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Status, Ecology, and Conservation of the Southwestern Willow Flycatcher

Abstract

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This publication was prepared in response to a need expressed by southwestern agencies and organizations for a comprehensive assessment of the population status, history, biology, ecology, habitats, threats, and conservation of the southwestern willow flycatcher (*Empidonax traillii extimus*). The southwestern willow flycatcher was federally listed as an Endangered subspecies in 1995. A team of flycatcher experts from multiple agencies and organizations identified components of the publication, wrote chapters, and cooperatively assembled management recommendations and research needs. We hope this publication will be useful in conserving populations and habitats of the southwestern willow flycatcher.

Key words: southwestern willow flycatcher, endangered species, riparian, Southwest, exotic woody plants, rivers, recovery, habitat restoration, Neotropical migratory bird, brown-headed cowbird

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Top left photo: *Adult southwestern willow flycatcher, White Mountains, Arizona. Photo by Suzanne Langridge*
Top right photo: *Southwestern willow flycatcher adult, nest, and nestlings, Kern River Preserve. Photo by Sean Rowe*
Bottom photo: *Southwestern willow flycatcher adult, nest, and nestlings, along irrigation ditch, Gila National Forest. Photo by Jean-Luc Cartron*

Status, Ecology, and Conservation of the Southwestern Willow Flycatcher

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Deborah M. Finch

Chapter 1:

Introduction of the Conservation Assessment Concept

The goal of this document is to describe the current status, ecology, habitat, and threats of the southwestern willow flycatcher (*Empidonax traillii extimus*); to offer guidance for managing and protecting this Neotropical migrant and its habitats; and to identify gaps in our knowledge of the bird and its requirements. Goals, processes, and target species for U.S. Forest Service (USFS) conservation assessments of southwestern organisms were first outlined at a meeting held by the USFS Southwestern Region on May 11-12, 1994. At that time, the Forest Service had identified the southwestern willow flycatcher in a general category called "riparian birds" whose conservation assessments would be drafted in 1999. Yet, by July 23, 1993, the U.S. Fish and Wildlife Service had proposed to list *E. t. extimus* based on findings of a petition submitted in 1992 (U.S. Fish and Wildlife Service 1993). When the southwestern willow flycatcher was federally listed as endangered in March 1995 (U.S. Fish and Wildlife Service 1995), the need for developing management guidance became a higher priority, and the date for completing the assessment was accelerated. In 1997, the USFS Southwestern Region asked the Rocky Mountain Research Station's Albuquerque office to prepare an assessment of the flycatcher that would provide guidance for conserving its populations on national forests.

Prior to and since its listing, federal, state, and municipal agencies have been working together and with private landowners and conservation organizations to survey riparian habitats in California, Arizona, New Mexico, western Texas, southern Utah, southern Nevada, and southern Colorado with the hope of finding and protecting additional flycatchers and their habitats. Because populations of the flycatcher reside on lands under mixed ownerships, I concluded that the most effective conservation strategy for this subspecies of the willow flycatcher (WIFL) would have to be developed by multiple stakeholders. With this in mind, I assembled a team comprised of representatives of several southwestern state and federal agencies, including U.S. Fish and Wildlife Service, U.S. Forest Service, U.S. Geological Survey, Bureau of Reclamation, Arizona Game and Fish, New Mexico Department of Game and Fish, and California Department of Fish and Game to prepare the conservation assessment. To ensure sufficient technical expertise, additional representatives of two nongovernmental organizations, Kern River Research Center and The Nature Conservancy, were also invited to participate in the development of specific technical review chapters. Biographical sketches and institutional affiliations of authors who contributed chapters to the assessment are given in the Appendix.

Our first meeting of the conservation assessment team was held in Albuquerque on May 6, 1997. At that time, we outlined the chapter topics, content, authors, and schedule needed for completing the conservation assessment. We agreed that most chapters of the assessment would be prepared by one or more experts on the chapter topic, but that the Management Recommendations and Research Needs chapters would be developed through a group consensus process. The team met on multiple occasions through the remainder of 1997 and part of 1998 to discuss management recommendations and research needs, and to review progress. On March 2, 1998, the team met to evaluate the final product and to initiate the review process. External reviews of the conservation assessment were solicited from a wide variety of stakeholders, and their input was considered in the final document. In addition, arrangements were made with The Ornithological Council to conduct a formal "blind review" of the document. The Council requested reviews of the entire document from three referees and received two thorough but favorable reviews in return which were forwarded to the Editors, Scott Stoleson and myself. We distributed the Council reviews to senior authors of each chapter with requests for revisions, and authors revised their individual papers accordingly. This document is therefore defined as peer-reviewed and should be cited as such.

In the context of WIFL habitat requirements and consistent with the goals of Forest Service Conservation Assessments, our report emphasizes the Chief's national priorities for protecting watersheds and riparian ecosystems, and restoring rangeland and forest health. This document is also consistent with the "Company's Coming" program that the USFS Southwestern Region implemented in 1997. One of three major components of Company's Coming focuses on sustainability of riparian ecosystems; a second component stresses forest and rangeland health. This report also emphasizes interagency collaboration in conserving flycatchers and their habitats, a strategy that dovetails well with the new Southwestern Interagency Initiative referred to as the Southwest Strategy (http://www.swstrategy.org) called for by the Secretaries of Agriculture and Interior in 1997. This initiative stresses the need for southwestern agencies and associated partners to work cooperatively together to develop strategies for managing natural resources. The Scientific Information Working Group has highlighted the southwestern willow flycatcher as a flagship species for initiating interagency research and conservation under the auspices of the Southwest Strategy.

In 1998, the U.S. Fish and Wildlife Service (FWS) initiated the process for developing a comprehensive recovery plan that involves input by numerous technical experts and other stakeholders (http://ifw2es.fws.gov/swwf). The conservation assessment presented herein was prepared as an interim document to help guide WIFL habitat management on southwestern national forests and other lands prior to the release of the recovery plan. Several members of the original Conservation Assessment Team (i.e., Deborah Finch, Rob Marshall, Susam Sferra, Mark Sogge, Sartor Williams III, and Mary Whitfield) were selected by FWS to be on the Recovery Team. Members of the Conservation Team circulated chapters of the Assessment to the Technical Subgroup of the Recovery Team. Information compiled and synthesized in this Assessment report served as a stepping stone and useful reference for drafting the technical portion of the recovery plan. Individual chapters of the Assessment report are cited liberally throughout the recovery plan. The management chapter provided in our Assessment report is viewed as interim guidance and should be promptly replaced by the Recovery Team's stepdown outline once the Recovery Plan is formally released.

For Internet information about the southwestern WIFL, the U.S. Geological Survey's Colorado Plateau Field Station hosts an excellent web site at http://www.usgs.nau.edu/swwf. For Internet information about the USFS Rocky Mountain Research Station's program of research on the flycatcher, refer to the Albuquerque Forestry Sciences Laboratory's web page: http://www.fs.fed.us/rm/albuq. For status and updates of the recovery plan, check the FWS Southwest Region's web site: http://ifw2es.fws.gov/swwf.

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Robert M. Marshall

Chapter 2:

Population Status on Breeding Grounds

In his review of the overall population status of the southwestern willow flycatcher, Unitt (1987) concluded that "Even if a few hundred pairs persist in New Mexico, the total population of the subspecies is well under 1000 pairs; I suspect 500 is more likely." Since Unitt's review, a substantial amount of information has been collected rangewide on the distribution and abundance of the southwestern willow flycatcher. The 1992 petition to list the flycatcher under the Endangered Species Act and the subsequent proposal by the U.S. Fish and Wildlife Service in 1993 to list the subspecies as endangered with critical habitat encouraged survey efforts rangewide. This chapter synthesizes these new distribution and population data to provide a current baseline from which to evaluate the conservation needs of this subspecies.

Unitt (1987) reviewed historical museum specimens and contemporary survey data for *E.t. extimus* to estimate subspecies' population status and geographic boundaries. Unitt identified critical gaps in museum specimen records which confounded the delineation of distinct sub-specific boundaries in the Central Valley of California, southern Nevada, south-central Utah, southwestern Colorado, and northern New Mexico. These gaps have resulted in confusion over management needs, particularly among state and federal agencies responsible for the conservation of this subspecies. To reduce confusion, some agencies have drawn up provisional boundaries which expand the known distribution of this subspecies, particularly in central Utah and Colorado. Data are presented in this chapter that include those areas for which the taxonomic status of the willow flycatcher remains unclear.

Methods

To document the current rangewide distribution and population status of the southwestern willow flycatcher, data were compiled from a variety of sources, including federal and state agency reports, reports prepared by private contractors available to the public, and from individuals working at specific study sites. Data were summarized for the years 1993 through 1996, the latter being the most recent year for which complete rangewide data are available. Data sources include the following: Arizona (Sogge and Tibbitts 1992, Sogge et al. 1993, Muiznieks et al. 1994, Sogge and Tibbitts 1994, Sferra et al. 1995, Sogge 1995a, Sogge et al. 1995, Peterson and Sogge 1996, Spencer et al. 1996, Sferra et al. 1997, Sogge et al. 1997b, McKernan 1997 in litt.); California (Camp Pendleton 1994, Whitfield 1994, Griffith and Griffith 1995, Holmgren and Collins 1995, San Diego Natural History Museum 1995, Whitfield and Strong 1995, Pike et al. 1995, Griffith and Griffith 1996 in litt., Haas 1996 in litt., Kus 1996, Whitfield and Enos 1996); Colorado (T. Ireland 1994 in litt., Stransky 1995); New Mexico (Maynard 1995, Cooper 1996, 1997, Skaggs 1996); Nevada (C. Tomlinson 1995 in litt.); Utah (McDonald et al. 1995, Sogge 1995b).

Since 1993 more than 800 historical and new locations have been surveyed rangewide to document the status of the southwestern willow flycatcher (some sites in southern California have been surveyed since the late 1980s). Statewide survey and monitoring efforts were conducted in Arizona and New Mexico, and smaller-scale efforts in Colorado, Nevada, and Utah. A small number of sites in California have been surveyed and/or intensively monitored by several dedicated individuals, but the state as a whole lacks a coordinated survey and monitoring program. Formal survey efforts have not been attempted in southwestern Texas, largely due to difficulties in gaining access to private lands. Survey efforts in some states were conducted under the auspices of state Partners In Flight programs (e.g., Arizona), which served as the coordinating body for survey training sessions and data reporting. Tibbitts et al. (1994) developed the first survey protocol, which served as the basis for training efforts held annually throughout the range of *E.t. extimus*. Sogge et al. (1997a) published an updated version of the survey protocol.

Both Tibbitts et al. (1994) and Sogge et al. (1997a) rely on the use of tape-playback to elicit responses from territorial birds. The revised protocol prepared by Sogge et al. (1997a) requires a minimum of three visits stratified among three survey periods. In addition to summarizing flycatcher biology and habitat use, the protocol provides guidance on interpreting field responses and a set of standardized reporting forms for data collection.

The basic unit of analysis for this dataset is the "site." In most cases, site refers to a manageable survey unit of one to several hectares that can be reported on standardized data forms provided in Tibbitts et al. (1994) and Sogge et al. (1997a). However, in some cases a site encompasses several relatively discrete breeding locations spread throughout a drainage (e.g., Whitfield's data for the South Fork Kern River in California where several breeding locations occur over the entire 5.6 km study area). Data were compiled for sites that had documented breeding, suspected or probable breeding, or confirmed territorial birds (Sogge et al. 1997a). Migrants and detections with inadequate data to confirm resident status were omitted from analyses.

All analyses represent a composite of data collected between 1993 and 1996. This was necessary because many sites were not surveyed annually and excluding them may bias population estimates. For sites with multiple years' data, the most recent years' data (with positive results) were used. This "composite" approach, however, also has potential biases. Data from 1993 are treated equally with data from 1996, leaving open the possibility of overestimating or underestimating population sizes for sites that were not surveyed in each year. For example, at several sites flycatchers were absent during one or more years. However, for this chapter I considered these sites extant and used the most recent years' data (with positive survey results) for estimating population status. While this approach may overestimate population abundance, survey coverage was not complete for any given drainage and local movement of breeding groups could have gone undetected.

Data on population status are summarized as the number of territories, pairs, and the total number of individual flycatchers. Estimates of the number of territories and pairs were taken directly from the data source, whereas the total number of individuals represents the sum of territories plus half the number of documented pairs. A territory is defined as an individual singing in the same location during each of the survey periods outlined in the protocol. It is the basic unit the protocol is designed to estimate. Data on the number of pairs probably represent minimum values, because documenting breeding status (i.e., unmated/mated and confirmation of breeding) requires considerable effort above what is required to estimate the number of territories (Sogge et al. 1997a). Site data were not always reported consistently across years. In some cases nearby sites were combined or spilt for survey or reporting purposes. Thus, there may be some minor discrepancies with the original reports in the total number of sites per state. In addition, territory estimates were sometimes reported as a range of values (e.g., six to seven territories). For the purposes of this summary, the larger value was used to compile population estimates.

Several additional attributes were determined for each site, including the site's land management status/ownership pattern (e.g., federal, state, private, etc.), the county and drainage in which the site was located, the elevation at which the site occurred, and the general habitat type (e.g., mixed native broadleaf, monotypic saltcedar).

Results and Discussion

Rangewide Distribution and Abundance

Southwestern willow flycatchers are currently found in six states from near sea level in southern California to 2700 m (9000 ft) in southwestern Colorado (Table 2-1). Their current status in southwestern Texas, northern Sonora, Mexico, and Baja California Norte is not known due to a lack of survey effort in those areas. Based on survey data collected between 1993 and 1996, the total known population of southwestern willow flycatchers is estimated to be 549 territories (Table 2-1). At least 386 (70%) of these territories were documented as confirmed or probable breeding pairs.

Table 2-1. Population status of the southwestern willow flycatcher by state (1993-1996).

State	Estimated No. of Territories	Estimated No. of Pairs	Estimated No. of SWWF	Estimated No. of Sites	No. of Drainages
New Mexico	223 (40)[a]	175 (45)	398 (42)	25 (23)	9
Arizona	163 (30)	113 (29)	276 (30)	44 (40)	11
California	121 (22)	80 (21)	201 (21)	22 (20)	13
Colorado	28 (5)	9 (2)	37 (4)	10 (9)	8
Utah	12 (2)	8 (2)	20 (2)	7 (6)	6
Nevada	2 (1)	1 (1)	3 (1)	1 (1)	1
Texas	—	—	—	—	—
Sonora, MX	—	—	—	—	—
Baja, MX	—	—	—	—	—
Total	549	386	935	109	43[b]

[a] Parenthetical data represent within-column percentages.
[b] The disparity between the number of drainages/state and the total reflects that flycatcher sites were found on portions of the Colorado, Gila, Virgin, and San Francisco rivers in multiple states (see Table 2-4).

Southwestern willow flycatchers have been documented at a total of 109 sites on 43 drainages throughout the southwestern U.S. (Table 2-1). The bulk of the population occurs in Arizona, California, and New Mexico. Combined, the three states hold 92% of all territories (Table 2-1). However, the majority of sites are comprised of small numbers of flycatchers; more than 70% (n=77) of all sites had only three or fewer flycatcher territories (Table 2-2). As a proportion of the rangewide population, those 77 sites contained 22% only of all flycatcher territories. Many of the smallest sites apparently lacked breeding pairs. In fact, 17% (19) of the 109 documented sites were comprised of single, unmated individuals.

Nearly half (47%) of all flycatcher territories were distributed among 99 sites containing ten or fewer territories; 14% of all territories were distributed among six sites containing 11 to 20 territories; 15% of all territories were distributed among three sites containing 21 to 30 territories; and 24% of all territories were found at one site which had an estimated 134 flycatcher territories (Table 2-2). Table 2-3 provides this breakdown by state and illustrates the widely-scattered nature of the larger sites (>10 territories), in particular.

Combining site data by drainage provides a population summary at a larger scale and eliminates biases associated with comparing sites of different sizes, habitat composition, etc.(Table 2-4). These data indicate that of the 43 drainages where southwestern willow flycatchers have been documented, 72% (31) had ten or fewer flycatcher territories; nine percent (4) of the drainages had between 11 and 20 territories; 12% (5) had between 21 and 30 territories; and seven percent (3) had more than 30 territories. Additional survey effort, particularly in California, may add to the overall number of sites and territories per drainage.

Table 2-2. Frequency distribution for the number of southwestern willow flycatcher territories per site (1993-1996).

No. of Territories/ Site	Frequency (number of sites)	Percent of Sites	Cumulative Percent
1	42	38.5	38.5
2	23	21.1	59.6
3	12	11.0	70.6
4	7	6.4	77.1
5	4	3.7	80.7
6	4	3.7	84.4
7	2	1.8	86.2
8	2	1.8	88.1
10	3	2.8	90.8
11	2	1.8	92.7
12	1	0.9	93.6
13	1	0.9	94.5
15	1	0.9	95.4
17	1	0.9	96.3
22	1	0.9	97.2
29	1	0.9	98.2
30	1	0.9	99.1
134	1	0.9	100.0
Total	109	100.0	100.0

However, given that approximately 13% of sites surveyed rangewide have yielded positive results, it is highly unlikely that the addition of new sites and territories will substantially change the distribution and abundance patterns described above.

During the four year study period, 53% of the southwestern willow flycatcher population occurred at just ten sites rangewide, and the remaining 47% occurred in small groups of ten or fewer territories spread out among 99 sites. The estimates of 549 territories and 109 sites rangewide should be viewed cautiously,

Table 2-3. Distribution of southwestern willow flycatcher sites by size and state (1993-1996).

	No. of Sites w/ ≤10 Terr.	No. of Sites w/ 11-20 Terr.	No. of Sites w/ 21-30 Terr.	No. of Sites w/ ≥ 31 Terr.
Arizona	41	2	1	
New Mexico	21	3		1
California	19	1	2	
Colorado	10			
Utah	7			
Nevada	1			
Total	99	6	3	1

Table 2-4. Southwestern willow flycatcher population estimates by state and drainage (1993-1996).

Drainage	Total No. of Territories	Total No. of Pairs	Total No. of SWWF
Arizona			
Colorado	32	21	53
San Pedro	30	28	58
Salt	22	18	40
Gila	19	8	27
Tonto Ck.	18	11	29
Little Colorado	13	10	23
Verde	11	8	19
Bill Williams	6	2	8
Big Sandy	5	2	7
Santa Maria	4	2	6
San Francisco	3	3	3
Subtotal	**163**	**113**	**273**
California			
S. Fork Kern	30	30	60
San Luis Rey	29	24	53
Santa Ynez	23	4	27
Santa Margarita	12	4	16
Colorado	7	6	13
Santa Ana	7	4	11
Mohave	4	4	8
Las Flores Ck.	3	3	6
Pilgrim Ck.	2	1	3
De Luz Ck.	1	—	1
Fallbrook Ck.	1	—	1
San Mateo Ck.	1	—	1
San Onofre Ck.	1	—	1
Subtotal	**121**	**80**	**201**
New Mexico			
Gila	156	150	306
Rio Grande	49	21	70
Rio Chama	6	1	7
Coyote Ck.	3	0	3
Nutria Ck.	3	0	3
Rio Grande de Ranchos	2	2	4
Zuni	2	—	2
Blue Water Ck.	1	1	2
San Francisco	1	0	1
Subtotal	**223**	**175**	**398**
Colorado			
Gunnison	10	2	12
Beaver Ck.	5	—	5

(con.)

Table 2-4. (Con.)

Drainage	Total No. of Territories	Total No. of Pairs	Total No. of SWWF
Colorado			
Anthracite Ck.	4	2	6
Plateau Ck.	3	3	3
Colorado	2	1	3
East	2	1	3
San Miguel	1	—	1
West Ck.	1	—	1
Subtotal	28	9	37
Nevada			
Virgin	2	1	3
Utah			
Panguitch Ck.	3	3	6
San Juan	3	2	5
Virgin	3	1	4
Panguitch Lk	1	1	2
Swamp Ck.	1	1	2
Yellow Ck.	1	0	1
Subtotal	12	8	20
Rangewide Total	**549**	**386**	**932**

however. During the study period a number of sites were either extirpated due to high, sustained levels of nest predation, cowbird parasitism and, possibly, drought, or suffered substantial habitat losses as a result of fire, habitat inundation, agricultural clearing, and clearing for roads and bridges (Table 2-5). In addition, some sites with relatively large populations suffered habitat losses or were threatened due to human activities (see Table 2-5; USFWS 1996, 1997a, 1997b). The scope and magnitude of adverse impacts and threats combined with the predominance of small breeding groups vulnerable to stochastic processes, alone, suggests that the population is probably fluctuating spatially and temporally. Without a more comprehensive, annual monitoring effort, however, our ability to track and respond in a management context to these changes is severely compromised.

Conservation Challenge

The overall distribution of flycatchers—many sites with small populations and a small number sites with larger populations—presents a difficult conservation challenge at best. The smallest sites (≤10 territories) comprise nearly half of the total population, but are the most vulnerable to demographic and environmental stochasticity. In some cases, we know that reproduction has not been sufficient for these sites to persist on their own, or to yield emigrants for colonization of other sites (Muiznieks et al. 1994, Maynard 1995, Sogge et al. 1997b). However, trends at these sites should not be used as justification for shifting conservation efforts away from sites with small numbers of flycatcher territories. For one, if this subspecies' population is comprised of a number of metapopulations, then some of these smaller sites probably are regional sources of colonizers, at least in some years. Second, we do not understand the processes or circumstances under which colonization of new sites occurs. Shifting management attention away from smaller sites because they are presumed to have less conservation potential may result in losses that further isolate remaining breeding groups and potentially disrupts regional population dynamics. And third, many opportunities have already been lost at some of the larger sites, which has considerably narrowed management options (see Table 2-5, USFWS 1996, 1997a, 1997b). In evaluating the current pattern of small breeding group size and the potential effects of recent or anticipated habitat and population losses, I speculated (in USFWS 1997b) that,

> "…variation in individual fitness of flycatchers probably translates to variation in responses to habitat loss/degradation and subsequent survivorship and reproductive success. Thus, not all flycatchers are likely to perish as a result of displacement [due to habitat loss] and not all flycatchers are likely to fail to attract mates and breed [after dispersal]. The more likely result would be a regional phenomenon of "loss-disperse-decrease" whereby: (1) large habitat patches occupied by the larger breeding groups are lost either by stochastic (e.g., fire) or deterministic processes (e.g., permitted Federal action); (2) surviving birds are forced to disperse elsewhere, most likely into smaller habitat patches; and (3) this dispersal causes decreases in the probabilities of

survival, of obtaining mates, and of reproducing successfully. This hypothesis is based on the assumption that there is a negative relationship between habitat isolation and flycatcher survival and reproduction. This phenomenon could actually lead to a short-term increase in the number of sites occupied regionally while masking an overall, long-term decrease in population size and fecundity."

The above quote addressed the specific case of the Lake Mead inflow on the Colorado River where inundation of 445 ha of occupied willow habitat was anticipated to result in habitat loss, nest loss, and forced dispersal of flycatchers from at least eight territories documented in 1996 and, potentially, up to 25 territories. In fact, three of seven nest attempts at Lake Mead were lost due to treefall in 1996 (McKernan 1997). In 1997, when inundation was more extensive due to rising lake levels, fewer flycatchers returned. Three breeding attempts were documented; one successfully fledged young, one nest was

Table 2-5. Impacts documented or anticipated at Southwestern willow flycatcher sites.

Affected Sites by State	Drainage	Type of Impact	No. of Territories at Site
Arizona			
Roosevelt Lake[a]	Salt & Tonto Ck.	Anticipated loss of habitat for up to 45 terr. from inundation[b]	40
Lake Mead Inflow	Colorado	1100 acres of habitat lost and nests losses due to treefall	≥8
PZ Ranch[c]	San Pedro	Habitat loss due to fire	8
Sanchez Rd.[d]	Gila	Habitat loss due to bridge construction; high levels of cowbird parasitism	4
Tuzigoot	Verde	Extirpation; high levels of predation & parasitism	2
Grand Canyon	Colorado	<3 sites extirpated; high levels of predation & parasitism	1-2
Middle Gila	Gila	~ 6 miles of occupied habitat lost due to fire	?
California			
Lake Isabella[a]	S. Fork Kern	>700 acres of habitat modified and nests lost due to inundation	≤14
Santa Ynez	Santa Ynez	Occupied habitat lost due to agricultural clearing	?
Colorado			
Escalante SWR	Gunnison	Occupied habitat loss due to fire	10
New Mexico			
Gila Valley[a]	Gila	Largest known site threatened by flood control efforts	>134
Fort West Ditch[a]	Gila	Habitat and nest loss due to intentional clearing	15
San Juan Pueblo Bridge[e]	Rio Grande	Habitat loss due to bridge construction & fire	13
San Marcial[a]	Rio Grande	Extirpated 1996, possibly due to drought	11
Bosque del Apache NWR[f]	Rio Grande	Habitat loss due to fire	?

[a] Site is one of ten rangewide with more than ten territories.
[b] Up to 45 territories were anticipated to be lost by USFWS, which was slightly higher than the number documented at both sites.
[c] Up to 18 territories were documented prior to fire.
[d] Only 1 territory was present in 1997 after habitat loss.
[e] However, additional survey effort revealed more territories after fire.
[f] Fire occurred in unsurveyed habitat adjacent to occupied flycatcher area.

lost to treefall, and one nest disappeared, the cause unknown.

Dispersal due to habitat loss is not unique to Lake Mead, but has also been documented at Lake Isabella on the South Fork Kern River in California (Whitfield and Strong 1995), at Elephant Butte Reservoir on the Rio Grande in New Mexico (Hubbard 1987), and is anticipated to occur at the Roosevelt Lake breeding sites in Arizona (USFWS 1996). These areas represent some of the largest known riparian habitat patches in the Southwest. In some cases the habitat modifications (i.e., inundation) occurred during the breeding season. Thus, flycatchers were, in all likelihood, forced to disperse to smaller patches potentially incurring increased risk of predation, increased competition for suitable habitat elsewhere, and delayed or foregone breeding opportunities.

One conclusion drawn from this line of thinking is that conservation efforts should focus aggressively on (1) protecting extant sites in order to provide breeding groups the greatest chance of persistence; and (2) on vastly increasing habitat options at least drainage-wide to provide local options in the event breeding groups are forced to disperse. In conjunction, research efforts should focus on identifying dispersal patterns and capabilities to better understand regional population dynamics and to determine habitat-specific demographic patterns so that local and regional conservation efforts are more effective.

