-fold increase in plasma triglycerides is associated with yolk production (Bacon et al. 1974, Challenger et al. 2001, Vézina and Williams 2003). Therefore, we concentrated our capture efforts during the month after females had finished egg laying and before the young fledged. Dates of capture were from 5 June to 7 July in 1999 and from 1 June to 30 June in 2000. In addition, triglyceride levels can rise sharply during the early-morning feeding and then level off after mid-morning (Jenni-Eiermann and Jenni 1997). In the same way, levels of BOHB are significantly lower in early morning as compared with other times of day. For this reason, we began sampling birds 3 h after sunrise, with daily capture times between 0800 and 1100 hours.

Birds were live-captured using a targeted mist-netting technique (Sogge et al. 2001), in which flycatcher songs and calls were broadcast to lure territorial flycatchers into nets. Flycatchers were removed from nets immediately upon capture, and fitted with an aluminum numbered federal band. We captured 130 adult flycatchers at 11 different breeding sites (Table 1). Fifty-five individuals were captured in exotic (saltcedar) habitats, and 75 in native habitats. For each bird we collected the following information: age, sex, subcutaneous fat (Helms and Drury 1960), wing chord, bill width, culmen length, and mass to the nearest 0.1 g. For birds that we could not reliably sex by presence of brood patch or cloacal protuberance (Pyle 1997), we sexed by genetic analysis, following Griffiths et al. (1998). We quantified the amount of visible subcutaneous fat deposited in the abdominal and furcular regions using a six-point scale (Helms and Drury 1960). An additional estimate of body condition was calculated by generating size-specific, fat-free body mass for each individual (as described by Ellegren 1992, Yong and Moore 1997). Individuals were grouped according to a common wing chord (1-mm increments). For each wing chord, body mass was regressed on fat score. In each regression, the *b*-intercept (equivalent to fat score = 0) provided an estimate of fat-free mass for the specific wing chord. Linear regressions were

Table 1. Location, elevation, and number of Southwestern Willow Flycatchers captured and sampled.

	Latitude, longitude	Elevation (m)	1999 (*n*)	2000 (*n*)	Total (*n*)
Exotic (saltcedar) sites					
Gila–Lower San Pedro River Confluence, Arizona	32.8°N, 110.7°W	600	5	8	13
Roosevelt Lake–Salt River Inflow, Arizona	33.6°N, 110.9°W	640	14	5	19
Roosevelt Lake–Tonto Creek Inflow, Arizona	33.8°N, 111.2°W	640	6	0	6
Middle Gila River, Arizona	33.1°N, 110.0°W	770	0	17	17
Total			25	30	55
Native sites					
Lower San Pedro River, Arizona	32.9°N, 110.7°W	660	11	15	26
Roosevelt Lake–Salt River Inflow, Arizona	33.7°N, 111.0°W	640	0	14	14
Middle Gila River, Arizona	33.1°N, 110.0°W	770	0	11	11
Cliff–Gila, New Mexico	32.9°N, 108.6°W	1,370	0	24	24
Total			11	64	75

performed for all wing chord lengths, and a second regression model was then produced by regressing fat-free mass on corresponding wing chord lengths. Using the equation generated by the second regression model, we calculated size-specific fat-free mass for each individual. We then subtracted fat-free body mass from body mass at capture to produce an estimate of stored fat (in grams).

Immediately following capture, a blood sample (50–125 μL) was taken via the brachial vein (26-gauge needle) and collected into heparanized capillary tubes. Capillary tubes were stored on ice. A drop of blood was placed on a glass slide and a thin smear was made using a beveled slide. Blood smears were air-dried, fixed with 100% methanol, and air-dried again. For identification of white blood cells, slides were stained with combination Wright and Giemsa stains. Absolute counts include all white blood cells (i.e. lymphocytes, monocytes, heterophils, eosinophils, and basophils) per 100 fields of view, using oil immersion (Campbell and Dein 1984). Total WBC count is expressed as the number of WBCs per 10,000 red blood cells (RBC). Changes in leukocyte number, whether leukocytosis (elevated leukocyte count) or leukopenia (depressed leukocyte count), reflect ongoing disease processes of bacterial, parasitic, or viral origin. Leukopenia may also indicate stress on the system by a nonetiological process, such as severe malnutrition (Gershwin et al. 1985) or strenuous exercise (Mackinnon 1992).

