



FIGURE 4. Willow Flycatcher winter habitat along Quebrada Pese, Panama. Sugar cane plantations surround the gallery forest and woodland.

growth of permanent towns and villages and conversion of native habitats to pasture land. This conversion from wooded areas to pasture has been one of the most significant changes in land use throughout Latin America (Hartshorn 1992, Kaimowitz 1996); overall, from 1981 to 1990, more than 75 million ha of forested land were converted to cattle pastures (Houghton *et al.* 1991). We found flycatchers using grazed areas that still contained scattered woody vegetation; thus, the presence of cattle itself did not

preclude presence of flycatchers. However, cattle ranching can cause major impacts to Willow Flycatcher habitat. The most extensive habitat impacts occur from the practice of clearing entire areas of shrubs and trees to create open pastures. These intensively cleared pastures are maintained by removing woody vegetation, rendering the site unsuitable for wintering Willow Flycatchers. Although grazing may have created Willow Flycatcher habitat by opening up areas in otherwise dense forests, lands intensively



FIGURE 5. Willow Flycatcher habitat at Laguna El Jocotal, El Salvador. Site was approximately 400 m from water at the time of surveys, but contained standing water from September through November.

managed for cattle pasture do not preserve or provide Willow Flycatcher winter habitat.

Large-scale permanent agriculture has also been encroaching on wetland habitats in Central America since the 1500s (Browning 1971), with modern agricultural practices playing a major role in the conversion of wetlands and woodlands, and the degradation and contamination of lowland areas (Murray 1994, Biesanz et al. 1999). Streams and rivers were diverted for irrigation, and in many areas, fertile wetlands were drained completely to make way for large-scale plantations and export crops such as cotton, rice, and African oil palm. As a result, freshwater wetlands are increasingly scarce along the Pacific slopes of Central America. Like intensive cattle grazing, most agricultural fields are cleared of trees and shrubs, rendering them unsuitable as Willow Flycatcher habitat. The few remaining trees (usually only one or two individuals wide) at these fields are generally planted along property lines and fence lines, or are remnant of the riparian forest once found along *quebradas* bordering the fields. Without the other key components of flycatcher habitat nearby, such strips of trees do not comprise suitable flycatcher habitat.

Our cursory examination revealed a high potential for agrochemical impacts at some sites in El Salvador (Laguna de Olomega, Laguna El Jocotal, Laguna San Juan, and Barra de Santiago) and Costa Rica (Bebedero, Canas, and Coto 44), where vegetable crops and sugar cane fields are in close proximity to shorelines, riverbanks, and major irrigation canals. Agrochemicals are widely used on crops throughout Central America; however, their effects on the surrounding environments and ultimately their effects on Neotropical migrants have not been well studied. These pesticides and herbicides leach into rivers and streams and/or enter the water directly as run-off. Although organochlorides such as DDT are rarely used in Costa Rica, Panama, and El Salvador, other highly toxic pesticides and herbicides are common. Many chemicals, though less persistent than organochlorides, can accumulate to toxic levels in birds, decrease local faunal diversity, and cause declines in insect populations (Eisler 1985b, Hooper et al. 1990, Iolster and Krapovickas 1999). If overwintering habitat suitability for insectivorous migrants, such as the Willow Flycatcher, is related to insect availability, agrochemicals that reduce local insect populations may increase competition for food, increase foraging costs, and reduce fat reserves and overall fitness (Gard and Hooper 1995).

#### THE ROLE OF PROTECTED AREAS

Neotropical migrants require suitable sites in which to over-winter, and protection of wintering habitat is one method to help ensure their conservation. However, conservation of natural resources and the establishment of national parks and preserves face many obstacles in Central America, including government and international funding constraints, lack of environmental education, and high demands on remaining natural resources. Furthermore, most protected areas are located in high elevation cloud forests, lowland rainforests, tidal and salt-water marshes, and coastal mangroves; thus, they do not include suitable Willow Flycatcher winter habitat. As of 2000, 14 of 24 Central American Ramsar sites (wetlands of international importance) were located in El Salvador, Costa Rica, and Panama (totaling 425,366 ha); only seven (one in El Salvador, four in Costa Rica, and two in Panama) contain freshwater *lagunas* or seasonally inundated floodplains (Ramsar List 2001) with potential for suitable Willow Flycatcher habitat. There may be a perception that the freshwater wetland areas that persist in Pacific lowland agricultural areas are so heavily impacted that they are of low habitat value and not deserving of conservation attention or funds; this is certainly not the case for the wetlands that support wintering Willow Flycatchers.

Despite administrative protection, deforestation and contamination continue to plague existing protected areas occupied by Willow Flycatchers. One example is Laguna El Jocotal in El Salvador, which was designated a nationally protected area in 1996, and is the country's only Ramsar site (Ramsar List 2001). In 2000, the El Salvador Ministry of Environment and Natural Resources acknowledged contamination and over-fishing at El Jocotal (Joma 2000); local park personnel now patrol the *laguna*, but regulations are rarely enforced. During our surveys, cattle were seen grazing the shorelines and in shallow waters. Local residents use the *laguna* to wash laundry with harsh detergents, and plastic containers from bleach and other products were seen along the shoreline. Despite such challenges, the protection of wetlands and associated habitat, even with minimal regulation, may be an important step for preserving the Willow Flycatcher.

#### RECOMMENDATIONS FOR FUTURE STUDIES

The relative lack of observations and records of Willow Flycatchers on the wintering grounds is in part due to the difficulties in positively identifying *Empidonax* species, and many general inventories, Christmas bird counts, and lists

provided by birders and ornithologists identify flycatchers only to the genus *Empidonax*. In order to develop and prioritize conservation and management strategies for the Willow Flycatcher, we need a better understanding of its distribution and ecology on the wintering grounds. Our study provides Willow Flycatcher distribution data for some areas of El Salvador, Costa Rica, and Panama, but many unsurveyed areas remain and may contain suitable habitat. Additional surveys are needed, particularly at the northern and southern extents of the winter range and along a wider range of elevations.

Quantitative habitat studies are needed to better understand habitat requirements and to more precisely identify habitat availability on the winter range. It would also be valuable to determine if remote-sensing data and GIS can be used to accurately identify areas of wintering habitat. Research is needed to determine if distribution and habitat use vary by sex and/or subspecies, to document overwinter survivorship, and to characterize the effects of seasonal water changes on habitat selection. Studies are also needed to determine if flycatchers move, within and between sites, in response to seasonal changes in the presence of surface water/saturated soil. Ongoing studies at relatively large flycatcher sites in Costa Rica (Koronkiewicz and Sogge 2000) suggest winter territoriality, and high return rates and site fidelity for wintering Willow Flycatchers. Comparative studies are needed to determine if this is also true for smaller, more isolated, and/or more fragmented winter habitats throughout the flycatcher's winter range.

Finally, quantitative data are needed to more accurately assess the threat of land management practices, particularly agrochemical use, to wintering Willow Flycatchers and their habitat. Our survey project was not designed to detect the presence of agrochemicals or other environmen-

tal contaminants in flycatchers or their habitats, or to determine what effects such chemicals might have on wintering flycatchers. Given our observations of contaminated waterways, and the nature and extent of the agricultural activities that occur near wintering sites, detailed contaminant studies are warranted. Chemical analysis of water and/or soil samples at flycatcher wintering sites could identify areas where contaminants pose a threat. Furthermore, as has been done on the breeding grounds (Mora et al. *this volume*), chemical analysis of insects and surrogate bird species at wintering sites would help determine if contaminants are likely accumulating at harmful levels within locally wintering flycatchers.

#### ACKNOWLEDGMENTS

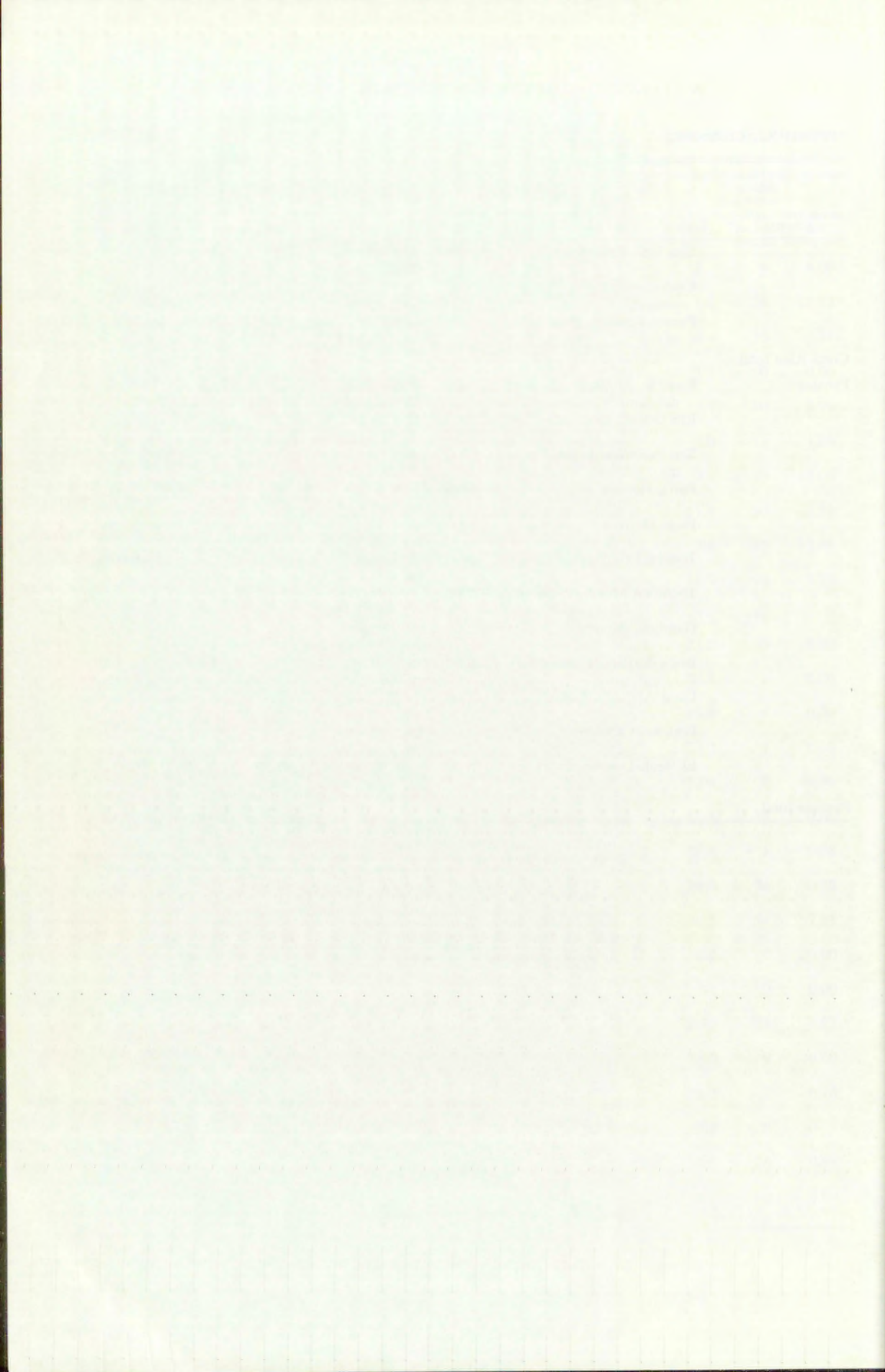
Financial support for this project was provided by the U.S. Bureau of Reclamation, (Phoenix, AZ), U.S. Geological Survey, U.S. Fish and Wildlife Service (Region 2, Albuquerque, NM), and the U.S. Forest Service. This work was made possible through collaboration with the Servicio de Parques Nacionales y Vida Silvestre and the Universidad de El Salvador in El Salvador, the Organization for Tropical Studies in Costa Rica, and the Smithsonian Tropical Research Institute in Panama. We thank P. Unitt and the San Diego Natural History Museum for administrative support, as well as S. Leon and S. Sferra for their encouragement and assistance with funding and contracts. Special thanks go to the dedicated members of the field crew: E. Cohen, C. Drost, K. Enos, J. Hart, M. Halterman, P. Heavin, M. Johnson, S. Langridge, M. J. Mendez, M. Santana, and S. Sferra. We thank G. Seutin and W. Rodriguez for their invaluable logistical and field support during the 2000 surveys, and the numerous people who provided us with information on current wintering locations, logistical advice, and assistance with permit applications. We are especially grateful to the many Central Americans who lent us their support and hospitality during our surveys. This manuscript was greatly improved by the comments of O. Komar and an anonymous reviewer.

## APPENDIX. WILLOW FLYCATCHER WINTER SURVEY EFFORT AND RESULTS FOR EL SALVADOR, COSTA RICA, AND PANAMA, JANUARY AND FEBRUARY 1998-2000

Country	Survey location	Year	Coordinates	Number of sites surveyed	Survey hours	Number of Willow Fly-catchers detected	Flycatchers per survey hour
El Salvador	Rio Paz, Ahuachapan	2000	N 13°47.71' W 90°06.77'	1	1	4	4.00
	Rio Guayapa, Ahuachapan	2000	N 13°43.32' W 89°59.06'	1	1.1	24	21.82
	La Barra de Santiago, Ahuachapan	2000	N 13°41.52' W 89°56.58'	1	8.4	35	4.17
	Lago Coatepeque, Santa Ana	2000	N 13°50.82' W 89°34.18'	1	1.5	0	0.00
	Colima, Cuscatlan	2000	N 14°02.75' W 89°07.39'	2	3.4	10	2.94
	Suchitoto, Cuscatlan	2000	N 13°58.34' W 89°01.54'	2	7.0	13	1.86
	Bosque Nancuchiname, Usulután	2000	N 13°20.48' W 88°43.14'	1	2	30	15.00
	Laguna de Olomega, San Miguel	2000	N 13°19.94' W 88°01.18'	11	11.9	30	2.52
	Laguna de San Juan, San Miguel	2000	N 13°22.08' W 88°09.58'	1	2.6	35	13.46
	Laguna El Jocotal, San Miguel	2000	N 13°19.15' W 88°14.59'	7	11.9	93	7.82
El Salvador total				28	50.8	274	
Costa Rica	Parque Nacional Santa Rosa, Guanacaste	1999	N 10°51.10' W 85°36.88'	5	21.5	0	0.00
	Bebedero, Guanacaste	1998	N 10°21.12' W 85°10.50'	4	24.5	1	0.04
	Canas, Guanacaste	1999	N 10°21.21' W 85°5.96'	2	13.8	0	0.00
	Tempate, Guanacaste	1999	N 10°22.10' W 85°43.18'	4	23.2	1	0.04
	Parque Nacional Palo Verde, Guanacaste	1999	N 10°20.90' W 85°16.92'	5	22.4	0	0.00
	Bolson, Guanacaste	1999	N 10°21.31' W 85°25.17'	5	43.4	26	0.60
	Puerto Humo, Guanacaste	1999	N 10°17.97' W 85°24.98'	2	12.8	1	0.08
	Santa Cruz, Guanacaste	1999	N 10°19.74' W 85°38.97'	5	34.6	26	0.75
	Solimar, Guanacaste	1999	N 10°16.54' W 85°8.80'	5	21.5	54	2.51
	Hojancha, Guanacaste	1998	N 10°6.30' W 85°22.01'	3	8.6	0	0.00
	Punta Piedra, Guanacaste	1998	N 9°42.57' W 85°1.00'	3	9.1	0	0.00
	Chomes, Puntarenas	1999	N 10°4.16' W 84°53.96'	4	23.0	28	1.22
	Boca de Barranca, Puntarenas	1999	N 9°53.42' W 84°40.75'	4	15.0	9	0.60
	Tarcoles/Agujas, Puntarenas	1999	N 9°51.05' W 84°33.90'	6	18.3	3	0.16
	Punta Coyote, Caletas	1999	N 9°45.59' W 85°16.07'	4	9.8	8	0
	Rio Palo Seco, Puntarenas	1999	N 9°34.35' W 84°18.70'	8	26.6	26	0.98
	Buenos Aires, Puntarenas	1999	N 9°6.65' W 83°20.46'	13	28.7	0	0.00

## APPENDIX. CONTINUED.

Country	Survey location	Year	Coordinates	Number of sites surveyed	Survey hours	Number of Willow Flycatchers detected	Flycatchers per survey hour
	San Vito, Puntarenas	1999	N 8°49.65' W 82°57.04'	3	5.8	0	0.00
	Coto Colorado/44, Puntarenas	1999	N 8°33.72' W 82°57.47'	8	32.4	10	0.31
	Puerto Jimenez, Puntarenas	1999	N 8°30.93' W 83°17.65'	7	33.5	9	0.29
Costa Rica total				100	428.5	202	
Panama	Road to Almirante, Bocas del Toro	2000	N 9°00.24' W 82°15.99'	2	2.8	0	0.00
	Río Guabo, Bocas de Toro	2000	N 8°56.99' W 82°11.29'	2	2	0	0.00
	San Felix/Las Lajas, Chiriqui	2000	N 8°10.61' W 81°51.63'	3	5.6	7	1.25
	Paris, Herrera	1999	N 8°6.18' W 80°34.01'	3	13.0	0	0.00
	Pese, Herrera	2000	N 7°53.20' W 80°32.43'	1	4.8	14	2.92
	Tonosí, Los Santos	2000	N 7°26.85' W 80°22.32'	3	19.7	18	0.91
	Tocumen Marsh, Panama	2000	N 9°04.09' W 79°22.43'	2	10.9	8	0.73
	Gamboa, Panama	2000	N 9°07.24' W 79°43.61'	2	5.1	3	0.59
	Boca de Pacora, Panama	2000	N 9°02.30' W 79°18.17'	2	2.5	0	0.00
	Lago Alajuela, Colon	2000	N 9°11.40' W 79°33.97'	2	2.3	0	0.00
	Portobelo, Colon	2000	N 9°33.95' W 79°34.58'	1	2	4	2.00
	El Real, Darien	2000	N 8°06.40' W 77°43.98'	3	11.3	12	1.06
Panama total				26	82.0	66	



## ECOLOGY AND BEHAVIOR—INTRODUCTION

MARY J. WHITFIELD, MARK K. SOGGE, SUSAN J. SFERRA, AND BARBARA E. KUS

As the broad title suggests, the papers in this section are diverse and cover a wide range of topics, including population size estimates, nesting ecology, breeding habitat descriptions, food habits, and singing behavior. They also cover a wide geographic area in the western U.S., with results reported from Oregon, California, Arizona, and New Mexico. Because the Willow Flycatcher has been the subject of several breeding ecology papers (e.g., King 1955, Walkinshaw 1966, Holcomb 1972, Flett and Sanders 1987, Brown 1988), two conservation assessments (Finch and Stoleson 2000, Green et al. 2003), and a book (McCabe 1991), some may question the need for more papers on the subject. However, aspects of the flycatcher's breeding ecology and habitat use can vary widely across its broad geographical and elevational range; therefore, it can be difficult to extrapolate the results of one study area to another. Indeed, McCabe (1991:22) recognized this dilemma when he noted "Field workers characteristically assume that what they observe is fact and that contrary observations are less than accurate or require special interpretation. The Little Green Bird [Willow Flycatcher], with its flexible life style, resists such pigeon-holing, as will be evident in many aspects of its biology."

This variability in life history traits is apparent in the results reported in the chapters within this section, especially those that focus on or contain information on habitat. While these papers support other published habitat descriptions that report Willow Flycatchers breeding in areas with shrubs or dense understory vegetation, usually within the lowest 2-3 m (e.g., McCabe 1991, Sedgwick 2000, Sogge and Marshall 2000, Uyebara and Whitfield 2000), the specifics of topography, proximity to water, and plant species composition differ widely. Anne King and Jon King, and Helen Bombay and colleagues describe Willow Flycatchers using deciduous riparian shrubs in montane meadows in California. Bob Altman and co-workers note that Willow Flycatchers in the Willamette Basin of Oregon breed in a variety of dense shrubby habitats, including 4-15 year-old clearcuts in coniferous forests, lowland riparian, and upland valley habitat. In Arizona, Linda Allison and co-authors report Willow Flycatchers using riparian woodland that mostly lacked shrubs, yet with dense vegetation up to 5-m high. However, in some areas, flycatcher habitat lacks dense un-

derstory within the first 2-3 m. For example, in the Gila River Valley, New Mexico, Scott Stoleson and Deborah Finch found Willow Flycatchers breeding in riparian forest patches which seldom had dense vegetation within the first 3-m above ground. Here, the densely vegetated areas were from 3-10 m high, and most Willow Flycatchers nested within this dense strata at about 7-m high.

Although qualitative descriptions of Willow Flycatcher habitat abound, only a few published studies (Brown 1988, Flett and Sanders 1987, Sedgwick and Knopf 1992, Uyebara and Whitfield 2000) have actually quantified Willow Flycatcher habitat characteristics. Several chapters in this volume provide much new data in this regards (Allison et al., Altman et al., Bombay et al., and Stoleson and Finch), and greatly increase the amount of published quantitative information on Willow Flycatcher habitat. Although this is an important step, more such data are needed for developing effective management guidelines that create and preserve Willow Flycatcher habitat.

Several papers in this section provide new data on subjects where little or no previously published information exists. Charles Drost and colleagues provide the first published data on the food habits of a population of Southwestern Willow Flycatchers. C.J. Ralph and Kim Hollinger report on the migration and movement patterns of Pacific-slope Flycatchers and Willow Flycatchers, and note the substantial differences between these two *Empidonax* species. Although Willow Flycatchers are considered to be a monogamous species (Sedgwick 2000), Rebecca Davidson and Linda Allison found polygyny common in two closely-monitored populations in Arizona, suggesting that this mating strategy may be more widespread than previously believed. They also examined how mating strategy (i.e., monogamy vs. polygyny) affected reproductive success of males and females. Finally, Helen Yard and Bryan Brown's study of Willow Flycatcher singing behavior documented that female Willow Flycatchers sing more often than previously known, and discuss the implications of this fact with regard to survey protocols and population estimates. Their work on female song during the breeding season complements recent research (Koronkiewicz 2002) documenting that female Willow Flycatchers use song (and other

agonistic behaviors) to defend individual territories on their wintering grounds.

#### FUTURE RESEARCH DIRECTIONS

Clearly, data that have been recently published in this volume and elsewhere (e.g., Sedgwick 2000, Stoleson and Finch 2000) have contributed greatly to our understanding of Willow Flycatcher breeding ecology and habitat. Just as clearly, however, the answers to many important questions remain uninvestigated and/or unknown.

The loss and degradation of habitat is widely recognized as the main cause of the decline of Willow Flycatcher populations in the West (Unitt 1987, Harris et al. 1987, USFWS 2002, Green et al. 2003, Altman et al. *this volume*). Thus, identifying those habitat features that influence Willow Flycatcher productivity, survivorship, and site fidelity is a crucial step for producing effective management strategies to protect and enhance Willow Flycatcher habitat. To date, Bombay et al. (*this volume*) have the only published paper that looks at this question with regard to the Willow Flycatcher. Because Willow Flycatcher habitat is so geographically variable, we need additional studies throughout its breeding range in order to determine the range of variability, document site-specific and regional patterns, and develop management guidelines that will be effective in specific locales.

An important consideration with regard to habitat characteristics and use is the issue of scale. Most Willow Flycatcher studies to date are centered on nest plot and territory, with only two published papers (Sedgwick and Knopf 1992, Bombay et al. *this volume*) simultaneously quantifying habitat at different scales. As Allison et al. point out, there is a great need for more habitat data at differing scales, such as at the breeding patch, drainage, and landscape levels.