Land Management Status

The data in Table 2-4 point to 43 potential conservation opportunities (river drainages) for the southwestern willow flycatcher. Portions of some of the drainages listed in Table 2-4 are already receiving some degree of management to benefit the southwestern willow flycatcher. For example, the Kern River Preserve and Kern River Research Center on the South Fork Kern River have been cowbird trapping since 1993, actively managing and restoring habitat throughout the South Fork, and have maintained a comprehensive monitoring and research program since 1989. The U.S. Forest Service removed livestock grazing on the San Luis Rey River in California to benefit both the endangered least Bell's Vireo (*Vireo bellii pusillus*) and southwestern willow flycatcher. Similarly, on the upper San Pedro River in Arizona the Bureau of Land Management removed livestock grazing from the entire Riparian National Conservation Area to benefit the high degree of biological diversity associated with that river corridor, including the flycatcher. On the lower San Pedro River, the Bureau of Reclamation, U.S. Fish and Wildlife Service, U.S.G.S. Biological Resources Division, Arizona Game and Fish Department, and The Nature Conservancy have initiated a comprehensive program of habitat protection, research, and monitoring to protect Arizona's largest breeding group of southwestern willow flycatchers. These programs are being carried out on both public and private lands demonstrating that cooperation among private and public entities can yield significant conservation gains. More of these programs will be necessary as the current distribution of flycatcher sites is spread out among mostly federal and private lands.

Data on land management status were available for 104 of the 109 sites studied. Table 2-6 reveals that 56% of all southwestern willow flycatcher sites occurred on lands managed by Federal agencies, while 32% were on private lands. While the threats to some of these locations are already known and are considerable, a coordinated, rangewide evaluation of the level of protection currently in place as well as the status of riparian habitats surrounding currently-occupied sites has not been completed.

The low overall population status of this subspecies and the potential isolation of breeding groups due to habitat fragmentation suggests several paths for management and research. First, extant breeding sites should be protected to maintain reproductive

Table 2-6. Land management status at southwestern willow flycatcher sites.

	Land Management Status					
State	Federal	State	Private	Tribal	Municipal/ County	Total
Arizona	27 (62)[a]	2 (5)	14 (31)	0	1 (2)	44
California	15 (71)	1 (5)	5 (24)	0	0	21
Colorado	3 (33)	2 (22)	4 (45)	0	0	9
New Mexico	9 (41)	2 (9)	7 (32)	4 (18)	0	22
Nevada	0	0	1 (100)	0	0	1
Utah	4 (57)	0	3 (43)	0	0	7
Total[b]	58 (56)	7 (7)	34 (32)	4 (4)	1 (1)	104

[a] Parenthetical values provide within-row percentages for each state.
[b] Parenthetical values represent proportion of the five land management categories.

potential and reduce population isolation. Second, habitat protection and management efforts should be focused near existing flycatcher breeding sites and should be incorporated into comprehensive monitoring programs. Third, an evaluation that identifies, in a spatially-explicit manner, gaps in protection as well as opportunities for protection and management is critically needed. And fourth, data on dispersal events (i.e., causes and spatial patterns) and subsequent reproductive success are needed to better understand population dynamics, including regional habitat needs over time and space. These efforts will require considerable resources and a commitment among the various private and public entities interested in promoting conservation and management for this species. The data summarized in this chapter provide a rangewide context from which such an effort could originate.

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Chapter 3: Threats

The continued survival of the southwestern willow flycatcher (*Empidonax traillii extimus*) is threatened indirectly by the loss, modification, and fragmentation of riparian habitat, and directly by factors that impact the survival and reproductive success of flycatchers. Because the impact of habitat loss on small populations can be particularly severe, we first discuss some of the population-level effects that may be influencing flycatcher population dynamics. We then review some contemporary cases of habitat loss and discuss other factors potentially impacting the flycatcher. The effects of brown-headed cowbird (*Molothrus ater*) parasitism on the southwestern willow flycatcher are discussed in detail in Chapter 8. For additional information on site-specific threats to the southwestern willow flycatcher readers should consult Greenwald (1998).

Effects of Habitat Loss and Fragmentation

Habitat loss and habitat fragmentation are interrelated processes that affect patterns of species' abundance and distribution at local and regional scales (Pulliam and Dunning 1994). Habitat loss is the reduction of the total amount of a particular habitat type in a landscape. Fragmentation is the apportionment of the remaining habitat into smaller, more isolated patches (Wilcove et al. 1986, Saunders et al. 1991). Habitat loss is often manifested as the conversion of one habitat type to another (e.g., conversion of a forested floodplain to agricultural fields). By reducing the amount of space that can be occupied, habitat loss reduces the total number of individuals that can occur at a particular location or throughout a region.

Riparian habitats in the Southwest are naturally rare and patchy, subject to periodic disturbance and occurring as widely-separated ribbons of woodland and forest within a primarily arid landscape. In Arizona, for example, riparian habitat comprises less than 0.5% of the landscape (Strong and Bock 1990). The actual extent of habitat suitable for the southwestern willow flycatcher is much less. Wide-ranging or highly mobile species that rely on naturally patchy and ever-changing habitats, such as the flycatcher, persist at regional scales as metapopulations, or local breeding groups that are linked together and maintained over time by immigration/emigration and dispersal (Hanski and Gilpin 1991, Pulliam and Dunning 1994). Persistence of local breeding groups is a function of the group's size (numbers of individuals), productivity, survivorship, and the ability of individuals to disperse from one breeding location to another (Harrison 1991). By isolating habitat patches, fragmentation reduces the chance of an individual successfully finding suitable habitat. Searching for increasingly isolated patches leaves individuals vulnerable to mortality from competition, starvation, or predation and can result in delayed or lost of breeding opportunities. Weins (1996) noted that habitat loss is probably the most important factor governing population dynamics when the landscape still contains a high proportion of suitable habitat, but "at a certain threshold of habitat loss, patch isolation may quickly come to dominate population dynamics."

Effects of Small Population Size

Demographic Effects

The overall southwestern willow flycatcher population is small with an estimated 549 territories rangewide (see Chapter 3). Moreover, these territories are distributed among a number of very small breeding groups and only a handful of relatively large breeding groups. The small size of flycatcher populations leaves them vulnerable to local extirpation through environmental stochasticity (e.g., floods, fire, severe weather events, disease), and demographic stochasticity (e.g., shifts in birth/death rates and sex ratios). Even moderate variation in stochastic factors that might be sustained by larger populations can reduce a small population below a threshold level from which it cannot recover. This is especially true with short-lived species such as the southwestern willow flycatcher (see Chapter 7).

The persistence of small populations frequently depends on immigration from nearby populations, at least in some years (Stacey and Taper 1992). The small, isolated nature of current southwestern willow flycatcher populations exacerbates the risk of local extirpation by reducing the likelihood of successful immigration among populations. McCarthey et al. (1998) presented data for 36 sites in Arizona where two or more years worth of survey work had been completed between 1993 and 1997. They documented extirpation at ten sites for a loss of 13 territories, and population declines at an additional 15 sites for a loss of 56 territories. Of the 25 sites that were extirpated or that experienced declines, all but four were small sites comprised of ten or fewer territories. Five of the 36 sites had no change in the number of territories and six sites saw increases in the number of territories for a total gain of 38 territories. Overall, at the 36 sites monitored there was a net loss of 18 territories.

Genetic Effects

Small populations tend to be characterized by low levels of within-population genetic variation, and possibly inbreeding. These conditions may lead to reduced survival, reduced fecundity, lowered resistance to parasites and disease, or physiological abnormalities (Allendorf and Leary 1986, Hartl 1988). Low effective population size also threatens small populations. Effective population size is an index of the actual number of individuals breeding and the number of offspring they contribute to the next generation. The effective population size for a species may be much smaller than the censused population size because of uneven sex ratios, uneven breeding success among females, polygyny (e.g., Sedgwick and Knopf 1989), and low population numbers which exacerbate the above factors.

Synthesizing recent empirical and theoretical studies on population genetics, Lande (1995) suggested that the number 500, long held by some in the conservation biology community to represent the minimum effective population size necessary to maintain a viable population of any species, is far too small. Lande contended that effective population sizes should be much larger (in the range of 5000) in order for a species to maintain normal levels of potentially adaptive genetic variance to counteract the effects of random genetic drift. Lande concluded that, because recovery goals for listed species are often not much higher than the actual population size at the time of listing, maintenance of adequate evolutionary potential and long-term genetic viability was doubtful unless populations were recovered to much larger sizes. Based on Lande's hypothesis, and considering the current status of the flycatcher rangewide, the effective population size for the southwestern willow flycatcher may be critically low.

Factors Contributing to Habitat Loss

Water Management

Dams and Reservoirs—Most of the major and many of the smaller Southwestern rivers support one or more dams that have severely altered the distribution, extent, and species composition of riparian habitats (e.g., Colorado River, Gila River, Kern River, Mojave River, Rio Grande, Salt river, San Diego river, Santa Ana River, Sweetwater River, Tijuana River, Verde River). For example, Mearns (1907; in Ohmart et al. 1988) estimated that the lower Colorado River contained more than 161,900 ha of native riparian habitat at the onset of the 20th Century (prior to the construction of any dams). Nearly 100 years later and with the addition of eight dams and diversions along the 660 km of river between Pearce Ferry and the border with Mexico, the U.S. Bureau of Reclamation (1996) estimated the current extent of native riparian habitat at approximately 1,800 ha, or one percent of its former estimated total.

Riparian habitats are modified, reduced, or lost downstream of dams as a result of changes in flood frequency and duration. Hydrological cycles below dams are modified such that minimum flow events occur with greater frequency and longer duration reducing instream flows and lowering watertables. In some cases, sustained high flows have caused loss of riparian stands from prolonged inundation. For example, Hunter et al. (1987a) documented the loss of a 120 ha stand of cottonwood-willow at the confluence of the Bill Williams River and the Colorado River in 1981 after 24 months of continual high flows released from Alamo Lake. Dams also inhibit annual cycles of flood-induced sediment deposition, floodplain hydration and flushing, and seed dispersal necessary for the establishment and maintenance of riparian habitats

Despite these modifications, some southwestern drainages still have the capacity to develop substantial stands of native cottonwood-willow. Several thousand acres of cottonwood and willow developed along the lower Colorado River below Yuma, AZ after the floods of 1993 (U.S. Bureau of Reclamation 1996). However, due to the diversion of Colorado River water upstream at Moreles Dam, those stands declined from desiccation. Restoration of flows to the lower portion of the Colorado River could substantially increase the extent of riparian habitat on that system simply by maintaining vegetation that becomes established after natural flood events.

The filling of reservoirs results in the loss of riparian habitats upstream of dams. For example, the flooding of Glen Canyon resulted in the loss of southwestern willow flycatchers, which Behle and Higgins (1959) considered a common species. Over time, however, some reservoir inflows have developed extensive deltas colonized by some of the largest stands of riparian trees and shrubs currently found in the Southwest, such as at the head of Elephant Butte Reservoir in New Mexico; at the Salt River and Tonto Creek inflows to Roosevelt Lake in Arizona; the Gila River inflow to San Carlos Reservoir in Arizona; the Colorado River inflow to Lake Mead in Arizona; and the inflow of the South Fork Kern River at Lake Isabella in California. In addition, these areas (except San Carlos Reservoir) support or have supported some of the largest southwestern willow flycatcher populations rangewide (Hubbard 1987, Whitfield and Strong 1995, Sferra et al. 1997, McKernan 1997).

However, current water management policies do not support management strategies to protect and maintain these significant riparian stands. As a result, occupied southwestern willow flycatcher habitat has been lost and flycatchers have suffered nest losses or been displaced. For example, inundation at the inflow to Elephant Butte Reservoir in New Mexico during the 1980s resulted in the loss of willow habitat and displacement of at least 10 flycatcher pairs (Hubbard 1987, T. Schrader U.S. Bureau of Reclamation, pers. comm.). Approximately 283 ha of willow habitat were modified (i.e., loss of understory vegetation) due to inundation at the South Fork Wildlife Area at Lake Isabella in 1995. That event resulted in loss of flycatcher nests and subsequent decline in the number breeding flycatchers in the South Fork Wildlife Area (Whitfield and Strong 1995, USFWS 1997a). Approximately 445 ha of occupied Goodding willow (Salix gooddingii) habitat at the inflow to Lake Mead were anticipated to be lost during the 1997 and 1998 growing seasons due to prolonged inundation (USBR 1996, USFWS 1997b). The number of flycatcher territories and nesting attempts at the inflow decreased in 1997 with increasing levels of inundation (see Chapter 3) . And finally, the habitat at Roosevelt Lake, which supports one of Arizona's largest flycatcher populations, is anticipated to be lost when inflows are sufficient to fill the newly-created reservoir conservation space (USFWS 1996). The deltas associated with these and other reservoirs represent some of the most significant management opportunities available to restore a portion of the extensive riparian habitats historically found on these drainages. They also represent significant opportunities to conserve the southwestern willow flycatcher and the suite of riparian-dependent species found in Southwestern riparian systems.

Diversions and Groundwater Pumping—Surface water diversions and groundwater pumping for agriculture, industrial use (e.g., mining), and municipal use are considered major factors in the deterioration of riparian habitats (USFWS 1993, Briggs 1996). Surface diversions and overdraft of groundwater lower watertables and reduce surface flows. The Arizona Game and Fish Department estimated that in Arizona, alone, more than 1448 km miles of formerly perennial stream are no longer perennial. One of the most extensive stands of native riparian habitat in Arizona along the upper San Pedro River is threatened by increased groundwater withdrawal by the nearby city of Sierra Vista (Davis 1995 [in Briggs 1996]). This threat is particularly ironic in light of the fact that ten years of livestock removal from the San Pedro Riparian National Conservation Area has resulted in a dramatic comeback of cottonwood-willow habitat as well as the return of breeding southwestern willow flycatchers (Krueper 1993, McCarthey et al. 1998). Similarly, human population growth in the Verde watershed has raised concerns that central Arizona's most important aquatic and riparian corridor, the Verde River, will not support riverine, riparian, and aquatic resources over the long term (Verde Watershed Association 1998).

The combination of severe drought and upstream diversion for agricultural use was thought to be the cause of southwestern willow flycatcher territory loss or abandonment of at least eight territories along the middle Rio Grande in the vicinity of San Marcial, New Mexico (D. Leal, USFWS, pers. comm., Cooper 1997).

Land-Use Practices

Channelization and Bank Stabilization—Flood control projects generally shorten, straighten, and narrow river channels with the aim of producing unobstructed pathways to convey floodwaters. These projects can severely reduce the extent of alluvial-influenced floodplain by cutting off main channels from side channels and adjacent floodplains and by reducing meander patterns, which slow stream velocity and dampen the effects of flooding (Poff et al. 1997). Channelization alters stream banks, typically elevating them well above groundwater levels and thus preventing the roots of most native riparian shrubs and trees from accessing groundwater. Overbank flooding necessary to deposit sediments, disperse seeds, rehydrate floodplain soils, and flush accumulations of salts, is reduced or precluded. Channel cutting further reduces water tables adjacent to the river, precluding seedling establishment because of the increased depth to groundwater (Szaro 1989). Channelization can increase the intensity of extreme floods, because reductions in upstream storage capacity produce accelerated water flow downstream. Channelization also reduces the width of wooded riparian habitats, increasing the proportion of edge. Avian species richness has been shown to increase with the width of wooded riparian habitats (Stauffer and Best 1980).

Bank stabilization is typically used to protect property and structures from the impacts of flooding. Various manmade structures are used to protect banks and reduce the likelihood and impact of floods. Bank armor, such as rip-rap and levees, can protect stretches of bank and adjacent riparian vegetation, but can also lead to eddying and increased scouring of unprotected banks (DeBano and Heede 1987). In addition, bank armor reduces over-bank flooding, and consequently the occurrence of germination and regeneration of riparian vegetation. Under some conditions, certain types of flood-control structures can protect or enhance riparian habitat. For example, streamflow separations are used to create low energy flows at the bank. In so doing, separators can increase sediment deposition and create extensive stillwater areas adjacent to banks (DeBano and Heede 1987).

The riparian habitat that contains the largest known population of southwestern willow flycatchers along the Gila River in southwestern New Mexico is threatened by a combination of bank stabilization structures and agricultural practices within the floodplain (Phelps-Dodge Corporation 1995). Much of the floodplain is devoted to agricultural and ranching uses. Levees are used extensively along the border of agricultural fields to protect from flood damage. Riprapping, earthen dikes, and other structures are used along channel banks to further minimize flood damage. In some cases, the structures protect occupied flycatcher habitat. However, the combination of flood control structures in the channel, appropriation of the floodplain for agricultural or other uses, and the use of levees to further protect the land-uses occurring within the floodplain, has resulted in a system that isolates most of the floodplain, including existing flycatcher habitat, from natural flood processes needed to sustain and regenerate extensive new habitats.

Given that 25% of all known southwestern willow flycatchers breed at this site, the ramifications of potential habitat loss are substantial. Beyond these ramifications, however, this scenario points to a problem observed throughout the range of the southwestern willow flycatcher—development within floodplains. Be it homes, other types of structures, agricultural lands, or roads and bridges, development within floodplains increases the economic justification for flood control projects, which generally decreases opportunities for maintenance and restoration of floodplain processes necessary for the continual regeneration of riparian habitats (Poff et al. 1997).

Agricultural Development—The availability of irrigation water, relatively flat land and rich soils has spawned wide-scale agricultural development in river valleys throughout the Southwest. For example, more than 75% of the Mohave, Parker, Palo Verde, and Yuma valleys on the lower Colorado River has been converted to agriculture (Ohmart et al. 1986). These areas formerly contained vast riparian forests captured in early photographs of the area and probably comprised the most important riparian corridor in the Southwest. Collections of southwestern willow flycatcher nests made in the vicinity of Yuma in 1902 indicate that the flycatcher was at least locally very abundant along the lower Colorado River (Huels in litt. USFWS 1997b). The clearing of floodplain riparian habitat for agriculture continues today. For example, in January 1996, up to 2 km of occupied flycatcher habitat was lost to agricultural expansion on the Santa Ynez River in California (USFWS in litt.).

Livestock Grazing—Overgrazing by livestock has been a major factor in the modification and destruction of riparian habitats in the arid western U.S. (Fleischner 1996, Ohmart 1996, Dobkin et al. 1988). Riparian areas are often disproportionately preferred by cattle over surrounding uplands because of access to water, abundant and palatable forage, a cooler and shadier microclimate, and moderate slopes allowing easy access (Ames 1977, Glinski 1977, Szaro 1989; Fleischner 1996, Ohmart 1996). On uplands livestock act as geomorphic agents. By reducing vegetation cover and compacting soil, heavy livestock grazing reduces infiltration and increases runoff, erosion, and sediment yield, which can destabilize stream channels and affect the extent and distribution of riparian habitats (Trimble and Mendel 1995).

Grazing affects riparian vegetation through removal and trampling (Kauffman and Krueger 1984, Marlow and Pogacnik 1985). Removal by browsing affects the structure, spacing, and density of vegetation (Rea 1983, Cannon and Knopf 1984, Kauffman and Krueger 1984, Sedgwick and Knopf 1991). In several studies, willow canopy coverage was eight to ten times greater in areas excluded from grazing than in grazed areas (e.g., Taylor 1986, Schulz and Leininger 1990).

Grazing can also alter the age structure and species composition of riparian areas. Cattle readily eat shoots of cottonwood and willow, and heavy grazing can completely eliminate regeneration of these species (Glinski 1977, Rickard and Cushing 1982, Boles and Dick-Peddie 1983, Kauffman et al. 1983, Ohmart 1996). In contrast, cattle tend to avoid less palatable species such as saltcedar and juniper. Prolonged grazing in a riparian area can act as a selective agent shifting the relative abundance of plant species over time (Szaro and Pase 1983, Kerpez and Smith 1987). Dobkin et al. (1998) found that livestock grazing in riparian meadows resulted in a loss of perennial flow and a conversion of obligate wetland plant species and riparian bird species to upland species. When livestock were removed, perennial flow returned, as did obligate wetland plant species and an avian community comprised of wetland rather than upland species.

Trampling by livestock contributes to soil compaction, streambank erosion, widening and deepening of channels, increased runoff, and physical destruction of vegetation (Kauffman and Krueger 1984, Marlow and Pogacnik 1985, Szaro 1989, Trimble and Mendel 1995). In turn, unstable stream banks lead to accelerated erosion and increased sediment loads, which can destabilize floodplains and threaten the persistence of riparian habitats.

The impacts of grazing on riparian vegetation vary with the intensity and season of grazing. Late autumn and winter grazing may have relatively little effect, at least compared with other disturbances such as flooding (Kauffman and Krueger 1984, Knopf et al. 1988, Sedgwick and Knopf 1991). However, late spring and summer grazing typically has severe impacts, and results in little or no recruitment of riparian vegetation. This produces even-aged, non-reproducing communities of mature cottonwoods and decadent willows, with little understory. Such decadent, park-like stands, which are common throughout grazed drainages in the Southwest, are not suitable for southwestern willow flycatchers (Kauffman and Krueger 1984, Knopf et al. 1988, see Chapter 9).

In several studies, Willow Flycatcher numbers increased following the reduction or elimination of cattle grazing in riparian areas (Taylor 1986, Taylor and Littlefield 1986, Knopf et al. 1988). Harris et al. (1987) reported a 61% increase in flycatcher numbers over five years after grazing was reduced. Recent removal of livestock from the Riparian National Conservation Area on the upper San Pedro River in Cochise County, Arizona has resulted in both a dramatic increase in the recruitment of riparian vegetation and in the abundance of avian species reliant on dense understories, including the southwestern willow flycatcher, which was recently confirmed as a breeding species on the upper San Pedro (Kreuper 1993, McCarthey et al. 1998).

Low-intensity grazing during the non-growing season may be compatible in certain floodplain systems (i.e., those in proper functioning condition [USBLM 1993] and containing the full complement of riparian plant species and successional habitat types). For example, the Kern River Preserve in Kern County, California permits occasional, short duration and highly supervised livestock grazing in a small portion of the Preserve where meadows interface with riparian forest (R. Tollefson, pers. comm.). Livestock use of the Preserve, however, is not part of any annual grazing scheme. Furthermore, use is based on current ecological conditions, permitted at the discretion of and with the supervision of the Preserve Manager, and only permitted during the non-growing season. In the Gila Valley in southwestern New Mexico, livestock grazing occurs in irrigated pastures adjacent to the riparian stringers occupied by the largest known concentration of southwestern willow flycatchers (Parker and Hull 1994). In that case livestock forage is provided in the adjacent irrigated pasture and livestock use the riparian habitat primarily for shade. Neither of these cases represent a typical grazing situation for the Southwest, however. In the context of riparian management for the southwestern willow flycatcher, the appropriateness of a particular livestock grazing regime (in the uplands or riparian areas) should be evaluated based on current ecological conditions, the ecological potential for an area to support flycatcher habitat in the absence livestock grazing, and on the potential for livestock to serve as a magnet for cowbirds.

Although not yet documented for the southwestern willow flycatcher, livestock have been documented destroying - through trampling - willow flycatcher nests placed low in vegetation (Valentine et al. 1988). This should be considered a threat at any site within the southwestern willow flycatcher's range where flycatcher nest placement averages 3 m or less and where livestock are present during the breeding season.

Wild ungulates can also adversely impact riparian habitats, particularly when population densities are high. Elk (*Cervus canadensis*) have been shown to preclude the recovery of willow habitats even after the cessation of livestock grazing (Case and Kauffman 1997). Where elk and livestock are sympatric, reversing impacts to riparian areas may require more intensive management of both species. Elk occur in areas currently inhabited by southwestern willow flycatchers, including the higher elevation flycatcher sites in Arizona, New Mexico, Colorado, and Utah. The extent to which elk are adversely affecting areas inhabited by southwestern willow flycatchers is thought to be substantial in certain areas, however, quantitative studies that characterize the nature of impacts (e.g., extent, season, numbers of elk) are lacking.

Phreatophyte Control—In some areas riparian vegetation is still removed from waterways (streams and irrigation ditches) by mowing, cutting, rootplowing or spraying of herbicides. The intent of these practices is to increase watershed yield, remove impediments to stream flow, and limit water loss through evapotranspiration (Horton and Campbell 1974). As a consequence, riparian habitat is eliminated entirely or is maintained as a mosaic of very early successional patches not suitable for breeding flycatchers. Willow flycatcher populations (*E. t. adastus*) at the Malheur National Wildlife Refuge increased following the elimination of willow cutting and spraying (Taylor and Littlefield 1986).

Recreation—In the Southwest, campgrounds and recreational activities are concentrated in riparian areas because of accessibility, the presence of water, fishing opportunities, shade, and aesthetic qualities. These recreational activities include off-road vehicle use, boating, fishing, hunting, camping, birdwatching, hiking, swimming, floating, picnicking, and river rafting. The magnitude of such activities can be considerable. For example, Johnson and Carothers (1982) reported that the Glen Canyon and Lake Mead National Recreation Areas in Arizona received eight to nine million visitors per year. Recreation can impact riparian vegetation through damage or destruction of plants, elimination of seedlings, promoting invasion by exotic species, increased incidence of fires, indirect effects from soil compaction, and bank erosion (Johnson and Carothers 1982).

Disturbance from human recreation can reduce both the density and diversity of avian communities (Aitchison 1977, Szaro 1980, Taylor 1986, Riffell et al. 1996). In riparian areas in Utah, the presence of willow flycatchers was negatively correlated with campgrounds (Blakesley and Reese 1988). Food scraps and garbage in areas of high recreational use attract larger birds (e.g., jays, ravens) and small mammals (skunks, squirrels) which prey on bird nests and recently-fledged young (Johnson and Carothers 1982, Blakesley and Reese 1988). However, Haas (pers. comm.) reported a pair of southwestern willow flycatchers successfully fledging young from a nest that was several meters from a picnic table used frequently on weekends.

Urban Development—Urban development can result in a multitude of impacts to riparian habitats, such as the placement of homes and buildings within floodplains; the development of reservoirs and flood control structures within natural channels; overdraft of groundwater supplies and dewatering of streams and rivers; degradation of plant communities from heavy recreational use; increases in native and exotic predators; and improper placement of bridges. Some of these threats are discussed elsewhere in this chapter. Bowler (1990) documented the loss of riparian habitats in southern California that resulted from urban growth. One area of particular importance to the southwestern willow flycatcher and riparian habitats is the impacts of roads and bridges.