For differential counts (i.e. heterophil:lymphocyte [H:L] ratio), 100 WBCs were counted and the relative proportion of each blood cell type estimated. H:L ratio is used to assess stress in birds (Gross and Siegel 1983, Vleck 2001). Studies show that the H:L ratio increases in response to a variety of stressors, including food or water deprivation, malnutrition, and injury (Gross and Siegel 1986, Tripathi and Bhati 1997, Vleck et al. 2000).

Within 6 h of blood collection, we spun the capillary tubes in a clinical centrifuge for 9 min at 14,000 rpm. Using digital calipers, we determined hematocrit by measuring height of RBC layer and dividing by height of total blood sample. Hematocrit is frequently used to assess a bird's nutritional state (Amand 1986), but interpretation of values is difficult. A low hematocrit can indicate anemia or other mineral deficiencies, or bacterial and parasite infections (Campbell and Dein 1984). However, dehydration or elevated oxygen consumption may cause a high hematocrit (Carpenter 1975). Hematocrit may also reflect the reproductive activity of birds, being higher in breeding males because of increased testosterone levels (Sturkie 1986).

Blood plasma was separated from RBCs,

stored frozen, and then shipped to The Ohio State University Department of Animal Sciences for plasma constituent analysis under the direction of W. Bacon. Plasma metabolites were assayed using standard reagent kits that require small amounts of blood, ranging from 3 to 12 μL. Glucose, uric acid, BOHB, glycerol, and triglyceride levels were determined by quantitative enzymatic tests (Sigma Chemical, St. Louis, Missouri) and NEFA (Wako Chemicals USA, Richmond, Virginia). Intra-assay coefficients of variation ranged from 0.2% (triglycerides) to 3.7% (glycerol) for the various assays. Inter-assay coefficients of variation ranged from 1.1% (glycerol) to 7.0% (uric acid). Birds gaining mass may exhibit higher levels of plasma triglycerides and glucose, though the latter is generally kept within narrow limits (Jenni-Eiermann and Jenni 1994, 1997). On the other hand, levels of plasma glycerol, NEFA, and BOHB will decrease in response to lipid catabolism (Jenni-Eiermann and Jenni 1994, 1998). Uric acid levels must be interpreted with caution, because high levels have been linked to a high-protein diet (Hochleithner 1994) and to short-term food stress (Jenni-Eiermann and Jenni 1994). Therefore, understanding the meaning of uric acid patterns requires consideration of the other measures of physiological condition.

Statistical analysis.—To obtain plasma levels of true triglycerides, we subtracted free glycerol from total triglycerides. The process of egg production causes exceptionally high levels of triglycerides. Therefore, females with triglyceride levels of ≥800 mg dL^{-1} were excluded from analysis. Not all variables were measured for all individuals (primarily owing to differences in the amount of blood taken per individual) and therefore, sample sizes vary among variables (Table 2).

We tested for the effect of habitat type and sex on variation in physiological condition of flycatchers with analysis-of-variance (ANOVA) models, using type III sums of squares. Statistical significance was set at $\alpha = 0.05$. All significance levels refer to two-tailed tests. White blood cell count and heterophil:lymphocyte ratio did not meet the assumptions of normality. However, while log-transforming the variables created normality, it did not affect the results of the analysis. Therefore, we present all nontransformed data for clarity. We performed all analyses using SPSS 12.0.