Exotic plants such as saltcedar and Russian olive are prevalent in many Willow Flycatcher breeding sites (Sogge et al. 1997a, USFWS 2002). Non-native or exotic-dominated habitats are sometimes thought of as being inferior to native habitats for many animal species, including the Willow Flycatcher (Tracy and DeLoach 1999). Because of this, and other ecological ramifications, major efforts are underway throughout the U.S. to eliminate or reduce exotics (Executive Order 13112). These programs will likely entail substantial costs, and will hopefully yield significant long-term ecological benefits. However, Southwestern Willow Flycatchers inhabit many areas that are dominated by exotic plants, and could be affected by the removal of these non-native plants, especially in

areas where the current hydrologic regime is unlikely to support native trees. Therefore, research is needed to determine the potential effects of exotic vegetation control within flycatcher habitats, and to develop ways to minimize any negative impacts. Accomplishing this requires additional studies focused on flycatcher productivity, survivorship, diet, and habitat use in exotic vs. native habitats. Because of the highly variable nature of flycatcher demographic and ecological patterns, such studies must be conducted in multiple areas and over multiple years, to determine whether large-scale control of exotics is appropriate in areas that Willow Flycatchers occupy.

Polygyny is typically considered to be uncommon for Willow Flycatchers (Prescott 1986, Sedgwick and Knopf 1989, McCabe 1991, Sedgwick 2000), yet polygyny appears to be fairly common in some populations of the Southwestern subspecies (Pearson 2002, Allison and Davidson *this volume*). Interestingly, populations with significant polygyny rates often harbor territorial but unmated males. This fact raises important questions regarding why the territories of some males have two or more females, while others have none. Research comparing habitat features, insect abundance, physical microclimate, and other factors within the territories of unmated vs. monogamous vs. polygynous males would help answer this question, and provide insights into important questions as to what constitutes good quality habitat.

Another important factor in habitat selection and use is food resources, yet we know almost nothing about how flycatcher diet varies in different habitats (e.g., saltcedar dominated vs. native dominated, conifer dominated vs. lowland habitat). Indeed, with only four published accounts of Willow Flycatcher diet (Beal 1912, Prescott and Middleton 1988, McCabe 1991, Drost et al. *this volume*), there is a paucity of information on flycatcher diet throughout its range. This is surprising given the fact that food resources can affect breeding site selection, habitat use, productivity, and survivorship. Clearly, additional studies of food availability, diet patterns, and foraging behavior are warranted.

As is the case with most neotropical migrant species, the vast majority of Willow Flycatcher ecology and habitat research has focused on the breeding grounds. Although migration behavior and habitat are important, little published information exists (but see Hussell 1991a,b; Yong and Finch 1997, Otahal 1998, Ralph and Hollinger *this volume*), and many questions need to be answered. Information on Willow Flycatcher wintering ecology and behavior is needed because they spend more than half the year on



their wintering grounds. With new information available on Willow Flycatcher winter distribution and ecology (Koronkiewicz 2002, Lynn and Whitfield 2003, Lynn *et al.* *this volume*), the opportunity to investigate critical questions is easier. What are the habitat characteristics of Willow Flycatcher wintering and migration areas? What do they eat during migration and winter? Do different habitats provide more or better food or energy resources than others; if so, which? What are the linkages between particular breeding and wintering populations? Do the different

Willow Flycatcher subspecies spatially segregate on the wintering ground, and/or migrate differentially in spring and fall? What are the major migration routes for Willow Flycatchers (especially in the southern U.S. and Central America)? What is needed in terms of type, size, and geographic spacing of migration stopover habitats? What are the major stressors or mortality factors during migration and on the wintering grounds? The answers to these, and other, unanswered questions have direct management and conservation implications.

## WILLOW FLYCATCHERS IN WARNER VALLEY, PLUMAS COUNTY, CALIFORNIA

ANNE M. KING AND JON R. KING

**Abstract.** Annual surveys for Willow Flycatchers (*Empidonax traillii*) have been conducted since 1996 in the Almanor Ranger District of the Lassen National Forest. Results from surveys in Warner Valley, Plumas County, California, in 1996–1998 suggested a population of as many as 45 breeding pairs. In 1998, we monitored this population to determine the number of territories and obtain preliminary information on their productivity. We mapped 32 territories and recorded 7 additional singing males during some surveys. Ten Willow Flycatcher nests were found; 7 successfully fledged at least one young, and there was no known parasitism by Brown-headed Cowbird (*Molothrus ater*). All of the nests were built in mountain alder (*Alnus incana*) shrubs, and 9 of the nests sites were surrounded by Lemmon's willow (*Salix lemmonii*) shrubs. Shrub cover within 5 m of the nests was comprised entirely of Lemmon's willow and mountain alder.

**Key Words:** *Empidonax traillii*, montane meadow, nest monitoring, Sierra Nevada, territory mapping, Willow Flycatcher.

The Willow Flycatcher (*Empidonax traillii*) is a neotropical migratory species that breeds throughout much of the United States and portions of southern Canada, and winters from southern Mexico to northern Central America (Sedgwick 2000). Four subspecies are generally recognized, and three breed in California. Historically, Willow Flycatcher was a common breeding species throughout the state (Grinnell and Miller 1944), but severe declines in populations led to the species being listed as Endangered in 1990 under the California Endangered Species Act (California Department of Fish and Game 1991). The subspecies *E. t. extimus*, which breeds in the southern portions of the state and elsewhere in the southwestern United States, is federally listed as Endangered (U.S. Fish and Wildlife Service 1995).

The other subspecies known to breed in California are *E. t. brewsteri* and *E. t. adastus*. The former was once common along California's Pacific Coast (Eliot 1923) and in the Sierra Nevada (Grinnell and Miller 1944). In California, *E. t. brewsteri* is now almost entirely restricted to montane meadows in the western Sierra Nevada and Cascades; a recently discovered breeding pair in Humboldt County is the only known current record from coastal California (R. Hewitt, pers. comm.). Within California, *E. t. adastus* breeds east of the Sierra Nevada and Cascade crestline from the Oregon border to Inyo County. It is not known which subspecies occurs at breeding sites near the crestline of the Sierra Nevada and Cascades, including our study area, and it is possible these birds are hybrids between *brewsteri* and *adastus* (Phillips 1948, Unitt 1987).

In an effort to update the status and distribution of Willow Flycatcher in California, the Cal-

ifornia Department of Fish and Game (CDFG) conducted surveys throughout the Sierra Nevada in 1982 and 1986 (Serena 1982, Harris et al. 1988), primarily on U.S. Forest Service and National Park Service lands, which resulted in an estimate of 150 pairs in the Sierra Nevada. Recent attempts by the Sierra Nevada Framework Project to synthesize Willow Flycatcher survey results led to a similar estimate of 300–400 individuals in the Sierra Nevada (R. Stephani, pers. comm.). In 1982 and 1986, 8 and 11 (respectively) singing males were detected on lands in, and adjacent to, the Almanor Ranger District (ARD) of the Lassen National Forest, at the northern boundary of the Sierra Nevada. In 1996, ARD biologists began annual Willow Flycatcher surveys in Warner Valley, a site not previously surveyed. Results suggested that Warner Valley supported one of the largest populations of breeding Willow Flycatchers in the Sierra Nevada (as many as 49 pairs). However, conclusions were based on single-day surveys conducted early in the breeding season, when migrant individuals are still passing through the area and may contribute to an overestimation of the population size.

The principal objective of the present study was to determine the number of breeding territories present in Warner Valley based on surveys conducted on multiple days throughout the season. Further, we obtained preliminary information on the productivity of the Warner Valley Willow Flycatcher population.

### METHODS

Warner Valley is a large (250 ha) montane meadow approximately 2 km long and 100–750 m wide, at approximately 1525 m elevation. It is located in northern Plumas County (Fig. 1) near the crestline of the far northern extent of the Sierra Nevada. Approximately

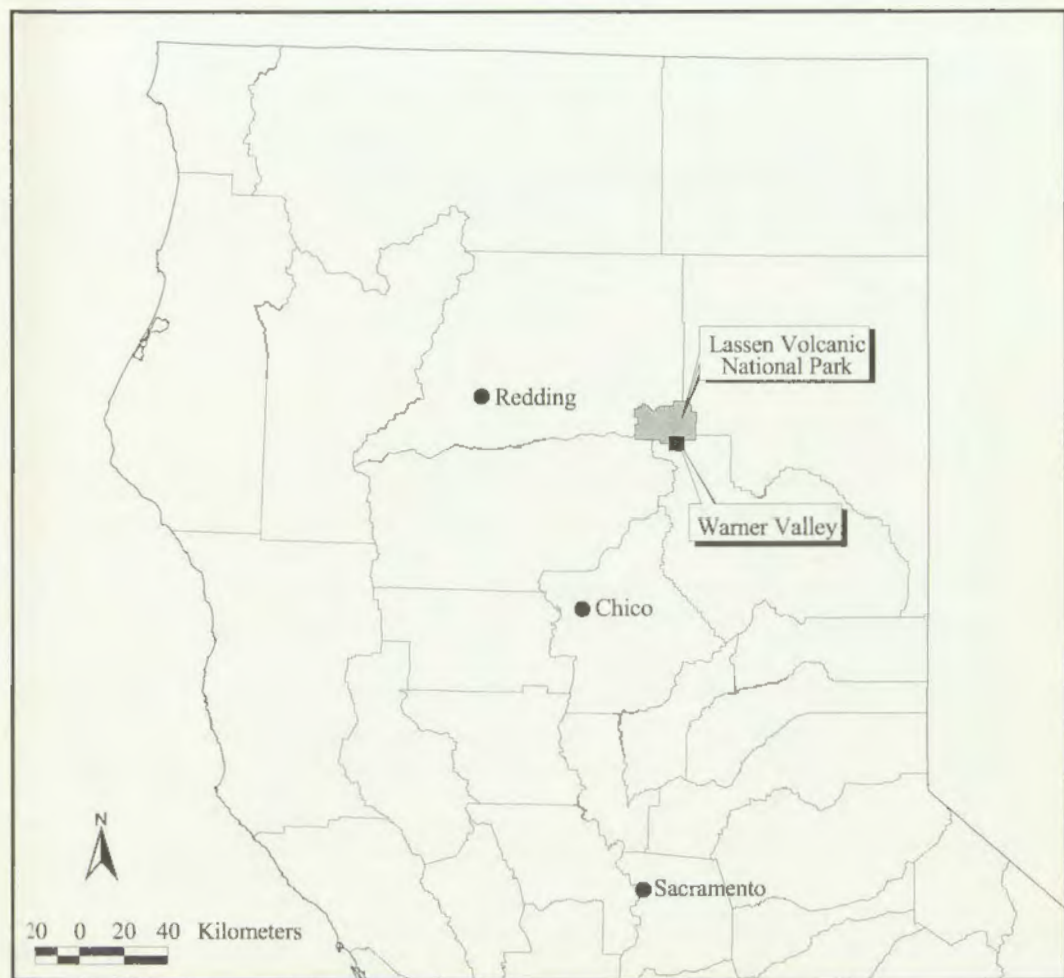


FIGURE 1. Location of Warner Valley, Plumas County, northern California.

90% of Warner Valley is a California Department of Fish and Game (CDFG) Wildlife Area, and the remaining portions are within the ARD and Lassen Volcanic National Park (LVNP). The habitat is primarily comprised of Lemmon's willow (*Salix lemmonii*) and mountain alder (*Alnus incana*) clumps interspersed with open herbaceous areas of grasses and sedges (*Carex* spp.). Mixed coniferous forest, dominated by lodgepole pine (*Pinus contorta*), surrounds the meadow and is present in pockets of higher ground within the meadow. Warner Creek generally flows along the western boundary of the meadow, and several large beaver ponds and numerous small channels of flowing water are present.

In 1998, we surveyed for Willow Flycatchers in Warner Valley 6 times between June 18 and July 20. Surveys began at sunrise and were concluded by noon. The starting point of each survey alternated between the northern and southern ends of the meadow. We slowly walked a meandering route through the meadow stopping periodically for up to ten minutes and

listening for Willow Flycatcher songs and calls (tape playback was not used). Each time a singing individual was encountered, we followed it for at least 10 minutes and mapped its movements on an aerial photograph. Detections of Brown-headed Cowbirds (*Molothrus ater*) were also noted.

Opportunistic nest searching was conducted during surveys; if nesting behavior was observed, up to 15 minutes were spent searching for the nest. Additional nest searching was conducted after morning surveys but was restricted to the most accessible territories and those where nesting behavior had been observed. Nests were monitored every 5–10 days until the outcome was determined, and the cause of failure was recorded when known. Nest searching and monitoring were conducted following Martin and Geupel (1993) to minimize disturbance and observer-influenced predation. Data on vegetation variables were collected at all nest sites soon after completion of the nesting attempt, and generally followed Breeding Biology Research and Monitoring Database guidelines (Martin et al. 1997).

Total shrub cover, cover of each shrub species, and ground cover (i.e., grass/sedge, shrub, forb, log, bare ground, and water) were estimated within a 5-m radius of the nest. Nest dimensions, nest height, number and size of supporting branches, substrate height, and canopy cover at the nest site were measured; dimensions of the nest clump and nest concealment were estimated.

## RESULTS

Thirty-two territorial male Willow Flycatchers were detected during multiple surveys throughout the census period. Seven additional singing males were detected during some of the surveys; these were likely migrant individuals that did not breed in the immediate area. The sex of the singing individuals was based on behavioral observations, such as singing locations and interactions with other individuals. The number of territories occupied by a breeding pair was not determined, though pairs were documented in many of the territories. Brown-headed Cowbirds appeared to be very scarce in the area; no more than three male cowbirds were detected during each of the five surveys, and no female cowbirds were detected.

Ten Willow Flycatcher nests were found. Monitoring observations provided some estimates of nest timing; dates of clutch initiation ranged from June 25 to July 19, hatching dates from July 10 to August 3, and fledging dates from July 22 to August 17. Clutch size was determined for six nests: four had a clutch size of four, and two nests had three-egg clutches. Seven of the 10 nests fledged at least one young; two of the failed nests were abandoned (one during building and one with eggs that may have been infertile), and the third was either abandoned during laying or partially depredated and subsequently abandoned. No cowbird eggs or young were found in any nest.

All 10 nests were built in mountain alder shrubs; nine were entirely surrounded by Lemmon's willow. Mean nest height was 1.3 m (SD = 0.31; range 0.9–1.9 m), and mean height of nest substrates was 2.8 m (SD = 0.9; range 1.8–5.0 m; Table 1). Shrub cover within 5 m ranged from 35% to 100% (mean = 56%; SD = 21.2) and was entirely comprised of Lemmon's willow and mountain alder (Table 1). Grasses and sedges accounted for an average of 96% of the ground cover within 5 m, with forbs and open water accounting for the remaining 4%. Although open water was a small portion of the total ground cover, the soil at all nest sites was completely saturated throughout the breeding season, and, in many cases, the herbaceous cover was growing in standing water.

TABLE 1. VEGETATION PARAMETERS FOR WILLOW FLYCATCHER NESTS FOUND IN WARNER VALLEY, PLUMAS COUNTY, CALIFORNIA, IN 1998 (N = 10)

Vegetation variable	Mean $\pm$ SD	Range
Nest height (m)	1.3 $\pm$ 0.31	0.9–1.9
Substrate height (m)	2.8 $\pm$ 0.92	1.8–5.0
Total shrub cover (%)	56.0 $\pm$ 21.2	35.0–100
Willow cover (%)	57.3 $\pm$ 26.5	32.5–98.3
Alder cover (%)	42.6 $\pm$ 26.4	1.8–71.3
Green ground cover (%)	98.5 $\pm$ 2.2	95.0–100

## DISCUSSION

Historically, Willow Flycatchers were widespread and abundant in montane meadows of the Sierra Nevada, including the Lassen region (Grinnell et al. 1930, Grinnell and Miller 1944). However, surveys conducted in 1982 and 1986 indicated dramatic declines and extirpation from many historical sites in this area (Serena 1982, Harris et al. 1988). After the species was listed as Endangered in California, many agencies and land managers began annual surveys of appropriate habitat on their lands to assess and monitor the status of the species. Warner Valley, first surveyed in 1996, was found to support a relatively large population of Willow Flycatchers.

Single-day surveys conducted by ARD biologists in 1996–1998 led to a population estimate of approximately 45 breeding pairs, but subsequent to our study, ARD surveys in 2000 and 2001 detected 35 and 29 singing individuals, respectively. Although these differences between years may have been a result of annual variation in population size, survey dates and seasonal conditions are likely contributing factors. Surveys in earlier years were conducted in early June, while in later years surveys were conducted in mid to late June. Although the 1998 ARD survey was conducted on June 17, it was a very heavy snow year, and migrants unable to continue to higher elevations may have been present in Warner Valley at the time of the survey.

We suggest that results of our study and ARD surveys in 2000 and 2001 may provide a more accurate estimate of the Warner Valley breeding population than earlier ARD surveys. Therefore, in 1998–2001 Warner Valley probably supported a breeding population of 30–35 territorial males, and perhaps as many breeding pairs. Although the flycatcher population in Warner Valley may not be as large as originally suspected, it is the largest known population at a single meadow

and accounts for approximately 20% of known Willow Flycatchers in the Sierra Nevada.

Warner Valley Willow Flycatcher nest success (70%) in 1998 was higher than values reported for central Sierra Nevada sites: 60% in 1997 ( $N = 25$ ), 48% in 1998 ( $N = 65$ ), and 26% in 1999 ( $N = 69$ ) (Bombay et al. 1999, Morrison et al. 1999a). However, small sample size and single-season data warrant additional data collection before concluding this population truly has higher nest success. The apparently high nest success in Warner Valley may be related to low nest predation and low cowbird parasitism rates. The use of mountain alder as a nest substrate was unexpected. Other studies in the Sierra Nevada have found Willow Flycatcher nests predominantly in willows (Bombay 1999). The sturdy structure of mountain alder stems may provide a more solid nest substrate, while the thicker foliage of Lemmon's willow may provide better cover for nest concealment.

Our results indicate Warner Valley supports a significant Willow Flycatcher population, apparently with relatively high nest success. Expanded study of this population could provide valu-

able demographic information on productivity, survival, and site fidelity. Future monitoring should investigate the potential importance of mountain alder and other features of the vegetation and physical environment of the meadow as a whole, and of individual territories and nest sites. This information would improve understanding of Willow Flycatchers habitat requirements in the Sierra Nevada and help guide management efforts to ensure the appropriate vegetation and hydrological characteristics are maintained at Warner Valley.

#### ACKNOWLEDGMENTS

This preliminary study was a component of a larger Point Reyes Bird Observatory avian monitoring project in the Lassen region, undertaken in cooperation with U.S. Forest Service Almanor Ranger District and Lassen Volcanic National Park. We are grateful to ARD and LVNP for many forms of support, and for access to their lands. We especially thank S. Armentrout (ARD) for arranging logistical and financial support of the Willow Flycatcher component of the study. ARD Wildlife staff conducted the one-day surveys mentioned. We also thank CDFG for permission to conduct work on their land. This is Point Reyes Bird Observatory contribution number 851.

## SCALE PERSPECTIVES IN HABITAT SELECTION AND ANIMAL PERFORMANCE FOR WILLOW FLYCATCHERS (*EMPIDONAX TRAILLII*) IN THE CENTRAL SIERRA NEVADA, CALIFORNIA

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**Abstract.** Habitat selection is often evaluated using a hierarchy of spatial scales, from coarse selection of general vegetation communities to fine selection of specific foraging or nesting locations. Rarely, however, are these differing scales examined to determine how they relate to habitat quality (as measured by animal performance). We examined how habitat selection at each of three scales (meadow, territory, and nest) constrained or influenced selection at other scales, and then assessed how these selections related to animal abundance, territory productivity, and nest success for Willow Flycatchers (*Empidonax traillii*) in the Sierra Nevada, California. During 1997 and 1998, we surveyed and monitored 104 meadows to document Willow Flycatcher abundance, territory, and nesting status. Vegetative and hydrologic variables were measured in association with all meadows, territories, and nest sites. We used multiple linear and logistic regression to determine which variables best predicted animal performance at each of the three spatial scales, and we used logistic regression to compare nest sites, territories, and occupied meadows with unused or adjacent areas at each scale. The patterns of selection were relatively consistent across scales, with riparian shrub cover a primary predictor of habitat selection for meadows, territories, and nest sites. At successively finer scales, Willow Flycatchers selected areas with higher riparian shrub cover. Increased shrub cover also predicted both Willow Flycatcher abundance and territory success, suggesting that the habitat characteristics selected by these birds also conferred high animal performance and thus habitat quality.

**Key Words:** animal performance, *Empidonax traillii*, habitat selection, habitat quality, meadow, reproductive success, riparian, *Salix*, Sierra Nevada, Willow Flycatcher.

Habitat selection occurs when there is a discrepancy between what is used by an organism and what is available (Johnson 1980). Habitat selection is an often-studied aspect of animal ecology. Because of the recent increase in preparation of habitat suitability indices, models, and recovery plans for endangered species, the accurate interpretation of what constitutes habitat has increased in importance (Verner et al. 1986, Hall et al. 1997). Many scientists have proposed that habitat selection should be viewed as a hierarchical process at multiple spatial scales (Johnson 1980, Hutto 1985; Wiens 1985, 1989b) in which an organism chooses habitat components at a number of scales; for example, meadow, territory location, nest location, and prey choice. These spatial scales exist in a hierarchy, such that selection at one scale is constrained by habitat selection at the scale above, and each choice constrains selection at the scale below (O'Neill 1989; Wiens 1989b, 1989c; Levin 1992). For example, organisms select territories in a non-random manner, which puts constraints on placement of nest or den sites.

Effective management may require more than simply exploring what is selected for use by an organism (Pulliam 1988, Hall et al. 1997). We can most effectively determine which habitat components imply high habitat quality by viewing how selection at one scale constrains and

influences selection at other scales, and then examining how these choices influence animal performance. For Willow Flycatchers (*Empidonax traillii*) we define animal performance as a measure of animal fitness that varies by spatial scale, including: relative abundance, territory/pair success, and nest success. Habitat quality is the relative ability of a given location to provide the conditions necessary for survival, reproduction, and persistence (Van Horne 1983, Hall et al. 1997).

We examined the relationship between selection and animal performance at multiple spatial scales for Willow Flycatchers in the central Sierra Nevada range. Our study took place along the zone of intergradation between two subspecies of Willow Flycatcher; *E. t. brewsteri* and *E. t. adastus* (Phillips 1948, Unitt 1987). These two subspecies are listed as endangered by the state of California, and designated as "sensitive" species in California by the U.S. Forest Service Region 5, and by the U.S. Fish and Wildlife Service Region 1. At this time it is unknown whether the birds at our study sites were *E. t. brewsteri*, *E. t. adastus*, hybrids between the two, or a combination.

The Willow Flycatcher is a neotropical migrant that winters from Mexico to northern South America, and breeds across North America (Bent 1942, Fitzpatrick 1980, Unitt 1987,

Sedgwick 2000). Breeding Willow Flycatchers in the Sierra Nevada occupy wet meadows and occasionally riparian thickets from 600 to 2500 m in elevation (Serena 1982, Valentine et al. 1988, Harris et al. 1987, Flett and Sanders 1987, Bombay 1999). Historical accounts and museum records indicate that this species was locally common as recently as the 1940s within Sierra Nevada meadow systems (Ray 1903, 1913; Ingersoll 1913, Orr and Moffitt 1971, Serena 1982, Klebenow and Oakleaf 1984, Gaines 1992; Western Foundation of Vertebrate Zoology, unpublished nest records). The current Sierra Nevada Willow Flycatcher population is estimated at only 300 to 400 individuals based on surveys completed between 1982 and 1998 (Serena 1982, Harris et al. 1987, CDFG 1991, Bombay 1999, Stefani et al. 2001).