Southwestern willow flycatchers have been directly affected by roads and bridges that bisect riparian habitat. For example, an Empidonax flycatcher (probably a willow flycatcher) was killed by an automobile on a rural road that bisects willow flycatcher habitat in the White Mountains of Arizona (Sferra et al. 1995). In the San Juan Pueblo of New Mexico, placement of a new bridge across the Rio Grande resulted in the direct loss of habitat that contained two flycatcher territories (USFWS 1996). In Arizona, construction of a new bridge across the Gila River resulted in the loss of approximately one-third of a 1.5 ha riparian patch that supported four flycatcher territories (USFWS 1996). The number of territories decreased to one following habitat loss at that Graham County site (McCarthey 1998).

Placement of roads and bridges may have long-term effects of reducing overall habitat suitability for the willow flycatcher. Foppen and Reijnen (1994) and Reijnen and Foppen (1994) documented reduced breeding success, lower breeding densities, and higher dispersal rates of willow warblers (*Phylloscopus trochilus*) breeding next to roads that bisect forested habitat. Sogge (1995a) noted that the population decline and changes in the distribution of willow flycatcher territories on the Verde River in Arizona were consistent with other studies documenting adverse effects of roads that bisect habitat. However, Sogge (1995a) noted that the small size of that population coupled with sustained, high levels of predation and cowbird parasitism, may also have been factors at that site.

While the small size of sites and small number of territories involved in the above instances may not seem to justify conservation attention at first glance, it is important to keep in mind that these small instances of riparian habitat loss are numerous, frequent, and widespread (USFWS 1996, 1997b). At the minimum, these losses increase habitat fragmentation and reduce the carrying capacity of an area. Taken across the range of this species, the cumulative effects of these and other adverse impacts addressed in this chapter may result in destabilization of regional population dynamics.

Other Factors Contributing to Habitat Loss

Fire—Fire is a critical threat to occupied and unoccupied flycatcher habitat. In June of 1995, a fire on the Gila River in Pinal, County, Arizona, burned approximately six miles of riparian habitat potentially occupied by southwestern willow flycatchers (USFWS *in litt.*, USFWS 1997b). In 1996, five flycatcher breeding sites were degraded or lost altogether to fire, including two sites on the Rio Grande in New Mexico, one of the largest flycatcher sites on the San Pedro River in Arizona (Paxton et al. 1996), and two additional areas on the Gila River in Arizona where approximately eight miles of riparian habitat burned. In 1997 a fire started by an adjacent landowner burned a 32-ha portion of the Escalante Wildlife Area near Delta, Colorado (Owen and Sogge 1997). That location comprised one of the largest known breeding sites for willow flycatchers in Colorado with approximately seven pairs occupying the site in 1996.

Although fires are known to have occurred in riparian habitats historically, riparian habitats are not fire-adapted nor are they fire-generated communities. Thus, fires in riparian habitat are typically catastrophic. Busch (1995) documented that the current frequency and intensity of fires in riparian habitats is greater than what occurred historically because: (1) a greater accumulation of fuels due to a reduced frequency of scouring floods; and (2) the expansion and dominance in many areas of saltcedar (*Tamarix chinensis*), which is highly flammable. The increased incidence of fire is causing profound alterations in riparian habitats throughout the Southwest. Both saltcedar and arrowweed (*Tessaria sericea*) recover more rapidly from fire and are more tolerant of fire-induced increases in salinity and decreases in soil moisture than are cottonwood and willow (Busch and Smith 1993, Busch 1995). Consequently, saltcedar and arrowweed are becoming increasingly dominant in low elevation riparian habitats, and cottonwood and willow less so. On the lower Colorado River alone, Busch and Smith (1993) and Busch (1995) documented 166 individual fires that burned more than 11,800 ha between 1981 and 1990. Given the rate and extent of loss documented by Busch and Smith, and that the remaining cottonwood-willow habitat on the lower Colorado River is virtually surrounded by saltcedar, the potential for fire to result in further losses of the remaining cottonwood-willow habitat is substantial.

Exotic Species—The exotic tamarisk, or saltcedar, was introduced from Asia as an ornamental and erosion-control agent in the 1800s. It began spreading rapidly throughout the Southwest during the early part of the 20^{th} Century (Tellman 1998). Today it has become dominant along many watercourses replacing multi-layered, multi-species native communities with monotypic stands uniform in structure. Hunter et al. (1987b) estimated that saltcedar dominated 49% of the area encompassed by riparian habitats in the Southwest, and occurred as a minor component in considerably more.

With its deep root system and extended production of seed from March through October, saltcedar thrives or persists where surface flow has been reduced or lost (Warren and Turner 1975, Horton 1977, Minckley and Brown 1982). The development of reservoirs and the concomitant change in flood regimes essential to the establishment of native riparian communities has enabled saltcedar to replace native broadleaf species. Furthermore, saltcedar establishment often results in a self-perpetuating regime of periodic fires. Fires were uncommon in native riparian communities prior to invasion by saltcedar, due to high moisture content in fuels and rapid removal of litter through decomposition and floods (Bradley et al. 1992). Consequently, native species are fire-intolerant. In contrast, saltcedar regenerates rapidly after fire (Busch and Smith 1993, Busch 1995). Areas with saltcedar that are not flooded regularly build up accumulations of salts in the soil, rendering the soil inhospitable for reestablishment of native species (Kerpez and Smith 1987).

Finally, the displacement of cottonwood-willow by saltcedar, particularly at elevations below 365 m, may reduce thermal buffering provided by the canopies of native riparian trees (C. Hunter pers. comm.). The absence or overall low reproductive success of mid-summer breeding birds at elevations below 365 m may be tied closely to a combination of (1) thermal tolerance of bird eggs being exceeded at ambient temperatures above 42° C (Walsberg and Voss-Roberts 1983); (2) predictable summer temperatures that frequently exceed 42° C during June and July (Hunter 1988, Hunter and Ohmart unpubl. manuscript); and (3) loss of most cottonwood-willow forests that may have provided effective thermal cover prior to the 1930s (e.g., Rosenberg et al. 1991). Hunter (pers. comm.) speculates that anticipated increases in average global temperature may exacerbate potential problems with productivity and distribution for mid- to late-summer breeding species such as the southwestern willow flycatcher.

In spite of the adverse impacts associated with the spread of saltcedar, this species is now a naturalized component of Southwestern drainages, particularly in Arizona, New Mexico, southern Utah, and southern Nevada. There is considerable irony in the fact that certain saltcedar habitats now provide what appears to be suitable nesting habitat for the endangered flycatcher (see Chapter 9)! That irony is reinforced by the fact that federal agencies responsible for recovering the southwestern willow flycatcher are also expending funds to "control" saltcedar. While saltcedar control may have some merit in systems for which the hydrological regime and water quality could truly support native riparian trees and shrubs, current control efforts and planning are focused almost exclusively on the symptoms rather than the root of the problem. Those involved in saltcedar management should heed Ewel's (1986) observation that "species invasions often reflect the conditions of the community being invaded rather than the uniquely aggressive traits of the invader." In the case of saltcedar, water management and water quality are the key factors. Control programs that do not consider these factors in the design of a restoration program run the risk of further reducing the biological diversity of an area, and, possibly, eliminating nesting habitat for the southwestern willow flycatcher. At a minimum, any area slated for saltcedar control or management should be thoroughly surveyed for flycatchers well in advance of physical alterations so that potential impacts to flycatchers can be fully evaluated and avoided.

Other exotic species have spread in riparian habitats throughout the range of the southwestern willow flycatcher. Russian-olive (*Elaeagnus angustifolia*) is abundant at middle elevations in New Mexico and Colorado (Szaro 1989). Where it occurs it is sometimes used for nesting by southwestern willow flycatchers (e.g., Skaggs 1996). Russian-olive appears to be less invasive than saltcedar and competitively inferior to native overstory species (Knopf and Olson 1984). Where found in mixed stands with native species, Russian-olive commonly occurs in less moist sites along the outer edge of riparian patches (Knopf and Olson 1984). Russian-olive supports a relatively high diversity and density of bird and mammal species, and may provide equivalent or better nesting habitat, although quantitative data are lacking (Knopf and Olson 1984). In California, giant reed (*Arundo donax*) is spreading rapidly. It forms dense monotypic stands unsuitable for flycatchers. Other exotic trees, such as Siberian elm (*Ulmus pumilis*) and tree of heaven (*Ailanthus simaruba*) occur in riparian areas within the flycatcher's range and do not appear to have any value as nesting substrates for flycatchers. At present their distribution is highly localized, which suggests that impacts to the flycatcher may be limited to local changes in riparian community composition.

Factors Directly Affecting Flycatchers

Cowbird Parasitism

Brood parasitism by brown-headed cowbirds (*Molothrus ater*) is a major threat to some populations of the southwestern willow flycatcher (Brown 1988, Harris 1991, Whitfield 1990, Sogge et al. 1997). The ecology of the cowbird is discussed in detail in Chapter 8. Originally thought to be commensal with American bison (*Bison bison*), cowbird numbers have increased tremendously with the expansion of livestock grazing, agriculture, and forest cutting (Laymon 1987, Robinson et al. 1993, Rothstein 1994). Cowbirds do not raise their own young, but rather lay their eggs in the nests of other species thus directly affecting their hosts by reducing nest success. Cowbird parasitism reduces host nest success in several ways. Cowbirds may remove some of the host's eggs, reducing overall fecundity. Hosts may abandon parasitized nests and attempt to renest, which can result in reduced clutch sizes, delayed fledgling, and reduced overall nesting success and fledgling survivorship (Whitfield 1994, Whitfield and Strong 1995). Cowbird eggs, which require a shorter incubation period than those of many passerine hosts, hatch earlier, giving cowbird nestlings a competitive advantage over the host's young for parental care (Bent 1960,McGeen 1972, Brittingham and Temple 1983).

Where studied, high rates of cowbird parasitism have coincided with southwestern willow flycatcher population declines (Whitfield 1994, Sogge 1995a, b, Whitfield and Strong 1995, Sogge et al. 1997), or, at a minimum, resulted in reduced or complete elimination of nesting success (Muiznieks et al. 1994, Whitfield 1994, Maynard 1995, Sferra et al. 1995, Whitfield and Strong 1995). Whitfield and Strong (1995) found that flycatcher nestlings fledged late in the season had a significantly lower rate of survival, and that cowbird parasitism was often the cause of delayed fledging.

A second brood parasitic species, the bronzed cowbird (*Molothrus aeneus*), is sympatric with *E. t. extimus* in portions of its range. However, except for one possible instance in the Gila River valley of New Mexico (Skaggs 1996) and one instance at Roosevelt Lake in Arizona (Sferra et al. 1995), the southwestern willow flycatcher is not known to be a host of this species (Lowther 1995). The bronzed cowbird is unlikely to pose any significant threat to *E. t. extimus* because it has a very limited distribution within the range of *E. t. extimus*, occurs at much lower densities than the brown-headed cowbird, prefers open habitats, and tends to prefer larger hosts, especially Icterids (Lowther 1995).

Predation

For many flycatcher populations, nest predation is the major cause of nest failure (Chapter 6). Most monitored populations experience high rates of nest predation ranging from 14 to 60% (Spencer et al. 1996, Whitfield and Strong 1995, Sferra et al. 1997, Sogge et al. 1997). Known or suspected nest predators include various snakes, predatory birds including corvids, owls, hawks, grackles and cowbirds, and small mammals including raccoons, ringtails, weasels, and rats (McCarthey et al. 1998).

Rates of predation may increase in human-altered landscapes. In the lower Colorado River valley, Rosenberg et al. (1991) noted increases in great-tailed grackles, a common nest predator. Increases in the extent of habitat fragmentation have been correlated with increased rates of nest predation in both forested and non-forested habitats (Picman et al. 1993, Askins 1993, Robinson et al. 1995). Whitfield (1990) noted that predation on flycatcher nests increased with decreasing distance to edge. Most small bird species in North America experience moderate rates of nest predation (30 to 60%) and the southwestern willow flycatcher, presumably, has adapted to similar rates. The key factor to determine is whether impacts, such as habitat fragmentation, are resulting in substantially higher rates of predation.

Parasites and Disease

Parasites and diseases can be critical factors affecting avian survival and reproduction, but tend to be poorly known (Dobson and May 1986). A variety of internal and external parasites have been recorded to affect willow flycatchers (Boland et al. 1989; Chapter 6 and references therein). However, the impact of such parasites or diseases on flycatchers is unknown.

Environmental Toxins

Where flycatcher populations are in proximity to agricultural areas, the use of pesticides poses a potential threat. Birds may be affected through direct toxicity or a reduction of their insect prey base. Although no quantitative data are available, physical deformities in willow flycatchers may indicate exposure to toxic compounds. Bill deformities and missing eyes have been reported from birds at sites in Arizona, Colorado and New Mexico (Paxton et al. 1997). In addition, flycatchers may be exposed to potentially toxic compounds on wintering or migration grounds.

In the lower Colorado River area, water management operations may exacerbate potential effects to flycatcher reproduction by concentrating naturally-occurring selenium. Selenium and other contaminants have been found in elevated levels in other birds within the lower Colorado River area (King and Andrews 1996). Selenium levels are known to be high at the Escalante State Wildlife Area in Colorado, where a willow flycatcher nestling was found with skull and bill deformities.

Summary

The above discussion illustrates the wide scope and magnitude of threats faced by this subspecies rangewide. The impacts documented during the last four years, alone, are alarming. Moreover, both small and large flycatcher populations have been adversely impacted or remain threatened. Haig et al. (1993) observed for the red-cockaded woodpecker, an endangered bird that still numbers from one thousand to several thousand pairs, that,

> "...species with such small populations are easily 'nickel and dimed' to extinction. That is, loss of a few small populations does not cause concern, but the cumulative effects of these losses could be dramatic. Therefore, a first step to species' recovery will be to stop these local extinctions."

The losses sustained by the flycatcher and current threats have been the subject of considerable conservation and research, public scrutiny, and litigation. However, we have yet to witness widescale application of what Haig et al. termed the "first step." This is evidenced by the numerous federal actions that have resulted in or are anticipated to result in the loss of flycatcher habitat and the displacement of flycatchers (USFWS 1997b). The cumulative effect of the threats and adverse impacts addressed in this chapter is substantial, and may account for the current low and relatively isolated population status for this subspecies. The rangewide scope and, in some cases, intense magnitude of these impacts underscores the critical need to protect existing flycatcher breeding groups and their habitat so as to not increase the degree of isolation among breeding groups. It also reinforces the concept of habitat conservation and management at the scale of the drainage (see Chapter 3), with the goal of decreasing habitat isolation and providing for population movement that results from population phenomena (i.e., emigration, dispersal), stochastic events (e.g., catastrophic floods, fires), or deterministic events (e.g., inundation of habitat).

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Chapter 4:

The Dynamic Environmental History of Southwest Willow Flycatcher Habitat: A Survey of Changing Riparian Conditions Through Time

The extent of riparian habitat in the southwestern United States during the past 100 years appears to have been reduced by modern land development, urban expansion, and a general increase in human populations (Finch 1996; Shaw and Finch 1996). Thousands of acres of river flood plain along the Rio Grande and Colorado rivers have been cleared for agriculture, construction of housing, and industrial development. River channels have been diverted and contained by dams, levies, and other water control structures in order to provide irrigation and drinking water, and to protect this investment in development from the destructive forces of periodic flooding (Tellman and others 1997; Wozniak 1995). Additionally, livestock grazing and the suppression of fire in upland ecosystems have detrimentally affected the overall conditions of riparian habitat (Thibault and others 1999).

The U.S. Fish and Wildlife Service added the Southwestern Willow Flycatcher (*Empidonax traillii*) to the endangered species list due to the brood parasitism of Brown-Headed Cowbirds and the destruction and modification of riparian habitats (U.S. Fish and Wildlife Service 1995). Cottonwood-willow riparian ecosystems are essential habitat for this species. While we can assume that industrial-era human expansion and land use have been responsible for Willow Flycatcher habitat loss, the environmental history of Southwestern cottonwood-willow ecosystems likely did not follow a linear trend of development or degradation.

Southwestern riparian ecosystems follow a dynamic regime of change and are not ecologically static. Prior to the installation of flood-control structures, periodic and catastrophic flooding replenished soil nutrients and served to “replant” riparian vegetation, while simultaneously removing large stretches of cottonwood-willow habitat from river flood plains (Whitney 1999). Human environmental manipulation, such as the burning of vegetation and clearing of land for agriculture, has been another factor of change to these already dynamic ecosystems. Although occurring at first on a limited scale, this interaction between people and the environment of the Southwest has occurred for at least 12,000 years (Cordell 1984). Archaeological research shows that not only were riparian plant and animal species used as sources of food, medicinal plants, and wood fiber for shelter and firewood, certain drainages in southwestern New Mexico were virtually stripped bare of trees during the eleventh and twelfth centuries A.D. (LeBlanc 1985).

According to ethnographic accounts, many American Indian cultures used and affected riparian habitats in a variety of ways. While some groups burned the vegetation along rivers and streams to provide clear hunting areas, others pruned and even planted riparian plants, willows for example, for future use (Blackburn and Anderson 1990; Fowler 1986 and 1996; Opler 1983a and b).

The overall effects of human land use changed in both method and intensity with Spanish conquest and settlement after 1540. This environmental change greatly intensified after 1846 when Anglo-American ranchers, farmers, and miners began to settle in the Southwest (Scurlock 1998; Wozniak 1996). Combined with the effects of modern development, this long-term, socioecological interaction has influenced and helped create the riparian conditions we see today.

We provide in this chapter a brief environmental history of Southwestern Willow Flycatcher habitat. Our geographical focus is the American Southwest (i.e., New Mexico, Arizona, and portions Southern California). We begin by describing the general changes and development of ecological conditions in the Southwest since the end of the Pleistocene. This description of the area's natural history provides a background for a discussion of human-environmental interactions with stream-side ecosystems, and importantly, illustrates the dynamic quality of Southwestern ecosystems. Within this context, we discuss Pre-Columbian and ethnohistorical evidence of riparian land use and manipulation. This is followed with a survey of historical observations of riparian habitat, first those of Spanish explorers, then more detailed accounts by Anglo-American trappers, military officers, and ornithologists. The section on exploration also provides accounts of direct sightings of Willow Flycatchers and the collection of vegetation and bird species. We then review the effects of European and Anglo-American expansion and settlement on the environment of the Southwest. Finally, we conclude with a discussion of how this historical ecological information may be useful in the management of Southwestern Willow Flycatcher habitat.

Ecological Conditions During the Holocene

By the end of the Pleistocene, c.12,000 to 10,000 years before present (B.P.), vegetation zones in the Southwest were 900 to 1,400 meters below present elevations. Sagebrush was more widespread during early- and full-glacial periods than it is today. Vegetation zones that had been at lower altitudes during the Pleistocene shifted to higher elevations during the transition from the glacial to post-glacial periods (Hall 1985:117). During the early-Holocene (10,000 to 7,000 B.P.) climatic conditions were generally more cool and moist than at present. This cool period was followed by a gradual warming and drying of the climate beginning approximately 7,000 B.P. and extending to 5,000 B.P. During this period of the middle-Holocene, average annual temperatures were between one and two degrees Celsius higher than today's annual temperatures (Mannion 1991:53-54). Pollen records from sites throughout the Southwest show that the middle-Holocene was extremely warm and dry relative to any other period. There was a reduction in woodland and riparian vegetation, and at alpine localities tree lines appear to have been as much as 70 meters above those of today. Alluvial valleys were eroded, resulting in the truncation of many alluvial pollen records (Hall 1985:118). After 5,000 B.P., there was a gradual increase in moisture levels and a correspondingly progressive increase in woodland and forest vegetation (Hall 1985:118). During the Little Ice Age, occurring during the late-Holocene from approximately A.D. 1450 until 1900, annual temperatures were one to two degrees Celsius cooler throughout the Northern Hemisphere than they are today (Kreutz and others 1997).

As demonstrated by the arid conditions of the middle-Holocene and cooler period of the Little Ice Age, the Holocene has been a period of climatic variability. Additionally, these broad-scale fluctuations were accompanied by more periodic climatic patterns. For example, historical records used to reconstruct more than four hundred and fifty years of El Niño-Southern Oscillation (ENSO) effects show that climate and moisture regimes varied extensively during the late-Holocene (Quinn and others 1987). By studying documented observations of abnormal weather, flooding, destruction of settlements, reductions in coastal fisheries, and other unusual natural events, Quinn and others identified moderate, strong, and very strong El Niño occurrences from 1525 to 1987. High-resolution alluvial sedimentary deposits in Ecuador show that the current periodicity of ENSO was established about 5,000 B.P. (Rodell and others 1999:518-519).

In the American Southwest, fire-histories show that years of increased or decreased regional burning have been closely related to the extreme ENSO phases (Swetnam and others 1999). Extensive drought and fire records, compiled for the Southwest from dendroclimatological data, show that extreme El Niño (high moisture) phases result in an accumulation of fuels. When followed by La Niña drought conditions, such fuels result in a greater number of fires on a regional scale (Swetnam and Betancourt 1998:3132-3136). Such patterns of climatic and moisture change would have affected levels of runoff and groundwater accumulation. This oscillating cycle of precipitation and fuel accumulation followed by drought and burning likely affected riparian vegetation as well as upland forests.

Native American Use of Riparian Ecosystems

For at least the past 12,000 years, humans have been living in and interacting with ecosystems throughout the Western Hemisphere (Cordell 1984; Frison 1991). The American Southwest has an abundance of archaeological and ethnographic resources that have the potential to enhance our understanding of riparian history. Archaeological research and excavation often includes the study of past environments through the examination of buried botanical remains collected from archaeological sites and other locations where pollen might be preserved, such as a peat bog or lake bottom (Birks and others 1988; Chambers 1993). Studying the remains of plants used by prehistoric and historic cultures can provide insights into human land use and environmental effects (cf. Pearsall 1989).

Prehistoric archaeological sites are often associated with riparian areas because of the presence of water and high resource availability. Riparian vegetation was used for firewood, construction material, shade, and food (Cordell 1984). Frequently, the macrofloral remains are well preserved in Southwestern archaeological sites, and pollen analysis of site sediments often reveals willow (*Salix* spp.), cattail (*Typha* spp.), and other riparian plants (Reinhard and others 1991:119; see also Cummings 1995a, b, 1997).

During the Paleo-Indian period (ca. 12,000 B.C. to 5,500 B.C.) and the Archaic period (5,500 B.C. to A.D. 400), people in the Southwest primarily foraged and hunted for subsistence (Cordell 1984). With the introduction of maize into the area, between 2,000 B.C. and 1,500 B.C. (Minnis 1992) until approximately A.D. 400, people continued to follow a hunting and gathering economy but with an increased dependence upon agriculture. Interestingly, during the Archaic period land use in some areas concentrated on upland landscapes that had high elevational diversity and therefore a greater range of resources to be exploited throughout the year (Tainter and Tainter 1996).

Between A.D. 400 and A.D. 600, until the beginning of Spanish colonization in A.D. 1540, agricultural groups began to build permanent settlements throughout what is now Arizona and New Mexico. Unlike those of earlier, Archaic period groups, these settlements were in some areas associated with large river-bottom environments (Tainter and Tainter 1996). Prehistoric farmers planted crops in riparian areas after clearing flood plains of vegetation (Cordell 1984; LeBlanc 1985). Agricultural societies in the Southwest had significant effects on riparian ecosystems. These societies included: the Patayan cultures located along the Colorado river in western Arizona; the Hohokam on the Gila, Verde, Salt, and San Pedro rivers in south-central Arizona; and the Anasazi of the Four Corners region in the San Juan, Little Colorado, and Rio Grande river basins. The Mogollon culture, which covered much of southern New Mexico, southeastern Arizona, and northern Sonora and Chihuahua, Mexico, was associated with the Rio Grande, Gila, Salt, the Rio Conchos, Rio Yaqui, and Rio de Sonora rivers (Cordell 1984).

In the southwestern corner of New Mexico archaeological and paleoenvironmental research in the Mimbres Valley reveals that prehistoric cultures had a profound effect on riparian ecosystems. A team of scientists headed by archaeologist Steven LeBlanc speculates that the Mimbres Valley underwent human-caused degradation during the period from A.D. 1000 to A.D. 1130 (LeBlanc 1985). Centuries of occupation and land use greatly reduced tree-cover in the river valley's riparian areas. Before A.D. 1000, cottonwood had been a common source of firewood and roof timbers but this source became depleted. Examination of wood charcoal shows that people were forced to use upland trees as substitutes when cottonwood was depleted. Clearing of the valley bottom for agriculture also likely affected the riparian plant community. After the valley was abandoned, most of the original vegetation returned. However, pollen analysis indicates that at least one species, sycamore (*Platanus wrightii*), was eliminated entirely from the ecosystem (1985:21).

Riparian-related vegetation was utilized as a resource by a variety of American Indian tribes throughout the Southwest and Great Basin. These cultures systematically tended riparian landscapes through the use of fire, pruning vegetation, and planting stands of willows and other plants in new locations (Anderson 1999; Blackburn and Anderson 1993b). The Timbisha Shoshone of Death Valley, California, used fire to clear riparian areas of dense willows and various grasses in order to promote the growth of certain types of seeds, particularly the white-stemmed blazing star (*Mentzelia albicaulis*) (Fowler 1996:40). The Timbisha routinely removed willows from springs and other water sources so that water could accumulate both for wildlife and for their own use (1996:98). As with pruning and selective harvest of riparian species, fire-use was localized and used for specific purposes (Anderson 1999). In order to produce straight willow stems for use in basketry, willow was pruned and coppiced by the Timbisha and other Shoshonean tribes in the Great Basin (Fowler 1986, 1996).

The Chiracahua Apaches of southwestern New Mexico and southeastern Arizona used the roots of tule (*Scirpus* spp.) and cattail (*Typha* spp.) for food and baskets. Sedge (*Carex* spp.) tubers and rootstocks of cattail were significant in the diet of the Mescalero Apaches of southeastern New Mexico and western Texas (Opler 1983a; Opler 1983b).

