

## ECOLOGY AND BEHAVIOR—INTRODUCTION

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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.