To facilitate meaningful conservation and management efforts for Willow Flycatchers and the meadows they occupy in the central Sierra Nevada, we examined flycatcher habitat selection and animal performance at three scales: the meadow, the territory, and the nest site. Our objective was to examine how habitat selection at each scale constrained or influenced selection at other scales (*sensu* Johnson 1980), and then to assess how these selections related to animal performance and therefore habitat quality (Van Horne 1983, Hutto 1985, O'Neill 1989; Wiens 1989b, 1989c; Levin 1992, Hall et al. 1997). Specifically, our goal was to create a hierarchical habitat model for the Willow Flycatcher in the central Sierra Nevada that (1) determined factors influencing habitat selection at the meadow, territory and nest site spatial scales, and (2) determined which habitat characteristics within these scales conferred high abundance and reproductive success.

#### STUDY AREA

Our study area included montane wet meadows within a 1.2 million-ha portion of the central Sierra Nevada (Fig. 1). This area included over one-third of the Willow Flycatchers known to exist within the Sierra Nevada at the time (Serena 1982, Harris et al. 1987, California Natural Diversity Database 1997, Stefani et al. 2001). Precipitation in the region falls mostly in the form of snow, with accumulations ranging from as little as 36 cm per year on the eastern slope, to 205 cm per year on the western slope.

The meadows within the study area were generally associated with streams or small headwaters rivers, but some also occurred along lake or pond margins, or were associated with springs and seeps at higher elevations (Ratcliff 1982, Weixelman et al. 1999). Vegetation usually consisted of a variety of grasses, forbs, sedges (*Carex* spp.), and rushes (*Juncus* spp.) depending on elevation, slope, hydrology, substrate, and management history (Ratcliff 1982, Weixelman et al. 1999, Dill 1999). Riparian deciduous shrubs were generally

distributed in a patchy manner across meadows, or in some cases restricted to the edges of the water course. Willows, particularly *Salix lemmonii* and *Salix geyeriana*, were the dominant shrubs within open meadows in our study area, although other willow species, mountain alder (*Alnus tenuifolia*), creek dogwood (*Cornus sericea*), aspen (*Populus tremuloides*), gooseberries (*Ribes* spp.) and lodgepole pine (*Pinus contorta*) also occurred (Storer and Usinger 1963; Ratcliff 1982, 1985; Weixelman et al. 1999).

#### METHODS

##### DISTRIBUTION AND ABUNDANCE OF WILLOW FLYCATCHERS

To assess habitat selection at the meadow scale we designated all meadows as occupied or unoccupied by Willow Flycatchers based on our survey results, with meadows being considered unoccupied if we did not observe at least one flycatcher. To assess animal performance we determined the relative abundance of Willow Flycatchers at each meadow. Relative abundance was defined as the percent of survey points where flycatchers were detected at a site.

We surveyed a total of 104 meadows during 1997 and 1998 to determine distribution and abundance of flycatchers relative to hydrologic and vegetative characteristics. Sites ranged from small meadows only a few ha in size to expansive riverine/meadow systems. Survey sites were limited to meadow and riparian communities, and included three subsets: (1) 28 meadows known to currently or historically support Willow Flycatchers based on surveys, journal articles, and nest records obtained from the Western Foundation of Vertebrate Zoology oological collection; (2) 66 meadows identified as having vegetation and hydrology with a potential to support flycatchers based on aerial photo analysis or field reconnaissance; and (3) a stratified random subset of 10 riparian or meadow sites between 600 and 2500 m in elevation and supporting some riparian deciduous shrubs (as delineated on U.S. Fish and Wildlife Service wetland survey maps or aerial photos).

We conducted surveys between first light and 10:00 hrs (PST), from 15 June through 31 July, in 1997 and 1998. These dates maximized the likelihood of detecting flycatchers, while minimizing chances of detecting migrants rather than breeders (Craig et al. 1992). We spaced survey points 100 m apart; at each point we first listened for spontaneous singing for 1 min, then played three to four bursts of a taped song and listened for responses. We repeated this process for a total of six minutes at each point. We conducted surveys once per site only.

##### MEADOW CHARACTERISTICS

We selected physical and biological variables measured at the survey sites (meadow scale) based on parameters that reflect structural and compositional aspects of meadow systems relevant to Willow Flycatchers, as indicated by previous research (Serena 1982, Flett and Sanders 1987, Valentine et al. 1988, Whitfield 1990, Sedgwick and Knopf 1992). We measured or estimated the following variables for each meadow surveyed: size of meadow (ha); elevation (m); total area of riparian shrub (m<sup>2</sup>); percent of meadow with

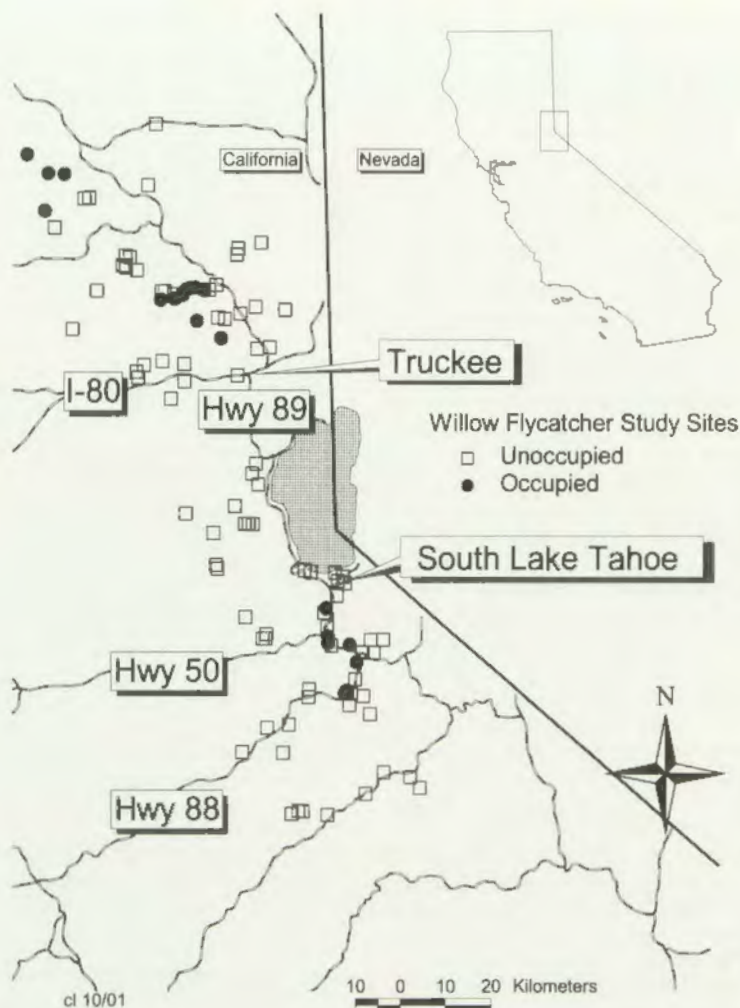


FIGURE 1. Locations of Sierra Nevada meadows surveyed for Willow Flycatchers in 1997 and 1998, and included as study sites.

riparian shrub matrix; proportion of riparian shrubs by species group; average shrub height (m); percent over-story canopy closure within the shrub matrix; dominant herbaceous vegetation (grass, forb, sedge, rush); presence/absence of standing or running water; percent of meadow covered by water, or with saturated soils; dominant type of water across the site and in the riparian shrub matrix (stream, seep, oxbow, in channel pool, snowmelt, pond, lake margin); average stream width (m); and presence/absence of beaver (*Castor canadensis*). Variables except for meadow size, elevation, and total riparian shrub were measured by ocular estimates during the flycatcher field surveys. We recorded elevation from topographic maps, and calculated meadow size and total area of shrub from aerial photos using a grid and photo scale for all survey sites. Approximately one third of the photos were taken in 1997, with the remainder taken between 1991 and 1995. Photo scale was generally designated as 1:

12,000 (Range 1:16,000–1:8000); however, because photo scale varies within a flightline, we calculated individual photo scale using 7.5 min, 1:24,000 U.S. Geological Survey topographic maps.

#### TERRITORY SELECTION AND SUCCESS

To examine habitat selection at the territory scale we compared Willow Flycatcher territories to adjacent meadow areas. To assess animal performance we placed all territories in one of two categories depending on whether or not they produced successful nests.

We mapped flycatcher territories by observing individual males and marking the locations of their singing perches and frequently used foraging areas on aerial photographs. To delineate general territory boundaries, we completed an initial 1.5 hr visit at each territory, then refined our boundary maps during each subsequent monitoring visits (described below). We conducted observations between approximately 1 June



and 31 August each year. Timing of territory mapping and nest searching took place between dawn and dusk.

We used standard nest searching techniques (Martin and Geipel 1993, Ralph *et al.* 1993) to determine reproductive status for all flycatcher territories. We observed each territory for 0.5–1.5 hr every two to seven days, until nests were found. We briefly visited each nest, at the same frequency, to determine if it was still active and if so, its stage (incubation, nestling, fledging). We considered territories successful if at least one nest therein fledged at least one flycatcher. We confirmed fledging when either fledglings were directly observed or adults were seen carrying food after the nest was empty (Vickery *et al.* 1992). We monitored each territory from its delineation until fledging, or until we observed that the territory was abandoned on three consecutive visits.

#### TERRITORY CHARACTERISTICS

We could not actually measure the availability of resources to Willow Flycatchers because we cannot know what is potentially accessible from the perspective of an organism (Johnson 1980; Wiens 1983, 1989a; Hutto 1990). Instead, we measured the abundance of a variety of resource variables and explored which variables were actually selected for use by individual flycatchers in their territories, and in what proportion relative to their abundance within meadows.

Because the abundance of Willow Flycatchers in the Sierra Nevada is already quite low, it is not reasonable to assume that: (1) all suitable meadows are saturated, or occupied; or that (2) unused meadows are unsuitable (Wiens 1983, 1989b; Capen *et al.* 1986, Noon 1986). Therefore we compared the abundance of specific habitat variables within 87 territories to their relative abundance within randomly selected adjacent plots in the same meadow, rather than comparing territories to areas defined as unsuitable or unused.

After territory boundaries were recorded and flycatcher fledglings had been out of the nest for approximately 10 days or nest failure had been documented, we collected vegetation and hydrology data for each territory. We used our territory mapping photos to locate the center point of the territory, and marked the point regardless of whether it fell within riparian shrub patches or the open meadow. We then centered a 60-m baseline over the territory center point; baseline direction was determined by adding a random number (between -15 and +15) to the compass bearing of the long axis of the territory. We also established four 20-m transects that alternated from right to left at 5, 20, 35, and 50 m along the baseline. After collecting data within each territory, we randomly selected a location 75 m from the territory center and constructed our comparison baseline and transects. The compass bearing for both baselines in each pair was the same.

We used the point intercept method to measure cover for individual woody plant species or herbaceous species groups (e.g., grasses, forbs, rushes, sedges), total plant and water cover, and percent cover by height class (USDI/USDA 1996, Kelly and Wood 1996, Elzinga *et al.* 1998). We collected data at 5-m intervals along the four transects and baseline (30 points), and recorded one hit for each species or species group

touching the measuring rod in any or all of the following height classes: 0–1 m, 1.01–2 m, and >2 m. We used two measures of total percent shrub cover. In the first, we pooled all height classes so that one hit was recorded for each of the 30 point intercept locations if there was any shrub hit in any height class ( $x/30$  points \* 100 = percent cover for all height classes pooled). In the second measure, we recorded two-dimensional cover by recording the presence or absence of shrub hits for each height class at each point intercept. As a result we had three vertical points at each of 30 point intercept locations ( $x/90$  points \* 100 = percent cover across all height classes). To provide an estimate of vegetative dominance at the intercept point, we listed species in descending order by the estimated number of hits on the pole. At all points that intercepted riparian shrubs, we measured the maximum height (m) of the live growth of the shrub, and the shortest distance (m) from the outside edge of the shrub to the outside edge of its two closest shrub neighbors. In 1998, we added two additional vegetative variables to our territory analyses. The first was a measure of foliar density that was essentially a finer measurement of the vegetation hits on the vertical pole. We divided the 1-m intervals on the pole into 0.2-m intervals and recorded the number of these 0.2-m intervals (0–5) that had hits. We did this for both the 0–1 m and 1.01–2 m height classes. We also measured the average height of herbaceous vegetation found within a 0.5-m radius of the vertical pole (m).

We recorded water depth (m) and water type for all points that intercepted streambeds, oxbows, or obvious depressions that were holding water during the data collection period or that were known to have held water earlier in the flycatcher breeding season (based on personal observation or the presence of aquatic plants). Soil moisture was also recorded as a number ranging from 0 (no moisture) to 10 (saturated) as measured by a soil moisture meter.

#### NEST SITE SELECTION AND SUCCESS

We evaluated habitat selection by Willow Flycatchers at the nest scale by examining characteristics of 87 nest sites relative to the abundance of hydrological and biological variables within the territory. The measure of animal performance at this scale was nest success; a successful nest was defined as one that fledged at least one flycatcher, and an unsuccessful nest was one that fledged none.

#### NEST SITE CHARACTERISTICS

Nest-related habitat variables described three aspects of nest sites: (1) description of the actual nest, (2) location of the nest within the riparian shrub patch, and (3) the physical and vegetative description of the area within 12 m of the nest (to approximate the 0.04 ha nest area standard described by Noon 1981).

We measured the height and diameter (cm) of each nest, and the number and average diameter (cm) of the supporting branches. We recorded the placement of the nest relative to potentially important habitat features in the immediate vicinity of the nest, including: proximity to water (m), nest height from the ground (m), distance from nest to top of shrub (m), distance from nest to nearest shrub edge and patch edge (m), average dis-

tance from nest to shrub edges and patch edges (m), nest shrub height (m), nest concealment (0-4), and distance from the nest to nearest elevated perch, nearest shrub neighbors, and nearest tree (m). The variables we chose to characterize the general area surrounding the nest and to compare with the overall territory included: total percent cover by all riparian shrub species combined and by height class, percent cover from each riparian shrub species, dominant herbaceous vegetation (forb, grass, sedge, rush), type of water present (ox-bow, stream, depression), mean depth of water (m), soil moisture (0-10), and average herbaceous height (m).

We set 12-m transects radiating away from each nest in each of the four cardinal directions (N, S, E, W), with point intercept locations every 2 m and at the nest location itself. Therefore, we recorded data at 25 points for each nest, following the territory scale protocol described above.

#### DATA SCREENING AND PRELIMINARY ANALYSES

Prior to conducting multivariate analyses addressing each hypothesis, we performed preliminary data exploration (Hosmer and Lemeshow 1989) and removed all variables that were present in less than 5% of cases. We tested the remaining variables for normality using the Kolmogorov-Smirnov test, and then examined for skewness and kurtosis.

To reduce the number of variables included in the following multivariate analyses, for each hypothesis we first examined the results of the t-tests, Mann-Whitney tests, and Chi-Square contingency tables for the appropriate variables. We removed those variables with  $P > 0.2$ , then conducted bivariate correlations for all remaining variables and removed one variable from each pair with a Pearson's correlation coefficient  $\geq 0.80$ , unless our knowledge of flycatcher biology suggested that both should be included (Hosmer and Lemeshow 1989). We based the selection of which correlated variable to retain on the member of the pair with the smallest P-value derived from t-tests or Mann-Whitney tests. In instances where P-values were similar or equal we retained the variable that we estimated to have the greater biologic importance and/or the one that would be easiest to interpret for management purposes. In addition, to avoid including variables with statistically, but not biologically, significant univariate relationships in our multivariate analyses, we removed variables if the absolute difference between group means was less than 3%. This helped us to protect against multivariate results being skewed by variables with large relative difference but small absolute difference (e.g., a cover variable with values of only 2% and 4% for used and unused sites, respectively), and therefore unlikely to be biologically meaningful. If after using these criteria, the number of variables in the final variable list was still  $>25\%$  of the sample size included in the analysis, we removed those variables with P-values  $> 0.1$ . In the case of very small sample sizes, we considered results to be exploratory in nature (Johnson 1981).

We pooled our data across all years because sample sizes were too small in 1997 to permit statistically valid analyses. Additionally, lumping of years and sites was preferred because our ultimate goal was to build

a model describing Willow Flycatcher habitat selection and animal performance at the study area scale (central Sierra Nevada).

#### MULTIVARIATE ANALYSES

In all but one multivariate analysis (animal performance at the meadow scale), we used forward stepwise logistic regression or logistic regression with forced variable entry. These methods were chosen because they are rigorous even with departures from parametric assumptions, and they allow the inclusion of both continuous and categorical variables in a single analysis (Brennan et al. 1986, Capen et al. 1986, Hosmer and Lemeshow 1989, Norman and Streiner 1994, Zar 1996, Morrison et al. 1998). Variables were entered into the forward stepwise models if the score statistic was  $<0.05$  and removed from the models if the likelihood ratio was  $>0.10$ . Models with fewer variables are more likely to be numerically stable, and are more easily generalized than models with many variables (Hosmer and Lemeshow 1989). For this reason we manually restricted the addition of new variables in the stepwise logistic regression process unless the additional variables improved the overall percent correct classification of the model by at least 5%.

To interpret final logistic regression models, we examined the odds ratio of each variable, which indicates how much more, or less, likely it is for the outcome (i.e., occupied or unoccupied) to occur with a one unit change in the independent variable. In cases where a one unit change was thought to be biologically insignificant relative to flycatcher habitat decisions (e.g., a 1% change in shrub cover across an entire meadow), outcomes were also described relative to a 10 unit change.

In examining habitat selection at the three spatial scales, we tested the null hypotheses that selection of meadows, territories, and nest sites for use by Willow Flycatchers was not dependent on hydrologic and vegetative characteristics. For these three tests we compared occupied to unoccupied meadows, territories to adjacent meadow areas, and nest sites to territories, respectively.

Because we had unequal sample sizes for occupied ( $N = 20$ ) and unoccupied meadows ( $N = 81$ ), we first conducted forward stepwise logistic regression analyses on ten equal sample size subsets, by randomly subsampling the larger outcome group (unoccupied meadows). We then determined which variables appeared in the results of more than 50% of the subsets and entered those variables in the final logistic regression using forced variable entry.

To assess animal performance at the territory and nest scales our null hypotheses were that the success of territories and nests was not dependent on the relative abundance of hydrological and vegetative characteristics. For both scales we first used the forward stepwise procedure with the entire territory and nest datasets.

At the territory scale, we included duplicate vegetation data for territories if two years of observation existed. This created some risk of increased error because these two cases were not independent of one another. To check for bias related to non-independence, we used forced entry of the variables selected with the

initial forward stepwise logistic regression model, and applied them to two independent samples of the territory data. For those territory locations with observations in multiple years we used only 1998 data for one test and only 1997 data for another test. Data from territory locations with only one year's worth of data (1997 or 1998) were included in both additional tests.

For the nest success analysis, the requirement of independence of all data points was not met because (a) in many cases the same territory produced more than one nest in a given year, and (b) some territory locations, with potentially the same male or female, produced nests in more than one year. For this reason, after building the forward stepwise model we used forced entry of variables to compare the model to those created by using independent subsets that eliminated all re-nests, and eliminated nests from 1998 or 1997 for those territory locations with two years of data.

To examine animal performance at the meadow scale we used stepwise linear multiple regression to evaluate whether relative abundance of flycatchers was significantly related to any of the biological and physical characteristics of meadows. In this test we used data only from those meadows currently occupied by Willow Flycatchers. Because the  $r^2$  statistic tends to be an over estimate of the population parameter, we used adjusted  $r^2$ , which compensates for this optimistic bias (Norusis 1998).

## RESULTS

### MEADOW SCALE HABITAT SELECTION

Data screening resulted in 17 variables for inclusion in the logistic regression procedure comparing unoccupied to occupied meadows. When we used these 17 variables to build logistic regression models by subsampling from the unoccupied meadow category, the following 12 physical and biological variables were included in at least one of the 10 models: total amount of riparian shrubs (ha); percent shrub matrix cover; dominance of forbs within the overall meadow (index: 0-4); dominance of grasses or forbs within the shrub matrix only (index: 0-4); shrub foliar density (index: 1-2); prevalence of small braided channels as a water source (index: 0-2); prevalence of single large channels as a water source (index: 0-2); prevalence of small depressions or oxbows with standing water (index: 0-2); average primary channel width (index: 1-3); and meadow size. Only the first three of these variables were included in at least 50% the models and therefore we entered the three variables into the final logistic regression model.

The logistic regression model found that meadows were 3% more likely to be occupied with each 1% increase in the percent of the site with a riparian shrub matrix; this equals a 30% increase in likelihood of occupancy with a 10% increase in riparian shrub matrix (Table 1). Meadows were 17% more likely to be occupied

TABLE 1. DESCRIPTIVE STATISTICS AND LOGISTIC REGRESSION RESULTS FOR HABITAT CHARACTERISTICS DISTINGUISHING BETWEEN MEADOWS OCCUPIED BY WILLOW FLYCATCHERS (N = 20) FROM UNOCCUPIED (N = 81) MEADOWS<sup>a</sup>

Habitat variable	Descriptive statistics		Logistic regression			
	Occupied mean $\pm$ SD	Unoccupied mean $\pm$ SD	Coef. (B) $\pm$ SE	Odds ratio	Wald statistic	P-value
Dominance of forbs within meadow	2.4 $\pm$ 0.8	3.4 $\pm$ 0.9			11.135	0.011
Forbs—low site dominance <sup>b</sup>			-1.033 $\pm$ 1.452	0.36	0.506	0.477
Forbs—moderately low site dominance			-1.919 $\pm$ 1.380	0.15	1.934	0.164
Forbs—moderately high site dominance			-5.297 $\pm$ 1.868	0.01	8.044	0.005
Forbs—high site dominance			0.031 $\pm$ 0.014	1.03	4.946	0.026
% riparian shrub matrix	60.3 $\pm$ 22.9	40.5 $\pm$ 25.3				
Total ha riparian shrubs	4.8 $\pm$ 2.7	3.0 $\pm$ 3.6	0.157 $\pm$ 0.090	1.17	3.037	0.081
Constant			-1.269 $\pm$ 1.541		0.678	0.410

<sup>a</sup> Model  $\chi^2 = 36.27$ ,  $P < 0.001$ , forced variable entry.

<sup>b</sup> Reference category.

TABLE 2. RESULTS OF MULTIPLE REGRESSION COMPARING HABITAT CHARACTERISTICS TO RELATIVE ABUNDANCE OF WILLOW FLYCATCHERS IN OCCUPIED MEADOWS (N = 20)<sup>a,b</sup>

Habitat variable	Coeff. (B) ± SE	P-value
% overstory cover from trees	-0.257 ± 0.039	<0.001
Elevation	0.001 ± 0.001	<0.001
% riparian shrub matrix	0.004 ± 0.001	0.004
Mean riparian shrub height	0.162 ± 0.500	0.005
Constant	-1.423 ± 0.297	<0.001

<sup>a</sup> Forward stepwise multiple regression (entry: 0.05, removal: 0.10).

<sup>b</sup> Model Adjusted R<sup>2</sup> = 0.835, P < 0.001.

with each 1 ha increase in absolute area of riparian shrub. Interpretation of the categorical variable related to forb dominance is slightly modified because a reference category (low forb dominance) is involved. Forbs were negatively associated with Willow Flycatcher presence and therefore analysis of odds ratios showed that meadows where forbs had moderately low dominance, moderately high dominance, and high dominance were 2.8, 6.8, and 200 times less likely to be occupied than meadows where forbs had low dominance within the herbaceous layer (Table 1;  $\chi^2 = 36.27$ , P < 0.001). We found that although these variables correctly classified 93% of unoccupied meadows, they only correctly classified occupied meadows 30% of the time; overall percent correct classification for both groups was 80%.