For native peoples, riparian ecosystems were highly productive and therefore attracted a high level of land use. This manipulation of vegetation likely occurred over thousands of years in both upland and lowland stream environments. Many of the stream-side areas encountered by European and Anglo-American explorers may have in fact been semi-managed ecosystems (Blackburn and Anderson 1993b).

Western Exploration and Settlement

In 1540, the viceroy of New Spain ordered Fray Marcos de Niza, who traveled ahead of the Coronado expedition, to take note of "the nature, fertility and climate of the land; the trees, plants, and domestic and wild animals…the rivers, whether they are large or small" (Hammond and Ray 1940). De Niza neglected to write about the natural world through which he passed, contrary to the viceroy's orders. Alvar Nuñez Cabeza de Vaca, in the chronicles of his journey from a shipwreck in Florida to New Spain (Mexico), described crossing the Rio Grande somewhere north of what is now El Paso; he suggests the presence of settlements and farms on the flood plain (Cabeza de Vaca 1542). Hernando de Alvarado and Fray Juan de Padilla, on their way to rendezvous with Coronado along the Rio Grande, noted the existence of cottonwoods near present day Albuquerque (Hammond and Ray 1940:183).

In general, the journals and documentation of Spanish explorers do not mention riparian or other vegetation in detail. Although Spain sent scientific expeditions to New Spain between 1785 and 1800, primarily for the purpose of recording plant and animal life in addition to mineral and other resources, none traveled through the American Southwest (Engstrand 1981).

Journals of explorers, trappers, and members of military expeditions contain information relevant to identifying historical environmental conditions during following the Spanish Colonial period (1540 to 1821) as well as during and following the Mexican period (1821 to 1848). American fur trappers entered the Southwest as early as 1831 (see Gregg 1905). The records of American military expeditions associated with the war with Mexico, 1846 to 1848, and the exploration of possible routes for transcontinental railways contain the most thorough observations of environmental conditions prior to the twentieth century (Abert 1962; Bell 1870; Pattie 1905; Pike 1966; Sitgreaves 1853; Wislizenus 1848).

During his explorations of New Mexico in 1805, Zebulon Pike observed that, "the cotton tree is the only tree of this province except some scrubby pines and cedars [juniper] at the foot of the mountains. They form borders on the banks of the Rio del Norte and its tributary streams. All the rest of the country presents to the eye a barren wild [wilderness] of poor land, scarcely to be improved by culture, and appears to be only capable of producing sufficient subsistence for those animals which live on succulent plants and herbage" (Pike 1966:47).

In 1826, fur trapper and trader James Pattie remarked that near Socorro, New Mexico, the river bottoms were thinly timbered and that the only growth was cottonwood and willow (Pattie 1905:86). However, during their first night on the Gila River, Pattie's group trapped over thirty beavers. The next day they journeyed along the river, and became "fatigued by the difficulty of getting through the high grass, which covered the heavily timbered bottom" (1905:87).

In the 1830s, explorer Josiah Gregg noted that the aspen along the upper portion of Santa Fe Creek were as "thick as cottonwoods in the Missouri bottoms" (Gregg 1905:282). However, the effects of human land use also were observed by Gregg. Commenting on the Rio Grande Bosque, he wrote that, "on the water-course there is little timber to be found except cotton-wood, scantily scattered along their banks. Those of the Rio del Norte are now nearly bare throughout the whole range of settlements, and the inhabitants are forced to resort to the distant mountains for most of their fuel" (1905:159). Similar observations of riparian vegetation along the Rio Grande were made by Adophus Wislizenus in 1846. The banks of the Rio Grande and south of Albuquerque, he observed, were bare of trees, with only occasional cottonwoods (Wislizenus 1848:34).

Beginning in 1846, American military expeditions resulted in some of the most detailed environmental descriptions of the Southwest during the nineteenth century. As part of Col. Stephen Kearny's expedition during the Mexican American War, engineer Lt. William H. Emory produced a detailed journal that contains numerous descriptions of riparian vegetation in the Southwest. On the Purgatory River, shortly after entering New Mexico, Emory remarks that, "the blighted trunks of cotton-wood and locust trees were seen for many miles along its course, but the cause of decay was not apparent" (Emory 1848:17). He also recorded sighting "black locust, the everlasting cotton-wood, willow, wild currents, hops, plums and grapes, artemesia [sic], *Clementis verginiana*, *salix*, in many varieties; and a species of angelica" (1848:17). On the Canadian River, Emory described the presence of a few cottonwoods (1848:19).

Emory carefully documented the birds he encountered on the expedition. While on the Canadian River he wrote that, "birds are rare, with the exception of the cow-bunting [cowbird?], which has been seen in great numbers on the whole route [from Bent's Fort] in a state so tame as to often alight on our horses" (1848:21). Additionally, he described healthy stands of willows and cottonwoods on the Cimarron and its tributary streams (1848:22).

Emory recounted that the area around Santa Fe was entirely cultivated through use of irrigation and that the expedition's horses had to be sent to graze 12 to 30 miles from the city (Emory 1844:35). He remarked that the area near Albuquerque was destitute of wood and that grass was sparse for the expedition's horses; however, he observed significant cottonwood and willow growth, along with evidence of beavers, south of Albuquerque (1848:47-48). At Polvadera, the river was fringed with large cottonwoods, and Emory observed flocks of geese "blue-winged ducks, plovers, doves and a few meadow larks" (1848:48). There were "immence [sic] flights of sand-cranes and geese well within gunshot of houses and the largest towns" (1848:48). He mentioned that as he traveled south, the cottonwood growth become more plentiful (1848:50).

South of Socorro, Emory's party encountered an area which he judged to be "the best in New Mexico; the valley is broader, the soil firmer, and the growth of timber, along the river, larger and more dense" (Emory 1848:53). Emory noted evidence of irrigation and two deserted towns in the area that had once been a successful Spanish settlement. After passing the Fra Cristobal Mountains, Emory remarked on shooting three quail and one small lark that resembled a "sparrow-hawk" (1848:54). Interestingly, at this point in the journal he made the statement that "game in New Mexico is almost extinct" (1848:54). In contrast, when the expedition reached the area located one mile north of San Felipe, he observed that their camp was, "well grassed and wooded, and apparently untrodden by the foot of man" (Emory 1848:55). For the first time in New Mexico, Emory's expedition saw abundant evidence of game (1848:55).

The expedition left the valley of the Rio Grande and traveled west toward the Gila River. After crossing over table lands and entering more hilly terrain, Emory observed a stream with "green trees and luxuriant foliage…. The stream was clear, limed, and cool, the first but one I had seen since crossing the Alleghenies, where water could be drunk without imbibing a due proportion of mud and sand" (1848:57). As the group progressed further, he noted that, "in the valley grows cotton-wood, a new variety of evergreen oak…and a new kind of walnut" (1848:57). Emory wrote that the sides and banks of the Rio Mimbres were "covered with a growth of stunted live oak," and the valley was "densely covered with cotton-wood, walnut, [and] ash" (1848:57). He stated that the river was filled with an abundance of fish "without scales [Roundtail Chub]" (1848:61-62). The Gila River valley, according to Emory, was covered with a luxuriant growth of trees, "chiefly cotton-wood, a new sycamore, mezquite [sic]…a few cedars, and one or two larch [Arizona Cyprus?]" (1848:62).

Lt. J. W. Abert, also under Col. Kearny's command during this period, traveled in a separate expedition and kept a journal much like the one recorded by Emory. Abert recorded specific bird sightings and like Emory made observations of the vegetation encountered. For example, on the Purgatory River, he observed, "we here saw several flickers, with red lined wings and tails…the common flicker, and large flocks of the yellow headed black bird" (Albert 1962:30). Further down the Purgatory River, he recorded sightings of "red shafted flickers" (1962:30-31). Like Emory, Abert also observed the "common cow bird" (1962:32). Abert described the riparian vegetation he encountered in much the same manner as Emory had; he described the campsites on the Canadian River as "shaded by large cottonwood trees and willow thickets" (1962:35).

In 1850, an expedition led by Captain L. Sitgreaves surveyed a segment of the Rio Grande, the Zuni River, and the Colorado River (Sitgreaves 1853). Like Emory and Abert, Sitgreaves reported on the vegetation he encountered. More detailed and technical observations, however, were made by S. W. Woodhouse, M.D., the surgeon and naturalist of the expedition. Woodhouse noted that, "From El Paso, passing up the Rio del Norte, the vegetation alters but little, the timber being principally cotton-wood, and mezquit [sic] extending as far as the Jornada del Muerto." From the Pueblo of Santo Domingo to Albuquerque, Woodhouse noted that there was little change in vegetation "with the exception of a few scattered cotton-wood trees…or occasionally a few cedars [junipers]" (1853:35). Significantly, Woodhouse made thorough and detailed observations of birds, and recorded sightings of "Trail's Fly-catcher" and the "Dwarf Fly-catcher" (1853:74-75). What he calls "Trail's Fly-catcher" is likely the Southwestern Willow Flycatcher (*Empidonax traillii extimus*).

Interestingly, when describing the Zuni River, Woodhouse remarked that they encountered "in but one place a few poplars (*Populus augustifolia*), and near these trees was a beaver dam, in which was growing cattails (*Typha latifolia*)" (Woodhouse 1853:36). He also noticed beaver lodges on the banks of the Little Colorado, although there was little timber.

However, he did mention "a species of swamp-willow (*Salix*)" (1853:36). As the expedition approached the San Francisco Mountains, he noted that the cotton-wood became more abundant (1853:39). Woodhouse wrote that the banks of the Little Colorado were "fringed with cotton-wood trees" and that at its confluence with the Colorado, he had trouble measuring the velocity of the of the river due to a "dense growth of willows and weeds" (1853:40).

Woodhouse noted several streams with willows, and upon finally reaching the "Colorado of the West," he remarked, "On the banks of this stream are growing willows (*Salix* spp.) of several kinds, one of which, the *Salix augustifolia*, affords good fodder for the mules; they oftentimes, whilst on this stream, had nothing else, and in fact we thought that we were doing well when we found this species of willow" (1853:39). Additionally, he observed that from the place where they first encountered the Colorado to the mouth of the Gila (Figures 4-1 through 4-3), "south to the entrance of the Great Desert," the vegetation varied little, being cottonwood, mesquite, and willow (Woodhouse 1853:39).

The extensive Wheeler railroad surveys, conducted from 1871 through 1874, produced seven volumes of information about the West (Wheeler 1878). Volume VI documents the vegetation encountered in detail (Figures 4-4 through 4-6). As reported in Volume V, ornithologist Henry W. Henshaw collected extensively in western New Mexico, Arizona, Utah, and Nevada. In all, his expedition procured more than 3,000 birds (Henshaw 1875). In 1874, his party, which included two other scientists, traveled from Santa Fe to Fort Wingate, New Mexico, through Arizona to Fort Crittenden near the Mexican border. From Fort Crittenden, they returned to New Mexico through eastern Arizona, then north along the Rio Grande to Santa Fe.

In his report, Henshaw recorded the species, sex, location, and the number of birds collected during the expedition. He stated that, "no birds have been introduced that have not actually been taken or observed by the expedition. In all cases where we have utilized the notes of observers other than members of the survey, attention is called to the fact" (Henshaw 1875:139).

As he traveled through the Gila valley Henshaw remarked that the avifauna was very much like that of the Colorado Valley (1875:140). In all, Henshaw collected and documented what were then classified as fifteen different species of "flycatcher," including the Willow Flycatcher (*Empidonax traillii*), which he referred to as the "Little Flycatcher" (1875:356-358). Henshaw's team collected Willow Flycatchers throughout Arizona, in the White Mountains, at Fort Apache, Fort Bowie, and Fort Crittenden. A list of these birds, and observations made by Henshaw, is provided in Appendix A. Reviewing the results of his other expeditions, Henshaw remarked that these birds (Southwestern Willow Flycatchers) were

> …exceedingly numerous near Provo, River [Utah] in willow thickets; sparingly so in eastern Nevada. Colorado, New Mexico, and Arizona are all included in the range of this flycatcher; its abundance being dependent upon the presence or absence of its favorite grounds…. Wherever willows are found growing in small clumps or fringing the streams, this flycatcher is almost certain to be found common (Henshaw 1875:357).

During the 1860s and 1870s, U.S. Army surgeon and ornithologist Elliott Coues collected and recorded birds and mammals as a member of numerous military expeditions in the West (Coues 1866, 1874, and 1878). Coues describes *Empidonax traillii* as being an abundant "Flycatcher of the West" and he observed that at "Fort Whipple, in Arizona, it is the commonest and characteristic species of its group," ranging from the central plains to the Pacific (Coues 1874:252-253).

Dr. Edgar Alexander Mearns recorded his observations of mammals and trees encountered during the Mexican Boundary Survey of 1892 to 1894. The survey party covered territory from Fort Worth, Texas, to San Diego, California, along the present border of the United States and Mexico. Mearns states that the streams along the route were lined with trees, including Fremont cottonwood, black willow, box elder, walnut, sycamore, oak, mulberry, and ash (Mearns 1907). He described cottonwood and willow as associated with every permanent stream, bordered with a broad zone of mesquite (1907 261:32-35d). Mearns estimated that about 160,000 to 180,000 hectares of riparian vegetation covered the Lower Colorado River flood plain between Fort Mojave and Fort Yuma (Rosenberg and others 1991:21).

In 1910, over a period of three months, ornithologist Joseph Grinnell surveyed the Colorado River from Needles, California, to Yuma, Arizona. During the expedition, Grinnell systematically collected and studied the plants and animals of the Lower Colorado Basin. The party collected 1,374 bird specimens, along with large numbers of other vertebrates (Grinnell 1914:52). Grinnell described cottonwood and willow as the dominant vegetation in the flood plain adjacent to the river, while the higher terrace was predominantly covered with mesquite and "salt-bush" (1914:60-61). He observed that the river landscape continually changed as floodwaters cut new channels and cleared areas of vegetation. New sediment was continually deposited on the inside curve of the river. Trees tended to grow in a successive pattern. The youngest cottonwoods and willows growing nearest to the water's edge, progressively older and taller trees growing away from the river.

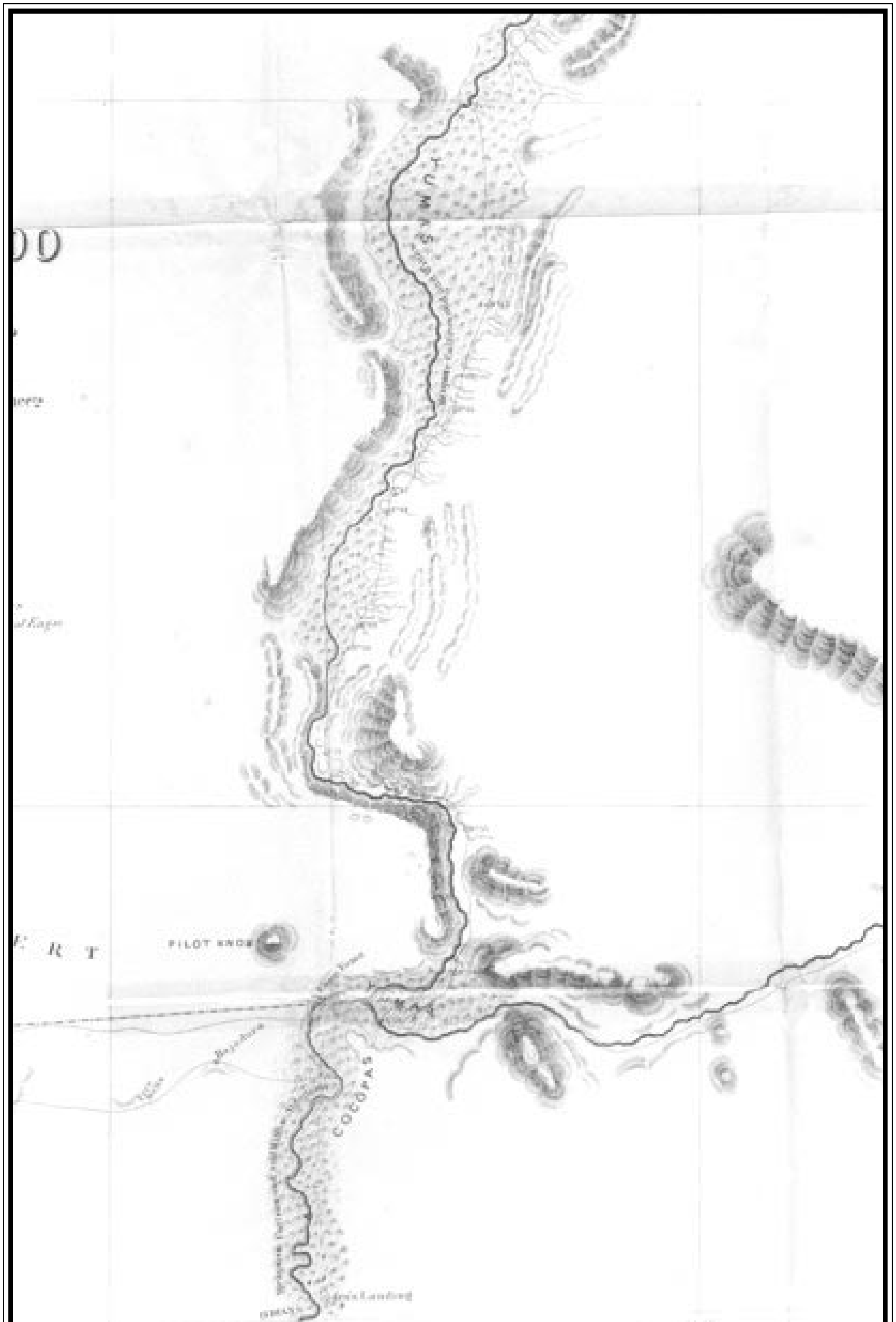

Figure 4-1. Lower portion of the Colorado River with large areas of mesquite, cottonwood, and willow represented. Map made from information collected during 1851 Sitgreaves expedition (Sitgreaves 1853).

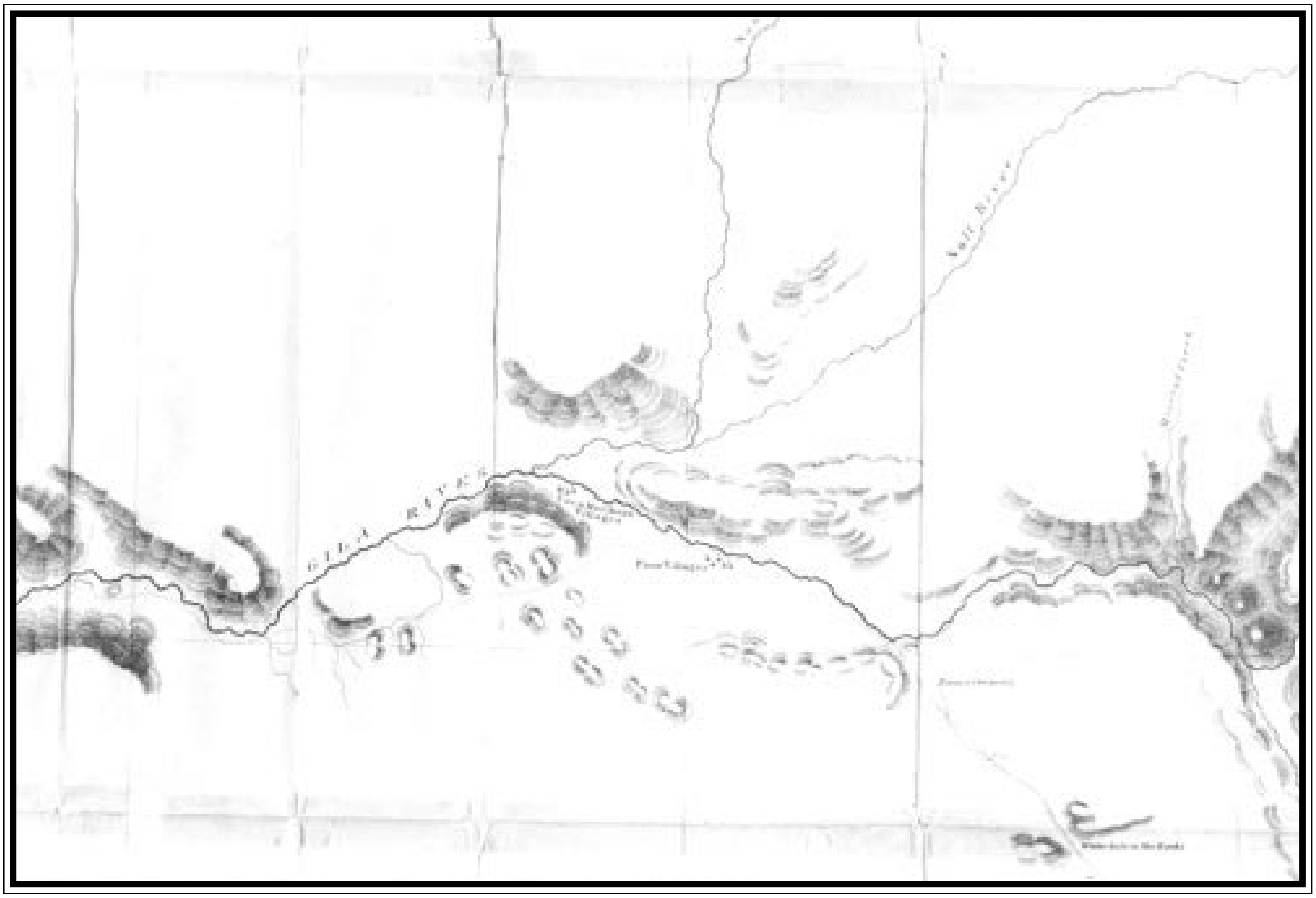

Figure 4-2. Middle portion of Gila River. Map made from information collected during 1851 Sitgreaves expedition (Sitgreaves 1853).

Grinnell also described the effects of Laguna Dam, which was completed in 1909, as already altering large areas of the Lower Colorado River landscape by 1910. The vegetation growing along a ten-mile stretch of the river had been decimated by rising water levels, while a prodigious amount of sediment was deposited over the flood plain. As water subsided, the original riparian vegetation was replaced by "vast mudflats growing arrowweed. All of this change, of course, involved the birds and mammals of the area affected, in addition to the plant life" (Grinnell 1914:61-62).

Grinnell observed and collected Willow Flycatchers (*Empidonax traillii*) during the 1910 survey, referring to the species as the "Traill Flycatcher" (Grinnell 1914). He first spotted several of the birds on the California side of the Colorado River and again sighted Willow Flycatchers five miles northeast of Yuma. Grinnell states that, "On both sides of the river in the vicinity of Pilot Knob the species [*Empidonax traillii*] was frequently observed" and that, "The birds were never detected away from dense willow growths close to water" (1914:151).

In California, Grinnell described "Western Traill Flycatchers" (*Empidonax traillii*) as being present in riparian ecosystems throughout the length the state, east and west of the Sierras." He stated that the birds "avoid in major part forested areas including north-west coast belt, the open deserts, and the higher mountains…this flycatcher exists in summer time practically wherever its special habitat exists" (Grinnell and Miller 1944:256). At that time, *traillii* could be found within the "Lower and Upper Sonoran zones, Transition [zones], and even Canadian [zones]. Altitudes of known nestings extend from within a hundred feet of sea level, for example at Alviso and Palo Alto, Santa Clara County, up to at least 8,000 feet, in the neighborhood of Mammoth, Mono County" (1944:256). The Flycatchers were primarily restricted to willow thickets, "along streams in broad valleys, in canyon bottoms, around mountain-side seepages, or at the margins of ponds or lakes" (1944:257).

In a 1908 study that focused on the San Jacinto Mountains of southern California, Grinnell and Swarth described *Empidonax traillii* as only occurring

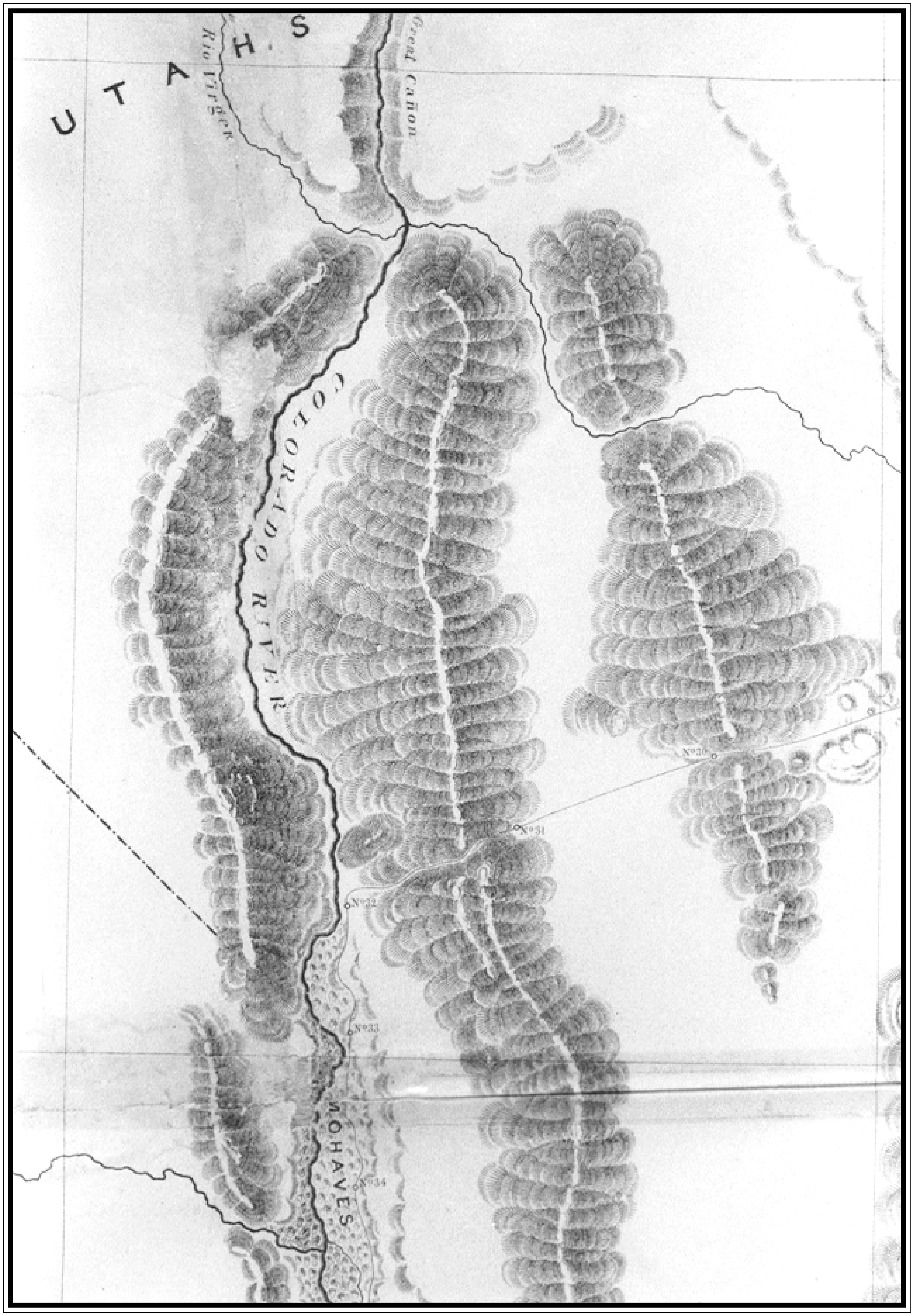

Figure 4-3. Colorado River along Arizona, California, and Nevada boundaries. Confluence of the Virgin River and the Colorado is show in upper portion of map (Sitgreaves 1853).