Results

We conducted preliminary analyses to determine whether the condition indices differed with year, date (day within breeding season), and time of sampling. NEFA was the only variable to vary between years ($F = 190.60$, df = 1 and 130, $P < 0.0001$). For all subsequent analyses, NEFA was separated by year. We found a significant time-of-sampling effect on male triglyceride levels ($r^2 = 0.12$, $F = 11.51$, df = 1 and 85, $P = 0.001$), such that triglyceride levels increased throughout the morning, with highest values observed later in the morning (Jenni-Eiermann and Jenni 1997). To control for the time effect, we regressed triglyceride level on time, saved residuals, and used residuals for subsequent analyses. Otherwise, no other condition variables were significantly related to time or date of sampling.

Overall, 50 females were sampled, most of which ($n = 36$) had fully vascularized brood patches, indicating that they were incubating eggs. The remaining females ($n = 14$) had either a smooth or no brood patch and no evidence of an egg in the oviduct, an indication that they were in the nest-building or prelaying stage. We found no statistical differences in the variables of physiological condition between these two groups of females. Therefore, all females were combined for subsequent analyses.

Plasma metabolites.—There were significant differences between habitats for triglycerides, glycerol, and uric acid, but not for BOHB, NEFA, or glucose (Table 2). Specifically, we found that triglyceride and uric acid levels were higher, and glycerol was lower, in flycatchers sampled in saltcedar habitats compared with those captured at native sites. We ran additional analysis on habitat differences in male triglyceride levels attributable to the significant time effect. Using residuals computed by regressing triglyceride level on time of sample, the habitat difference in triglyceride levels was still significant ($F = 4.28$, df = 1 and 70, $P = 0.042$). We found significant differences by sex for all plasma metabolites except NEFA (Table 2). Females had higher levels of glucose, triglyceride, and uric acid, and lower levels of BOHB than males. Glucose showed a significant interaction effect between sex and habitat (Table 2), in that males in saltcedar had lower glucose levels than those in native habitats, whereas females showed the opposite trend.

Table 2. Descriptive statistics (means ± SD) and effect of habitat type and sex on variables of physiological condition of Southwestern Willow Flycatchers captured in Arizona and New Mexico during the breeding season of 1999 and 2000.

	Male				Female				*F*		
	Native	*n*	Saltcedar	*n*	Native	*n*	Saltcedar	*n*	Habitat	Sex	Habitat * Sex
Triglycerides	65.32 ± 16.54	40	78.22 ± 25.32	32	107.30 ± 60.37	26	124.22 ± 63.40	15	6.59**	23.83***	2.37
BOHB	20.42 ± 7.18	35	19.70 ± 7.37	16	11.91 ± 5.86	18	14.57 ± 6.98	5	0.23	11.23**	0.68
Uric acid	16.84 ± 6.32	41	20.16 ± 6.65	32	19.36 ± 7.64	28	26.00 ± 7.85	14	12.12***	9.83**	1.04
Glycerol	43.58 ± 10.7	40	41.10 ± 10.91	33	39.44 ± 16.68	27	31.74 ± 10.71	15	4.19*	7.38**	1.10
Glucose	329.40 ± 47.13	41	313.54 ± 49.82	32	332.08 ± 67.8	24	327.89 ± 53.41	13	1.22	7.55**	1.10
NEFA (1999)	3.52 ± 0.08	6	3.45 ± 0.19	15	3.49 ± 0.17	5	3.54 ± 0.27	7	0.02	0.34	1.18
NEFA (2000)	2.98 ± 0.19	35	2.98 ± 0.16	17	2.94 ± 0.16	19	3.12 ± 0.20	8	3.92	1.23	3.82
WBC count	12.39 ± 13.56	37	10.16 ± 5.90	27	25.68 ± 23.48	26	29.49 ± 15.35	12	0.13	21.08***	0.30
H:L ratio	0.49 ± 0.58	34	0.91 ± 1.97	20	0.42 ± 0.35	25	0.31 ± 0.16	11	0.74	2.07	1.09
Hematocrit	0.51 ± 0.02	39	0.50 ± 0.02	26	0.48 ± 0.03	27	0.48 ± 0.03	13	0.60	18.17***	0.18
Stored fat (g)	0.12 ± 0.77	39	0.61 ± 0.83	29	1.68 ± 0.97	27	1.84 ± 0.88	13	3.08	57.10***	1.04
Mass (g)	12.16 ± 0.79	41	12.37 ± 0.76	31	11.97 ± 0.85	27	12.13 ± 0.70	13	0.71	1.36	0.02
Fat score	0.67 ± 0.58	39	0.59 ± 0.61	34	1.80 ± 0.77	28	1.41 ± 0.99	16	1.79	51.64***	0.96

* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$; abbreviations: NEFA = non-esterified fatty acids, BOHB = beta-hydroxybutyrate, H:L = heterophil:lymphocyte ratio, WBC count = white blood cell (leukocyte)/10,000 red blood cells.

Leukocyte counts.—We found no habitat differences in WBC or H:L ratio (Table 2). WBC count differed significantly by sex (Table 2); females had higher WBC counts in both native and saltcedar habitats. H:L ratio did not differ between sexes for either habitat type.

Hematocrit.—We found no habitat-related differences in hematocrit, but there was a significant main effect difference between sexes (Table 2). Females had lower hematocrits in both native and saltcedar habitats.

Body condition indices.—Although mass, fat score, and stored fat did not differ significantly by habitat, there were significant main effect differences between the sexes for fat and stored fat (Table 2). In both habitat types, females had higher fat scores and stored fat than males.

Discussion

Body mass, fat levels, and plasma metabolites depend strongly on food intake; therefore, differences in daily patterns of food intake (caused by weather, differences in diet, etc.) may cause differences in daily patterns of these indicators of condition (Jenni-Eiermann and Jenni 1994). Hematological variables (e.g. WBC, H:L ratio) may reflect acute or chronic stressors, such as food or water limitations, injuries, or disease processes (Campbell and Dein 1984, Gershwin et al. 1985, Maxwell 1993, Vleck 2001). Therefore, the variables of physiological condition we measured should provide insights into environmental stressors that might be associated with breeding in saltcedar habitats as compared with native habitats, and between the energetic–physiological stressors on breeding males and females.

Habitat differences.—The indicators we measured showed no evidence that the physiological condition of flycatchers is lower in saltcedar habitats. Only 3 of the 12 variables differed between habitats (Table 2), and the patterns in 2 of these 3 variables suggested that saltcedar provided better energetic–dietary conditions than native habitats. Higher triglyceride and lower glycerol levels indicated that the flycatchers in saltcedar had deposited fat more recently (e.g. producing and storing more fat) than those in native habitat (Jenni-Eiermann and Jenni 1994, Schaub and Jenni 2001). The significantly higher uric acid levels (Table 2) for flycatchers nesting in saltcedar could be interpreted in two ways: flycatchers in saltcedar may be (1) consuming a higher-protein diet (Hochleithner 1994) or (2) experiencing food stress and metabolizing body protein (Anthony et al. 1990). The former interpretation is more consistent with our observed patterns in fat levels, mass, condition indices, and other plasma metabolites.

Our results may not be intuitive, given studies documenting lower arthropod diversity and abundance in saltcedar habitats (see DeLoach et al. 2000). One possible explanation is that earlier studies did not specifically investigate the relationship between saltcedar, associated arthropods, and flycatcher diet. Flycatchers consume a relatively diverse array of invertebrates (Drost et al. 1998, 2003), and the simple fact that flycatcher diet differs in different habitats does not mean that one habitat is inferior to another from the perspective of food availability. Although the greater variety of prey in native habitat may offer some buffer against a temporary shortage of any particular prey species, the large number of pollinator species attracted to flowering saltcedar appears to provide a very good source of prey in this habitat (Drost et al. 1998). Given that saltcedar flowers during much of the flycatcher breeding season at our study sites, abundance of large prey items (e.g. pollinators) may more than compensate for reduced diversity of available prey types.