#### MEADOW SCALE ANIMAL PERFORMANCE

The following nine variables were included in the multiple regression analysis comparing Willow Flycatcher abundance to physical and biological variables in occupied meadows: elevation; mean riparian shrub height; percent overstory canopy cover; presence or absence of tree species other than lodgepole pine (0/1); percent mountain alder cover; sedge dominance within the meadow (index: 0-4); prevalence of lake margins as sources of standing water (index: 0-2); percent riparian shrub matrix cover; and percent of the shrub matrix formed by willow species.

Based on the multiple regression analysis, four variables were significant predictors of Willow Flycatcher relative abundance. Flycatcher relative abundance increased with increasing riparian shrub matrix, mean height of riparian shrubs, and elevation, but decreased with increasing overstory cover from trees (Table 2; Adjusted Model  $r^2 = 0.835$ ; P < 0.001).

#### TERRITORY SCALE HABITAT SELECTION

Seventeen variables were included in the logistic regression analysis related to territory selection, including: percent *Salix geyeriana* cover in the 1.01-2-m height class; percent *Salix lem-*

*monii* cover in the >2-m height class; percent cover from gooseberry; percent total cover from riparian shrubs (all height classes pooled); mean shrub height; shrub dispersion; percent shrub foliar density in the 0-2-m height class; mean height of herbaceous vegetation; percent cover from grasses, forbs, sedges, and rushes; percent of points dominated by grasses, forbs, and sedges; percent ground cover of standing and running water; and water depth.

In the final model, only total riparian shrub cover was a significant predictor of territory selection. An area was 11% more likely to be a territory for every 1% increase in total riparian shrub cover (Table 3; Model  $\chi^2 = 66.49$ ; P < 0.001), or 110% more likely if shrub cover increased by 10%. When examining the ability of this model to correctly predict areas used as territories, we found that total shrub cover correctly classified 80% of adjacent areas and 80% of territories; overall total correct classification was 80%. It is important to note that total shrub cover was highly correlated with two-dimensional shrub cover ( $r = 0.962$ , P < 0.001), and shrub cover in the 0-1-m ( $r = 0.912$ , P < 0.001), 1.01-2-m ( $r = 0.965$ , P < 0.001), and >2-m ( $r = 0.797$ , P < 0.001) height classes independently; therefore, it is difficult to be certain whether different portions of the shrub layer are more or less important to the species at the territory scale (Bombay 1999).

#### TERRITORY SCALE ANIMAL PERFORMANCE

Six variables were included in the logistic regression procedure comparing successful to unsuccessful territories: percent herbaceous cover from forbs; percent shrub cover in the >2-m height class; percent total shrub cover (all height classes pooled); percent shrub foliar density in the 0-1-m height class; and water depth for standing water only, and for standing and running water combined. Only total shrub cover was a significant predictor of territory success. With every 1% increase in total shrub cover, territories were 5% more likely to be successful (Table 4; Model  $\chi^2 = 9.908$ ; P = 0.002); a 10% increase in shrub cover improved the likelihood

TABLE 3. DESCRIPTIVE STATISTICS AND LOGISTIC REGRESSION RESULTS FOR HABITAT CHARACTERISTICS DISTINGUISHING WILLOW FLYCATCHER TERRITORIES (N = 66) FROM ADJACENT MEADOW AREAS (N = 64)<sup>a</sup>

Habitat variable	Descriptive statistics		Logistic regression			
	Territories mean ± SD	Adjacent areas mean ± SD	Coef. (B) ± SE	Odds ratio	Wald statistic	P-value
% shrub cover (height classes pooled)	48.4 ± 13.5	22.4 ± 17.1	0.100 ± 0.017	1.11	36.678	<0.001
Constant			-3.465 ± 0.621		31.129	<0.001

<sup>a</sup> Model  $\chi^2 = 66.49$ ;  $P < 0.001$ ; forward stepwise variable selection.

success by 50%. Using only shrub cover this model correctly classified successful territories 70% of the time and unsuccessful territories 60% of the time; overall percent correct classification was 65%.

Because some territories had two years of data and were therefore represented twice within the preceding test, we repeated the logistic regression on two independent subsets using forced entry of total shrub cover. In subset one, the shrub cover correctly identified 36% of unsuccessful territories and 78% of successful territories, for an overall correct classification rate of 59% (Table 4; Model  $\chi^2 = 2.514$ ;  $P = 0.113$ ). In data subset two, the original model correctly classified 66% of unsuccessful territories and 72% of successful territories, for an overall correct classification rate of 69% (Table 4; Model  $\chi^2 = 10.481$ ;  $P = 0.001$ ).

#### NEST SCALE HABITAT SELECTION

Eleven variables were included in the logistic regression procedure comparing nest sites to territories: percent cover from sedges and forbs; percent of herbaceous layer dominated by grasses; percent cover in the 0–1-m shrub height class, and across all height classes (two dimensional); percent foliar density in the 0–1-m shrub height class; mean shrub height; mean shrub dispersion; percent ground covered by running water; and mean standing and running water depths. Only two variables were significant predictors of nest site selection. With every 1% increase in total shrub cover across all height classes (two dimensional), areas were 5% more likely to be nest sites. Nest sites were negatively associated with foliar density within the 0–1-m height class; therefore with each 1% increase in foliar density in the 0–1-m portion of the shrub layer, areas were 12% less likely to be selected as nest sites. (Table 5; Model  $\chi^2 = 32.79$ ;  $P < 0.001$ ). Together these two variables correctly classified 61% of territories and 75% of nest sites 76%; overall percent correct classification for both groups was 69%.

#### NEST SCALE ANIMAL PERFORMANCE

Seven variables were included in the logistic regression procedure comparing successful to unsuccessful nests: maximum live height of nest shrub; maximum dead height of nest shrub; mean distance from nest to shrub edge; distance from nest to nearest shrub patch opening; percent foliar density in the 0–1-m height class at the nest; distance from nest to nearest tree; and mean supporting branch diameter. Only distance from nearest tree was a significant predictor of nest success. With every 1 m increase in distance from the nearest tree (which ranged up to

TABLE 4. DESCRIPTIVE STATISTICS AND LOGISTIC REGRESSION RESULTS FOR HABITAT CHARACTERISTICS DISTINGUISHING SUCCESSFUL FROM UNSUCCESSFUL WILLOW FLYCATCHER TERRITORIES USING THE FULL DATA SET AND TWO INDEPENDENT SAMPLES

Habitat variable	Descriptive statistics		Logistic regression			
	Successful mean $\pm$ SD	Unsuccessful mean $\pm$ SD	Coeff. (B) $\pm$ SE	Odds ratio	Wald statistic	P-value
Model A: Full data set (N = 46; 42) <sup>a</sup> % shrub cover (height classes pooled) Constant	51.7 $\pm$ 14.1	42.7 $\pm$ 13.1	0.051 $\pm$ 0.017 -2.310 $\pm$ 0.844	1.05	8.579 7.498	0.003 0.006
Model B: Subset 1 (N = 36; 28) <sup>b</sup> % shrub cover (height classes pooled) Constant	50.5 $\pm$ 13.8	45.2 $\pm$ 12.8	0.031 $\pm$ 0.020 -1.213 $\pm$ 0.975	1.03	2.387 1.548	0.122 0.214
Model C: Subset 2 (N = 32; 32) <sup>c</sup> % shrub cover (height classes pooled) Constant	53.5 $\pm$ 12.4	43.1 $\pm$ 12.6	0.068 $\pm$ 0.023 -3.279 $\pm$ 1.158	1.07	8.481 8.024	0.004 0.005

<sup>a</sup> Model A:  $K^2 = 9.908$ ;  $P = 0.002$ ; forward stepwise variable entry.

<sup>b</sup> Model B:  $K^2 = 2.514$ ;  $P = 0.113$ ; forced variable entry.

<sup>c</sup> Model C:  $K^2 = 10.481$ ;  $P = 0.001$ ; forced variable entry.

500 m), nests were 1% more likely to be successful (Table 6; Model  $\chi^2 = 7.135$ ;  $P = 0.008$ ); with each 50 m increase, nests were 50% more likely to be successful. Although the model using this variable correctly classified nests as unsuccessful 84% of the time, the correct classification rate for successful nests was only 34%. Overall percent correct classification for both groups was 59%.

Because some nests occurred within the same territory in either the same year, separate years, or both, we repeated the logistic regression test on two independent subsets using forced entry of distance to nearest tree. In subset one, the original model correctly classified 84% of unsuccessful nests and 48% of successful nests, for an overall correct classification rate of 65% (Table 6; Model  $\chi^2 = 10.092$ ;  $P = 0.002$ ). In data subset two, the original model correctly classified 88% of unsuccessful nests and 50% of successful nests, for an overall correct classification rate of 71% (Table 6; Model  $\chi^2 = 10.897$ ;  $P = 0.001$ ).

## DISCUSSION

We found that Willow Flycatchers showed consistent preference for areas with greater riparian shrub cover at all scales, and in our study area willow made up 85%, 98%, and 99% of riparian shrubs at occupied meadows, territories, and nest sites, respectively (Bombay 1999). Thus, Willow Flycatchers in the Sierra Nevada select meadows with a large proportion of area covered by a riparian shrub matrix, and within these meadows, flycatchers select territories in the areas with the most riparian shrubs. Again, within the constraints of the territory boundaries, flycatchers select nest locations with the highest total shrub cover across all three height classes. Interestingly, riparian shrub cover was also a good indicator of animal performance, and therefore habitat quality at meadow and territory scales. When examining both habitat selection and habitat quality, riparian shrub cover was most highly predictive at the territory scale; in fact, it was the only variable selected at this scale, while at the meadow and nest scale it contributed less towards model fit. Although consistently selected by our models, shrub cover was not the only variable of importance for flycatchers.

## MEADOW SCALE HABITAT SELECTION

We found a consistent negative relationship between occupied meadows and the predominance of forbs within the herbaceous layer. The dominance of forbs within Sierra Nevada meadows is often related to lowered water tables, and is considered an indicator of early seral stage, or

TABLE 5. DESCRIPTIVE STATISTICS AND LOGISTIC REGRESSION RESULTS FOR HABITAT CHARACTERISTICS DISTINGUISHING WILLOW FLYCATCHER NESTS (N = 66) FROM TERRITORIES (N = 64)<sup>a</sup>

Habitat variable	Descriptive statistics		Logistic regression			
	Nests mean ± SD	Territories mean ± SD	Coeff. (B) ± SE	Odds ratio	Wald statistic	P-value
Shrub foliar density (0–1.0-m)	40.3 ± 6.5	47.5 ± 10.1	-0.110 ± 0.030	0.90	13.719	0.0002
% shrub cover (across height classes/3-D)	39.8 ± 15.8	31.2 ± 10.3	0.052 ± 0.014	1.05	12.718	0.0004
Constant			3.219 ± 1.340		5.768	0.0163

<sup>a</sup> Model  $\chi^2 = 32.786$ ,  $P < 0.0001$ ; forward stepwise variable selection.

the result of disturbance caused by human-associated uses (Ratliff 1985, Ratliff et al. 1987; Weixelman et al. 1997, 1999). The positive relationship between riparian shrub cover and Willow Flycatcher occupancy at the meadow scale suggests that a relatively abundant riparian shrub community is important at the meadow scale of habitat selection. This finding agrees with Bent (1942), Grinnell and Miller (1944), King (1955), Serena (1982), Harris et al. (1987), Sedgwick and Knopf (1992), and Sedgwick (2000).

Although our total percent correct classification for the logistic regression model at this scale was 80%, our model's ability to correctly identify occupied meadows was only 30%. This means that although we could identify unoccupied meadows most of the time (93%), we had very inconsistent results in predicting meadows that were selected by flycatchers. This suggests that the Willow Flycatcher population is now at such low numbers that it may not be fully occupying all areas that could support them. Alternatively, these inconsistent correct classification rates could mean that at the scale measured, differences in habitat variables between occupied and unoccupied meadows were not biologically significant.

#### MEADOW SCALE ANIMAL PERFORMANCE

In addition to more shrub cover, meadows with more Willow Flycatchers were characterized by having taller shrubs and being at higher elevations, compared to sites with fewer flycatchers. Taller shrubs suggest the flycatchers are using sites with more mature stands of riparian shrubs, with less intense grazing pressure or other disturbance factors, and/or sites with better growing conditions. Elevation is more difficult to understand since Willow Flycatchers were known to historically occur at lower elevations within our study area (Ray 1903, 1913; Klebenow and Oakleaf 1984). Perhaps higher elevation sites have undergone less dramatic habitat changes due to fewer types and intensities of human activities. Percent overstory cover from trees had a negative relationship with flycatcher abundance, suggesting that birds settled in greater numbers in broad open meadow systems with little encroachment from lodgepole pine, or with a smaller edge to interior ratio. This could indicate preference for less disturbed meadows with higher water tables, where lodgepole pine do not become established as easily, or wide open floodplain settings where there is less edge per hectare of meadow (Benedict 1984, Ratliff 1985, Kattelman and Embury 1996, Dull 1999). Because this analysis was based on a small sample size of only 20 occupied meadows, inferences about animal perfor-

TABLE 6. DESCRIPTIVE STATISTICS AND LOGISTIC REGRESSION RESULTS FOR HABITAT CHARACTERISTICS DISTINGUISHING SUCCESSFUL FROM UNSUCCESSFUL WILLOW FLYCATCHER NESTS USING THE FULL DATA SET AND TWO INDEPENDENT SUBSETS

Habitat variable	Descriptive statistics		Logistic regression			
	Successful mean $\pm$ SD	Unsuccessful mean $\pm$ SD	Coeff. (B) $\pm$ SE	Odds ratio	Wald statistic	P-value
<b>Model A: Full data set (N = 44; 43)<sup>a</sup></b>						
Distance to tree	82.4 $\pm$ 101.0	40.4 $\pm$ 35.8	0.009 $\pm$ 0.004	1.01	4.691	0.030
Constant			-0.500 $\pm$ 0.306		2.680	0.102
<b>Model B: Subset 1 (N = 27; 25)<sup>b</sup></b>						
Distance to tree	113.7 $\pm$ 117.8	40.3 $\pm$ 37.8	0.014 $\pm$ 0.006	1.01	5.166	0.023
Constant			-0.830 $\pm$ 0.436		3.620	0.057
<b>Model C: Subset 2 (N = 22; 24)<sup>c</sup></b>						
Distance to tree	126.4 $\pm$ 127.5	40.5 $\pm$ 37.8	0.014 $\pm$ 0.006	1.01	5.883	0.015
Constant			-1.109 $\pm$ 0.449		6.114	0.013

<sup>a</sup> Model A:  $\chi^2 = 7.135$ ,  $P = 0.008$ ; forward stepwise variable entry.

<sup>b</sup> Model B:  $\chi^2 = 10.092$ ,  $P = 0.002$ ; forced variable entry.

<sup>c</sup> Model C:  $\chi^2 = 9.869$ ,  $P = 0.002$ ; forced variable entry.

mance at this scale should be viewed as preliminary (Johnson 1981).

#### TERRITORY SCALE HABITAT SELECTION

Because flycatchers selected meadows with an extensive shrub matrix and a late seral herbaceous community, territory placement was confined by those conditions. We were surprised to discover that Willow Flycatcher territories did not have significantly more ground covered by water than adjacent areas, though Sedgwick and Knopf (1992) had similar results. Sedgwick and Knopf (1992) postulated that the lack of a significant difference was due largely to the overall mesic nature of the meadows being occupied by Willow Flycatchers. In our study area, occupied meadows had 57% of their area covered by standing water or saturated soils, while territories and comparison transects had 44% and 42% cover from standing water, respectively (Bombay 1999). It is possible that because selected meadows are wet, they are constraining territory choices to areas with relatively uniform mesic conditions.

#### TERRITORY SCALE ANIMAL PERFORMANCE

Willow Flycatchers selected territories with higher shrub cover than was present in adjacent areas, and within this constraint, territories with the highest levels of shrub cover provided the highest habitat quality. High shrub cover values across territories may allow for a greater choice of possible nest locations, and this could be important when multiple re-nesting attempts are needed (Martin 1992). Shrub cover and shrub configuration may also have implications relating to nest parasitism or predation, post fledging survival, thermal cover (for nests and adults), foraging efficiency, and territorial defense by males (King 1955, Norman and Robertson 1975, Anderson and Storer 1976, Freeman et al. 1990, McCabe 1991, Martin 1992, Sedgwick and Knopf 1992, Staab and Morrison 1999, Sedgwick 2000, Uyehara and Whitfield 2000). The importance of riparian shrubs to this combination of many life history factors may explain why increased shrub cover predicted increased territory success even though it did not predict individual nest outcomes.

Our ability to predict animal success was best at the territory scale with percent correct classifications for successful territories between 70–78%, and overall percent correct classification between 59–69%. As suggested by Laymon and Barrett (1986), this may indicate that the territory is a better scale for evaluating the physical and biological variables that drive animal performance and therefore habitat quality, particularly when developing management prescriptions.



Although the results varied somewhat between our original territory success model and the models based on two independent subsets, the general pattern of the relationship between successful and unsuccessful territories remained constant. This suggests that the use of the same territory locations by flycatchers between years did not overly bias the original model results.

#### NEST SCALE HABITAT SELECTION

Territory selection constrained nest placement to areas with high shrub cover. We found that two-dimensional shrub cover (percent cover across all height classes) was significantly higher in nest areas than across territories overall (40% and 31%, respectively). The negative association with foliar density (0–1 m) in nest areas is likely due to our observation that the amount of leafy vegetation is decreased in the lower interior portions of large shrub clumps (where nests are frequently placed) due to shading. Placement of nests based on these two variables may help minimize nest predation and parasitism (Sanders and Flett 1989, Martin 1992, Uychara and Whitfield 2000), and buffer against mean nighttime low temperatures of 2.4°C (June through August, 1997–2001), as well as summer snowstorms and hailstorms (Ingersoll 1913, Sanders and Flett 1989, Western Regional Climate Center 2001).

#### NEST SCALE ANIMAL PERFORMANCE

Nest success was negatively associated with proximity to the closest tree. This variable was much better at explaining unsuccessful nests than at predicting successful ones. Perhaps nests that are close to trees experience more predation pressure from the combination of meadow and edge predators, while nests far away still have predation from meadow predators, but have lower overall predation pressure without the edge predators (Wilcove 1985, Cain 2001). Additionally, trees may provide locations for visual predators to search for nests (Anderson and Storer 1976, Gates and Gysel 1978, Freeman et al. 1990, Rosenfield and Bielefeldt 1993). These factors may explain why only 59% of the successful nests could be predicted by distance to the nearest tree. Alternatively, poor correct classification rates could mean that at the scale measured, differences in habitat variables between successful and unsuccessful nests were not biologically significant.

Although the results varied somewhat between our original nest success model and the models based on two independent subsets, the general pattern of the relationship between successful and unsuccessful nests remained constant. This suggests that the use of similar nest

locations by flycatchers between years and the use of data from multiple nest attempts did not overly bias the original model results.

Our model predicting nest success failed to select any habitat characteristics associated with the area directly surrounding the nest, most notably shrub cover. It is possible that the variables that we choose to measure, or the 12 m area that we examined around the nest site, were not appropriate for the assessment of nest outcome. Another scenario is that nest outcome may be largely affected by the level of chance involved in nest searching by predators, as well as fluctuations in predator populations and weather patterns (Martin 1992). Given this, it may take a larger sample size over more years to differentiate the effects of these variations from those of habitat characteristics.

#### CONCLUSIONS

Our findings indicate that although the variables we used to describe riparian shrub cover changed between scales (percent shrub matrix within meadow, percent cover within territory, and percent cover within 12 m of nest), shrub cover nonetheless remained linked to Willow Flycatchers across all scales. When considering that riparian shrub cover also predicted flycatcher abundance and territory success at the meadow and territory scales, our confidence in shrub cover as a measure of habitat quality is strong.

Based on the fact that animal performance was predicted by the same characteristic at two spatial scales, one might be inclined to assume that in the case of Willow Flycatchers in the Sierra Nevada, relative abundance alone could indicate habitat quality. Our model of individual nest success, however, did not select a shrub related variable, but rather distance to the nearest tree. Assumptions about habitat quality would be somewhat premature since only two (relative abundance, reproductive success) of Van Horne's (1983) parameters for habitat quality were included in our models. Only when long term results on survival and reproductive trends are applied to a habitat model can we be sure that relying on a single measure of both habitat selection and animal performance is adequate for habitat management of a population at risk (Van Horne 1983).

Although additional information is necessary to fully understand habitat selection and habitat quality issues for Willow Flycatchers, a 10% increase in riparian shrub cover resulted in 30, 110 and 50% increases in the likelihood of a meadow, territory, and nest area being selected by flycatchers, respectively. Additionally, territories were 50% more likely to produce successful nests with each 10% increase in riparian shrub

cover. As a result, where the goal is to restore or maintain Willow Flycatcher habitat in montane settings, management efforts that at a minimum provide the conditions necessary for riparian shrub regeneration and recruitment appear warranted at this time.

#### ACKNOWLEDGMENTS

We thank T. M. Benson, T. Benson, J. Bombay, S. Bosworth, A. Chatfield, M. Flett, C. Gaulden, C. Loff-

land, L. Loffland, D. Queheillalt, J. Steele, D. Walker, and G. Wilson for their assistance, and the folks at Webber Lake Ranch and Carpenter Valley for access to their land. Thanks also to San Francisco State University's Sierra Nevada Field Campus, and University of California's Sagehen Creek Field Station. Funding was provided by the U.S. Forest Service, Region 5, Partners in Flight Program, to California State University, Sacramento, Department of Biological Sciences.

## WILLOW FLYCATCHER NESTING ECOLOGY AND HABITAT RELATIONSHIPS IN THE WILLAMETTE BASIN, OREGON

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**Abstract.** The Little Willow Flycatcher (*Empidonax traillii brewsteri*) nests in both riparian and upland habitats within low elevation valley and higher elevation forest in the Willamette Basin of northwestern Oregon. Nesting habitat in early-seral conifer forest occurs approximately 4–15 years following even-aged timber harvest or natural events that remove most or all of the forest canopy and allow for extensive growth of a shrub layer. Nesting habitat in the valley occurs in riparian or upland shrub-dominated habitats with an interspersed of herbaceous openings. Our two-year nesting study in the Willamette Basin revealed a Mayfield estimate of seasonal nest success of 40.5% (N = 147). We did not find significant differences in nest success between riparian and upland habitats or between valley and forest habitats; however, there were significant yearly differences. The rate of cowbird parasitism was low (4%), and all parasitism occurred within valley habitats (8% of valley nests). Nest success was significantly higher in western bracken fern (*Pteridium aquilinum*) than other primary nest substrates. Nest habitat selection in early-seral conifer forests was most positive for vine maple (*Acer circinatum*) and trailing blackberry (*Rubus ursinus*), and the best habitat selection model included western bracken fern and vine maple. The greatest concerns for Willow Flycatcher populations in the Basin are the location, type, and timing of management activities, and continued loss and fragmentation of riparian habitat.

**Key Words:** *Empidonax traillii brewsteri*; habitat relationships; Little Willow Flycatcher; nest success; Oregon; Willamette Basin.