Figure 4-4. Riparian habitat at the head of the Conejos River in south central Colorado. Photo taken during Wheeler railroad surveys of the 1870s (Wheeler 1878).

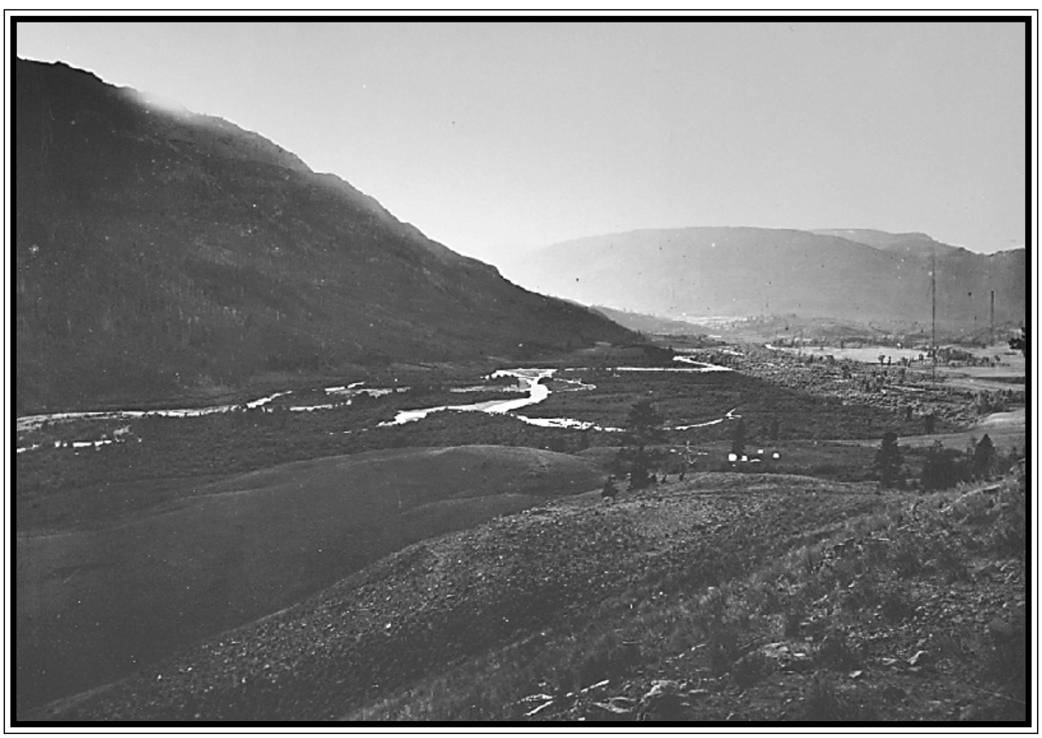

Figure 4-5. Braided stream and riparian habitat along the Conejos River in south central Colorado. Photo taken during Wheeler railroad surveys of the 1870s (Wheeler 1878).

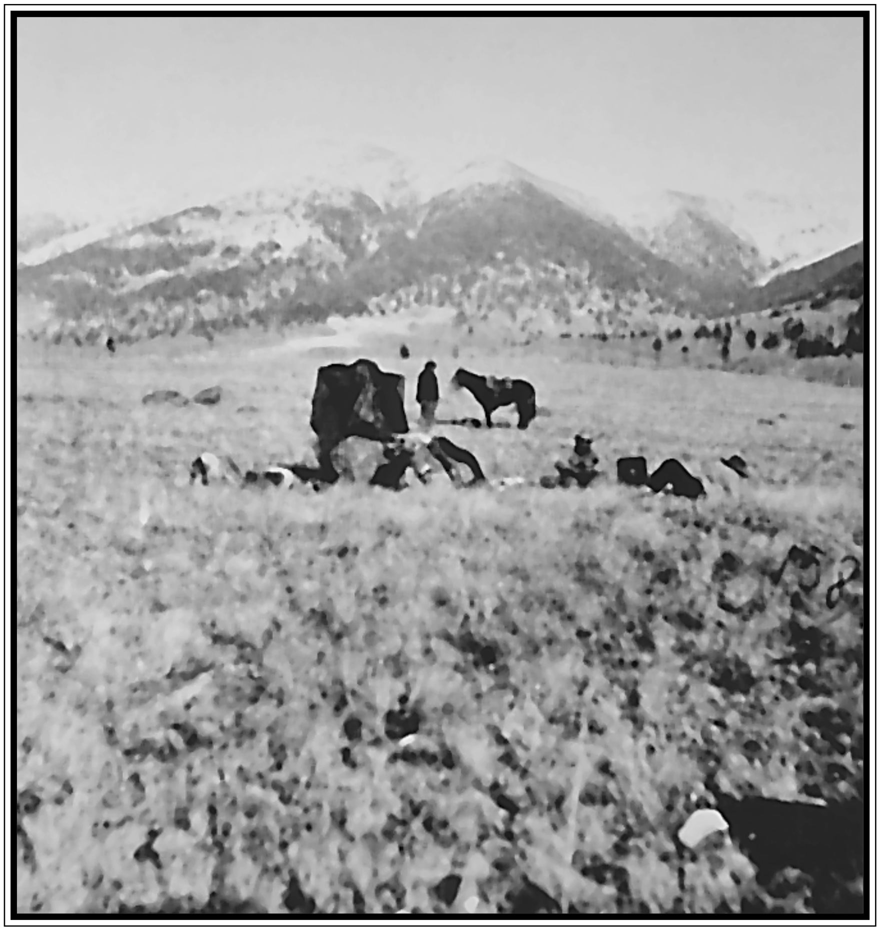

Figure 4-6. Base of the San Francisco Mountains in Arizona with Wheeler survey party and photographic equipment in the foreground (Wheeler 1878).

on the desert side of the mountain range during spring and in late summer moving to other locations in the San Jacinto area (Grinnell and Swarth 1913). Their group collected *traillii*, which appear to have been abundant, at Cabezon and Dos Palmos. The birds were found in thickets of desert willow at Carrizo Creek and Palm Canon and in other areas up to 3,000 feet above sea level. Grinnell and Swarth collected 19 *traillii* specimens during the survey (1913:256). Additionally, Grinnell and Kellogg each mention *Empidonax traillii* as occurring in the Trinity region of northern California (Grinnell 1916:404; Kellogg 1916:382).

Euro-American Impacts on Southwestern Riparian Ecosystems

Beginning with Coronado's *entrada* (1540 to 1542), native cultures began to change. Throughout the world, European contact with indigenous societies has disrupted native cultures in a number of ways (Ferguson 1992a and b). Coronado's expedition likely effected environmental change by pressuring Puebloan groups to produce food and fuel for his soldiers (thereby putting additional pressure on flood plain resources) and by introducing metal tools with which native people could more effectively clear trees (Wozniak 1995). European contact with Native Americans also introduced previously unknown diseases into a native population with no immunity to European illness. This caused a vast decline in population and a disruption of the cultural and economic activities focused on resource production (Ramenofsky 1987), such as burning undergrowth, harvesting native plants, producing crops, and managing water, all of which would have affected vegetational patterns.

By 1598, Spanish settlement affected environmental change on a large scale. Spanish colonists introduced domesticated livestock, intensive ditch and flood irrigation, a plethora of European plants, use of metal tools, and the plow. This resulted in tremendous changes in water systems, the clearing of larger tracts of land, grazing pressures, and the expansion of nonnative plants (Scurlock 1998:105-119).

Fur trappers were some of the first Americans to affect Southwestern riparian areas primarily by trapping beaver. Trappers often traveled in groups, or "brigades," that would trap *all* of the beaver from a drainage before moving on to the next river system (Vandiveer 1971; Ross 1956; Karamanski 1983; Chittenden 1935). The destruction of beaver dams likely resulted in a narrowing of riparian areas due to less water retention in certain drainages. This caused a change in riparian vegetation. The clearing and regeneration pattern would have been less dynamic.

By the time of the first major cattle drives from Texas to the California gold fields in 1850, there were already indications of overgrazing in the Southwest. Hispanic ranchers were raising tens of thousands of sheep and cattle, along with goats and horses (Raish 1995; Scurlock 1988; Scurlock 1998). Texan cattlemen established two major routes from west Texas to California: one trail crossed New Mexico near Albuquerque and then proceeded west across Arizona to Los Angeles; the other cattle trail passed along the region of what is now the Mexican-American border through southeastern New Mexico, to Tucson, then to San Diego. Despite the fact that this enterprise was only marginally successful, due to the extremely long distances and shortages of grass and water (Beck and Haase 1989:29-30), the cattle drives had significant effects on those areas through which they passed (Emory 1857).

During the 1870s and 1880s, numbers of cattle and sheep grew dramatically in the Southwest. Anglo-American ranchers accumulated vast herds numbering in the millions, and the ecological conditions of rangeland and riparian areas worsened. Native American herds grew and had a lasting effect on the lands as well (Scurlock 1998:96-97). Topsoil stripped of vegetation eroded with wind and runoff, which increased stream sediment and the down cutting of streams (see Abruzzi 1995; Scurlock 1988 and 1998; Tellman and others 1997; Widdison 1959; Wilson 1988; Wozniak 1995).

Timber cutting also significantly altered the river bottoms of the Southwest. Cottonwood was cut for steamboat fuel along the Colorado, while pine and other soft woods were removed from mountain ranges (Rosenberg and others 1991). Around the perimeters of settlements such as Albuquerque, firewood had become scarce by the time the American military arrived during the late 1840s (Emory 1848; Rosenberg and others 1991; Whipple 1856; Wislizenus 1848; Sitgreaves 1853). Removal of tree-cover resulted in increased runoff, and subsequently high sediment loads.

The arrival of the railroads during the late 1870s and early 1880s brought new settlers, resulting in the expansion of urban areas. This greatly increased the amount of river land under cultivation (Wozniak 1995). With the railroads, ranchers were able to ship their cattle and sheep to eastern markets. These new transportation systems facilitated the availability of an increased number of industrial and agricultural technologies, thus allowing the development of even more arable land, an increase in the number of sawmills, and other industrial enterprises (Hess 1992; Worster 1993).

Since the 1890s, numerous rivers and streams in the Southwest have been dammed, pushed between levies, and diverted to satisfy the ever-increasing demands of urban landscaping, industry, drinking water, and irrigation. Agricultural lands replaced cottonwood-willow habitat, and although the numbers of range stock have decreased, riparian areas continue to be impacted by cattle grazing. Additionally, nonnative plants such as salt cedar and Russian olive, after their introduction early in the twentieth century, began out-competing native riparian vegetation, in part due to altered hydrological regimes (Scurlock 1998; Tellman 1997).

Discussion

This chapter provides a sketch of a vast and complex historical and ecological topic. The dynamic climatic, vegetational, and human history of the Southwest demonstrates the remarkable changeability of its environment. Riparian habitats in the Southwest are not now, nor have they ever been, in a state of equilibrium (Swetnam and others 1999:1201). These dynamics of change include long-term climatic variation and human-environmental interaction. While climatic variation, drought, and periodic flooding continually have changed drainage and vegetation patterns, humans also have manipulated Southwestern ecosystems since the end of the Ice Age.

Archaeological research shows that not only were riparian species used for food and medicinal purposes, but also that certain southwestern drainages were virtually stripped bare of trees by prehistoric horticulturists. Large areas were cleared for agriculture and riparian vegetation was used for construction and firewood (LeBlanc 1985). The archaeological record contains riparian-related macroremains and pollen, however many archaeological investigations have not focused on overall anthropogenic environmental effects. Although the presence of willow and cattail pollen in archaeological sites does not provide an indication of past riparian conditions, such evidence does demonstrate that humans utilized the resources available in these streamside ecosystems. Long-term burning, pruning, and planting of riparian vegetation by native peoples likely helped to create current conditions, and knowledge of their techniques may in fact present a model for future restoration efforts (Anderson 1999). Further review of the ethnographic record can provide a wealth of information about past Native American land use.

Historical observations made by explorers and biologists shows that the Willow Flycatcher was locally common in the cottonwood-willow habitats of the southwest in the 1800s. The first-hand observations discussed here were made by a few individuals traveling along primary routes, and therefore provide only a sample image of past riparian conditions. The ability to draw conclusions about the extent of riparian vegetation and the distribution of Willow Flycatchers could be enhanced by further review of archival material at the state, county, and community level.

It is necessary to discuss the broad spectrum of historical conditions of riparian systems in the Southwest. Conducting environmental history requires an interdisciplinary approach incorporating the expertise of multiple scientific and humanistic fields (Worster 1993:156). Ecosystem conditions of the recent and distant past need to be evaluated using a variety of information sources (e.g., paleobotany, geomorphology, as well as local historical documents). Additionally, local historical societies, family journals, legal documents, and photographs could be significant sources in developing a local-level environmental history of riparian ecosystem conditions for specific project areas.

Managing Willow Flycatcher habitat is ecologically and socially complex and challenging. An ecosystem must be studied and evaluated prior to the establishment of appropriate target conditions and objectives concerning the restoration of various components (Dahm et al. 1995:225). Managing riparian ecosystems (i.e., re-establishing Willow Flycatcher habitat), requires clear understanding of the ecological complexity and linkages between biotic communities and the abiotic environment, recognition of the dynamic character of ecosystems, and knowledge of humans as ecosystem components (Christensen and others 1996:669-670). These ecological factors need to be understood at the local and regional scale and temporally over the short- and long-term (Swetnam and others 1999:1190). The so-called "range of historical variability" for the Southwest has been quite broad. Considering the dynamic nature of Southwestern landscapes, it would be misguided to designate a specific point in time from which to establish a desired future condition for riparian restoration (Swetnam and others 1999:1201; Sprugel 1991).

Having knowledge of all the dynamic forces that helped to shape riparian habitat will give decision-makers a greater range of opportunities and options when considering the management and reestablishment of cottonwood-willow vegetation. Understanding these changes in riparian ecosystem conditions, and dynamics behind them, can provide an invaluable perspective that applies to the re-establishment and management of Southwestern Willow Flycatcher habitat within the limits of modern human social and resource demands.

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Appendix A

WHEELER SURVEY BIRD DATA (Henshaw 1875)

The following lists only those species that are referred to as "Flycatcher" by Henshaw.

Ash-throated Flycatcher (*Myiarchus cinerascens*)

Where Collected	Survey Year	Number of Birds
Fort Wingate, AZ	1873	3
Inscription Rock, NM	1873	1
Camp Apache, AZ	1874	2
Camp Bowie, AZ	1874	1
Camp Crittenden, AZ	1874	1

Notes

"Having a distribution nearly coincident with that of the preceding species, though extending somewhat farther to the north into Utah, Nevada, and Colorado. It is less abundant than the preceding [Cassin's], and inhabits much the same style of country, affecting rough, rocky country sparsely wooded, or the brushy creek bottoms, even extending its range out to a considerable distance on the dry plains" (Henshaw 1875:345-346).

Recorded as the **Yellow-bellied Flycatcher** (*Myiodynastes luteiventris*), now known as the **Sulphur-bellied Flycatcher**

Where Collected	Survey Year	Number of Birds
Chiricahua Mountains, AZ	1874	5

Notes

"This peculiar flycatcher appears to be a summer resident of the Chiricahua Mountains, Southern Arizona, were I obtained a pair of old birds, together with three young . . ." (Henshaw 1875:346-347).

Olive-sided Flycatcher (*Contopus borealis*)

Where Collected	Survey Year	Number of Birds
Nevada	1871	1
Near Ft. Garland, CO	1873	5
Rio Grande, CO	1873	2
Camp Apache, AZ	1873	2
Willow Springs, AZ	1874	1
Indian Valley, CO	1874	1
Bowie Agency, AZ	1874	2
Trinchara Creek, CO	1874	1
Conejos River, CO	1874	1
Mount Graham, AZ	1874	2
Black River, AZ	1874	1

Notes

"The Olive-sided Flycatcher appears to be much more abundant through the West generally than at the East, and in parts of Utah and Colorado has been found by our parties in considerable numbers. It is a highly characteristic bird of the pine region, ranging from about 7,000 feet up to timber line."

"We found it almost as numerous in Eastern Arizona, quite far to the south, as in Colorado; but I supposed that it was only thus present during the migrations. The past season [1873], however, specimens were taken near Camp Apache in July, which doubtless were breeding, and later, about the middle of August, young and old were secured near Camp Bowie, within one hundred miles of Mexico. Its replacement, therefore, in this region by *Contopus pertinax* would appear to be only partial, and the two breed in the same districts." (Henshaw 1875:350-351).

Little Flycatcher (*Empidonax trailli*, var. *Extimus*)

Where Collected	Survey Year	Number of Birds
Humboldt River, NV	1871	1
Provo, UT	1872	23
Wahsatch Mountains, UT	1872	1
Fort Garland, CO	1873	5
White Mountains, AZ	1873	1
Camp Apache, AZ	1873	1
Near Camp Apache, AZ	1873	2
Pueblo, CO	1874	1
Camp Bowie, AZ	1874	4

Fort Garland, AZ	1874	1
Camp Crittenden, AZ	1874	1
Pagosa, CO	1874	1

Notes

"Exceedingly numerous near Provo River in willow thickets; sparingly so in Eastern Nevada. Very quick and nervous in its movements, constantly crossing and recrossing the river and catching insects.... Colorado, New Mexico, and Arizona are all included in the range of this flycatcher; its abundance being dependent upon the presence or absence of its favorite grounds.... Wherever willows are found growing in small clumps or fringing the stream, this flycatcher is almost certain to be found common, and it is rarely seen in the summer in other situations. Its habits and notes appear to be identical with those of its eastern analogue, from which it differs mainly in its paler coloration. The nest is placed in the upright fork of a bush or sapling a few feet from the ground, and is composed of grasses and fibrous material, rather loosely woven together, and lined with fine grasses. Its general appearance is much like that of the nest of the Yellow Warbler, *D. aestiva*, but it is not nearly so compact nor artistic." (Henshaw 1875:356-358).

Least Flycatcher (*Empidonax minimus*)

Where Collected	Survey Year	Number of Birds
Denver, CO	1873	1

Henshaw's notes state that the habitat and behavior of this bird are much like that of *Empidonax trailli* (Henshaw 1875:358-359).

Recorded as the **Western Yellow-bellied Flycatcher** (*Empidonax flaviventris*, var. *Difficilis*), now known as the **Cordilleran Flycatcher** (*Empidonax occidentalis*)

Where Collected	Survey Year	Number of Birds
Rio Grande, CO	1873	1
Fort Wingate, NM	1873	1
Inscription Rock, NM	1873	1
Willow Springs, AZ	1874	2
Mount Graham, AZ	1874	1
Camp Bowie, AZ	1874	1

Henshaw's notes state that the habitat and behavior of this bird are much like that of *Empidonax trailli*(Henshaw 1875:359-360).

Wright's Flycatcher (*Empidonax obscurus*)

Where Collected	Survey Year	Number of Birds
Bull Run, NV	1871	2
Provo, UT	1872	1
Snake Creek, NV	1872	1
Denver, CO	1873	2
Fort Wingate, NM	1873	1
Inscription Rock, NM	1873	1
Camp Apache, AZ	1873	3
South of Camp Apache, AZ	1873	2
Santa Fe, NM	1874	2
Camp Bowie, AZ	1874	2
Fort Garland, CO	1874	3

Henshaw's notes state that the habitat and behavior of this bird are much like that of *Empidonax traillii* (Henshaw 1875:360-361).

Hammond's Flycatcher (*Empidonax Hammondi*)

Where Collected	Survey Year	Number of Birds
Beaver, UT	1872	1
Cedar, UT	1872	1
Rio Grande, NM	1873	1
Camp Apache, AZ	1873	5
Gila River, AZ	1873	4
Fort Bayard, NM	1873	1
Navajo Creek, NM	1874	1
Mount Graham, AZ	1874	6
Gila River, AZ	1874	1

Henshaw's notes state that the habitat and behavior of this bird are much like that of *Empidonax trailli* (Henshaw 1875:362-363).

Buff-breasted Least Flycatcher (*Mitrephorus fluvifrons*, var. *Pallescens*)

Where Collected	**Survey Year**	**Number of Birds**
Inscription Rock, NM	1873	5
Camp Apache, AZ	1873	1
Bowie Agency, AZ	1874	1

Notes

Little noted for this bird (Henshaw 1875:364).

Red Flycatcher (*Pyrocephalus rubineus*, var. *Mexicanus*)

Where Collected	**Survey Year**	**Number of Birds**
Pueblo Viejo, AZ	1873	1
Sonoita Valley, AZ	1874	3
Camp Lowell, AZ	1874	4
Gila River, AZ	1874	1

Notes

Little noted for this bird (Henshaw 1875:365).

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Chapter 5:

A Survey of Current Breeding Habitats

The distribution and abundance of a species across a landscape depends, in part, on the distribution and abundance of appropriate habitat. If basic resource needs such as food, water, and cover are not present, then that species is excluded from the area. Scarcity of appropriate habitat is generally the key reason for the status of most rare and endangered species. An understanding of an endangered species' habitat characteristics is crucial to effective management, conservation and recovery.

The southwestern willow flycatcher (*Empidonax traillii extimus*) breeds in dense riparian habitats in all or parts of seven southwestern states, from sea level in California to over 2600 m in Arizona and southwestern Colorado. Although other willow flycatcher subspecies often breed in shrubby habitats away from surface water (Bent 1942, McCabe 1991), *E.t. extimus* breeds only in dense riparian vegetation near surface water or saturated soil. Other habitat characteristics such as dominant plant species, size and shape of habitat patch, canopy structure, vegetation height, etc., vary widely among sites. Our objective in this chapter is to present an overview of southwestern willow flycatcher breeding habitat, with an emphasis on gross vegetation characteristics. Although quantitative studies of habitat have begun in some areas (e.g., Spencer et al. 1996, Whitfield and Enos 1996, McKernan and Braden 1999, Paradzick et al. 1999), we focus here on qualitative information on plant species composition and structure. Although many of the details of vegetation characteristics differ among breeding sites, we will draw attention to those common elements or themes that are shared by most sites. All of the breeding sites described herein are within the geographic range currently administered as the southwestern subspecies (*E.t. extimus*) by the U.S. Fish and Wildlife Service. Several on-going studies could ultimately change the accepted boundary designations for *E.t. extimus*. Thus, some of the breeding sites described may eventually be removed from *E.t. extimus* range, while new sites could be added. Any such changes may provide new perspectives on southwestern willow flycatcher habitat.

What is "Habitat"?

Birds and bird communities have played a major role in the development of the concept of habitat, yet specific definitions of the term habitat are often vague and/or differ from one another (Block and Brennan 1993). However, a common theme among different definitions and terms is that "habitat" includes the physical and biological environmental attributes that influence the presence or absence of a bird species (Morrison et al. 1992). Thus, habitat involves many components in addition to vegetation composition and structure. Environmental features (climate, food, patch size or area), predation, competition, parasitism, disease, disturbance, past history and even chance influence the current distribution and abundance of species (Wiens 1989a, 1989b). Research is usually focused on those habitat components that are most easily or reliably quantified and/or considered most likely to influence the bird community, and no single study can address all of the factors that may influence bird species use in a system.

Many factors underlie habitat selection and these factors do not act equally for all species or even for all populations of a single species (Wiens 1989a, 1989b). A species' morphological and physiological traits allow it to exploit subsets of resources and, hence, certain habitats (Morrison et al. 1992). Life-history traits such as foraging behavior and mating strategies are also mechanisms that underlie habitat selection in a species (Hansen and Urban 1992). Proximate factors such as song perches, nest sites, and the structure and composition of the vegetation determine whether a bird settles in a habitat. These are part of a habitat selection "template" (Wiens 1989a) that results from both an individual's genetic makeup and information learned through experience with different areas and habitats. Ultimately, the suitability of a particular habitat is a function of reproductive success and survivorship. Thus, mere occupancy of a habitat does not imply the habitat is optimal, only that it meets the selection template for those individuals breeding there. There has yet to be developed a comprehensive habitat model for the southwestern willow flycatcher that enables one to determine which breeding habitats, or parts of a single breeding patch, are better than others based on vegetation characteristics alone.

General Vegetation Composition and Structure

Southwestern willow flycatcher breeding habitat can be broadly described based on plant species composition and habitat structure. These two habitat characteristics are the most conspicuous to human perception, but are not the only important components. However, they have proven useful in describing known breeding sites, evaluating suitable survey habitat, and in predicting where breeding flycatchers may be found.

We have organized habitat descriptions into three broad types - native vegetation dominated, exotic vegetation dominated, and mixed native/exotic. These broad habitat descriptors reflect the fact that southwestern willow flycatchers now inhabit both native and non-native dominated riparian habitats. Saltcedar (*Tamarix ramosissima*) and Russian olive (*Elaeagnus angustifolia*) are used as nesting substrates and in some cases, flycatchers breed where these species dominate the canopy or occur in nearly monotypic stands. Data on the most conspicuous plant species at 106 flycatcher breeding sites (Table 5-1) demonstrate the widespread use of both native and exotic trees and shrubs.