Recently, Durst (2004) reported on the diet and potential arthropod prey base of flycatchers at Roosevelt Lake, Arizona. Flycatcher diet differed between habitats. Birds in saltcedar consumed more Homoptera, and less Lepidoptera and Ananeae, than those in native habitats. Further, biomass of several invertebrate taxa differed significantly between habitats. However, total arthropod biomass was not different, and Durst (2004) concluded that there were no differences in relative quality of food resources between native and exotics habitats. This conclusion is consistent with our physiology results, both at Roosevelt Lake and at the other sites we sampled.

Our finding that flycatchers breeding in saltcedar habitats do not suffer negative physiological consequences does not mean that all saltcedar-dominated riparian areas would provide suitable breeding habitat. Although our samples came from sites that support most of the flycatchers breeding in Arizona and New Mexico, these sites were located in an elevational

range of 560–1,370 m and typically within 200 m of surface water or moist soil. Furthermore, the riparian habitats at our study sites were usually embedded within a local matrix of desert shrub uplands (often dominated by mesquite [*Prosopis* spp.]) or irrigated croplands. These adjacent habitats may have provided a source for many strong-flying invertebrates (e.g. bees, wasps) that are attracted to flowering saltcedar (Drost et al. 2003). Many of the earlier studies of saltcedar, its invertebrate communities, and its reduced value to wildlife were conducted at sites that were lower in elevation, hotter, and drier than those included in Durst (2004) and the present study. Indeed, in many of the extensive monotypic saltcedar stands along the lower Colorado River and elsewhere in the deserts of the Southwest, high temperatures, dry conditions, or lack of invertebrate prey may preclude breeding by flycatchers. These potential regional and site-specific differences in suitability underscore the reality that not all saltcedar habitats are equal with regard to habitat quality.

Sex differences.—We found substantial sex-based differences in the condition of male and female Southwestern Willow Flycatchers; 10 of the 12 physiological condition indices differed significantly between the sexes (Table 2). In all cases where male and female condition differed, the differences suggested that males experienced higher stress or lower food intake and were in poorer condition than females, regardless of habitat type. In both native and exotic habitats, higher levels of fat, body condition, glucose, and triglyceride indicated that females were gaining more mass than males, and lower levels of BOHB and glycerol demonstrated that females were catabolyzing their fat reserves to a lesser degree than males (Jenni-Eiermann and Jenni 1994, 1997). Judging from these patterns, the higher uric acid levels in females probably reflected a higher-protein diet. The higher hematocrit in males may be attributable to dehydration or to higher energy demands. (Carpenter 1975, Work et al. 1999), which is consistent with our plasma metabolite results. Our findings agree with other studies that found sex-related differences in hematocrit and immunological variables (Gavett and Wakeley 1986, Hõrak et al. 1998, Ots et al. 1998).

Male flycatchers appear to be more energetically challenged than females during the nesting season. One probable explanation is the different activity patterns of males and females. During the breeding season, male flycatchers are strongly territorial (Sogge 2000) and active, spending much of their time singing and defending against conspecifics' intrusions. By contrast, female flycatchers (during the early nesting period that we sampled) are relatively inactive, periodically foraging and singing but spending most of the day incubating (M. K. Sogge unpubl. data). The higher activity level of males entails higher energy demands, with subsequent heightened physiological stress.

Our comparison of the effects of breeding in saltcedar versus native habitats was conducted within a specific geographic region and stage within the breeding season. The patterns that we found may differ in other parts of the flycatcher's range. Also, there are other ways in which differences in habitat suitability may be manifested, including differences in clutch size, productivity (number of young fledged per female per season), adult or juvenile mortality and survival, site fidelity, and breeding population age and density. None of this information is available, and additional studies and data analyses are needed to determine whether such differences exist at our study sites and elsewhere in the Southwest. However, our results show that there is no evidence that flycatchers breeding in saltcedar habitats are suffering negative physiological effects and reinforce the fact that such negative effects should not be assumed *a priori*.

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