There has been increased interest in the status of Willow Flycatcher subspecies and populations since the Southwestern Willow Flycatcher (*Empidonax traillii eximus*) was listed as endangered in 1995 (U.S. Fish and Wildlife Service [USFWS] 1995). The Oregon Department of Fish and Wildlife (ODFW 1997) listed the Little Willow Flycatcher (*E. t. brewsteri*, hereafter Willow Flycatcher) as State Sensitive in 1997 due to concerns about declining populations and a lack of information on species ecology. *E. t. brewsteri* was formerly a Federal Candidate species (USFWS 1994), and a Federal Species of Concern in Oregon (G. Miller, pers. comm.). The Willow Flycatcher also is a Focal Species for conservation in the Westside Lowlands and Valleys Bird Conservation Planning Region of the Oregon–Washington Chapter of Partners in Flight (Altman 2000).

*E. t. brewsteri* breeds west of the Sierra Nevada/Cascade Mountains crest north from Fresno County, California to the east coast of Vancouver Island and the Fraser Lowlands in British Columbia (Unitt 1987, Sedgwick 2000). In the Willamette Basin (hereafter Basin) of northwestern Oregon, it occurs in both lowland valley and higher elevation forest habitats. From around the turn of the century through the mid 1900s, all ornithologists used the word “common” in their description of Willow Flycatcher abundance in the Willamette Valley (hereafter Valley) (e.g., Johnson 1880; Anthony 1886,

1902; Gabrielson and Jewett 1940, Gullion 1951).

Breeding Bird Survey (BBS) data for the last 30+ years indicate significant population declines of 3.6% per year for *E. t. brewsteri* in western Oregon and Washington and northwestern California (Sauer et al. 2000). In that same time period, the Valley population trend has mirrored the regional trend (i.e., declining at 4.1% per yr), although the trend is not significant and the sample size (N = 11) is small. Descriptive analysis of BBS data in the Valley indicated that the Willow Flycatcher population has declined from a mean of approximately 11–13 birds per route in the early 1970s to 4–5 birds per route throughout the 1990s. However, on forest BBS routes in the Basin (N = 12), mean number of birds per route has remained relatively steady around 4 birds per route.

We initiated a two-year study in the Basin in 1999 to identify conservation and management needs for Willow Flycatcher. The two primary objectives were: (1) examine nest success as a potential factor in population declines, especially differences in nest success between geographic regions (high elevation forest and low elevation valley), habitat types (riparian and upland), and other parameters (e.g., nest substrate, human activity levels, proximity to water, roads, etc.); and (2) identify important habitat features at nests to help direct habitat management.

## METHODS

### STUDY AREA

The Basin encompasses ca. 7200 sq km between the crest of the Cascade and Coast Ranges in northwestern Oregon (Wentz and McKenzie 1991). The Basin is approximately 75 km long, and ranges from 30–60 km wide. It includes the broad alluvial floodplain of the Valley floor (ca. 2100 sq km), and is bounded by mountain slopes and foothills on three sides and by the Columbia River on the north. Elevations range from 100 m at the mouth of the Willamette River near Portland to 3423 m in the Cascade Mountains. Land uses are predominantly forestry and recreation in the mountains, and urban and agriculture in the lowlands.

Historical vegetation in the Valley included wet and dry prairies, riparian forest and shrub, and *Quercus* woodlands and savannah. Most of the native vegetation has been converted to agricultural and urban uses. The Valley comprises 12% of Oregon's area, yet has >70% of its human population (Keisling 2000); land ownership is >90% private (Puchy and Marshall 1993).

The climax forest association in most of the Basin is western hemlock (*Tsuga heterophylla*)—western redcedar (*Thuja plicata*) (Franklin and Dyrness 1973); however, much of the study area is dominated by the seral species Douglas-fir (*Pseudotsuga menziesii*). Ownership within the forested portion of the Basin is an approximately equal mix of public and private lands.

### SITE SELECTION

We selected two forest watersheds, Molalla and Lake Creek, based on land ownership of project co-operators, and equal representation from the Cascade Mountains and Coast Range respectively. We randomly selected a pool of 10–12 early-seral forest sites of <15 ha within each watershed; each was clearcut 5–20 years prior to our study. Final site selection, made in the field based on access and personnel limitations, resulted in eight study sites in the Molalla watershed and four sites in the Lake Creek watershed.

Private land ownership precluded systematic sampling in the Valley. We opportunistically selected numerous riparian and upland sites considering presence and abundance of Willow Flycatchers, geographic distribution, accessibility, habitat type, and permission to access.

### NEST MONITORING

We located nests by observing behavioral cues, then marked and revisited them in a manner designed to reduce predator attraction and investigator-induced predation (Martin and Geupel 1993). Each nest was monitored every three to four days until either the young fledged or the nest failed. We considered a nest successful if at least one young was observed as a fledgling or indirect evidence (e.g., flattened nest rim, extensive fecal matter in nest and on rim) on the final visit suggested fledging. Failed nests were examined to identify cause of failure. If nest contents (eggs or nestlings) were removed, the nest was considered depredated.

We subjectively categorized the level of human ac-

tivity within 50 and 15 m of each nest as low (occasional or no human activity), moderate (few people on most days), or heavy (daily use by many people).

### HABITAT CHARACTERIZATION

Data collected at each nest included nest height; nest substrate and substrate height; an ocular estimate of nest concealment from above and below with the nest centered in a 0.3 m box (poor = <20% concealed; fair = 20–60%; good = 60–90%; excellent = >90%); and distances to the nearest road and water. We collected nest vegetation data within a 1-m<sup>2</sup> plot centered on the nest with the corners oriented in each cardinal direction (referred to as nest), and in 5- and 11.3-m radius circular plots centered on the nest (referred to as nest area). Data collected at each plot scale included ocular estimates (to the nearest 5%, totaling 100%) of percent vegetation cover by growth form (i.e., grass/forb, shrub layer, tree layer), by species, and also for non-vegetation (i.e., litter/residue, bare ground, rock, water).

We categorized a nest location as riparian if any hydrophytic vegetation (e.g., willow [*Salix* sp.], Douglas spirea [*Douglasii spiraea*], red-osier dogwood [*Cornus stolonifera*]) was present within an 11.3 m radius of the nest.

### NEST HABITAT SELECTION

We assessed nest habitat selection at three different sites in the Molalla Watershed; two revegetating harvest units in 1999, and a different harvest unit in 2000. We collected data at plots randomly located from the center of the study site. The number of random points sampled was equivalent to the number of nests located within the study site. Data collection followed the same protocol as that at nests except for nest-specific data.

### DATA ANALYSIS

#### *Nest success*

We estimated nest success using the Mayfield method (Mayfield 1975) and proportional measures of nest success (i.e., number of successful nests versus number of nests monitored). We calculated 95% normal confidence intervals (CI; Zar 1996) about the Mayfield estimates to determine whether significant differences in nest success occurred between categories. Paired habitat comparisons included forest versus valley (riparian and upland combined), riparian versus upland, and valley upland versus forest upland. We also compared nest success among nest substrate plant species, and between exotic and native nest plant substrates. Mayfield estimates were considered statistically different at the two tailed  $\alpha = 0.05$  if the CI did not overlap.

We conducted two-sample *t*-tests using a pooled standard deviation to compare percent cover variables for growth form and several nest characteristics between successful and failed nests.

#### *Resource selection*

We modeled Willow Flycatcher nest habitat selection by fitting multivariate logistic regression models with stepwise model selection procedures in PROC LOGISTIC in SAS (SAS Institute 2000) using nests

TABLE 1. WILLOW FLYCATCHER NEST SUCCESS IN THE WILLAMETTE BASIN, OREGON, 1999–2000

Category	Nests	Proportional nest success <sup>a</sup>	Exposure days	Daily survival rate	Mayfield success estimates <sup>b</sup>	95% CI
All nests	147	0.585	2055	0.970	0.405	na
Forest	72	0.583	1052.5	0.972	0.420	0.304–0.536
Valley	75	0.586	1002.5	0.969	0.390	0.277–0.503
Riparian	31	0.613	447	0.973	0.441	0.263–0.620
Upland	116	0.578	1618	0.970	0.397	0.306–0.488
Forest upland	69	0.594	1018.5	0.973	0.433	0.314–0.553
Valley upland	47	0.553	589.5	0.964	0.337	0.204–0.487

<sup>a</sup> Proportional success is percentage of successful nests of the total nests monitored.

<sup>b</sup> Mayfield success estimates are calculations of nest success based on days of observation.

as used data and random plots as available data. Two models were fit with all variables (percent cover for either growth form or species) for a given location and year. We report test results as significant ( $P < 0.10$  or  $P < 0.05$ ) or highly significant ( $P < 0.01$ ).

## RESULTS

### NESTING CHRONOLOGY

Most Willow Flycatchers arrived in the Basin in the last week of May with peak arrival in the first week of June. The earliest observation of nest building was June 9 and the earliest date of a nest with eggs was June 14; most nest-building and egg-laying occurred in mid- to late June. The earliest hatch date was June 21 and the earliest fledging was July 8. Most hatching occurred in early to mid-July and fledging in the last 10 days of July and the first week of August. Nearly one-third of the nests (31%,  $N = 46$ ) were still active in August, including nine (20%) that still had eggs. Most of the nests active in August fledged during the first week of August (70%,  $N = 32$ ); the latest fledge date was August 22.

### REPRODUCTIVE SUCCESS

We located and monitored 147 nests (Table 1); 86 (58%) were successful (Mayfield nest success = 40%). Among the six habitat nest location categories, Mayfield estimates were lowest in valley upland (34%) and highest in riparian (44%). Mean clutch size of nests for which there was complete information was 3.4 eggs (range 2–4,  $N = 115$ ). Mean number of young fledged per nest (successful and unsuccessful) was 1.7. There were no significant differences in clutch size or fecundity between forest and valley habitats or between riparian and upland habitats.

We did not find significant differences in the two-year Mayfield estimates between valley (39%  $\pm$  0.1 SE) and forest (42%  $\pm$  0.1 SE) habitats, or between riparian (44%  $\pm$  0.1 SE) and upland (40%  $\pm$  0.04 SE) habitats (Table 1). However, when the data were separated by year, nest

success was significantly different between riparian and upland habitats in each year: greater in upland in 1999 and greater in riparian in 2000. Nest success also was significantly different for riparian habitats between each year (2000 > 1999).

Among the four predominant nest substrates, Mayfield estimates of nest success were lowest in vine maple (*Acer circinatum*; 17%) and highest in western bracken fern (*Pteridium aquilinum*; 78%) (Table 2). Nest success was significantly higher in western bracken fern than Himalayan blackberry (*Rubus procerus*) and vine maple, and higher (but not significantly so) than Scot's broom (*Cytisus scoparius*). Nest success was not significantly different between exotic (35%  $\pm$  0.1 SE) and native plants (45.9%  $\pm$  0.1 SE E).

There was no significant difference in mean percent cover of any plant growth form between successful and failed nests (Table 3), and among the nest and nest site variables only nest height differed (higher at successful nests,  $P = 0.098$ ; Table 4). Proportional nest success was 56% ( $N = 25$ ) and 55% ( $N = 55$ ) where human activity was moderate or heavy within 15 m and 50 m, respectively. Proportional nest success was similar (approximately 55–60%) over differing distances up to 50 m from the nearest road, then increased from 51–100 m (Fig. 1). Nest success also increased as the distance to water decreased (Fig. 1).

Nests were parasitized at three sites, and the overall rate of cowbird parasitism was low (4%,  $N = 6$ ). All parasitism occurred in valley habitats (8% of valley nests), and 5 of the 6 parasitized nests failed.

### NESTING HABITAT

We located nests in 17 different plant species, but four species (Himalayan blackberry,  $N = 47$ ; western bracken fern,  $N = 21$ ; Scot's broom,  $N = 19$ ; vine maple,  $N = 19$ ), accounted for 71% of the nests. Mean nest height ( $N = 144$  nests) was 1.1 m  $\pm$  0.4 SD, mean height of the nesting

TABLE 2. WILLOW FLYCATCHER NEST SUCCESS, BY PLANT SUBSTRATE, IN THE WILLAMETTE BASIN, OREGON, 1999-2000

Category	Nests	Proportional nest success <sup>a</sup>	Exposure days	Daily survival rate	Mayfield success estimates <sup>b</sup>	95% CI
Himalayan blackberry	47	0.553	639.5	0.967	0.368	0.227-0.509
Western bracken fern	21	0.857	367	0.992	0.781	0.601-0.961
Scot's broom	19	0.526	288	0.969	0.385	0.162-0.608
Vine maple	19	0.421	193	0.943	0.175	0.000-0.345
Exotic species	71	0.465	959	0.966	0.350	0.237-0.463
Native species	76	0.632	1096	0.974	0.459	0.345-0.573

<sup>a</sup> Proportional success is percentage of successful nests of the total nests monitored.

<sup>b</sup> Mayfield success estimates are calculations of nest success based on days of observation.

substrate was  $2.0 \text{ m} \pm 0.7 \text{ SD}$ , and mean distance from the nest to the edge of the shrub patch was  $5.9 \text{ m} \pm 11.1 \text{ SD}$ .

Shrub layer vegetation dominated the cover at nest sites ( $80\% \pm 25.3 \text{ SD}$ ; Table 3). There were no significant differences in mean percent cover by growth form or plot scale between successful and failed nests. In the habitat selection models for percent cover by growth form, shrubs (+) were the only variable in the best model (two of the three sites).

Habitat selection for nest plant species was most pronounced for vine maple (highly significant at all three sites) and trailing blackberry (highly significant at two sites) (Fig. 2). Cover of Himalayan blackberry and Scot's broom were significantly greater at nest plots at one site each, while cover of western bracken fern was significantly greater for nests at one site and at random plots for another site. Species selected against as nesting habitat (i.e., significantly more cover at random plots) were California hazel (*Corylus cornata*; highly significant at all three sites), Douglas-fir (highly significant at one site and significant at another site), and cascara (*Rhamnus purshiana*; significant at one site).

Two of the three sites had significant variables in the model for percent cover by species. Cal-

ifornia hazel, western blackcap (*Rubus nigerrimus*), Douglas-fir, and western redcedar (all -) were in the best model at the Bureau of Land Management (BLM) 1999 unit. Western bracken fern and vine maple (both +) were in the best model at the Willamette 2000 unit.

## DISCUSSION

### HABITAT

The Willow Flycatcher is a characteristic species of many shrub-dominated habitats in the Basin. Nesting habitat in early-seral conifer forest occurs approximately 4-15 years following even-aged timber harvest or natural events that remove most or all of the forest canopy and allow for extensive growth of a shrub layer. Nesting habitat in the Valley occurs in riparian or upland shrub-dominated areas with an interspersed of herbaceous openings, and with or without the presence of scattered trees.

The strong association of Willow Flycatcher with upland habitats in the Basin is in contrast to its obligate association with riparian habitats in the arid parts of western North America. The consistent habitat features throughout its range are moisture and the dominance of shrubs or a dense shrub layer of vegetation. In most of the

TABLE 3. DIFFERENCES IN MEAN PERCENT COVER BETWEEN SUCCESSFUL AND FAILED WILLOW FLYCATCHER NESTS, BY GROWTH FORM AND PLOT SCALE, IN THE WILLAMETTE BASIN, OREGON, 1999-2000

Growth form	Scale (m)	Successful nests (N = 85)		Failed nests (N = 60)		P
		Mean $\pm$ SD	95% CI	Mean $\pm$ SD	95% CI	
Herbs	1	10.5 $\pm$ 15.2	7.3-13.8	12.2 $\pm$ 17.7	7.6-16.7	0.551
	5	25.3 $\pm$ 19.8	21.0-29.6	29.1 $\pm$ 19.4	24.1-34.1	0.255
	11.3	19.1 $\pm$ 18.5	15.1-23.1	21.5 $\pm$ 18.0	16.9-26.1	0.441
Shrubs	1	80.2 $\pm$ 24.6	74.9-85.5	79.0 $\pm$ 26.6	72.1-85.9	0.784
	5	57.1 $\pm$ 23.2	52.1-62.1	54.2 $\pm$ 22.0	48.5-59.8	0.438
	11.3	66.1 $\pm$ 24.4	60.8-71.4	66.8 $\pm$ 24.4	60.5-73.1	0.862
Trees	1	9.0 $\pm$ 23.2	4.01-14.0	7.9 $\pm$ 22.6	20.1-13.8	0.780
	5	14.5 $\pm$ 17.2	10.8-18.2	12.1 $\pm$ 13.1	8.7-15.5	0.367
	11.3	12.0 $\pm$ 18.6	8.0-16.0	8.7 $\pm$ 16.5	4.4-12.9	0.267

TABLE 4. DIFFERENCES BETWEEN SUCCESSFUL AND FAILED WILLOW FLYCATCHER NESTS, BY NEST AND NEST SITE CHARACTERISTICS, IN THE WILLAMETTE BASIN, OREGON, 1999–2000

Characteristic	Successful nests (N = 85)		Failed nests (N = 59)		P
	Mean $\pm$ SD	95% CI	Mean $\pm$ SD	95% CI	
Activity within 15 m	1.5 $\pm$ 0.5	1.1–1.3	1.2 $\pm$ 0.5	1.1–1.4	0.774
Activity within 50 m	1.5 $\pm$ 0.7	1.4–1.7	1.5 $\pm$ 0.8	1.3–1.7	0.975
Nest concealment above	3.1 $\pm$ 0.7	2.9–3.2	2.9 $\pm$ 0.8	2.7–3.1	0.234
Nest concealment below	2.3 $\pm$ 0.8	2.1–2.5	2.1 $\pm$ 0.7	1.9–2.3	0.216
Distance to edge (m)	4.0 $\pm$ 3.6	3.2–4.8	3.2 $\pm$ 3.4	2.3–4.1	0.185
Nest height (m)	1.2 $\pm$ 0.5	1.0–1.3	1.0 $\pm$ 0.3	0.9–1.1	0.098
Nest substrate height (m)	2.0 $\pm$ 0.71	1.8–2.1	2.0 $\pm$ 0.7	1.8–2.2	0.690

arid West, moist shrubby conditions occur only in riparian habitat. In the temperate rainforests of northwestern Oregon, the Willow Flycatcher is a regularly occurring species in shrub-dominated upland habitats because moisture is not a limiting factor in vegetation growth, and a dense shrub layer can develop exclusive of riparian areas.

Although Willow Flycatchers nested in upland habitats in both the valley and forest, the higher nest success in riparian habitats and the progressively higher nest success with proximity of nest to water indicates a consistent positive pattern with riparian habitat. These data and the strong association of Willow Flycatcher with riparian habitat in the West suggest that conditions associated with riparian shrub habitat in the Valley may be most suitable. Upland habitats, particularly in the Valley, may be used because of the limited availability of riparian habitat, but these may be functioning as less than optimal habitat.

Willow Flycatcher nesting habitat in early-seral stages of managed forests of the Basin has

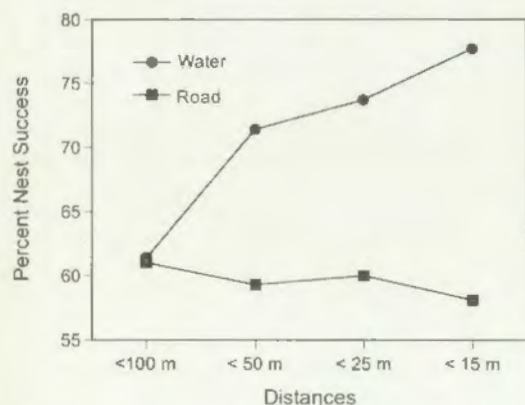


FIGURE 1. Relationship between Willow Flycatcher nest success and distance to roads and water in the Willamette Basin, Oregon, 1999–2000.

a life span of approximately 10–12 years. However, the amount of this habitat across the landscape at any point in time is likely to be consistent where forests are managed using even-aged silviculture with standard rotations for sustainable wood production. Thus, the conservation issue for Willow Flycatcher in managed forests is not loss of habitat, but the shifting of habitat and the ability of the species to locate and colonize habitat as new areas become available. This is apparently not a problem because Willow Flycatchers occur at some sites <3 years post-harvest if patches of deciduous vegetation have been retained or resprouted, and sites that are 4–6 years post-harvest are often densely populated with flycatchers.

Willow Flycatcher use of forest habitats in the Pacific Northwest likely increased with the advent of large-scale clearcutting in the last 50–100 years. Additionally, the amount of upland non-forest habitats dominated by exotic shrubs such as Himalayan blackberry and Scot's broom has likely increased in the last 50 years. Both these factors may be compensating for loss of the flycatcher's riparian nesting habitat, in terms of regional habitat availability. Riparian habitat in the Valley is highly fragmented and much smaller in extent than at the time of European settlement (Titus et al. 1996), and continues to be reduced in extent in recent years (Frenkel et al. 1983).

#### NESTING

Nest success among Willow Flycatcher subspecies has been reported to be highly variable, but generally lower for Southwestern Willow Flycatcher than the other three subspecies (Stoleson et al. 2000b). Our Mayfield estimate of nest success (40%) matches that reported for a population of *E. t. brewsteri* in the Sierra Nevada (40%, N = 90; Bombay 1999). Small nest sample sizes for other populations of *E. t. brewsteri* limit the validity of other comparisons; however, our proportional nest success (58%) is sim-

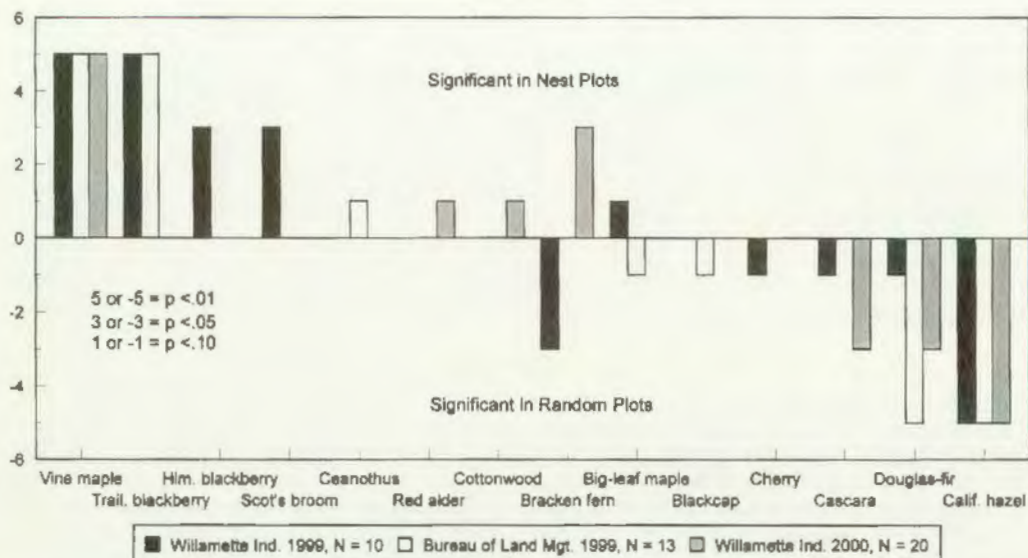


FIGURE 2. Vegetative cover of plant species significantly associated with Willow Flycatcher nest sites and random plots in three revegetating harvest units in the Molalla watershed, Oregon, 1999–2000.

ilar to that reported in the Sierra Nevada (54.5%,  $N = 11$ ; Sanders and Flett 1989), and higher than another site in the Sierra Nevada (37.5%,  $N = 8$ ; Kings River Conservation District 1985) and in British Columbia (33%,  $N = 6$ ; Campbell et al. 1997).

Our proportional nest success rate compares favorably with nest success rates for open-cup nesting passerines in North America, which range from approximately 38–70% with a mean of 52% (Nice 1957, Martin 1993). However, these multi-species summaries include many species with different reproductive strategies than the Willow Flycatcher (e.g., double or triple-brooding, larger clutch size). Other species' nest success rates may not be comparable with a species like Willow Flycatcher, which is mostly single-brooded in the Basin and has a relatively low reproductive capability. Nest success for a single-brooded species generally needs to be greater than that of multiple-brooded species in order to sustain populations. Murphy (1983) suggested that flycatchers in general, most of which are single-brooded, have evolved the need to have a relatively high nest success rate.