Narrative descriptions of the general vegetation types used throughout the southwestern willow flycatcher's range are provided below, with a focus on the dominant tree and shrub components. The habitat types described include a continuum of plant species composition (from nearly monotypic to diverse assemblages) and vegetation structure (from simple, single stratum patches to complex, multiple strata patches). Because pictures are often more effective than verbal descriptions at conveying the general nature of a riparian patch, we include one or more photographs of each type of occupied breeding habitat. The intent of the descriptions and photographs is to provide a basic understanding of the types of habitat occupied by the flycatcher, not to create a standardized definition or classification. All known breeding sites are not described or illustrated, so every potential variant is not shown. However, the sites presented capture most of the known range of patch floristics, structure, and size.

Native Vegetation Dominated

Many of the areas used by breeding southwestern willow flycatchers are dominated by native trees and shrubs, especially, as one might expect based on the bird's common name, willows (*Salix* spp.). The floristic and gross structural variation of occupied native-dominated habitats is quite broad. Occupied sites vary from monotypic, single strata patches to multi-species, multi-layered strata with complex canopy and subcanopy structure. Overall, low to mid-elevation sites and high elevation sites differ substantially, and are treated separately below.

Low to Mid-Elevation Native Sites:

General characteristics: These sites range from single plant species to mixtures of native broadleaf trees and shrubs including (but not limited to) Goodding's (*Salix gooddingii*) or other willow species, cottonwood (*Populus* spp.), boxelder (*Acer negundo*), ash (*Fraxinus* spp.), alder (*Alnus* spp.), and buttonbush (*Cephalanthus occidentalis*). Average canopy height can be as low as 4 m or as high as 30 m. Gross patch structure is generally characterized by trees of different size classes, often forming a distinct overstory of cottonwood, willow or other broadleaf tree with recognizable subcanopy layers and a dense understory of mixed species. Although some descriptions of flycatcher breeding habitat emphasize these multi-species, canopied associations, flycatchers also breed at sites with tall (>5 m or greater) monotypic willow.

Table 5-1. Frequency of occurrence of different types of southwestern willow flycatcher breeding sites based on whether the tree and shrub components are dominated by native or exotic species, or a mixture of both. Data are for 106 known breeding sites (as of 1998) from Ahlers and White (1999), Sferra et al. (1997), McKernan and Braden (1998), Cooper (1997), and USFWS unpublished data.

State	Native Dominated	Exotic Dominated	Mixed Native/Exotic	Total
Arizona	12	3	30	45
California	11	0	8	19
Colorado	8	0	2	10
New Mexico	14	0	10	24
Nevada	0	0	1	1
Utah	4	2	1	7
Total	49	5	52	106

Exotic or introduced trees and shrubs may be a rare component at these sites, particularly in the understory. In an unusual site along the upper San Luis Rey River in San Diego County, CA, willow flycatchers breed in a streamside area dominated by live oak (*Quercus agrifolia*), where willows once predominated but were eliminated by a phreatophyte control program several decades ago (W. Haas, pers. comm.).

Examples

South Fork Kern River at Lake Isabella, Kern County, CA. Elevation 780 m. (see Whitfield and Enos 1996). This is one of the largest tracts of monotypic native-dominated flycatcher habitat in the Southwest (Figure 5-1). The site includes roughly 500 ha of riparian woodland dominated by a dense overstory of red willow (*Salix laevigata*) and Goodding's willow, interspersed with open areas often dominated by nettle (*Urtica dioica*), mule fat (*Baccharis salicifolia*), cattails (*Typha* spp.), and tules (*Scirpus* spp.). Canopy height is typically 8 to 12 m. This site has numerous river channels, sloughs, and marshes that provide surface water and saturated soils throughout most of the breeding season (Figure 5-2).

Santa Ynez River, Santa Barbara County, CA. (see Holmgren and Collins 1995). Willow flycatchers breed

Figure 5-1. Breeding site at the South Fork, Kern River, CA. Note the canopy height and breadth of floodplain at this cottonwood-willow dominated site. Photo by Mark Sogge.

Figure 5-2. Breeding site at the South Fork, Kern River, CA. Note the dense tangle of willow understory and small openings directly above surface water. Photo by Mark Sogge.

at several areas along the perennial Santa Ynez River between Buellton (elevation approximately 150 m) and the ocean. These species-rich riparian sites (Figure 5-3) are comprised of red willow, black cottonwood (*Populus trichocarpa*), and box elder, with dense, shrubby thickets of willows (*Salix lasiolepis* and *S. exigua*), mulefat, poison oak (*Toxicodendron diversilobum*), and blackberry (*Rubus* spp.). Beaver dams pond water in may areas along the river, creating slow-water and emergent marsh conditions.

San Pedro River, Pinal County, AZ. Elevation 600 m. (see Spencer et al. 1996). Several flycatcher breeding sites along this narrow riparian system are dominated primarily by cottonwood and willow, with some ash

Figure 5-3. Breeding site on the Santa Ynez River, CA. Note the structural complexity and density of the multiple native broadleaf species, and the proximity to surface water. Photo by Mark Sogge.

and boxelder overstory. Understory is comprised of younger trees of these same species, with saltcedar as a major to minor component in some areas. Overstory canopy height averages 15 to 20 m. Open water, marshes and seeps (including cattail and bulrush; Figure 5-4), and saturated soil are present in the immediate vicinity.

Gila River, Grant County, NM. Elevation 1,480 m. (see Skaggs 1996, Stoleson and Finch 1998). The largest known population of breeding southwestern willow flycatchers is found in a series of riparian patches distributed over a 13 km stretch of the Gila River. Flycatchers breed in two distinct structural types; riparian scrub and riparian forest. Riparian scrub (Figure 5-5) is dominated by 4 to 10 m tall shrubby willows and seepwillow (*Baccharis glutinosa*) that grow along the river bank or in old flood channels. These shrub strips are sometimes less than 10 m wide

Figure 5-4. Breeding site on the San Pedro River, AZ. Note the emergent plants bordering the dense willow and buttonbush-dominated patch. Surface water is present throughout this site. Photo by Mark Sogge.

Figure 5-5. Breeding site on the Gila River, NM. Note the stringers of riparian "scrub," some of which are less than 10 m wide, but in total form a wider mosaic. The exposed banks are the result of past livestock grazing. Photo by Rob Marshall.

and rarely more than 20 m. Riparian forest patches (Figure 5-6) were 100 to 200 m wide, and dominated by trees such as Fremont cottonwood (*Populus fremontii*), Goodding's willow, Arizona sycamore (*Plantanus wrightii*) and boxelder. Understory includes young trees of the same species. Canopy height generally ranges between 20 and 30 m. Much of this forest vegetation is sustained by water from the river and small, unlined water diversions that function much like a dendritic stream system.

High-Elevation Native Sites

General characteristics: As a group, these sites are more similar than low elevation native sites. All known high elevation (1,900 m and above) breeding sites are comprised completely of native trees and shrubs. Most sites are dominated by a single species of willow, such as Coyote willow (*Salix exigua*) or Geyer's willow (*S. geyeriana*). Average canopy height is generally only 3 to 7 m. Gross patch structure is characterized by a single vegetative layer with no distinct overstory or understory. There is usually very dense branch and twig structure in the lower 2 m, with high live foliage density from the ground to the canopy. Tree and shrub vegetation is often associated with sedges, rushes, nettles and other herbaceous wetland plants. These willow patches are usually found in mountain meadows and are often associated with stretches of stream or river that include many beaver dams and pooled water.

Examples

Little Colorado River near Greer, Apache County, AZ. Elevation 2500 m. (see Spencer et al. 1996, Langridge and Sogge 1997). This 14 ha site is a mosaic of dense, shrubby Geyer's willow (Figure 5-7), dense herbaceous ground cover, and open water. The river and associated beaver ponds create marshes, wet meadows and saturated soil conditions. Average willow canopy height is 4 to 6 m. The willow matrix is a combination of clumps and thin (3 to 5 m wide) strips. The shrubby vegetation is structurally composed of a single layer of live vegetation, with dense branch and twig structure and high live foliage density from ground level to canopy. Habitat surrounding the broad valley is primarily ponderosa pine (*Pinus ponderosa*) and scattered houses and cabins.

Beaver Creek, Dolores County, CO. Elevation 2,440 m. (see Owen and Sogge 1997). This is a large site, at least 3,200 m long and 400 to 500 m wide, located in a broad, wide mountain valley. The shrubby vegetation (Figure 5-8) is dense, almost monotypic willow with small amounts of hawthorne (*Crataegus rivularis*). Numerous stream channels and associated beaver ponds create wet or flooded substrates, as well as openings within the dense vegetation.

Exotic Vegetation Dominated

General characteristics: Exotic plant species such as saltcedar and Russian olive were not introduced or

Figure 5-6. Breeding site on the Gila River, NM. Note the openings within the dense cottonwood and boxelder and the channel with agricultural tailwater in the bottom foreground. Photo by Rob Marshall.

Figure 5-7. Breeding site on the Little Colorado River in the White Mountains, AZ. Note the dense shrubby appearance of these high elevation willows not yet fully in leaf. Beaver dams retain surface water throughout the patch during the breeding season. Photo by Mark Sogge.

Figure 5-8. Breeding site on Beaver Creek, CO. Another site where beaver dams pond surface water. Note density and height of willows and patch opening in foreground. Photo by Jen Owen (USGS).

widespread in southwestern riparian systems until approximately 100 years ago. Thus, southwestern willow flycatchers evolved in and until fairly recently (from an evolutionary perspective) bred exclusively within thickets of native riparian vegetation such as willows, cottonwoods and seepwillow. However, southwestern willow flycatchers have responded to the widespread loss and modification of native riparian habitats by nesting within some exotic-dominated habitats. From the standpoint of flycatcher productivity and survivorship, the suitability of exotic-dominated sites is not known. Flycatcher productivity in some exotic-dominated sites is lower than in some native-dominated habitats (Sferra et al. 1997, Sogge et al. 1997), but other factors such as small patch size may be more important correlates of productivity at those sites. The reverse is also true, with some saltcedar-dominated sites having similar or higher flycatcher productivity than nearby native sites (McKernan and Braden 1999, Paradzick et al. 1999). Thus, there is currently no clear evidence that the exotic-dominated habitats in which southwestern willow flycatchers now breed are generally suboptimal.

Southwestern willow flycatchers do not nest in all exotic species that have invaded and sometimes dominate riparian systems. For example, flycatchers do not use arundo (*Arundo donax*) or tree of heaven

(*Ailanthus altissima*). Even in the widespread saltcedar, flycatchers tend to use only two conspicuous life forms: (a) low to mid-stature saltcedar (3-6 m tall) found as a component in the understory of a native cottonwood-willow gallery forest, or (b) tall (6-10 m) mature stands of saltcedar that have a high percentage of canopy closure. Thus, willow flycatchers are largely absent as a breeding species throughout most of the saltcedar habitats of the Southwest, where saltcedar stands are often too short, sparse, or dry.

Most exotic habitats range below 1,200 m elevation. As a group, they show almost as much variability as do low elevation native-dominated sites. Most exotic sites are nearly monotypic, dense stands of exotics such as saltcedar or Russian olive that form a nearly continuous, closed canopy (with no distinct overstory layer). Canopy height generally averages 5 to 10 m, with canopy density uniformly high. The lower 2 m of vegetation is often very difficult to penetrate due to dense branches. However, live foliage density may be relatively low from 0 to 2 m above ground, but increases higher in the canopy.

Examples

Roosevelt Lake, Gila County, AZ. Elevation 640 m. (see Spencer et al. 1996, Sferra et al. 1997). Two of the largest known southwestern willow flycatcher populations in Arizona breed in large, contiguous stands of dense, mature saltcedar at the Tonto Creek and Salt River inflows to Roosevelt Lake (Figures 5-9 and 5-10). The Salt River site is monotypic saltcedar, while the Tonto Creek site includes a few scattered, large cottonwood trees that emerge above the saltcedar canopy, which averages 8 to 12 m in height. Within the patches, there are numerous small openings in the canopy and understory. As is usually the case in such mature saltcedar stands, there is little live foliage below a height of 3 to 4 m within the interior of the patch (although live foliage may be continuous and thick at the outer edges of the patch), and virtually no herbaceous ground cover. However, numerous dead branches and twigs provide for dense structure in the lower 2 to 3 m strata (Figure 5-11). In normal or wet precipitation years, surface water is adjacent to or within the saltcedar patches.

Figure 5-9. Breeding site on Salt River inflow to Roosevelt Lake, AZ. Note dense, tall, monotypic stand of saltcedar with openings in the patch interior. No surface water was present when photo was taken. Photo by Mark Sogge.

Figure 5-10. Breeding site on the Salt River inflow to Roosevelt Lake, AZ. Note the breadth of this floodplain habitat and the numerous openings interspersed within the dense mature saltcedar stand. Surface water was present when this photo was taken in June 1996 by the U.S. Bureau of Reclamation.

Figure 5-11. Breeding site at Topock March, Colorado River, AZ. This illustrates the dense vegetative structure (often dead branches) in the lower 3 to 4 m, and the numerous small branches providing potential nest sites, common to occupied saltcedar stands. Photo by Mark Sogge.

Colorado River in Grand Canyon, Coconino County, AZ. Elevation 850 m. (see Sogge et al. 1997). The willow flycatcher breeding sites along the Colorado River in the Grand Canyon (Figure 5-12) are very small (0.6 to 0.9 ha), dense patches of mature saltcedar, bordered on the upslope side by acacia (*Acacia greggii*) and along the river's edge by a thin band of willow. Saltcedar canopy height averages 8 to 12 m. Live foliage is dense and continuous along the edge of the patch, but does not begin until 3 to 4 m above ground within the patch interior. A dense layer of dead branches and twigs provides for a thick understory below the live vegetation. These sites have almost no herbaceous understory due to a dense layer of fallen saltcedar branches and needles. All patches are no further than 5 m from the river's edge.

Rio Grande at San Juan Pueblo, Rio Arriba County, NM. Elevation 1,800 m. (see Maynard 1995, Cooper 1997). Southwestern willow flycatchers breed in dense riparian vegetation (Figure 5-13) dominated

Figure 5-12. Colorado River in Grand Canyon, AZ. Tall, dense saltcedar borders a backwater channel on the Colorado River. Note the dense live vegetation from ground to upper canopy along the outer edge of the patch. Photo by Mark Sogge.

Figure 5-13. Breeding site on Rio Grande, NM. This dense Russian olive-dominated patch is bordered by emergent marsh and slough channel adjacent to the Rio Grande. Photo by Mark Sogge.

by Russian olive. Several large cottonwoods rise above the Russian olive canopy. The patch is bordered by emergent marsh on one side and the Rio Grande on the other. Canopy height of the Russian olive averages 8 to 12 m in height.

Mixed Native and Exotic Habitats

General characteristics: Many southwestern willow flycatcher breeding sites are comprised of dense mixtures of native broadleaf trees and shrubs mixed with exotic/introduced species such as saltcedar or Russian olive. The exotics are often primarily in the understory, but may be a component of overstory. At several sites, saltcedar provides a dense understory below an upper canopy of gallery cottonwoods, forming a habitat that is structurally similar to the cottonwood-willow habitats in which flycatchers historically nested. A particular site may be dominated primarily by natives or exotics, or be a more-or-less equal mixture. The native and exotic components may be dispersed throughout the habitat or concentrated in distinct, separate clumps within a larger matrix. Sites almost always include or are bordered by open water, cienegas, seeps, marshes, and/or agricultural runoff channels. However, during drought years surface water at some sites may be gone early in the breeding season. Generally, these habitats are found below 1,200 m elevation.

Examples

San Pedro River, Pinal County, AZ. Elevation 600 m. (see Spencer et al. 1996). Parts of the extensive riparian tracts of the lower San Pedro River are dominated by cottonwood and willow, but include substantial amounts of dense saltcedar. In some cases, the saltcedar occurs as a dense understory amidst a cottonwood, willow, ash or boxelder overstory (Figure 5-14), while in others it borders the edge of the native vegetation (Figure 5-15). Overall canopy height ranges from 10 to 18 m.

Verde River at Camp Verde, Yavapai County, AZ. Elevation 940 m. (see Spencer et al. 1996). Southwestern willow flycatchers breed here in a mixture of willow, cottonwood, and saltcedar habitat (Figure 5-16). Most of the territories are found in a cluster of dense decadent saltcedar (6 to 8 m tall) bordered by narrow bands of young willow, which in turn are surrounded on one side by a large (>50 ha) stand of mature cottonwoods and willows (15-20 m tall) with little understory. Although the patch itself is located on a sandy terrace approximately 4 m above typical summer river level, the Verde River flows along the eastern edge of the patch and a small intermittently flowing irrigation ditch provides water to a small pond adjacent to the saltcedar and willows. Patches of herbaceous ground cover are scattered throughout the site, but are absent under the saltcedar canopy.

Figure 5-14. Breeding site on the San Pedro River, AZ. Note the dense 5 to 6 m tall saltcedar interspersed with the taller cottonwood overstory. Photo by Renee Netter (USGS).

Figure 5-15. Breeding site on San Pedro River, AZ. Note the height, density and openings at this mixed native-exotic site. Surface water is present outside the frame. Photo by Eben Paxton (USGS).

Figure 5-16. Breeding site on the Verde River at Camp Verde, AZ. Note the tall cottonwoods and willows mixed with saltcedar. Photo by Mark Sogge.

Virgin River, Washington County, UT. Elevation 1,100 m. (USFWS unpublished data). Along one portion of Virgin River riparian corridor near St. George, flycatchers breed in a mixture of dense willow, Russian olive and saltcedar near an emergent marsh (Figure 5-17). The native trees form a tall (10-12 m) overstory, which is bordered by a shorter (10-12 m) band of saltcedar, and a strip of 4 to 8 m tall willow. The stretch of occupied habitat is approximately 60 m wide and 100 m long, and is located in an old meander channel through which the river no longer flows. In normal and wet years return channels and river flows seasonally inundate the base of the vegetation.

Patch Size and Shape

The riparian patches used by breeding flycatchers vary greatly in size and shape. They may be a relatively dense, linear, contiguous stand or an irregularly-shaped mosaic of dense vegetation with open areas. Southwestern willow flycatchers have nested in patches as small as 0.6 ha in the Grand Canyon (Sogge et al. 1997), and as large as 100 ha or more at Roosevelt Lake (Spencer et al. 1996) and Lake Mead (McKernan 1997). Most sites fall between these two extremes, and overwhelmingly toward the smaller end (probably because large blocks of suitable riparian habitat are uncommon). Flycatchers have not been found nesting in narrow, linear riparian habitats where the entire patch is less than approximately 10 m wide, although they will use such linear habitats during migration.

Figure 5-17. Breeding site on Virgin River, UT. This dense mixture of native and exotics is bordered by slough channels which create openings within the patch. The person in foreground is on a terrace 2 to 3 m higher than the terrain in which the riparian vegetation is rooted. Photo by Mark Sogge.

Except in the extreme smallest cases (such as the saltcedar patches in the Grand Canyon), all flycatcher breeding patches are larger than the sum total of the flycatcher territory sizes at that site. This is because flycatchers, typically, do not pack their territories into all available space within a habitat. Instead, some territories are bordered by additional riparian vegetation that is not defended as a nesting territory, but may be important in attracting flycatchers to the site and/or in providing an environmental buffer (from wind or heat) and in providing post-nesting use areas. Based on numerous habitat use studies (Whitfield and Enos 1996, Paxton et al. 1997, Sferra et al. 1997, Sogge et al. 1997) it is clear that flycatchers often cluster their territories into small portions of riparian sites, and that major portions of the site may be occupied irregularly or not at all. It is currently unknown how size and shape of riparian patches relate to factors such as flycatcher site selection and fidelity, reproductive success, predation, and brood parasitism.

Presence of Water

Flycatcher breeding habitats usually include or are near open water, cienegas, marshy seeps, or saturated soil. In many cases, nest plants are rooted in or overhang standing water (Sferra et al. 1997, Whitfield and Enos 1996). As a general rule, flycatcher territories are seldom farther than a few dozen meters from water or saturated soil. However, it is critical to keep in mind that in the Southwest, hydrological conditions at a site can vary remarkably within a season and between years. At some locations, particularly during drier years, water or saturated soil is only present early in the breeding season (i.e., May and part of June). At other sites, vegetation may be immersed in standing water during a wet year, but be hundreds of meters from surface water in dry years. This is particularly true of reservoir sites such as the Kern River at Lake Isabella, Tonto Creek and Salt River at Roosevelt Lake, and the Rio Grande near Elephant Butte Reservoir. Human-related factors such as river channel modifications (e.g. by creation of pilot channels) or altered subsurface flows (e.g. from agricultural runoff) can temporarily or permanently dry a site. Similarly, where a river channel has changed naturally (Sferra et al. 1997), there may be a total absence of water or visibly saturated soil for several years. In such cases, the riparian vegetation and any flycatchers nesting within it may persist for several years. However, we do not know how long such sites will continue to support riparian vegetation and/or remain occupied by breeding flycatchers.

Other Habitat Components

Other potentially important aspects of southwestern willow flycatcher habitat include distribution and isolation of vegetation patches, hydrology, prey types and abundance, parasites, predators, and interspecific competition. Population dynamics factors such as demography (i.e. birth and death rates, age-specific fecundity), distribution of breeding groups across the landscape, flycatcher dispersal patterns, migration routes, site fidelity, philopatry, and conspecific sociality also influence where flycatchers are found and what habitats they use. Environmental factors (e.g. temperature, humidity), may play an important role in habitat selection, breeding success and persistence, particularly in lowland desert riparian areas. Most of these factors are poorly understood, but may be critical to understanding current population dynamics and habitat use.

Common Factors and Mechanism for Selection

Clearly, willow flycatchers breed in widely different types of riparian habitat across a large elevational range and geographical area in the Southwest. Breeding patch size, configuration, and plant species composition can vary dramatically across the subspecies' range. However, certain patterns do emerge and are seen at most sites. Regardless of the plant species composition or height, occupied sites always have dense vegetation in the patch interior. In most cases this dense vegetation occurs within the first 3 - 4 m above ground. These dense patches are often interspersed with small openings, open water, or shorter/sparser vegetation, creating a mosaic that is not uniformly dense. In almost all cases, slow-moving or still surface water and/or saturated soil will be present at or near breeding sites during wet or normal precipitation years.

These themes common to flycatcher breeding sites – dense vegetation and proximity to water – probably relate directly to the underlying mechanisms driving habitat selection and site suitability. For example, breeding riparian birds in the desert Southwest are potentially exposed to extreme environmental conditions (Hunter 1988, Rosenberg et al. 1991). Dense riparian vegetation with surface water or saturated soil may be needed to provide suitable micro-climatic conditions, therefore limiting the distribution of flycatchers to a subset of available riparian habitats. Given that willow flycatchers are one of the latest nesting birds in Southwestern desert riparian systems (Hunter 1988), their nests may require substantial buffering against extreme environmental conditions. Dense vegetation and surface water may also function to reduce nest predation and cowbird nest parasitism, both of which may be important factors in site suitability.

Currently, we can not distinguish the relative importance of each of the many factors that influence southwestern willow flycatcher habitat use. The relative importance of particular factors may vary geographically, and at the local scale males and females may be selecting for different factors or habitat characteristics (Sedgwick and Knopf 1992). All of this complicates our ability to develop quantitative predictions of flycatcher habitat use. Ongoing and future research (e.g., Paradzick et al. 1999, McKernan and Braden 1999, Ahlers and White 1999, others) on local and landscape patch configuration, vegetation characteristics, productivity, and environmental factors will better determine the mechanisms responsible for habitat use patterns and spur development of accurate and comprehensive habitat suitability models for the southwestern willow flycatcher.

Habitat Suitability

The ultimate measure of habitat suitability is not simply whether or not a site is occupied. Suitable habitats are those in which flycatcher reproductive success and survivorship results in a stable or growing population. Without long term data showing which sites have stable or growing populations, we cannot determine which habitats are suitable or optimal for breeding southwestern willow flycatchers. Some occupied habitats may be acting as population sources, while others may be functioning as population sinks (Pulliam 1988).

What is not Southwestern Willow Flycatcher Breeding Habitat

Cottonwood-willow gallery forests that are devoid of an understory and that appear park-like do not provide nesting habitat for southwestern willow flycatchers. Similarly, isolated, linear riparian patches less than approximately 10 m wide generally do not provide nesting habitat. However, mosaics made up of aggregations of these small, linear riparian "stringers" may be used by breeding flycatchers, particularly at high elevations. High-elevation willow patches devoid of live vegetation structure in the lower strata (0-2 m from ground) are not used for nesting. Short stature (< 4 m) saltcedar stands, as well as sparse stands of saltcedar characterized by a scattering of trees of any height, also do not provide nesting habitat for flycatchers. See Figures 5-18 – 5-21 for examples of some of the common riparian habitat types that are not suitable for nesting southwestern willow flycatchers.

Migrant willow flycatchers may occur in non-riparian habitats and/or be found in some riparian habitats unsuitable for breeding. Such migration stopover areas, even though not used for breeding, may be critically important resources affecting local and regional flycatcher productivity and survival. Furthermore, such sites may be appropriate candidates for restoration efforts designed to create additional willow flycatcher breeding habitat.

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Figure 5-18. Native riparian vegetation that is not suitable flycatcher breeding habitat. This park-like gallery forest along a river in Colorado is tall and wide, but devoid of understory does not provide breeding habitat for the flycatcher. Photo by Mark Sogge.

Figure 5-20. High-elevation native riparian vegetation that is not suitable flycatcher breeding habitat. The cropping of these willow is a result of livestock grazing. The low stature, low density, and lack of breadth keeps this area from attaining the attributes necessary for flycatcher breeding. Photo by Mark Sogge.

Figure 5-19. Native riparian vegetation that is not suitable flycatcher breeding habitat, along Crystal Creek in the Grand Canyon, AZ. Such extremely narrow, linear riparian habitats do not provide breeding habitat for the flycatcher. Photo by Tim Tibbitts (NPS).

Figure 5-21. Saltcedar-dominated riparian vegetation that is not suitable flycatcher breeding habitat. This sparse, low-stature saltcedar stand at Roosevelt Lake, AZ does not provide the tall, dense overall vegetative structure needed by breeding flycatchers. Photo by Mark Sogge.