Willow Flycatchers in the Valley often nested close to areas of moderate or high human activity, but human activity did not appear to be a factor in nest success. Where human activity was moderate or heavy, nest success (55%) was nearly the same as overall proportional nest success (58%), and proportional nest success in val-

ley habitats (59%,  $N = 75$ ) where most of the human population occurs.

Despite the dominant agricultural landscape of the Valley, cowbird parasitism did not appear to be a limiting factor for Willow Flycatcher populations. The Brown-headed Cowbird population trend in the Valley is similar to that of Willow Flycatcher; i.e., a non-significant declining trend of 2.4% per year (4.1% for Willow Flycatcher) with a mean relative abundance of 9 birds per route (6.2 for Willow Flycatcher; Sauer et al. 2000). Our parasitism rate was similar to that reported for *E. t. brewsteri* in British Columbia (7%,  $N = 45$ ; Campbell et al. 1997).

We found no evidence or indication of double-brooding (i.e., raising a second brood after successfully fledging a first), and this is considered rare in northern populations of Willow Flycatchers (Sedgwick 2000). The range of our fledging dates, coupled with the fact that a complete reproductive cycle for successful nests takes approximately 30–35 days, suggests that double-brooding is probably a rare event in the Basin.

Despite a concerted effort to locate nests in riparian habitat, especially in 2000, our riparian nest sample was disproportionately low. This could have arisen due to logistical inefficiencies in sampling riparian areas and/or fewer birds nesting in riparian habitat. Most riparian shrub patches are small, linear, and patchily distributed across the landscape with single pairs or small



populations. Sparse and patchy habitat logistically requires more time to locate and monitor nests than those in continuous habitat. Conversely, upland shrub patches in the valley and in the forest often are extensive enough to support numerous pairs, thus requiring less time to find and monitor nests.

#### MANAGEMENT AND CONSERVATION

Riparian shrub habitat should be emphasized when management for Willow Flycatcher is being considered in the Valley. Anecdotal references confirm the historic association of Willow Flycatcher with riparian habitat, and current knowledge of the loss of riparian habitat coincides with recent declining population trends (i.e., BBS data). Our data also suggested an emphasis on riparian habitat because nest success was higher there and lower in upland valley habitat.

Management to control deciduous shrub vegetation in revegetating clearcuts, often via spraying or hand removal, is a concern for Willow Flycatcher populations in early-seral forests of the Basin. Because nearly all the nesting substrates in early-seral forest were deciduous shrub or shrub-layer vegetation, removal or killing of such deciduous vegetation should be discouraged where Willow Flycatcher management is a priority.

Two of the four plant species in which most nests were found (Himalayan blackberry and Scot's broom) are both aggressive exotic species that outcompete native shrubs and form shrub monocultures. Much of the current habitat restoration work in the Valley includes removal of these species, which could be detrimental to nesting Willow Flycatchers at that site. If the long-term management at such sites does not (as is often the case) include restoring a shrub-dominated community, the negative impacts could be long-term. However, concerns about the adverse impact of exotic plant control on Willow Flycatcher habitat and populations in the Valley are tempered by several factors. First, restoration activities are not widespread, and the degree to which restoration activities remove Himalayan blackberry and Scot's broom may not keep ahead of the rate at which new areas are overtaken by both species. Secondly, populations in early-seral forest habitats are not impacted by restoration activities and these habitats support a substantial portion of the Willow Flycatchers in the Basin. Finally, some habitat restoration work in the Valley includes development of riparian shrub vegetation, which has the potential for providing suitable Willow Flycatcher habitat in the future.

The most immediate concern about adverse

impacts of restoration and management activities on Willow Flycatchers in the Basin is the timing of the actions, especially because nearly one-third of Willow Flycatcher nests were still active in August. Where protocols call for restoration activities outside the breeding season, the terminal date of breeding is often given as July 15 or August 1. Activities initiated immediately after the former date would impact most Willow Flycatcher nesting, and after the latter up to one-third of the nests. If management and restoration actions are scheduled to avoid or minimize impacts on nesting Willow Flycatchers, August 15 should be considered the end of the nesting season. Management conducted prior to this date could result in a local population that loses a partial or entire cohort, which would impact not only that breeding season but subsequent ones as well.

We speculate that the high nest success in western bracken fern may be related to the fragile nature of the plant. Most potential nest predators (e.g., squirrels, chipmunks, snakes) would likely not be supported by the vegetation in their approach to the nest, except perhaps for small mammalian predators such as mice. Willow Flycatcher nesting in western bracken fern has been reported in the Basin from the late 1800s (Anthony 1886). Most nests of *E. t. brewsteri* in British Columbia (43%,  $N = 44$ ) were in western bracken fern (Campbell et al. 1997). Western bracken fern is a native species that readily occupies open forest habitats that are not intensively managed for timber. It should be considered a high priority for retention if a management goal is to support nesting Willow Flycatchers.

We are uncertain about the value of vine maple to Willow Flycatchers in early-seral forests. Vine maple was positively associated with nesting habitat at all three sites and was a positive variable in the best habitat model for one of the sites. However, nest success in vine maple was extremely low. Unlike western bracken fern, vine maple may provide more opportunities for mammalian predation because it has a woody and well-branched structure for a climbing predator. Thus, vine maple may provide unique cover or foraging habitat that is selected for in the nest area, but it may be deficient when selected as the actual nest substrate.

Despite significant population declines for *E. t. brewsteri* as indicated by the BBS, Willow Flycatcher is a regularly occurring species in both forest and lowland shrub-dominated habitats in the Basin. Our data indicated that nest success was not significantly influenced by location (forest or valley), habitat (riparian or upland), human activity, or cowbird parasitism.

The greatest concerns for Willow Flycatcher populations in the Basin are the location, type, and timing of management activities, and continual loss and fragmentation of riparian habitat. Willow Flycatcher conservation in the Basin will require balancing maintenance of suitable conditions in early-seral forests with efforts to enhance the capacity of riparian habitat in the Valley to support expanded populations. We suggest that both of these approaches will be most successful if management supports factors related to habitat selection and higher nest success as described in this study.

#### ACKNOWLEDGMENTS

We are most grateful to R. Goggans, ODFW, for initiating the project and assistance in securing funding. The project benefited greatly from financial support from the ODFW, U.S. BLM (Salem and Eugene Offices), Willamette Industries Inc., U.S. Army Corps of Engineers, USFWS (Oregon State Office), and the USDA Forest Service (Mt. Hood National Forest). We are indebted to a dedicated field crew of B. McCullough (2 years), K. Viste-Sparkman (2 years), T. Bray, L. Fish, J. Jebusek, R. Keister, J. Martin, D. Rosenthal, and D. Vandenbroek. Statistical analysis was conducted by Western EcoSystems Technology Inc.

## A CHARACTERIZATION OF VEGETATION IN NESTING AND NON-NESTING PLOTS FOR SOUTHWESTERN WILLOW FLYCATCHERS IN CENTRAL ARIZONA

LINDA J. ALLISON, CHARLES E. PARADZICK, JAMES W. ROURKE, AND TRACY D. MCCARTHEY

**Abstract.** We described habitat features at nesting plots of Southwestern Willow Flycatchers (*Empidonax traillii extimus*) in two study areas in central Arizona, and identified features that discriminated between nesting and non-nesting plots. Flycatchers showed preferences for nest placement close to breaks in the canopy and where there was more foliage at nest height and below; these preferences have also been described for Willow Flycatchers in other parts of the range. Other preferences we identified seemed unique to this region, reflecting the dominance of non-native saltcedar in nesting areas but also that the remaining native woody vegetation serves as an indicator of nesting habitat. High foliage density above the nest may be important for creating a suitable microclimate in the low desert landscape in which these birds nest.

**Key Words:** Arizona, canopy, *Empidonax traillii extimus*, nest height, nesting plots, Southwestern Willow Flycatcher, vegetation.

The endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*) breeds in riparian vegetation across the southwestern United States. Throughout this range, riparian habitat has been affected by the last century of land management practices. Prior to the 1880s, riparian habitats along low-elevation rivers and streams in Arizona were wetter than at present, and supported primarily native tree and shrub species (Minckley and Brown 1994). Since then, river channelization, impoundment and diversion, groundwater withdrawal (Stromberg 1993), and excessive livestock grazing (Amour et al. 1991) have created a less favorable environment for regeneration of native riparian plants. Overall, up to 90% of riparian habitat in Arizona has been degraded (Governor's Riparian Habitat Task Force 1990), which has restricted breeding Southwestern Willow Flycatchers to isolated sites within a few locations in the state. The future status of Arizona's Southwestern Willow Flycatcher populations is related to our ability to identify, protect, and conserve its breeding habitat.

Roosevelt Lake, at the confluence of Tonto Creek and the Salt River, hosts one of the largest breeding Southwestern Willow Flycatcher populations in Arizona (up to 115 territories; Paradzick and Woodward *this volume*), but current nesting habitat will flood and be destroyed when lake waters rise to the level of the newly renovated dam (U.S. Fish and Wildlife Service 1996). Characterization of nesting habitat at Roosevelt Lake is important as a description of nesting habitat in general, but also for comparison to vegetation in other areas to which these birds might relocate. The closest known breeding area to Roosevelt Lake is at the Gila/San

Pedro River confluence, where at least 76 territories have been supported each year since 1997 (Paradzick and Woodward *this volume*). At both areas, nesting territories of Southwestern Willow Flycatchers are spatially clustered within patches of even-aged vegetation. This has led to speculation that some suitable nesting habitat remains unoccupied in each area, and that flycatchers displaced from Roosevelt Lake may relocate to the Gila/San Pedro River confluence (U.S. Fish and Wildlife Service 1996). It is also possible that characteristics within the patches of even-aged vegetation explain selective nest placement and clustering, and could inform wildlife managers about features to preserve and protect in these and other possible breeding areas.

Studies of nesting habitat of various subspecies of Willow Flycatchers have been conducted in California (*E. t. adastus*; Flett and Sanders 1987), along the Colorado River in the Grand Canyon (*E. t. extimus*; Brown 1988), and in Colorado (*E. t. adastus*; Sedgwick and Knopf 1992). These studies concluded that compared to other areas in the same vegetation patches, flycatcher nests were usually built closer to surface water and were surrounded by higher density of vegetation at nest height and below. Beyond these generalities, however, each study described different species of nesting tree, canopy structure, and nest placement within vegetation. Because Willow Flycatcher nesting habitat can vary substantially by region (Sedgwick 2000), data from central Arizona can yield insights into Willow Flycatcher habitat use in a desert landscape.

Here, we describe vegetation characteristics measured in Southwestern Willow Flycatcher nesting plots and in non-nesting plots within the same vegetation patches at two sites in central

Arizona. Our goals were to identify specific variables that describe potential Willow Flycatcher breeding habitat locally and to contribute to understanding of general features that characterize breeding habitat throughout the range. Our objectives were (1) to understand how plots within patches used by nesting Willow Flycatchers differ from those that are not used, (2) to describe how features of nesting habitat in the two study areas compare, and (3) to distinguish attributes shared by nesting Willow Flycatchers in other parts of their range from those that are specific to central Arizona. Because riparian vegetation is often modified by seasonal high water flow and is characterized by rapid growth, and because flycatchers often moved to new patches between years, we also use our data to describe how vegetation features around Southwestern Willow Flycatcher nests differ substantially from year to year.

## METHODS

### SELECTION OF SITES AND DATA COLLECTION

The study areas in central Arizona, Roosevelt Lake (Gila County) and the Gila/San Pedro River confluence (Pinal County), are between 555 and 658 m in elevation, and are riparian corridors within the arid Sonoran desertscrub biome (Minckley and Brown 1994). Roosevelt Lake includes one site at the Salt River inflow, and another at the Tonto Creek inflow. The Gila/San Pedro River confluence area included one site on the Gila River and six sites on the San Pedro River. Vegetation occurred in even-aged stands within each site; stands that contained one or more Southwestern Willow Flycatcher territories were called patches. Many sites consisted of only one patch; however, four sites (Salt River inflow, Tonto Creek inflow, Dudleyville, and Indian Hills) contained more than one patch, and although the same sites were used both years, not all patches were consistent between years. Saltcedar (*Tamarix ramosissima*) was the dominant woody plant at all 19 patches in this study. Canopy and woody shrub vegetation also included seepwillow (*Baccharis salicifolia*), Goodding willow (*Salix gooddingii*), velvet mesquite (*Prosopis velutina*), and Fremont cottonwood (*Populus fremontii*).

We described and measured vegetation and habitat features in 1998 and 1999. So that each nesting plot represented an independent sampling unit, we took precautions to identify and measure features of only the first active nest (i.e., containing eggs) each year for each female (Rourke et al. 1999; Paradzick et al. 1999, 2000). We treated nests of the same female in different years as independent attempts because females usually switch mates and territories between seasons (Luff et al. 2000). Females feed young within the territory for up to two weeks after fledging (C. Paradzick, pers. obs.); to avoid disrupting this activity, we measured vegetation in August when the nest, territory, and adjacent flycatcher territories had been inactive for at least this long.

We measured vegetation and habitat characteristics at non-nesting plots in August 1999. We assigned plot

centers at the Gila/San Pedro River confluence by placing a gridline transparency over aerial photographs of each patch, randomly selecting grid intersections, and locating these points in the field. For the larger Roosevelt Lake patches, non-nesting plot centers were randomly selected from Universal Transverse Mercator (UTM) coordinates within patches. Because patch boundaries were delineated and non-nest plots were located in the field with global positioning units (which have inherent spatial error), some randomly chosen non-nesting plots were in obviously unsuitable vegetation. Use of these plots would have exaggerated differences between nesting and non-nesting plots within the same patch, so we only used non-nesting plots that contained a saltcedar, Goodding willow, Fremont cottonwood, or velvet mesquite tree over 5 m tall (approximate average nest hgt; Paradzick et al. 1999, 2000). Non-nesting plots in both breeding areas were only measured if canopy cover was at least 70%, if they were at least 25 m from any active flycatcher nest, and if they had no nesting flycatcher activity. Flycatcher activity was determined following the protocol of Sogge et al. (1997a); if flycatchers were present adjacent to a non-nesting plot, the plot was extensively searched multiple times to confirm the absence of nests.

We measured vegetation and habitat variables within an 11.3 m radius circle (0.04 ha; James and Shugart 1970) centered on the nest or, for non-nesting plots, centered on the randomly determined point. Plots of this size are likely to be large enough to describe variability within a territory without measuring areas outside the territory (Sedgwick and Knopf 1992). Vegetation and habitat variables measured were taken or modified from the BBIRD protocol (Martin et al. 1997, Rourke et al. 1999). We also measured vertical foliage density (MacArthur and MacArthur 1961), but used a color microvideo pin-hole camera (lens: 3.7 mm 90°) to estimate density as the percentage of a 0.5 × 0.5 m checkerboard obscured by vegetation. The camera and board were placed 2 m apart and raised in parallel, and measurements were recorded at various heights up to 7.6 m; above this height, poles were difficult to manipulate, so we recorded only whether vegetation was present.

We counted the number of stems of saltcedar, seepwillow, Goodding willow, velvet mesquite, Fremont cottonwood, and snags; other woody plant species that occurred in fewer than 5 plots were not analyzed. We also recorded nest height, vegetation measurements, and distance of the nest to nearest native shrub or tree, nearest break in the vegetation, and nearest surface water. Surface water included both the natural stream channel and any supplemental water present at the site (e.g., irrigation run-off).

### MODIFICATION OF VARIABLES FOR ANALYSIS

The number of variables measured at plots varied from 404 in 1998 to 314 in 1999 (Appendix). Thirteen of these variables could only be measured in conjunction with a nest, and were not reported for non-nesting plots. The number of descriptive variables far outnumbered the nesting plots, so some variables were modified or consolidated before any analysis (Appendix). (1) Vertical foliage measurements were averaged

across all heights and cardinal directions at a given distance from the nest, across all distances and cardinal directions at a given height, or across all distances at a given cardinal direction and height. (2) Canopy cover was averaged across all cardinal directions. (3) To reduce the number of classes with zero counts, stem counts were summed across all quadrants. (4) Saltcedar stem count categories were further combined into three groups according to diameter of stem at breast height (dbh): small shrubs (<2.5 cm dbh), large shrubs (2.5–8.0 cm dbh), and trees (>8.0 cm dbh). (5) Each of the native species were described as either shrubs (<8.0 cm dbh) or trees (>8.0 cm dbh), and were scored as present or absent. The Appendix also identifies variables that departed strongly from normality and were appropriately transformed before principal components analysis and before any averaging was done to generate composite variables.

#### STATISTICAL ANALYSES

##### *Describing variability of vegetation at nesting plots*

We used principal components analysis (PCA) to describe habitat variation at nesting plots. Because only continuous variables perform well in PCA, we excluded any species for which stem count was only reported as presence or absence. We examined a plot of decreasing eigenvalues (scree plot) to decide the number of components to extract (Dunteman 1989) and followed with varimax rotation to improve interpretation of components. For each principal component, scores were used to build ANOVA models to test whether variation could be accounted for as an effect of year or breeding area. Patches were included in the models as a factor nested within breeding areas.

##### *Describing differences between nesting and non-nesting plots within a patch*

Data from nesting and non-nesting plots were used to build a logistic regression model to classify future plots based on their potential to be used in a nesting territory. A best subsets technique was used to reduce the number of variables retained in the analysis. The procedure involved ranking the *P*-values of variables in the first model from lowest to highest, rebuilding the model without the variable with the lowest *P*-value, and repeating the process until four models had been explored. Variables were permanently removed from the model if the sum of their rank scores was higher than any variable that had ever scored in the lowest 20. The same procedure was followed again, using the lowest 15, then the lowest 10 ranking *P*-values.

Although application of logistic regression does not require assumptions about the underlying data distribution, some transformations facilitate interpretation of odds ratios. Odds ratios indicate the multiplicative effect on the odds for every unit change in an independent variable. Once the set of variables in the final model was identified, some were transformed to other units. For instance, because there were as many as 973 small-diameter saltcedar stems in a plot, we were more interested in describing how the odds change with a 10% increase in the number of stems, rather than with an increase of a single stem.

#### RESULTS

We gathered data from 85 first nests in 1998 and 130 in 1999, and measured vegetation and habitat characteristics at 123 non-nesting plots in 1999.

##### VARIABILITY OF VEGETATION AT NESTING PLOTS

PCA identified six gradients that described variation in habitat at nesting plots. Sixteen variables had loadings > |0.50| on these principal components (PC; Tables 1 and 4). Based on variable loadings, the first four PCs were similar for the full model (Table 1) and for models built separately with each year of data. Thus, correlations between variables were similar each year and overall. Combining data from both years resulted in description of an additional two PCs; overall the six PCs explained 66.6% of the variance between plots (Table 1).

PC1, PC2, and PC5 described the size classes of woody species and snags and the structure of this vegetation, represented by stem counts and canopy height and density (Table 1). PC1 described a gradient from plots with many small-diameter saltcedar stems and small snags to plots with a high, dense canopy. PC2 captured the fact that Southwestern Willow Flycatchers nested in plots with many native shrubs and trees but also in plots with many large-diameter saltcedar and small snags. As described by PC5, nesting plots in some patches were farther from water and had few large-diameter snags; those that were closer to water had more large-diameter snags.

PC1, PC3, PC4, and PC6 described the range of densities of foliage and canopy cover that characterized nesting plots (Table 1). PC1 reflected the range of canopy heights and densities, whereas PC3 and PC4 described vegetation density at or below average nest height ( $4.5 \text{ m} \pm 1.41 \text{ SD}$  units,  $N = 192$ ), either within 1 m of the nest (PC3) or averaged at three distances from 1 to 11 m from the nest (PC4). PC6 was attributable to variability in distance of each nest to the nearest break in the canopy.

ANOVAs for each of the six PCs indicated that nesting plots were more similar within than between patches except possibly for PC3 (Table 2). Species composition of woody vegetation did not change between years within a patch. However, because a different set of patches was used for nesting each year, statistically significant interaction effects for year-by-study area for PC1 and PC2 scores indicated that changes in patch use also resulted in use of areas with different species composition and structure. In 1999, patches used at Roosevelt Lake had shorter, less dense canopies and more small diameter saltcedar and snags (Fig. 1). This description also

TABLE 1. ROTATED PCA LOADINGS, EIGENVALUES, AND CUMULATIVE PERCENT VARIATION EXPLAINED IN VEGETATION AMONG SOUTHWESTERN WILLOW FLYCATCHER NESTING PLOTS IN 1998 AND 1999 AT ROOSEVELT LAKE AND THE GILA/SAN PEDRO RIVER CONFLUENCE IN ARIZONA

Variable	PC1	PC2	PC3	PC4	PC5	PC6
Vertical foliage >1 m N and S of the nest, 7.6 m high	-0.79	0.14	0.02	0.13	-0.11	0.06
Number of saltcedar stems <2.5 cm diam	0.77	-0.19	0.11	0.19	0.07	0.23
Vertical foliage <1 m N and S of the nest, 7.6 m high	-0.73	0.00	0.12	0.08	-0.01	0.17
Number of saltcedar stems 2.5-8.0 cm diam	0.72	-0.08	0.11	0.12	0.25	0.40
Canopy height	-0.64	-0.24	-0.21	-0.15	0.14	-0.13
Distance to nearest native over 5 m high	-0.09	0.82	-0.03	-0.22	-0.05	-0.17
Number of saltcedar stems greater than 8 cm diam	-0.35	0.76	-0.06	0.15	-0.07	0.13
Number of snags less than 8 cm diam	0.42	0.60	-0.10	0.16	0.30	0.07
Vertical foliage <1 m N and S of the nest, 2 m high	-0.02	-0.07	0.74	0.06	-0.14	-0.15
Vertical foliage <1 m N and S of the nest, 5 m high	0.05	-0.05	0.72	-0.03	0.17	0.16
Percent canopy cover	-0.20	-0.18	-0.23	0.77	0.03	0.03
Vertical foliage >1 m N and S of the nest, 5 m high	0.18	0.21	0.22	0.59	-0.02	0.22
Vertical foliage >1 m N and S of the nest, 2 m high	0.29	-0.01	0.36	0.52	0.21	-0.27
Number of snags greater than 8 cm diam	0.05	0.14	-0.15	-0.07	-0.82	-0.08
Distance to water	0.29	0.33	-0.19	-0.02	0.63	-0.14
Distance to canopy opening	0.09	-0.02	-0.02	0.06	0.00	0.86
Eigenvalue	3.6	2.0	1.6	1.3	1.2	1.0
Cumulative percent variance	22.6	35.2	45.0	53.0	60.5	66.6

fit nesting plots in patches at the Gila/San Pedro River confluence in 1998. Overall, Roosevelt Lake had fewer native woody plants and more large saltcedar and small snags (Fig. 1). As reflected by PC4, in both years, nests at Roosevelt Lake had more canopy cover and denser foliage at nest height and below, at least 1 m to the north and south of the nest than did nests at the Gila/San Pedro River confluence. Both study areas scored higher on PC4 in 1998 than in 1999. The statistically significant interaction effect of year and study area for PC1 and PC3 scores characterized nesting plots at Roosevelt in 1999 and Gila/San Pedro River confluence in 1998 for their greater canopy height, higher foliage density above average nest height, and denser foliage in the immediate vicinity of the nest, at and below average nest height (Fig. 2). The statistically significant effect on PC6 of patches and of the interaction effect of year and study area (Table 2) reflected the fact that nests were a similar distance from canopy openings both years at the Gila/San Pedro River confluence, whereas at Roosevelt Lake, nests were built much closer to canopy openings in 1998 than in 1999. Thus, the model reflects significant between-year differences due to use of different patches at Roosevelt.

#### DIFFERENCES BETWEEN NESTING AND NON-NESTING PLOTS WITHIN A PATCH

There were 15 variables in the final logistic regression model (Table 3). As distance to canopy opening doubled, the odds of a plot being occupied by Southwestern Willow Flycatchers decreased 44%. Doubling distance to water decreased the odds 24%, though the change was not significant at the  $\alpha = 0.05$  level. For each meter in canopy height, odds of being occupied more than tripled. Foliage density, reflected by percent canopy cover and vertical foliage measurements at 2 and 5 m height, increased the odds of a tree being used for nesting. Plots were more attractive to nesting flycatchers if they held more small-diameter ( $\leq 8$  cm) velvet mesquite, more mid-sized (2.5 cm-8.0 cm) saltcedar stems, fewer small diameter ( $\leq 2.5$  cm) or large diameter ( $\geq 8$  cm) saltcedar, velvet mesquite, and Goodding willow. Descriptive statistics for these variables are presented in Table 4.

Some variables in the final logistic regression model did not contribute to the description of nesting plots (Table 3), although all had performed well in interim models. Goodding willows with diameters less than 8 cm rarely occurred on our plots, were almost always associated with nesting plots (30 of 34 instances),

TABLE 2. UNIVARIATE ANOVA TESTS ON PCA SCORES DESCRIBING VEGETATION GRADIENTS BETWEEN SOUTHWESTERN WILLOW FLYCATCHER NESTING PLOTS IN CENTRAL ARIZONA

PC	Source	Sum of Squares	df	F	P
1	Study area	0.236	1	0.05	0.849
	Year	0.025	1	0.00	0.965
	Patch	55.177	15	7.42	<0.001
	Study area*Year	8.173	1	16.48	<0.001
	Error	85.809	173		
2	Study area	21.324	1	6.35	0.048
	Year	0.000	1	0.00	0.996
	Patch	79.770	15	17.42	<0.001
	Study area*Year	3.038	1	9.95	0.002
	Error	52.815	173		
3	Study area	0.133	1	0.06	0.827
	Year	1.238	1	0.37	0.653
	Patch	22.464	15	1.62	0.073
	Study area*Year	3.366	1	3.64	0.058
	Error	159.955	173		
4	Study area	6.000	1	3.53	0.070
	Year	6.236	1	7.87	0.006
	Patch	49.310	15	4.15	<0.001
	Error	137.835	174		
5	Study area	0.000	1	0.00	0.993
	Year	0.368	1	0.79	0.376
	Patch	83.873	15	11.96	<0.001
	Error	81.316	174		
6	Study area	1.088	1	0.08	0.821
	Year	22.764	1	0.78	0.540
	Patch	37.965	15	4.71	<0.001
	Study area*Year	29.238	1	54.46	<0.001
	Error	92.885	173		

Notes: Patches were nested within study areas. Interactions were retained in models when  $P < 0.10$ .

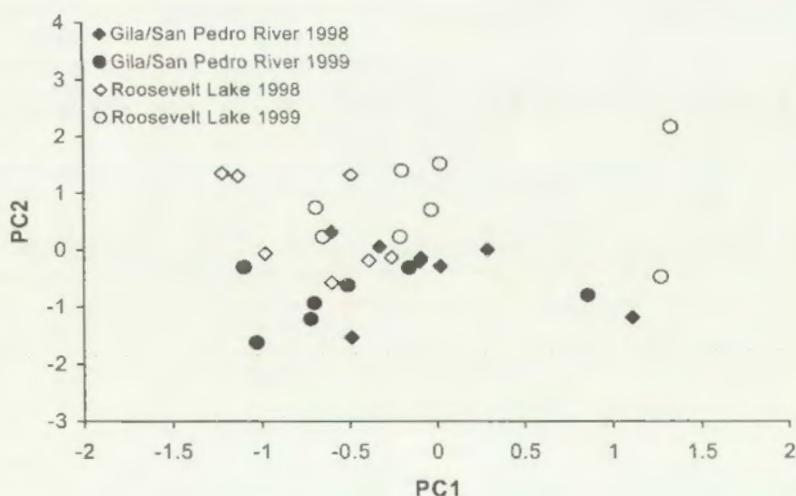


FIGURE 1. Average PC1 and PC2 scores within breeding patches for vegetation measurements at Southwestern Willow Flycatcher nest plots in central Arizona. Low PC1 scores described plots with high, dense canopy, while high scores indicated many small diameter saltcedar stems and snags. High PC2 scores indicated presence of many large saltcedars but few native shrubs and trees.

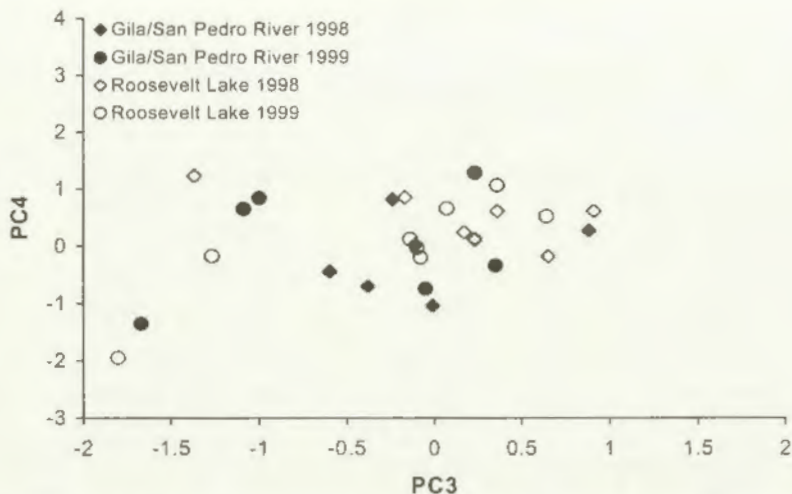


FIGURE 2. Average PC3 and PC4 scores within breeding patches for vegetation measurements at Southwestern Willow Flycatcher nest plots in central Arizona. Scores on both axes increased with density of vegetation at and below nest height within a one meter radius of the nest (PC3) or at a distance from one to 11 meters (PC4). PC4 was also positively correlated with percent canopy cover.

and were negatively correlated with presence of larger Goodding willows. As a result, the parameter estimate for Goodding willow was inflated and unstable. Two variables (vertical foliage to the south and 7.6 m high, and saltcedar stems larger than 8 cm diam) have high *P*-values and odds ratios so close to 1 that they do not add more information when combined with other variables in the model. These two variables were highly correlated with canopy height and vertical foliage to the north at 5 m high, respectively, so their lack of importance in the final model is best explained as a result of multicollinearity.

## DISCUSSION

Habitat characteristics affect survival and reproductive success in birds; consequently, we expect species to have developed preferences for particular elements in their environment. Even for broad-ranging species like the Willow Flycatcher, we expect to uncover similar habitat features at nesting sites across their range. On the other hand, we also expect development of preferences that are not shared range-wide, but enable the species to exploit and accommodate each of the particular regions in which it breeds. Our description of habitat use in central Arizona clarifies common elements of flycatcher nesting habitat across its range, and focuses attention on nesting habitat preferences of Southwestern Willow Flycatchers within the desert landscape in particular.

Three types of variables characterized placement of nests within stands of even-aged vegetation: location, structural components, and flo-

ristic composition. Our finding that nests were located near canopy breaks matches the results of Flett and Sanders (1987), but differs from those of Sedgwick and Knopf (1992). The apparent difference in results may reflect differences in vegetation type and structure. Sedgwick and Knopf (1992) examined nests in shrub-willow clumps (mean height = 3.4 m) within larger herbaceous riparian stretches. In this study, nests were placed in large stands of trees (saltcedar, Fremont cottonwood, Goodding willow) that form a uniformly closed canopy (mean height at nest = 8.4 m; Table 4). Whereas Sedgwick and Knopf (1992) found that female-selected nest sites were more distant than randomly chosen points from openings in vegetation, in our more thickly vegetated sites, female Southwestern Willow Flycatcher selection of canopy breaks may reflect a foraging preference of aerial insectivores. In the relatively more open habitat described for other Willow Flycatcher populations, habitat structure that enables aerial foraging may be more readily available, and females can choose more closed nesting habitat but still be close to foraging habitat.

Nesting vegetation at our study sites was characterized by dense foliage up to 5 m high, approximately the same as the average nest height. Although plant species composition and height differed in specifics from that at our sites, both Flett and Sanders (1987) and Sedgwick and Knopf (1992) reported selection of high foliage density at nest height for other Willow Flycatchers. This preference may improve fledging success through enhanced concealment from pred-



TABLE 3. ODDS RATIOS FROM THE FINAL LOGISTIC MODEL DESCRIBING DIFFERENCES BETWEEN SOUTHWESTERN WILLOW FLYCATCHER NESTING AND NON-NESTING PLOTS IN THE SAME PATCH OF RIPARIAN VEGETATION IN CENTRAL ARIZONA.

Variable	Definition of unit increase	Odds ratio	95.0% C.I.		P
			Lower	Upper	
Location in patch					
Distance to canopy opening	Doubling of distance	0.56	0.332	0.955	0.033
Distance to water	Doubling of distance	0.76	0.542	1.056	0.100
Amount of foliage					
Canopy height	1 m (up to 10)	3.19	1.776	5.740	<0.0005
Percent canopy cover	5% increments over 70%	1.45	0.920	2.281	0.110
Vertical foliage >1 m to the south, 7.6 m high	10%	1.22	0.916	1.622	0.173
Vertical foliage >1 m to the north, 5 m high	10%	1.45	1.077	1.951	0.014
Vertical foliage 9–11 m from the nest, 2 m high	10%	1.50	1.127	1.999	0.005
Species composition					
Distance to nearest native shrub/tree	5 m increments to 50 m	0.78	0.656	0.932	0.006
Saltcedar stems greater than 8 cm diam	Doubling of density	0.91	0.563	1.476	0.707
Saltcedar stems up to 2.5 cm diam	Doubling of density	0.34	0.171	0.670	0.002
Saltcedar stems 2.5–8.0 cm diam	Doubling of density	4.97	2.300	10.729	<0.0005
Velvet mesquite greater than 8 cm diam	Presence/absence	0.04	0.004	0.294	0.002
Velvet mesquite less than 8 cm diam	Presence/absence	9.92	1.899	51.864	0.007
Goodding willow greater than 8 cm diam	Presence/absence	0.04	0.006	0.320	0.002
Goodding willow less than 8 cm diam	Presence/absence <sup>a</sup>				0.636

<sup>a</sup> Only 34 of 226 plots contained small-diameter Goodding willow; all but four of these were nesting plots. The odds ratio estimate for this variable therefore had high variance and changed dramatically as different logistic regression models were fitted; however, the odds ratio computed from a simple contingency table is 7.34.

TABLE 4. MEAN (AND SD) OF VEGETATION CHARACTERISTICS IN CENTRAL ARIZONA THAT CHARACTERIZED DIFFERENCES BETWEEN NESTING AND NONNESTING PLOTS AND/OR DESCRIBED CHARACTERISTICS THAT ARE HIGHLY VARIABLE BETWEEN NESTING PLOTS

Variable	Nesting plots	Non-nesting plots	Distin- guished nesting and non- nesting plots	Source of vari- ability among nesting plots
Distance to canopy opening (m)	9.2 (1.34)	13.7 (2.31)	X	X
Distance to surface water (m)	66.5 (5.22)	150.7 (2.07)		X
Distance to nearest native plant >5 m high (m)	12.9 (18.55)	24.4 (23.03)	X	X
Canopy height (m)	8.4 (0.32)	7.2 (0.41)	X	X
Percent canopy cover	95.0 (0.56)	88.9 (2.82)		X
Vertical foliage on north-south line at >1 m from nest tree (% of board obscured)				
2 m high	39.0 (13.70)	38.6 (17.90)	X	X
5 m high	49.8 (18.15)	31.6 (20.89)	X	X
7.6 m high	37.2 (24.28)	20.0 (23.33)		X
Vertical foliage bracketing nest tree on north-south line (% of board obscured)				
2 m high	38.0 (29.27)	37.2 (31.68)		X
5 m high	57.5 (31.56)	37.7 (32.94)		X
7.6 m high	46.4 (39.68)	21.7 (34.00)		X
Tree (diam >8 cm) count by species				
Saltcedar	24.7 (5.03)	16.4 (10.38)	X	X
Goodding willow	1.4 (3.46)	0.1 (1.00)	X	
Velvet mesquite	0.0 (0.39)	0.8 (2.49)		X
Snag	0.9 (3.17)	2.7 (3.08)		
Shrub (diam 2.5-8 cm) count by species				
Saltcedar	49.5 (7.88)	27.9 (11.84)	X	X
Goodding willow	0.4 (1.56)	0.0 (0.29)	X	
Velvet mesquite	0.8 (3.43)	1.3 (4.92)	X	
Snag	116.8 (23.75)	72.4 (32.63)		X

ators (Martin and Roper 1988) and/or by providing a more favorable microclimate at the nest (Walsberg 1981). One additional feature of nest placement at our study sites may provide improved microclimate at the nest. Nesting plots had higher canopy cover than non-nesting plots; this was not reported at other Willow Flycatcher breeding areas that experience lower average temperatures and less solar radiation during the breeding season.

Other elements of nesting plots in central Arizona are also revealing about the habitat available in this region. Saltcedar, a non-native plant, dominated all breeding patches in our study. However, Southwestern Willow Flycatcher females did not use all sizes/ages of saltcedar equally; nesting plots contained disproportionately more saltcedar stems that were 2.5-8 cm dbh, and fewer stems from both larger and smaller size classes. This is similar to the description of saltcedar use in the Grand Canyon (Brown 1988). We caution that selective use of a vegetation type or plant species (in this case, use of 2.5-8.0 cm dbh saltcedar) does not imply high quality habitat, perhaps associated with

high reproductive rates (Van Horne 1983). Our study addressed flycatcher preferences but not habitat quality.

Note that although native trees and shrubs are not usually a dominant component of the vegetation at our study areas, presence of small-diameter Goodding willow or velvet mesquite nearby increased the odds of finding a Southwestern Willow Flycatcher nest (Table 3). We have no information to explain this association, but because younger shrubs require a higher water table than do larger trees, plants at this seral stage may indicate a particular humidity and/or microclimate that the birds prefer.

Some vegetation measurements were important for distinguish nesting and non-nesting plots in 1999, but also showed considerable variability among nesting plots that were measured in 1998 and 1999 (Table 4). For instance, in 1999, Southwestern Willow Flycatcher nest plots had denser vegetation at and below average nest height than non-nest plots. However, in a pattern that was also repeated with other variables, analysis of associated principal component scores from 1998 and 1999 indicated that there is con-

siderable variation in foliage density among plots, arising from between-year differences in vegetation type and/or availability at each breeding area.

Overall, variation in available habitat at the two study areas was similar. Changes in reservoir level and seasonal flooding along the rivers have led to loss of some stands and new growth of others. This successional process is important for generating mid-sized saltcedar and Goodding willow stands that are apparently favored by Southwestern Willow Flycatchers. Such stands provide a possible example of habitat that is preferred but occasionally available only in limited quantities. Although our analyses showed that older trees generally characterize non-nesting plots, some nesting plots (especially at Roosevelt Lake) did include older trees. The between-year and between-area variation in habitat captured in our analysis might be related to the dynamic nature of riparian systems in central Arizona. We speculate that it is possible and expected that in some years there will be less preferred habitat available, so Southwestern Willow Flycatchers will nest in habitat that is available but not necessarily preferred. Spatial and temporal variability in habitat availability mean that in order to assure sufficient suitable nesting habitat in most years, managers may need to secure larger stretches of riparian vegetation than the nesting territories would actually cover in a given year. Habitat variability should be considered when determining the scale at which conservation efforts for this species will prove effective.

The scale at which we described habitat use

by Southwestern Willow Flycatchers must also be carefully examined. This study was precipitated in part by the observation that nesting territories are often spatially clustered within what initially appeared to be homogeneous vegetation stands. Our analysis of variables centered on the nest represents one level of habitat selection and does not address selection questions at other scales. For instance, at the study area scale, use of only riparian habitat is evidence that distance to water is an important characteristic. However, distance to water did not differ significantly between nesting and non-nesting plots within a particular patch of riparian habitat. Study of stands that are used and those that are not may reveal that it is at this scale that distance to water describes habitat used by Southwestern Willow Flycatchers. Fine-scale habitat selection may also differ among sexes; Sedgwick and Knopf (1992) cautioned that nest placement describes only one aspect of breeding bird biology, and male Willow Flycatchers may select for different characteristics than do females, e.g., more exposed perch sites for advertisement and territorial defense. Our results provide insight into one scale of habitat use by Southwestern Willow Flycatchers in this dynamic, patchy, and fragmented landscape.

#### ACKNOWLEDGMENTS

We gratefully acknowledge R. F. Davidson, M. W. Sumner, and seasonal project field crews for much of the work collecting vegetation measurements. Funding for this project was provided by the U.S. Bureau of Reclamation (Cooperative Agreement 98-FC-32-0050), voluntary contributions to Arizona's Nongame Wildlife Checkoff Fund, and the Arizona Game and Fish Department's Heritage Fund.

## APPENDIX. VARIABLES MEASURED IN PATCHES OCCUPIED BY SOUTHWESTERN WILLOW FLYCATCHERS IN CENTRAL ARIZONA

Variable	Year		Measurement location		
	1998	1999	Cardinal directions	Meters from plot center	Transformation <sup>a</sup>
Plot center relative to patch features					
Distance to open canopy	X	X			L
Distance to surface water	X	X			L
Distance to nearest native shrub/tree	X	X			
Canopy characteristics					
Height of canopy	X	X			
Seepwillow canopy cover >40%	X	X			
Fremont cottonwood canopy cover >40%	X	X			
Velvet mesquite canopy cover >40%	X	X			
Goodding willow canopy cover >40%	X	X			
Saltcedar canopy cover >40%	X	X			
Canopy cover	X	X	N, S, E, W		A, M
Foliage density at given height					
Vertical foliage at 2 m	X	X	N and S	2, 6, 10	M
Vertical foliage at 5 m	X	X	N and S	2, 6, 10	M
Vertical foliage at 7.6 m	X	X	N and S	2, 6, 10	M
Vertical foliage around nest tree at 2 m	X	X	N to S	0	
Vertical foliage around nest tree at 5 m	X	X	N to S	0	
Vertical foliage around nest tree at 7.6 m	X	X	N to S	0	
Foliage presence around nest tree at >7.6	X	X	N to S	0	
Vertical foliage around nest tree at 2 m	X		E to W	0	
Vertical foliage around nest tree at 5 m	X		E to W	0	
Vertical foliage around nest tree at 7.6 m	X		E to W	0	
Foliage presence around nest tree >7.6 m	X		E to W	0	
Vertical foliage at 2 m	X		<sup>b</sup>	2	M
Vertical foliage at 5 m	X		<sup>b</sup>	2	M
Vertical foliage at 7.6 m	X		<sup>b</sup>	2	M
Vertical foliage at 2 m	X		<sup>b</sup>	6	M
Vertical foliage at 5 m	X		<sup>b</sup>	6	M
Vertical foliage at 7.6 m	X		<sup>b</sup>	6	M
Vertical foliage at 2 m	X		<sup>b</sup>	10	M
Vertical foliage at 5 m	X		<sup>b</sup>	10	M
Vertical foliage at 7.6 m	X		<sup>b</sup>	10	M
Presence of canopy >7.6 m	X		<sup>b</sup>	2	
Presence of canopy >7.6 m	X		<sup>b</sup>	6	
Presence of canopy >7.6 m	X		<sup>b</sup>	10	
Stem counts					
Snag stems of diameter <8 cm	X	X	N, S, E, W		S, M
Snag stems of diam >8 cm	X	X	N, S, E, W		S, M
Goodding willow stems of diam <8 cm	X	X	N, S, E, W		M
Goodding willow stems of diam >8 cm	X	X	N, S, E, W		M
Fremont cottonwood stems of diam <8 cm	X	X	N, S, E, W		M
Fremont cottonwood stems of diam >8 cm	X	X	N, S, E, W		M
Velvet mesquite stems of diam <8 cm	X	X			M
Velvet mesquite stems of diam >8 cm	X	X			M
Seepwillow stems of diam <8 cm	X	X	N, S, E, W		M
Saltcedar stems of diam <2.5 cm	X	X	N, S, E, W		S, M
Saltcedar stems of diam 2.5-8 cm	X	X	N, S, E, W		S, M
Saltcedar stems of diam >8 cm	X	X	N, S, E, W		S, M

<sup>a</sup>L = Log 10, S = square root, A = Arcsine square root, M = Average over measurements taken in different cardinal directions or locations in the plot as indicated. Transformations were used before PCA and before creating variables by averaging.

<sup>b</sup>All four cardinal directions measured in 1998; only north and south measurements taken in 1999.

## MICROHABITAT USE BY BREEDING SOUTHWESTERN WILLOW FLYCATCHERS ON THE GILA RIVER, NEW MEXICO

SCOTT H. STOLESON AND DEBORAH M. FINCH

**Abstract.** The endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*) breeds at numerous sites throughout its range that vary greatly in floristics, vegetation structure, and the extent of human alteration of the habitat. Here we present information on nesting habitat characteristics of Willow Flycatchers in the largest extant population of the subspecies along the upper Gila River in New Mexico. We compared 19 habitat variables between nest sites and sites not included in flycatcher territories. A logistic regression model identified three variables as significant predictors of flycatcher use: foliage density in the subcanopy, percent canopy cover, and number of boxelder (*Acer negundo*) stems. In mature riparian woodland, flycatchers displayed a significant preference for nesting in boxelder, and used two willow species less than expected by chance. Flycatchers in the Gila Valley tended to place nests rather high (mean = 7.6 m). The relative nest height, preference for dense foliage, and proximity to water were typical for the subspecies.

**Key Words:** Cliff-Gila Valley; *Empidonax traillii extimus*; habitat selection; nest site; New Mexico; Southwestern Willow Flycatcher.

Habitat structure and floristics can strongly affect the distribution and productivity of birds (Martin and Roper 1988, Block and Brennan 1993, Martin 1998). For endangered bird species, recovery often depends on identifying, preserving, and possibly restoring suitable habitat. A clear understanding of what comprises suitable habitat is especially important when habitat loss constitutes the primary cause of a species' decline or when a species has narrow habitat preferences.

The Southwestern Willow Flycatcher (*Empidonax traillii extimus*) is a riparian obligate inhabiting dense streamside thickets and woodland (Sedgwick 2000, Sogge and Marshall 2000). In the past century, most of the riparian habitat in the Southwest has been destroyed or degraded due to urban and agricultural development, water management, channelization, overgrazing, recreation, and invasion by exotic saltcedar (*Tamarix ramosissima*; Patten 1998, Cartron et al. 2000, Marshall and Stoleson 2000). The Southwestern Willow Flycatcher has shown a concomitant decline (Unitt 1987), resulting in it being listed as an endangered species in 1995 (U.S. Fish and Wildlife Service 1995). The most recent population estimates total 986 known territories rangewide (Sogge et al. *this volume*).

Recovery of this endangered subspecies will depend on the identification of preferred habitat as targets for preservation and as goals for restoration. A clear, quantitative understanding of what constitutes preferred habitat has been hindered by the fact that occupied sites vary greatly in floristics and vegetation structure (Sogge and Marshall 2000). Currently, flycatchers breed in numerous altered or degraded sites, including many dominated by exotic saltcedar (Paradzick

et al. 1999, U.S. Fish and Wildlife Service 2001).