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Chapter 6: Breeding Season Ecology

The willow flycatcher (*Empidonax traillii*) breeds across much of the conterminous United States and in portions of extreme southern Canada. As might be expected in such a wide-ranging species, willow flycatchers in different portions of the range exhibit differences in appearance, song, and ecological characteristics. The intent of this chapter is to provide information on the breeding-season ecology of the southwestern subspecies, *E.t. extimus*. However, most ecological studies to date have dealt with other willow flycatcher subspecies. Relatively few studies have been published on *E.t. extimus*, and much of what is currently known is presented in unpublished literature (e.g., agency and consulting firm reports); these sources are relied upon heavily in this chapter. This chapter does not address habitat characteristics in depth, other than for nest sites (refer to *A Survey of Current Breeding Habitats* for additional details). Although southwestern willow flycatchers are frequent victims of nest parasitism by brown-headed cowbirds (*Molothrus ater*), this chapter will not address the topic of parasitism and its effect on breeding ecology (refer to *The Ecology of Brown-headed Cowbirds and their Effects on Southwestern Willow Flycatchers* for details). Readers interested in more details of willow flycatcher biology and ecology are encouraged to read McCabe's (1991) treatise, which is based on over a decade of willow flycatchers research in Wisconsin and includes comparisons with other populations and subspecies.

Breeding Range and Taxonomy

The willow flycatcher is one of 11 *Empidonax* flycatchers that breed in North America. Although the *Empidonax* flycatchers are considered a very difficult group to identify by sight alone, each has unique morphological features, vocalizations, habitats, behaviors, and/or other traits that have allowed taxonomists and biologists to characterize each species. The willow flycatcher differs from most other *Empidonax* in lacking a conspicuous eye-ring, and having both a completely yellow lower mandible and a whitish throat that contrasts with a pale olive breast. While these differences may be subtle, the willow flycatcher also has a distinctive song (often termed *fitz-bew*; see below) that clearly separates it from all other bird species.

The willow flycatcher was first described by J.J. Audubon, who collected a specimen in the woods along the Arkansas River in the early 1800s (Audubon 1831) and named it *Muscicapa traillii*. Since that time, the species has undergone a series of name changes and species/subspecies designations (see Aldrich 1951, Browning 1993). Prior to 1973, the willow flycatcher and alder flycatcher (*Empidonax alnorum*) were treated together as the Traill's Flycatcher (A.O.U. 1957), but subsequent work proved that they do not interbreed (Stein 1958, 1963), have different vocalizations (Stein 1958), and are genetically distinct (Seutin and Simon 1988). The American Ornithologist's Union (1973) accepted the separation of willow and alder flycatchers in 1973. McCabe (1991) reviews the many common names historically given to the willow flycatcher.

The southwestern subspecies was first described by Phillips (1948). Unitt (1987) re-evaluated the subspecies taxonomy of the willow flycatcher and recognized four subspecies, each with a distinct breeding range and differentiated primarily by subtle differences in color and morphology. Browning (1993) performed a similar evaluation and proposed five subspecies, rather than four. Both authors, however, reconfirmed the validity of *E.t. extimus*, which has also been accepted by most authors (Aldrich 1951, Behle and Higgins 1959, Phillips et al. 1964, Oberholser 1974, Monson and Phillips 1981, Schlorff 1990, USFWS 1993). Based on Unitt (1987) and Browning (1993), the breeding range of the southwestern willow flycatcher (Figure 6-1) includes southern California (from the Santa Ynez River south), Arizona, New Mexico, southwestern Colorado, extreme southern portions of Nevada and Utah, and western Texas (although recent breeding records from west Texas are lacking). Records of probable breeding southwestern willow flycatchers in Mexico are few and restricted to extreme northern Baja California del Norte and Sonora (Unitt 1987, Wilbur 1987).

The southwestern willow flycatcher is generally paler than other willow flycatcher subspecies (Unitt 1987), although this difference is indistinguishable without considerable experience and training, and without study skins as comparative reference material. All three western subspecies differ from E.t. traillii in wing formula (Unitt 1987). Differentiation of subspecies in the field is not reliable, due to the subtlety of morphological differences, inconsistent conditions for comparisons, and the inability to repeat or reassess the identifications of individual specimens (Hubbard 1999).

Vocalizations

Willow flycatchers are suboscines, and their songs appear to be innate, rather than learned (Kroodsma 1984). In fact, even hatching-year flycatchers can sing (Kroodsma 1984, Sogge 1997). As with most birds, singing behavior is regulated by hormone levels, which in turn are influenced by a number of factors including photoperiod, time of day, and auditory and visual stimuli from other birds of the same species (Kroodsma 1984, Catchpole and Slater 1995).

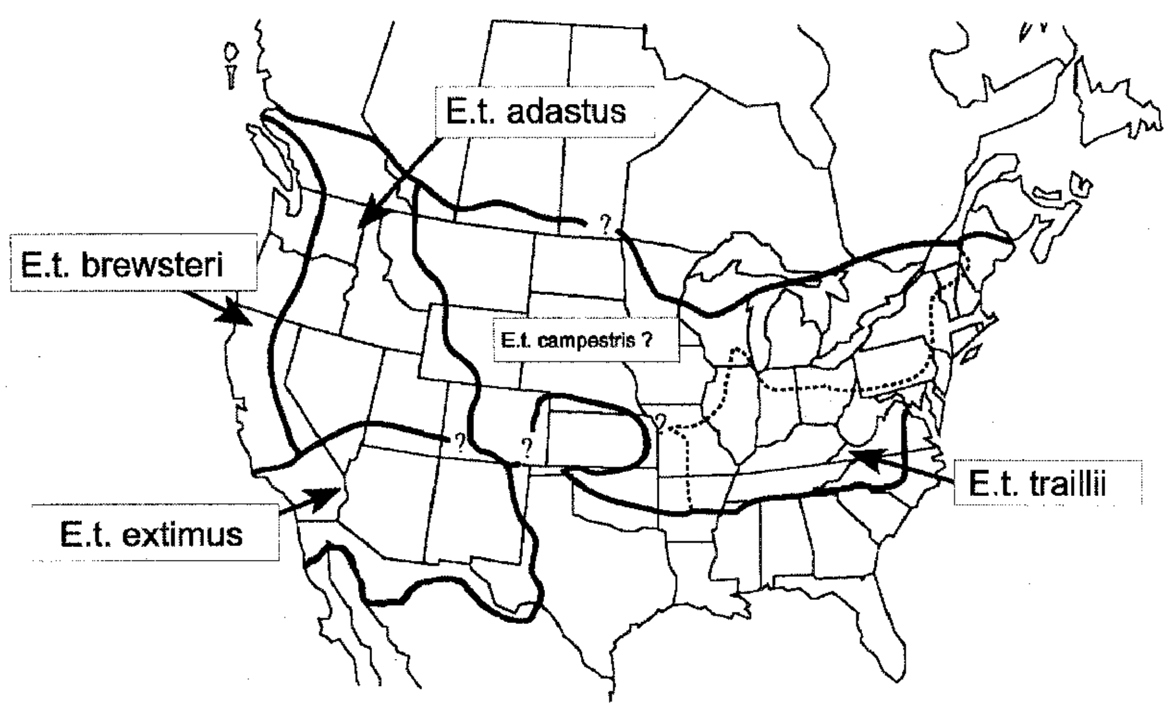

Figure 6-1. Breeding range distribution of the subspecies of the willow flycatcher (*Empidonax traillii*). Adapted from Unitt (1987), Browning (1993) and Sogge et al. (1997a).

The willow flycatcher has a distinct primary song, often referred to as *fitz-bew*, that distinguishes it from all other *Empidonax* flycatchers, and from other birds in general (refer to Stein 1963 for a detailed discussion). This is the primary territory advertising song of male willow flycatchers, and all subspecies sing *fitz-bew*. Singing bouts are usually comprised of a series of *fitz-bews*, sometimes interspersed with *creet* notes, lasting from less than a minute to over a half-hour.

Breeding males sing to advertise their territory to prospective mates and other nearby males. Males sing from a series of song perches throughout their territory, usually from tall perches but sometimes from within dense vegetation. Weydemeyer (1973) and McCabe (1991) described willow flycatchers singing during flight in the evenings, but this has been observed only rarely in *E.t. extimus*. Migrant willow flycatchers often sing from tall song perches during spring migration, in much the way that territorial birds do (Johnson and Sogge 1997). Sogge et al. (1997b) found that migrants accounted for up to 64% of the spontaneously singing flycatchers found each year along the Colorado River in the Grand Canyon. This makes it difficult if not impossible to separate territorial birds from migrants based on singing behavior alone.

Female willow flycatchers also sing, at least in some circumstances. Seutin (1987) reported female willow flycatchers singing in response to tape-playback experiments in southern Canada. Although he clearly established that females sing, the extent of female song under non-experimental conditions was unknown. Until recently, it was generally assumed that females seldom sang, and/or that their songs were quieter and/or not given from song perches in the way that males sing (Sedgwick and Knopf 1992). New research, much of it with banded individuals of known sex, has shown that female southwestern willow flycatchers regularly sing (though not nearly as often as males). Female flycatchers sometimes sing more quietly than males and sometimes near the nest (Sogge et al. 1997b, M. Whitfield unpublished data), but will also sing loudly and persistently from song perches, as is characteristic of males (Paxton et al. 1997). The true extent and function of female song awaits further research, but it is clearly incorrect to assume that all loudly singing willow flycatchers are males.

Male willow flycatchers sing most persistently early in the breeding season, but song rate declines as the season progresses, particularly once the male finds a mate and nesting efforts begin. Territorial flycatchers often begin singing well before dawn (as early as 0330 hrs standard time), and song rate is generally highest early in the morning. Short periods of predawn singing often continue as late as July (Sogge et al. 1997b). In breeding groups with many territorial males, song rate may remain high throughout most of the breeding season. Males may sing up to 60 songs per minute (H. Yard and B. Brown unpublished data). Unmated males and males with territories near other willow flycatchers tend to vocalize more than males in isolated territories (M. Sogge and M. Whitfield, unpublished data).

Being highly territorial, willow flycatchers readily sing and/or call in response to broadcast tapes of willow flycatcher song (Gorski 1969, Tibbitts et al. 1994), which they apparently perceive as an intruding flycatcher. This ready response to taped vocalizations forms the basis of standardized survey protocols currently in use (Craig et al. 1992, Sogge et al. 1997a). In many cases, willow flycatchers that are not vocalizing when surveyors first arrive at a site begin singing in response to a broadcast taped song. Territorial breeding males and females, migrants, and (perhaps rarely) even recently fledged (6-8 week old) willow flycatchers will respond to tape playback (Sogge 1997, Sogge et al. 1997a). However, much as with the general song patterns, response to tape playback declines over the course of the breeding season, and breeding flycatchers may not respond strongly after nesting has begun.

Another common vocalization used by flycatchers is the *whitt* call, which is frequently given by both sexes. *Whitts* are given as an alarm call and during interactions between flycatchers. *Whitt*s are often the most common vocalization used during mid- and late breeding season. Many other bird species have similar *whitt* calls, so unlike the *fitz-bew*, the *whitt* is not generally considered unique to willow flycatchers.

Foraging and Food

Foraging Behavior

The willow flycatcher, as the name implies, is primarily an insectivore. It is an agile aerialist, capable of catching flying insects on the wing. It often does so by darting quickly out on short flights, catching an insect in its bill, then returning to the same or a nearby perch. Another common foraging behavior is gleaning, where they hover to pick insects off of leaves and other vegetation. Willow flycatchers will also drop to the ground to capture insects, and females sitting on nests will sometimes reach out and pluck insects that are crawling nearby. Larger prey (such as dragonflies or butterflies) is often beaten against the perch, killing and softening it prior to consumption. Flycatchers forage within and above the canopy, along the patch edge, in openings within their territory, and above surface water.

Prescott and Middleton (1988) reported that willow flycatchers in Ontario spent 5 percent of time foraging and 63 percent sitting, corresponding to a “sit and wait" foraging tactic whereby birds can simultaneously engage in vigilance, food searching and capture, territorial advertisement, and resting. Preliminary studies on southwestern willow flycatchers documented foraging rates 0 to 4.6 foraging events per minute, with foraging rate highest early and late in the day, and during the nestling period (H. Yard and B. Brown, unpublished data).

Prey Items

All North American *Empidonax* flycatchers appear to have generally similar diets during the breeding season (e.g., predominantly small to mid-sized insects; Beal 1912). Most available information on specific prey items of willow flycatchers comes from studies of subspecies other than *E.t. extimus*, which demonstrate that the species is somewhat of a generalist. Overall, wasps and bees (Hymenoptera) are the most common food items, with beetles (Coleoptera), flies (Diptera), and butterflies/moths and caterpillars (Lepidoptera) being other major components (Beal 1912). Vegetable foods such as berries and small fruits have been reported (Beal 1912, Roberts 1932, Imhof 1962), but overall do not appear to be a significant food source during the breeding season (McCabe 1991).

A study of diet of adult southwestern willow flycatchers (Drost et al. 1997) found a wide range of prey taken. Major prey items were small (flying ants) to large (dragonflies) flying insects, with Hymenoptera, Diptera, and Hemiptera comprising half of the prey items. Willow flycatchers also took non-flying species, particularly Lepidoptera larvae. Plant material was negligible, consisting of a few seeds in several samples.

McCabe (1991) studied the insects brought by adults to nesting willow flycatchers (*E.t. traillii*) in Wisconsin. He found 33 families of invertebrates in a total of 214 food items sampled from eight nests. The most prevalent items were flies (Diptera), butterflies (Lepidoptera), spittlebugs (Homoptera), and beetles (Coleoptera). Immature and non-flying adult insects comprised 30 percent of the total; spiders accounted for 26 percent of the non-flying food items. This suggests that nestlings are fed similar, if perhaps somewhat smaller, food items to those consumed by adults.

Breeding Chronology

A neotropical migrant, southwestern willow flycatchers generally spend only three to four months on their breeding grounds. The remainder of the year is spent on migration or in wintering areas south of the United States (see the Migration and Wintering section). During the relatively short time they are on their breeding grounds, willow flycatchers must find a territory and a mate, build the nest, lay and incubate eggs, raise their young, and care for the fledged young. Figure 6-2 presents a generalized breeding chronology for the southwestern willow flycatcher (based on Unitt 1987, Brown 1988, Whitfield 1990,

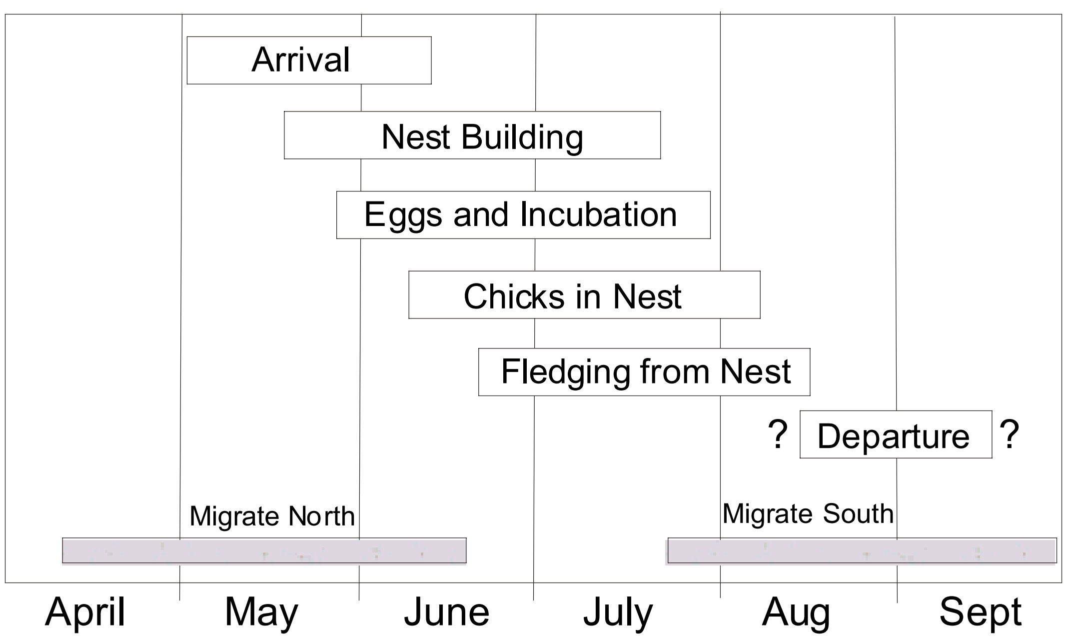

Figure 6-2. Generalized breeding chronology of the southwestern willow flycatcher (from Sogge et al. 1997a). Dates for a given stage may vary a week or more at a given site or during a given year.

Skaggs 1996, Sogge 1995, Maynard 1995, Sferra et al. 1997, and Sogge et al. 1997b). Record or extreme dates for any stage of the breeding cycle may vary as much as a week from the dates presented. In addition, flycatchers breeding at higher elevation sites, and other subspecies in more northerly areas, usually begin breeding efforts several weeks later than those in lower, southern areas.

Southwestern willow flycatchers typically arrive on breeding grounds between early May and early June, although a few individuals may establish territories in very late April (Unitt 1987, Maynard 1995, Skaggs 1996, Sferra et al. 1997). Because arrival dates vary geographically and annually, northbound migrant willow flycatchers (of all subspecies) pass through areas where *E.t. extimus* have already begun nesting. Similarly, southbound migrants (again, of all subspecies) in late July and August may occur where southwestern willow flycatchers are still breeding (Unitt 1987). Therefore, it is only during a short period of the breeding season (approximately 15 June through 20 July) that one can assume that a willow flycatcher seen within *E.t. extimus* range is most likely of that subspecies.

Nest building usually begins within a week of pair formation. Egg laying begins (rarely) as early as late May, but more often starts in early to mid-June. Chicks can be present in nests from mid-June through early August. Young typically fledge from nests from late June through mid-August; later fledglings are often products of renesting attempts. Adults depart from breeding territories as early as mid-August, but may stay until mid-September if they fledged young late in the season (M. Whitfield and W. Haas, unpublished data). Almost nothing is known regarding movements and ecology of adults and juveniles after they leave their breeding sites. Males that fail to attract or retain mates, and males or pairs that are subject to significant disturbance (such as repeated nest parasitism, predation, etc.) may leave territories by mid-July (Sogge 1995, Sogge et al. 1997b). Fledglings probably leave the breeding areas a week or two after adults; in Southern Ontario southward migration dates of immatures occurred 15 days later than for adults (Hussell 1991).

Mating and Territoriality

The southwestern willow flycatcher breeds only in dense riparian habitats, from sea level in California to over 2600 m in Arizona and southwestern Colorado (Sogge et al. 1997a). Although other willow flycatcher subspecies may breed in shrubby habitats away from water, *E.t. extimus* breeds only in dense riparian vegetation near surface water or saturated soil. Other characteristics such as dominant plant species, size and shape of habitat patch, canopy structure, vegetation height, etc., vary widely among sites (refer to *A Survey of Current Breeding Habitats*).

The first flycatchers to arrive at a breeding site are generally males, which establish a territory by singing and aggressive interactions with other flycatchers. Willow flycatchers are very territorial, and will sing almost constantly throughout the day when establishing their territory. Females tend to arrive later (approximately a week or two) and settle on the territory of a male. It is not known exactly what factors a female uses to select a territory, though it may be related to some factor of habitat quality or potential quality of the male. Second year males arrive at about the same time as females (M. Whitfield, unpublished data).

Males are usually monogamous, but annual polygyny rates of approximately 10-15% have been recorded at the Kern River Preserve in California (Whitfield and Enos 1996, 1998). Polygyny has also been recorded in Arizona (Sferra et al. 1997, Sogge et al. 1997b, Langridge and Sogge 1997, Paradzick et al. 1999). Polygynous males typically have only two females in their territory, but there have been several cases of a male with three and four females in a single year (Whitfield and Sogge, unpublished data). Preliminary genetic evidence also suggests that extra-pair copulation occurs, wherein one or more nestlings in a nest are fathered by a flycatcher other than the territorial male for that nest (Paxton et al. 1997).

Initial data from studies of color-banded populations in Arizona (Paxton et al. 1997, Netter et al. 1998) suggest that between-year mate fidelity may be low, and that during a breeding season some flycatcher pairs break up and subsequently pair and breed with other individuals. Whitfield (1980, unpublished data) also documented two cases where pairs that were together early in the season broke up and mated with other flycatchers later that same season. Such pair "reshuffling" may be related to initial nest failure, but additional data are needed to test this.

Southwestern willow flycatcher are strongly territorial, and will defend their breeding area from other flycatchers. Flycatcher territories (defined as a defended area, per Noble 1939) are often clumped together, rather than spread evenly throughout a habitat patch. This has led some authors to label willow flycatchers as "semi-colonial" (McCabe 1991), although they do not fit the true definition of a colonial species and regularly breed at sites with only one or a few pairs (Sferra et al. 1997, Sogge et al. 1997a and 1997b). The Least Flycatcher (*Empidonax minimus*) also tends to breed in groups (Briskie 1994).

Territory size varies greatly, probably due to differences in population density, habitat quality, and nesting stage. Early in the season, territorial flycatchers may move several hundred meters between singing locations, although this has been documented only at sites with one or two territorial males (Sogge et al. 1995, Petterson and Sogge 1996, R. Marshall pers. comm.). During incubation and nestling phases territory size, or at least the activity centers of pairs, can contract and be very small. Mapped breeding territory sizes are 0.06 to 0.2 ha for flycatchers occupying 0.6-0.9 ha patches on the Colorado River, AZ (Sogge et al. 1997b), 0.2 to 0.5 ha in a 1.5 ha patch along the Verde River, AZ (Sogge 1995), and 0.14-2.3 ha along the Kern River, CA (Whitfield and Enos 1996). Estimated territory sizes at the Gila River near Cliff, NM ranged from approximately 0.2 to >1 ha per territory (Skaggs 1996). Reported territory sizes of other willow flycatcher subspecies are also variable; 0.09 ha (Trautman 1940), 0.3 ha (McCabe 1991), 0.4 ha (Walkinshaw 1966), and 1 ha (Gorski 1969). However, only Gorski's (1969) study was based on detailed observations of color-banded individuals, and territory sizes for other studies must be viewed as approximations.

Territories of polygynous males are often larger than those of monogamous males (M. Whitfield pers. comm.). Flycatchers may use a larger area than their initial territory after their young are fledged, and utilize non-riparian habitats adjacent to the breeding area. Even during the nesting stage, adult flycatchers sometimes fly outside of their territory (often through the "air space" of an adjacent territorial flycatcher) to forage for their nestlings.

Site Fidelity

It is often assumed that most passerine birds, particularly those that are highly territorial, exhibit strong breeding site fidelity between and within years. Until recently, this was thought to be the case with the southwestern willow flycatcher. Repeated annual survey efforts on unbanded willow flycatcher populations (Sogge 1995, Sferra et al. 1997, Sogge et al. 1997b) found that the location and boundaries of individual flycatcher territories were often very similar in successive years, leading to speculation that the same male was holding the territory each year and that site fidelity was therefore high.

Evidence gathered during multi-year studies of color-banded populations (Figure 6-3) shows that although most male flycatchers return to former breeding areas, southwestern willow flycatchers regularly move among sites within and between years. Between 1996 and 1997, 29 percent of banded willow flycatchers in Arizona returned to the breeding site of the previous year, while 11 percent moved to other breeding areas within the same major drainage (Paxton et al. 1997). The remaining 60 percent of flycatchers were not relocated in 1997, and may have died or moved to undiscovered breeding sites. Distance moved ranged from 2 to 30 km, and movements were not always to the next closest breeding area. Among those flycatchers returning to the same breeding site between years, 23 percent moved to a different part of the habitat patch. Distance moved ranged from 20 to 900 m. There were also two cases of movement (>500 m) within a breeding site during the course of a breeding season. Thus, although most returning flycatchers showed site fidelity to breeding territories, a significant number move within and among sites. The mechanisms controlling the decision to return or move, as well the adaptive value of movement between sites, are unknown. Such movement does increase gene flow among breeding groups, which provides for higher genetic diversity than if movements did not occur.

In some cases, willow flycatchers are faced with a situation that forces movement, such as when catastrophic habitat loss occurs. In 1996 and 1997, occupied flycatcher breeding habitat was destroyed by fire at two sites, one along the San Pedro River in Arizona (Paxton et al. 1996) and the other along the Gunnison River in southwestern Colorado (Owen and Sogge 1997). In Arizona, the willow-cottonwood habitat was completely burned during the breeding season as nesting was underway, destroying all or most of seven territories. At least four nests were lost, and all willow flycatchers abandoned the site within a week after the fire and were not seen again that year. No willow flycatchers attempted to breed in the burned area in 1997. Seven displaced flycatchers were resighted in 1997; two had moved to unburned areas within the breeding site, and five moved to other breeding areas

Figure 6-3. A color-banded southwestern willow flycatcher. Photo by Michael Moore.

between 2 and 28 km away. In Colorado, virtually all of the tamarisk (*Tamarix ramosissima*) and willow habitat was destroyed, leaving only charred sticks and a few small scattered live willows. Surprisingly, some flycatchers returned to the burned areas and attempted to breed, even in areas without any live vegetation. However, pairing success and subsequent productivity was negatively affected. Several southwestern willow flycatcher breeding populations also face potential habitat loss due to flooding from rising reservoir levels. Where and how far these displaced flycatchers will move is uncertain and the subject of on-going studies (e.g., Paxton et al. 1997).

Nests and Eggs

Southwestern willow flycatchers build open cup nests constructed of leaves, grass, fibers, feathers, and animal hair; courser material is used in the nest base and body, and finer materials in the nest cup (Figure 6-4). Willow flycatcher nests sometimes have 2-15 cm of loose material dangling from the bottom of the nest. In tamarisk-dominated habitats, nests may be constructed completely of tamarisk leaves and have no hanging material from the bottom (Figure 6-5). Nests are approximately 8 cm high and 8 cm wide (outside dimensions), exclusive of any dangling material at the bottom.

Figure 6-4. Willow flycatcher nest placed in a willow near Alpine, AZ. Photo by Mark Sogge.

Females build the nest, with little or no assistance from the male, over a period of four to seven days (although renests are often built in as little as two or three days). McCabe (1991) conducted detailed studies of nest building *E. t. traillii* and found that females brought and added material to the nest every 7 to 10 minutes. Most nests are used only once, although females will often use some fibers and materials (particularly the lining) from the original nest when constructing a subsequent nest during the same season (McCabe 1991). There are only a few recorded instances of reuse of the same nest during a breeding season (H. Yard, B. Brown, and Arizona Game and Fish Department unpublished data) and no records of reuse between years.