We describe the nest site and nesting microhabitat characteristics of a population of Willow Flycatchers along the upper Gila River in New Mexico. This valley supports the largest known breeding concentration of *E. t. extimus* (estimated at 243 pairs in 1999; S. Stoleson and D. Finch, unpubl. data). Birds in this population exhibit nest site and microhabitat characteristics that differ in some respects from those reported elsewhere (Stoleson and Finch 1999b, Sedgwick 2000, Sogge and Marshall 2000). Information on nest site preferences for this population has previously been reported only in unpublished reports (e.g., Skaggs 1996). The data presented here should help to provide a more complete picture of the habitats used by breeding Willow Flycatchers in the Southwest and provide insights into important habitat components.

### METHODS

#### STUDY SITE

This study was conducted in the Cliff-Gila Valley of Grant County, New Mexico, (32° 58' N, 108° 34' W) in 1997-2000. Most of this broad floodplain is private land (the U Bar Ranch) consisting of irrigated and dry pastures used for livestock grazing and hay farming. Adjacent areas include protected lands of The Nature Conservancy and the Gila National Forest. Elevations range from 1335 to 1420 m. The Gila River and nearby earthen irrigation ditches are lined with riparian woodland patches of various ages and composition. Most patches support a mature woodland (>25 m canopy) composed primarily of Fremont cottonwood (*Populus fremontii*), Goodding's willow (*Salix gooddingii*), boxelder (*Acer negundo*), velvet ash (*Fraxinus velutinus*), Arizona walnut (*Juglans major*), Arizona sycamore (*Platanus wrightii*), Arizona alder (*Alnus oblongifolia*), and Russian olive (*Elaeagnus an-*

*gustifolia*). The understory is composed of shrubs including three-leaf sumac (*Rhus trilobata*), false indigo (*Amorpha fruticosa*), New Mexico olive (*Forestiera neomexicana*), forbs, and grasses. Fewer patches support a shrubby, early successional growth of seepwillow (*Baccharis glutinosa*), coyote and bluestem willows (*Salix exigua* and *S. irrorata*), and saplings of the species mentioned above. Most habitat patches are less than 5 ha in area, and the total area of riparian woodland included in this study is approximately 75 ha.

#### FIELD METHODS

We searched for nests in occupied patches daily throughout the breeding seasons (May–Aug.) of 1997–2000 during spot-mapping censuses, area searches, and focused nest searches (Martin and Geupel 1993). We found nests in approximately 70–85% of territories each year, based on spot-mapping data. At each nest, we recorded tree species, height, and diameter, and nest height. We also calculated the relative height of nests as nest height/nest tree height. We identified the dominant tree for nest sites where one tree species made up  $\geq 50\%$  of stems within 8 m of the nest. All vegetation measurements were performed after flycatcher breeding activity in the area had ceased (27 Jul–3 Sept).

Within occupied patches, we sampled microhabitat characteristics at 127 nest sites and 89 randomly selected non-use sites using a modified BBIRD methodology (Martin et al. 1997). Vegetation at nest sites was measured in a sample plot centered on the nest tree (see below). Southwestern Willow Flycatchers at this site often reused nest trees within and among years, and resighting of color-banded individuals suggests a high degree of site fidelity (S. Stoleson and D. Finch, unpubl. data). We also detected no significant yearly variation in habitat preferences (variables in Table 2, ANOVA, all  $P > 0.29$ ). Thus, to avoid any problems of non-independence, we took a conservative approach and included in analyses only nest plots with no spatial (8-m radius) overlap within or among years. Non-use sites were randomly selected from points on spot-mapping grids that were at least 33.5 m away from the nearest Willow Flycatcher nest, as most flycatcher territories at this site appeared to have radii much smaller than 33.5 m (S. Stoleson and D. Finch, unpubl. data). We assumed that all riparian habitat within spot-mapping grids was available to arriving flycatchers to set up territories.

At each nest and non-use site, we established a 0.02-ha circular sample plot (radius = 8 m). Sample plots at non-use sites were centered on the closest tree to the spot-map grid point. At the center of the plot and at eight other points (4 and 8 m from the center in each of the four cardinal directions), we measured canopy height using clinometers, percent canopy cover using densimeters, and estimated percent ground cover. Vertical foliage density was measured at 2, 4, 6 and 8 m from the center tree in each cardinal direction by counting hits of vegetation against a 10-m vertical pole marked in 1-m increments. We recorded the number and size class (dbh) of all trees ( $\geq 10$  cm dbh) within the 8-m radius plot, and the number and size class of shrubs and saplings ( $< 10$  cm dbh) within a 4-m radius of the center tree.

For each sample plot, we calculated average ground and canopy cover and average canopy height (mean of 9 measurements per plot); foliage density index (count of 1-m increments touched by foliage) for understory (0–3 m in height, for a maximum score of 48 per plot) and mid-canopy (3–10 m in height, for a maximum score of 112 per plot); and the sum of shrub/sapling ( $< 10$  cm diam) stems and tree ( $\geq 10$  cm diam) stems by species and size class ( $< 1$  cm, 1–4.9 cm, 5–7.4 cm, 7.5–9.9 cm, 10–29.9 cm, 30–49.9 cm, 50–70 cm,  $> 70$  cm). From these values we also calculated the total number of stems of each woody plant species per plot, an estimate of the total basal area of woody species per plot, woody plant species richness (number of species of trees and shrubs per plot), and plant species diversity (using the Shannon diversity index). We calculated several variables to estimate the degree of habitat heterogeneity within each sample plot: patchiness (the Shannon diversity index of total foliage density among the four cardinal directions); and the coefficient of variation in measures of canopy cover, canopy height, and ground cover within each plot. We also measured horizontal distance from each sample plot center to the closest surface water and closest edge of the habitat patch.

We compared habitat values between non-use sites and nest sites using either independent sample t-tests when data were normally distributed or could be normalized through standard transformations, or Mann-Whitney U-tests when data could not be normalized. Habitat variables found to differ significantly (using Bonferroni's adjustment for multiple tests on a single data set; Rice 1989) between nest and non-use sites were included in a logistic regression model (Menard 1995). We used a value of  $P \leq 0.10$  to enter and  $\geq 0.05$  to remove individual variables from the model. We chose the most parsimonious logistic regression model with equal numbers of parameters using Akaike's Information Criterion (AIC) and used likelihood-ratio chi-square tests to test for significant effects between nested models (Anderson et al. 2000). We compared the likelihood of occurrence of the six most frequent herbaceous groundcovers between nest and non-use sites using chi-square analyses. All means are presented  $\pm 1$  SD.

We also tested the hypothesis that Southwestern Willow Flycatchers chose nest trees randomly by comparing tree species usage with availability. Flycatcher nests were found in vegetation of all size classes  $\geq 1$  cm diameter, so we considered all stems in these classes as potential nest substrates. A composite stem count for each species was calculated from all nest plots. We assumed counts of stems at ground level were representative of the relative abundances of tree species available to flycatchers for nest placement. For each tree species we compared the (arcsine-transformed) proportion of stems used for nesting with their relative availability (proportion of all stems) using chi-square analyses.

## RESULTS

### NEST SUBSTRATES

We located a total of 488 Southwestern Willow Flycatcher nests. The majority (76%) of

TABLE 1. WILLOW FLYCATCHER NEST SUBSTRATES AND HEIGHTS IN THE CLIFF-GILA VALLEY, 1997-2000

Plant species	No. (%) nests		No. (%) stems		Nest heights		
					Mean	SD	Range
Boxelder	371	(76.0)	2188	(43.3)	8.4	3.4	1.8-19.0
Goodding's willow	36	(7.4)	1007	(19.9)	4.6	2.6	1.7-13.2
Fremont cottonwood	22	(4.5)	150	(3.0)	7.2	4.8	2.0-24.1
Russian olive	19	(3.9)	197	(3.9)	4.3	1.9	1.0-8.0
Coyote willow	15	(3.1)	857	(16.9)	2.6	0.9	1.5-4.2
Arizona alder	13	(2.7)	132	(2.6)	6.3	2.5	2.3-10.0
Saltcedar	4	(0.8)	25	(0.5)	2.7	0.5	1.9-3.1
Seepwillow	3	(0.6)	131	(2.6)	2.0	0.1	1.9-2.0
Arizona sycamore	2	(0.4)	18	(0.3)	11.0	4.2	8.0-14.0
Rose ( <i>Rosa multiflora</i> )	1	(0.2)	2	(<0.1)	4.0	—	—
Canyon grape ( <i>Vitis arizonica</i> )	1	(0.2)	34	(0.7)	1.5	—	—
Siberian elm ( <i>Ulmus pumila</i> )	1	(0.2)	27	(0.5)	3.6	—	—
Total/mean	488	(100.0)	5058	(94.3) <sup>a</sup>	7.6	3.7	1.0-24.1

<sup>a</sup> Figure does not total to 100% because it omits plant species not used by flycatchers for nesting.

these were placed in boxelder trees. Goodding's willow was the second most frequent nesting substrate (7% of nests), with the remaining nests found in ten other plant species (Table 1). In the Cliff-Gila Valley, flycatchers placed nests in cottonwood and seepwillow only in young stands.

Flycatchers did not select nest tree species in proportion to their availability ( $\chi^2 = 26.4$ ,  $df = 4$ ,  $P < 0.01$ ; Table 1). Boxelder was used significantly more than would be expected if birds chose nest trees randomly ( $\chi^2 = 22.6$ ,  $df = 1$ ,  $P < 0.01$ ). It comprised 43% of the woody stems over 1 cm diam, yet contained 76% of all nests. In contrast, Goodding's willow was used less than expected by chance ( $\chi^2 = 6.4$ ,  $df = 1$ ,  $P = 0.01$ ); it comprised almost 20% of all stems but was used for less than 8% of nests. Coyote willow was also used less than expected ( $\chi^2 = 10.7$ ,  $df = 1$ ,  $P < 0.01$ ). Other substrates were used too infrequently for meaningful comparisons of use versus availability (Table 1).

Willow Flycatchers tended to build nests in the numerically dominant woody plant species within nest plots; 81% were placed in the most frequent tree species within the plot. Flycatchers placed nests in boxelder at 139 of 141 (99%) nest sites dominated by boxelder. However, they also placed nests in boxelder in 4 of the 16 nest sites dominated by Goodding's willow and in over a third (36%) of the 39 nest sites dominated by species other than boxelder, either willow, or Russian olive.

#### NEST HEIGHTS

The mean height of all nests found was  $7.6 \pm 3.7$  m, with a median height of 7.0 m (range 1.0-24.1 m; Table 1). Heights varied considerably among different nesting substrates (Table 1). Boxelder nests were significantly higher ( $8.4$

$\pm 3.4$  m) than nests in all other substrates combined (mean =  $4.9 \pm 3.3$  m;  $t = -10.6$ ,  $df = 202.9$ ,  $P < 0.01$ ). Nest trees averaged  $12.3 \pm 5.0$  m tall (range 2.2-27.0 m), with diameter of  $22.4 \pm 16.7$  cm (range 0.5-142.7 cm). The relative height of Willow Flycatcher nests within nest trees averaged  $0.62 \pm 0.17$ .

#### MICROHABITAT OF NEST VS. NON-USE SITES

Microhabitat around nest sites differed substantially from that at non-use sites. In univariate comparisons, 9 of 19 habitat variables differed significantly ( $P < 0.01$ ) between nest and non-use sites (Table 2). Nest sites typically had less ground cover, greater canopy cover that was less variable, greater foliage density between 3 and 10 m, greater foliage density patchiness, more trees and boxelder stems, and fewer stems of cottonwood (Table 2). Logistic regression analysis identified three of these variables as significant predictors of flycatcher nesting. The best model was  $\text{logit}(p) = -10.69 + 0.09$  (subcanopy foliage density) +  $0.28$  (% boxelder stems) +  $0.09$  (mean canopy cover). The likelihood of a site being used for nesting by flycatchers increased with greater foliage density, greater proportion of boxelder, and greater mean canopy cover.

Used sites also differed from non-use sites in the occurrence of certain species of common understory herbaceous plants. Nest sites were significantly more likely to have wetland forbs such as spearmint (*Mentha spicata*;  $\chi^2 = 4.4$ ,  $df = 1$ ,  $P = 0.03$ ) and nettles (*Urtica dioica*;  $\chi^2 = 9.0$ ,  $df = 1$ ,  $P < 0.01$ ). In contrast, non-use sites were significantly more likely to have horehound (*Marrubium vulgare*;  $\chi^2 = 5.3$ ,  $df = 1$ ,  $P = 0.02$ ), four o'clocks (*Mirabilis* spp.;  $\chi^2 = 16.8$ ,  $df = 1$ ,  $P < 0.01$ ), jimsonweed (*Datura*

TABLE 2. UNIVARIATE COMPARISONS OF CONTINUOUS HABITAT VARIABLES BETWEEN WILLOW FLYCATCHER NEST SITES AND NON-USE SITES

Variable	Nest sites (N = 127)	Non-use sites (N = 89)	Test statistic <sup>a</sup>	df	P <sup>b</sup>
Average ground cover (%)	30.0 ± 23.4	39.2 ± 19.3	t = 3.17	208.4	<0.01
CV ground cover	1.0 ± 0.5	0.7 ± 0.4	t = 1.28	214	0.20
Average canopy cover (m)	88.7 ± 7.9	78.8 ± 12.4	U = 2641.0		<0.01
CV canopy cover	0.1 ± 0.1	0.2 ± 0.2	U = 4952.0		<0.01
Average canopy height (m)	13.9 ± 4.7	17.4 ± 9.7	t = -0.22	150.5	0.83
CV canopy height	0.3 ± 0.2	0.4 ± 0.3	t = 2.46	135.5	0.02
Foliage density 1-3 m	12.2 ± 6.6	13.8 ± 6.3	t = 2.87	214	0.01
Foliage density 3-10 m	41.7 ± 12.6	25.9 ± 13.7	t = -8.76	214	<0.01
Foliage height diversity	1.5 ± 0.2	1.1 ± 0.2	t = -2.42	157.9	0.02
Foliage density patchiness	1.34 ± 0.05	1.29 ± 0.13	U = 3573.0		<0.01
Total of shrub stems (<10 cm)	29.3 ± 44.5	19.7 ± 25.6	U = 5535.0		0.01
Total of tree stems (≥10 cm)	9.8 ± 4.7	5.8 ± 3.6	t = -4.69	146.1	<0.01
Total of boxelder stems	6.0 ± 4.1	1.6 ± 2.6	t = -6.10	214	<0.01
Total of willow stems	9.9 ± 37.9	3.7 ± 8.0	U = 8023.0		0.61
Total of cottonwood stems	0.5 ± 1.7	1.6 ± 3.4	U = 6911.0		<0.01
Plant species diversity	0.6 ± 0.5	0.7 ± 0.5	t = 1.26	214	0.21
No. of woody plant species	3.0 ± 1.7	2.9 ± 1.5	t = -0.28	214	0.78
Distance to nearest water (m)	41.2 ± 53.8	63.0 ± 58.9	t = 2.83	214	<0.01
Distance to nearest edge (m)	9.9 ± 8.6	9.7 ± 7.0	t = -0.18	423	0.86

<sup>a</sup>t-tests when data met assumptions of normality, Mann-Whitney U-tests when data could not be normalized.

<sup>b</sup>P-values in boldface were statistically significant based on Bonferroni's correction for experiment-wise error rate (Rice 1989).

*wrightii*;  $\chi^2 = 6.0$ ,  $df = 1$ ,  $P = 0.02$ ) and morning glories (*Convolvulus* spp.;  $\chi^2 = 28.4$ ,  $df = 1$ ,  $P < 0.01$ ).

## DISCUSSION

### NEST SITES

Southwestern Willow Flycatchers in the upper Gila River Valley of New Mexico differed from other known populations both in the high average placement of their nests and in the predominant nesting substrate (Sedgwick 2000, Sogge 2000b). The high use of boxelder appears to be unique to this population. This likely reflects the fact that in the Southwest, boxelder occurs primarily above 1200 m elevation, higher than most sites occupied by Southwestern Willow Flycatchers (Boles and Dick-Peddie 1983, Szaro 1989, U.S. Fish and Wildlife Service 2001). Unlike many other areas of the Southwest, where willows tend to dominate riparian areas, flycatchers in the Cliff-Gila Valley underutilized willows as nesting substrates (Szaro 1989, Sogge 2000b, U.S. Fish and Wildlife Service 2001). Our findings are congruent with those of McCabe (1991:49) from his study of *E. t. traillii* in Wisconsin, in which he suggested that where the bird has a choice of willows or other substrates, willow tends not to be preferred. The relatively frequent use of exotic Russian olive in this mostly native habitat is noteworthy in light of its encroachment into riparian habitats in the region (Olson and Knopf 1986).

Our results suggest potential working hypotheses to test whether the apparent habitat preferences reported here confer fitness benefits to breeding flycatchers, perhaps through reduced vulnerability to predation or brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). Boxelder may provide such potential benefits simply because flycatchers nest higher than in other substrates. The likelihood of brood parasitism was inversely correlated with nest height in the closely related Least Flycatcher (*Empidonax minimus*; Briskie et al. 1990). In this population, rates of brood parasitism were significantly lower in boxelder than in Russian olive, even when nest height and distance from edge were controlled for (S. Stoleson and D. Finch, unpubl. data), suggesting possible benefits from boxelder not related to nest height. Our results also suggest that riparian restoration in the Southwest need not be focused solely on willows to provide suitable habitat for flycatchers; planting of boxelder may be appropriate in some middle and upper-elevation areas.

In the Cliff-Gila Valley, Willow Flycatchers tended to nest considerably higher than in all other known populations (Sedgwick 2000). However, the high placement of nests was not uniform at our site. Birds placed nests unusually high in boxelder, cottonwood, alder and sycamore (Table 1). Mean nest height in willow (4.0 m) and saltcedar (2.7 m) was similar to nests in those trees elsewhere in the Southwest (Sogge



2000b). Although absolute heights of Willow Flycatcher nests in the Cliff-Gila Valley were unusually high, the relative position of those nests within the nest tree was very typical. The mean relative height here (0.62) was very similar to that reported by McCabe (1991) for his shrub-inhabiting *E. t. traillii* population (0.62,  $N = 601$  nests). Similarly, the mean relative nest height in Arizona (based on mean values for nest and tree heights for nests located in 2000) was 0.60 ( $N = 202$ ; Paradzick et al. 1999). This suggests nest placement by flycatchers may be based on relative position within the nest tree, and absolute height may simply reflect the stature of the habitat.

#### HABITAT PREFERENCES

The only significant predictors of flycatcher use indicated by logistic regression were foliage density in the subcanopy, number of boxelder stems, and average canopy cover. This suggests flycatchers may preferentially establish territories in dense, shady thickets of boxelder, their preferred nest tree in this habitat. Univariate comparisons indicated that flycatchers also tended to settle near water and where foliage was heterogeneous. Except for the boxelder, these results are congruent with descriptions of Willow Flycatcher nesting habitat elsewhere in the West (Whitmore 1977, Flett and Sanders 1987, Sedgwick and Knopf 1992, Sogge et al. 1997b). Our results should be combined with similar habitat assessments conducted elsewhere in the range of *E. t. extimus* in a meta-analysis (Arnqvist and Wooster 1995) to develop a comprehensive, quantitative habitat model for the subspecies.

Although almost half of the habitat variables examined differed significantly between nest sites and non-use sites, only three were signifi-

cant predictors of flycatcher use. There are several possible explanations for this lack of discriminatory power. Our assessment was based on, and measured around, nest sites, but avian territories serve additional functions including providing song perches and an adequate food base (Prescott and Middleton 1988, Sedgwick and Knopf 1992). Our methods may have assessed correlates of these other functions only poorly. Alternatively, settlement patterns of flycatchers may be more closely associated with habitat features at larger spatial scales, such as patch or watershed (Freemark et al. 1995, Saab 1999). Within New Mexico's Gila Valley, numerous areas of riparian habitat remain unoccupied by Southwestern Willow Flycatchers (S. Stoleson and D. Finch, unpubl. data). These patterns may reflect habitat preferences of the flycatcher at the patch and landscape scales; suitable microhabitat may exist in unsuitable landscapes. Alternatively, there may be too few flycatchers to saturate the area. Future research should concentrate on identifying patterns of flycatcher habitat selection at these larger spatial scales.

#### ACKNOWLEDGMENTS

We thank G. Bodner, K. Brodhead, P. Chan, J. Garcia, B. Gibbons, D. Hawksworth, R. Hunt, M. Means, G. Sadoti, B. Trussell, H. Walker, and H. Woodward for field assistance; R. King for biostatistical guidance; P. Boucher, J. Monzingo, and R. Pope of the Gila National Forest, T. Bays, C. Rose, and T. Shelley of Phelps Dodge Corp., and L. and A. Ortiz for logistical support; and T. and D. Ogilvie for their hospitality and for allowing us to use their livelihood as a laboratory. Comments by M. Sogge, R. R. Wilson, and two anonymous reviewers improved the manuscript. The Gila National Forest, Phelps Dodge Corporation, National Fish and Wildlife Foundation, and The Nature Conservancy of New Mexico provided funding.

## 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 veg-

etative 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 goodingii*) 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 "Calyptate 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 <sup>a</sup>
Year	1996	18
	1997	40
Month	June	8
	July	43
	August	1
Age	Adult	16
	Nestling	34
Sex <sup>b</sup>	Female	11
	Male	5

<sup>a</sup> 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.

<sup>b</sup> 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 simi-

lar). 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 <sup>a</sup>
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

<sup>a</sup> 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

<sup>a</sup> 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 Cyclorhapha). 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

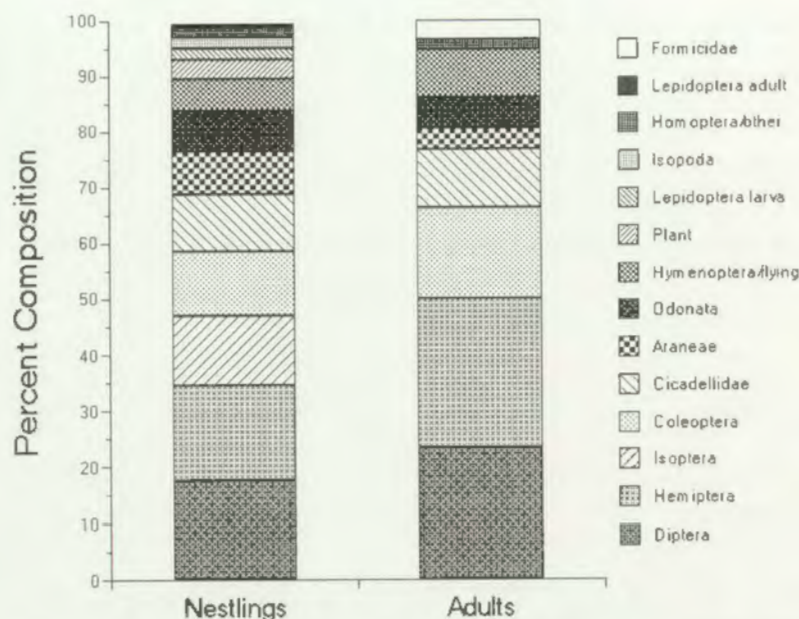


FIGURE 1. Diet composition (based on total number of prey individuals in major prey taxa) of nestling and adult Southwestern Willow Flycatchers, from the Kern River Preserve in southern California.  $N = 33$  nestlings and 16 adults.

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 feed-

ing 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

Taxon	Mean proportion in sample			
	Adults	Nestlings	$F_{1,35}$	$P^a$
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

<sup>a</sup> 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, sphecids 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 oc-

currence) 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