Typical nest placement is in the fork of a branch with the nest cup supported by several small-diameter vertical stems. The main branch may be oriented vertically, at an angle, or (rarely) horizontally and stem diameter for the main supporting branch can be as small as 2 to 4 cm. Vertical stems supporting the nest cup are typically 1 to 2 cm in diameter. The nest materials are interwoven among the supporting branches and twigs, such that nests cannot readily be separated from the branches without destroying the nest. McCabe (1991) studied details of *E. t. traillii* nest placement, and found that a network of main and support branching stems are the key to nest placement. Main nest support stem diameter averaged 1.3 cm, and support branches averaged between 2 and 5 cm diameter. Each nest included an average of five support branches, most of which angled upward between 40 and 70 degrees (with a peak at 50 to 60 degrees). Such supporting branch systems are typical of southwestern willow flycatcher nests as well.

Nest height varies considerably (from 0.5 to 18 m), and may be correlated with height of nest plant, overall canopy height, and/or the height of the vegetation strata that contains small twigs and live growth. In Arizona and California, flycatchers using mainly native broadleaf riparian habitats often nest relatively low (usually 2 to 3 m above ground; Sferra et al. 1997, Whitfield and Enos 1996), whereas those using mixed native/exotic and monotypic exotic riparian habitats often nest higher (usually 4 to 7 m above ground; Sferra et al. 1997, Sogge et al. 1997b). However, in any habitat type, nests may be found wherever the appropriate twig structure and plant cover occurs, at almost any height and location (near the center or

Figure 6-5. Southwestern willow flycatcher nest placed in tamarisk at Roosevelt Lake, AZ. Photo by Renee Netter.

on the edge of the nest bush). For example, flycatchers sometimes nest >10 m high in native-dominated habitats along the San Luis Rey River, CA (W. Haas, unpublished data) and the Gila River, NM (Stoleson and Finch 1999). At such sites nest height is linked to the tree species that dominates the site.

Prior to 1950 the vast majority of southwestern willow flycatcher nests were found in willows (Grinnell and Miller 1944, Phillips 1948, Phillips et al. 1964, Hubbard 1987, Unitt 1987). This is not surprising, given that willows were prevalent in streamside riparian stands in the southwest and that young willows can provide the dense cover and fine branching structure favored by nesting flycatchers. However, as the southwest experienced reduction and loss of native riparian vegetation and the invasion of several exotic plants, the willow flycatcher adapted to new host plants and now nests in both native and introduced species.

At high elevation sites in Arizona and southwestern Colorado, Geyer (*Salix geyeriana*) and other willows are used almost exclusively for nesting (Owen and Sogge 1997, Sferra et al. 1997). Along the Gila River in Grant County, New Mexico, 76 percent of southwestern willow flycatcher nests were placed in boxelder (*Acer negundo*), the dominant understory species, with the remainder in other native and exotic plants (Skaggs 1996). Saltcedar is the most frequent nest substrate in Arizona (Brown 1988, Paradzick et al. 1999) and New Mexico (Hundertmark 1978, Hubbard 1987, S. Williams pers. comm.), and is also used for nesting in Colorado, Nevada, and Utah (Owen and Sogge 1997, Langridge and Sogge 1998, McKernan and Braden 1999; M. Sogge unpublished data). Nests are often placed in tamarisk even when native vegetation is present and/or predominant in a territory (Sferra et al. 1997, Owen and Sogge 1997, Paradzick et al. 1999, USFWS unpublished data). However, not all tamarisk habitat appears suitable for nesting flycatchers. Willow flycatchers nest in Russian olive (*Elaeagnus angustifolia*) at some New Mexico breeding sites (Hubbard 1987, Maynard 1995, Cooper 1996 and 1997). In California, most nests are in native vegetation including willow and stinging nettle (*Urtica* spp.; Holmgren and Collins 1995, Whitfield and Enos 1996). In a very unusual situation along the San Luis Rey River in San Diego County, California, approximately 90 percent of flycatcher nests were in live oak (*Quercus agrifolia*), which became the dominant plant species adjacent to the river following willow removal in the 1950s (W. Haas, pers. comm.). McCabe (1991) demonstrated somewhat similar switching between nest substrates in Wisconsin as substrate availability changed among years. Southwestern willow flycatcher nests have also been found in buttonbush, black twinberry (*Lonicera involucrata*), Fremont cottonwood, alder (*Alnus* spp.), blackberry (*Rubus ursinus*), baccharis (*Baccharis* spp.) and other plants. Overall, the plant species appears less important than the appropriate live foliage density and twig structure.

Willow flycatcher eggs are buffy or light tan, generally with brown markings in a wreath at the blunt end but occasionally unspotted (Bent 1942). Eggs are approximately 18 mm long and 14 mm wide, and weigh about 1.6 g (McCabe 1991). Clutch size is usually 3 or 4 eggs for first nests, and is typically smaller in Arizona and New Mexico (usually 3) than in California and elsewhere in the species' range (usually 4; McCabe 1991, M. Whitfield unpublished data). The reasons for these differences are not known, but may be related to food availability or condition of the breeding female (Lack 1954). Female flycatchers lay one egg per day, although some four egg clutches may take five days to lay.

Females generally do not begin incubating until the entire clutch has been laid. Incubation generally lasts 12-15 days from the date the last egg is laid. McCabe (1991) gave a mean incubation period for *E.t. traillii* of 14.84 days (n=50 nests), and found that in 97 and 82 percent of three and four egg clutches, respectively, all eggs in a nest hatch within 48 hrs of each other. He also recorded a 3 percent rate of infertile or addled eggs. After hatching, females carry the eggshell fragments away from the nest.

Most incubation is by the female, although males have been recorded incubating in Arizona (H. Yard, B. Brown, and Arizona Game and Fish Department unpublished data). Incubating females sit tightly in the nest cup, with head and tail protruding over the nest edge. Females spend approximately 50 percent of the day attending (incubating or shading) the eggs (H. Yard and B. Brown unpublished data), and incubate throughout the night (Arizona Game and Fish Department unpublished data). Daytime incubation and shading bouts last from less than one to more than 60 minutes. Shading females stand on the nest rim or within the nest cup, positioned to provide shade to the eggs when the nest received direct sunlight. When shading during the heat of the day, females often appear heat-stressed, panting with mouth open.

Nestlings and Parental Care

Nestlings hatch out (on day 0) weighing only 2 g, mostly naked with only sparse gray down and the yolk sac still visible. Young hatch with the help of an egg tooth, which is no longer visible after the first week (King 1955, McCabe 1991). The edge of the bill and inside of the mouth of nestlings are bright yellow (Figure 6-6), as opposed to the orange mouth linings of brown-headed cowbirds (Tibbitts et al. 1994). Recently hatched flycatchers are unable to lift their head or move about, and motor coordination does not develop until days 2 or 3. Nestlings grow rapidly, reaching about 14 g by day 10. Feather development also occurs quickly, with most body and flight feathers emerging from the feather tracts by day 5 or 6, and feathers unsheathing on days 7 through 10. By days 10 or 11, nestlings are well feathered (with noticeable buffy wing bars), are able to perch on the edge of the nest and often actively preen. Wing flight feathers are unsheathed, although the tail is still very short and underdeveloped. By day 12, nestlings engage in much wing flapping in preparation for fledging and flight.

Figure 6-6. Nestling southwestern willow flycatcher. Note the yellow edge of bill and mouth lining. Photo by Eben Paxton.

For the first few days after the chicks hatch, the female performs most of the care of the young. As the nestlings grow and demand for food increases, the male brings food to the nest more often and by days 8-10 both parents feed the young about equally. Only the female broods the young, although both parents will shade nestlings if the nest is exposed to full sun. McCabe (1991) presents many details of parental care in willow flycatchers (*E.t. traillii*). Nest attendance decreased with nestling age, with females spending less than 10 percent of their time at the nest after day 7. The number of feeding trips peaked at approximately 30 trips per hour during days 5 through 10.

Young willow flycatchers usually leave the nest (fledge) at 12 to 15 days of age, but will fledge prematurely as early as day 10 if a nest is disturbed (e.g., by a predator or researcher). After fledging, young flycatchers stay close to the nest and each other for 3 to 5 days. Recently fledged birds may repeatedly return to and leave the nest during this period (Spencer et al. 1996), up to three times per hour (McCabe 1991). Fledglings stay in the natal area a minimum of 14 to 15 days after fledging, possibly longer. Male and female adults both feed the fledged young, which beg loudly (typically a "*peep*" call) as they perch or move about in the dense vegetation. The period following fledging is a time of high energy demand for fledglings, and parental feeding rates can be as high as 30 nest visits per hour.

Renesting

Second clutches within a single breeding season are uncommon if the first nest is successful, though this may vary between sites and years. M. Whitfield (unpublished data) has recorded only 5-10 percent renesting following successful first nesting. Most attempts at double brooding occur if the young fledge from the first nest by late June or very early July. On the other hand, willow flycatchers usually attempt another nest if the first nest is lost or abandoned due to predation, parasitism, or disturbance. Replacement nests are built in the same territory, and may be close to (even in the same plant) or far from (up to 20 m) the previous nest (McCabe 1991, Sogge et al. 1997b). McCabe (1991) found no differences in nest placement parameters between first nests and renests in *E.t. traillii*. Females usually begin construction of replacement nests within a day or two following the loss of the first nest, and replacement nests are usually constructed more quickly than first nests. Replacement nest building and egg laying can occur (uncommonly) as late as late-July or early August. Pairs may attempt a third nest if the second fails (Sferra et al. 1997, M. Whitfield pers. comm.), and Harris (1991) documented one female attempting six nests in one season. Clutch size (and therefore potential productivity) generally decreases with each nest attempt (Holcomb 1974, McCabe 1991, Whitfield and Strong 1995).

Post-Breeding Dispersal

Few specifics are known about when breeding pairs and their young leave their territory after nesting is completed. Adults that are successful in raising young may remain at breeding sites through mid-August and early September. Pairs with unsuccessful first and/or second nests sometimes abandon their territories midway through breeding season. In at least four cases, members of unsuccessful pairs have moved to other breeding sites within the same season and made second breeding attempts with new mates (Whitfield 1990, Paxton et al. 1997, M. Whitfield unpublished data). In Arizona, unmated males remained on territory through the early part of the breeding season but left by mid-July (Sogge 1995, Sogge et al. 1997b). The exact departure dates of most flycatchers are unknown, and it is not known if post-breeding flycatchers immediately begin their southward migration, or if they disperse and explore local riparian systems prior to heading south.

Competitors

In order for competition to occur, two or more species must attempt to utilize the same limiting resource (Lack 1954, Schoener 1982, Rosenberg et al. 1982). Individuals of the same species are often assumed to be competing (intraspecific competition), at least to some degree, particularly if they establish and defend separate breeding territories. Limiting resources are usually assumed to be food, nest sites, and/or mates. Interspecific competition should be strongest between closely related species that utilize resources in similar ways.

Empidonax flycatchers are very similar in morphology and food habits, and so present the most potential as competitors. Several studies suggest this may be the case. McCabe (1991), for example, found that willow and alder flycatchers maintained mutually exclusive territories at his study site in Wisconsin. Frakes and Johnson (1982) found similar diet and foraging behavior, and little territorial overlap, between coexisting willow and western (*Empidonax difficilis*) flycatchers in Washington. Johnson (1963) noted interspecific territoriality among *Empidonax* species, as did Beaver and Baldwin (1975). In the Southwest, however, the willow flycatcher is usually the only *Empidonax* flycatcher breeding within the dense riparian habitats that it favors, and no evidence has been seen of competition with other flycatchers.

Other less closely-related bird species are less likely to be significant competitors, even where they may share some ecological characteristics (such as nest placement or dietary overlap). McCabe (1991) found no evidence of intraspecific competition between willow flycatchers and co-occurring species such as yellow warblers (*Dendroica petechia*) and American Goldfinches (*Carduelis tristis*), which utilize similar habitat and resources.

There is little evidence that food is a limited resource at southwestern willow flycatcher breeding sites (although food availability may play a role in breeding site selection). For example, insects are usually abundant in flycatcher breeding patches, and nestling starvation is rarely recorded in unparasitized nests. Furthermore, willow flycatchers are to a large degree dietary generalists, and can select among differing prey types depending upon availability. Thus, although flycatchers share their breeding habitats with many other insectivorous birds, competition for food is probably negligible.

In terms of nest site competition, willow flycatchers can build nests in a variety of substrates and locations where suitable branching structure occurs. Several other birds, including yellow warblers and yellow-breasted chats (*Icteria virens*), occur in flycatcher sites and sometimes build nests of similar structure and placement. However, these species do not exclude willow flycatchers from their territories (based on many examples of overlapping territories), and suitable nest sites are usually abundant and unlikely limiting, so competition is not likely.

The one resource for which evidence suggests possible intraspecific competition is mates. Male willow flycatchers are strongly territorial, and establish and defend territories through singing and aggressive interactions. At many southwestern willow flycatcher breeding sites, some territorial males fail to secure mates (Whitfield and Enos 1998, Ahlers and White 1999, Paradzick et al. 1999). This implies that females may be limited in some breeding groups, and that males are competing for this reproductively critical resource, with some males more effective than others. On the other hand, at several of these same sites, some males are polygynous and mate with more than one female in their territory (Whitfield and Enos 1998, Paradzick et al. 1999). The criteria and mechanism by which females evaluate and select males are unknown, but could include song (form, rate, volume, etc.), aggression, or other factors. Females may also be selecting a patch of habitat or breeding territory, whereby the male at that location becomes her mate by default.

Predation and Predators

Predation, particularly during the nesting phase, is a significant factor in the natural history and population dynamics of most small birds, and the southwestern willow flycatcher is no exception. Being a small bird with an open-cup nest, flycatchers are exposed to a wide suite of potential predators. In fact, predation can be the single largest cause of nest failure in some years (e.g., Whitfield and Enos 1996, McCarthey et al. 1998, Paradzick et al. 1999), and most of what we do know about predation and flycatchers involves nest predation. Predation events on adults of most passerine birds are rarely observed, and we have virtually no data of this kind for the southwestern willow flycatcher.

Potential predators observed at or near willow flycatcher territories include a variety of snakes, and small and mid-sized mammals such as chipmunks, weasels, raccoons, foxes, and domestic cats (McCabe 1991, Sogge 1995, Langridge and Sogge 1997, Paxton et al. 1997, Sferra et al. 1997). Predatory birds such as corvids (jays, crows and ravens), hawks (especially accipiters), and owls are regularly found in occupied flycatcher habitat. Brown-headed cowbirds, found in virtually every known flycatcher breeding site, effectively function as predators when they remove a flycatcher egg during parasitization events. Cowbirds have also been documented killing nestling Kentucky warblers (*Oporornis formosus*; Sheppard 1996) and other small songbird chicks (Tate 1967, Beane and Alford 1990, Scott and McKinney 1994), and may be acting as predators on southwestern willow flycatcher chicks (M. Whitfield and Arizona Game and Fish Department unpublished data).

There are four documented cases of nest predation on willow flycatchers. In Wisconsin, McCabe (1991) captured a milk snake (*Lampropeltis triangulum*) that was being harassed by adult willow flycatchers and found it had eaten a complete clutch of four eggs. Paxton et al. (1997) reported two predation events in Arizona. In one, a common king snake (*Lampropeltis getulus*) ate two nestlings, while a third survived by jumping out of the nest. At a second nest, an adult Cooper's hawk (*Accipiter cooperii*) took two nestlings (one at a time) from a nest. As with the king snake event, one nestling survived by jumping from the nest. At the Gila River in New Mexico, three nestlings were taken from the same nest by a Great Horned Owl (*Bubo virginianus*; S. Stoleson unpublished data).

Parasites and Disease

Although individuals of virtually all natural bird populations are exposed to diseases and are hosts to one or more species of internal or external parasites, little is known regarding the role of disease and parasites on most species or populations. Historically, avian parasite and disease literature focused only on documenting occurrence and development of host lists. Recently, increasing attention has been focused on the ecology of bird-parasite interactions (e.g., see Loye and Zuk 1991). Disease and parasites clearly may become a significant factor in periods of environmental stress, during particular portions of a life cycle, or if an exotic/introduced parasite or disease is introduced into a new or naive host (Karstad 1971, Atkinson and van Riper 1991, van Riper 1991). It remains difficult, however, to determine the effect of most parasites on most host species.

The willow flycatcher is host to a variety of internal and external parasites. Bennett et al. (1982) listed *E. traillii* as host for blood parasites such as *Haemoproteus*, *Leucocytozoon*, *Microfilaria* and *Tyrpanosoma*. Boland et al. (1989) and Sabrosky et al. (1989) recorded blow fly (*Protocalliphora* sp.) larvae on nestling willow flycatchers. Pence (1975) reported Traill's flycatcher as host to two species of nasal mites. Most, if not all, avian species (including *Tyrannid* flycatchers) are susceptible to viral pox (Karstad 1971), therefore this disease probably occurs in willow flycatchers (though specific records could not be found). Although these sources provide information on the identity and occurrence of parasites in willow flycatchers, there is no information on what impact, if any, parasites have on the infected birds. McCabe (1991) identified mites

(*Ornithonyssus sylviarum*) in 43 percent of flycatcher nests, but noted no obvious impairment of young. He also recorded blowfly larvae in 32 percent of nests, but again found no evidence of negative effects to nestling flycatchers.

There is virtually no published information available on diseases or parasites in the southwestern willow flycatcher. Recent preliminary examination of blood samples (C. van Riper and M. Sogge, unpublished data) found that *E.t. extimus* is host to several blood parasites, including *Haemoproteus* sp., *Leucocytozoon* sp., and *Plasmodium* sp. (avian malaria). As with other parasites, nothing is known regarding the ecological effects of these blood parasites on the willow flycatcher.

Data Needs

Although the southwestern willow flycatcher received relatively little research attention prior to 1990, a number of studies and monitoring programs initiated since that time have provided us with much useful information relative to the basic ecology of the flycatcher. New studies are being initiated every year. Research programs at the Kern River Preserve (CA), Roosevelt Lake and San Pedro River (AZ), Lower Colorado River (AZ, CA, NV, UT), Rio Grande (NM), and the Gila River (NM) are expected to continue for several more years and will yield valuable data on long-term patterns. Thus, while we have learned a tremendous amount in the last 10 years, we are positioned to discover even more during the next few years.

Unfortunately, there are still large gaps in our knowledge and understanding of southwestern willow flycatcher ecology, including many topics of considerable management and conservation interest (refer to the Research Needs chapter for a more complete listing of research needs and priorities). We need more precise delineation of the subspecies' northern range boundary, based on morphological and genetic examination of breeding populations. Another issue of key importance is the relative suitability of the native and exotic riparian habitats where flycatchers breed. More information is needed on how breeding patch size, shape, and landscape features are related to flycatcher breeding site selection and success. We lack an understanding of how microclimate characteristics influence breeding and nest site selection, especially in low and mid-elevation riparian areas. Data on nest predators are scant even though nest predation may be responsible for the majority of lost productivity. We know very little about the details of and mechanisms behind flycatcher breeding site selection, site fidelity, dispersal, and post-breeding movements, yet these are critical aspects of the flycatcher's habitat use and metapopulation dynamics. Hopefully, future research will be directed at these and other important questions.

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Chapter 7: Migration and Winter Ecology

The willow flycatcher (*Empidonax traillii*) is a Neotropical migrant that breeds in North America, but winters in Central and northern South America. Little specific information is known about migration and wintering ecology of the southwestern willow flycatcher (*E. t. extimus*) (Yong and Finch 1997). Our report applies principally to the species as a whole and not just to the endangered subspecies. In this chapter, we describe timing of migration, migration routes, stopover behavior and ecology, winter distribution, and migration and winter habitats of the willow flycatcher species complex. We also explore the topic of possible threats to migrating and wintering flycatchers associated with habitat loss and pesticide use.

A round-trip journey of 2,000 to over 5,000 miles, depending on departure locations and destinations of individuals, is required by willow flycatchers to migrate between their wintering areas and breeding grounds. Migration and wintering periods account for over half of the annual cycle of the flycatcher and are thus important for understanding the ecology, population changes, and distribution of willow flycatchers. Resource limitations, habitat disturbances, and inclement weather can reduce survivorship of Neotropical migrants during winter and migration periods (Rappole 1995, Moore *et al.* 1995), but data clarifying these relationships with respect to willow flycatchers are limited. While most protection and recovery efforts in the United States emphasize the breeding grounds, conservation strategies for the willow flycatcher would be incomplete if we neglected attention to threats and management actions on the wintering and migration grounds (e.g., Moore 2000). Population declines of the southwestern willow flycatcher may be related to problems that arise during any part of the species' annual cycle.

Migration Ecology

Willow Flycatcher Identification During Migration

Willow flycatchers are difficult to distinguish from alder flycatchers (*Empidonax alnorum*) in the field during migration (Stein 1963, Pyle *et al.* 1997) except by song, and subspecies of willow flycatchers are even more difficult to distinguish from each other (Hubbard 1987, 1999). Most individuals of willow and alder flycatchers can be separated in the hand using Stein's (1963) formula, which combines several wing measurements and bill length. To demonstrate that the migrants captured on the middle Rio Grande were willow flycatchers, Finch and Kelly (1999) applied Stein's formula and found that 88.5% of birds identified as willow flycatchers could be confirmed as willow rather than alder flycatchers (Figure 7-1). Given that Stein's formula only separates 90% of birds known to be willow flycatchers (Stein 1963), that the presence of an alder flycatcher has never been confirmed in New Mexico (Williams 1997), and that young willow flycatchers are less distinguishable from alder flycatchers than adults, Finch and Kelly (1999) concluded that unconfirmed birds captured along the middle Rio Grande were also likely to be willow flycatchers.

Reference to specimen skins increases the probability of accurately identifying live individuals of different subspecies in the hand (Hubbard 1999, Unitt pers. comm.). Yong and Finch (1999) note, however, that collecting voucher specimens of endangered species is generally not approved under endangered species permits, limiting the availability of this option for identifying willow flycatcher subspecies captured in the Southwest. According to Unitt (1987), 90% of birds in which primary 10 is longer than primary 5 are the *E. t. traillii* subspecies and 90% of birds in which primary 10 is shorter than primary 5 are western (*extimus*, *brewsteri*, or *adastus*). Using Unitt's primary-feather criteria to distinguish subspecies, we analyzed 253 middle Rio Grande migrants for this paper and found that 99 (20%) sorted into the eastern subspecies (*E. t. traillii*) class (P10 > P5). Owing to the difficulty of obtaining reference specimens of endangered species, Yong and Finch (1997, 1999) attempted to separate net captures of all four subspecies of willow flycatchers during migration using wing, tail, wing formula (relative length of flight feathers), coloration of the head and neck and its contrast with the back, and the contrast between the breast-band and the throat based on Unitt's (1987) analyses, but these measures do not guarantee accurate identifications (Hubbard 1999). Finch and Kelly (1999) applied principal components analysis of tail length, wing length, bill length, wing formula, and tarsus length of migrant willow flycatchers but found no single or combination of morphological features that readily distinguished among subspecies.

An unpublished report by Unitt (1997) provides further assistance and clarification in separating subspecies, and a peer-reviewed publication of his analysis would aid in resolving discrepancies in methods for identifying willow flycatcher subspecies. At this time, however, we conclude that in the absence of voucher specimens or proven methods to verify subspecies identification, willow flycatcher subspecies should be lumped together when reporting migration results in the Southwest.

Migration Routes

The willow flycatcher as a species breeds as far north as Alaska and winters as far south as northern South America (Unitt 1997). Stevenson (1957) reported that

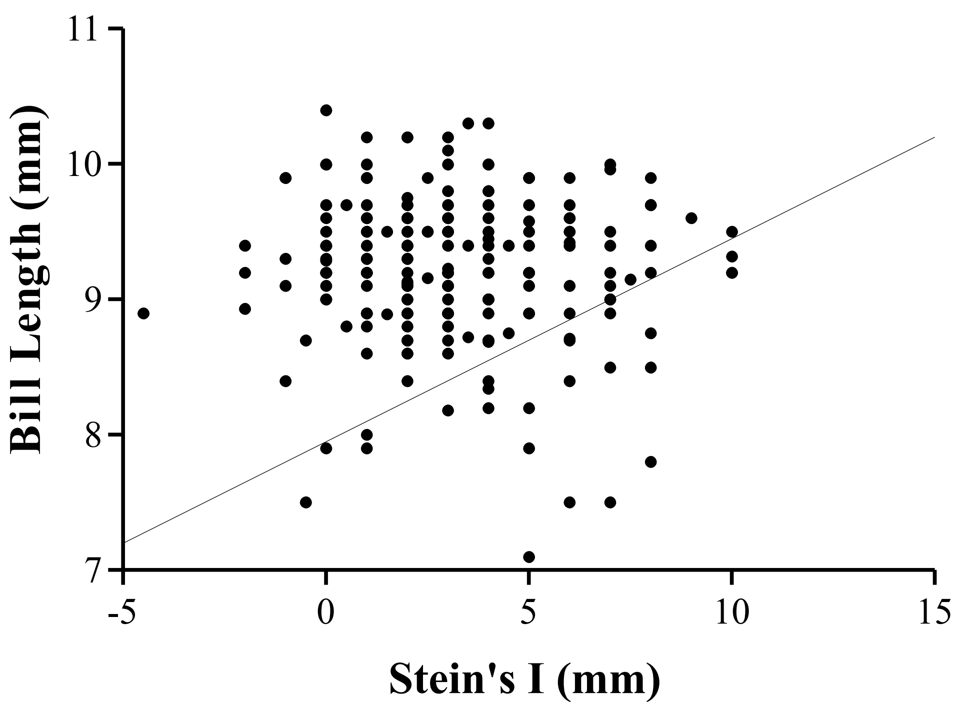

Figure 7-1. Bill length plotted against Stein's I [(length of longest primary minus length of the 6th primary) - length of the 5th primary - length of the 10th primary)]. The equation of the line is bill length = 7.95 + 0.15(I). Stein found that this line separated 90% of Willow and Alder Flycatchers. (Data from the middle Rio Grande, Finch and Kelly 1999).

trans-gulf migration of *Empidonax* flycatchers was not uncommon, but adequate support for use of this migration pattern by the willow flycatcher has not been established. Spring migration route(s) of the willow flycatcher from its winter range in the Neotropics to the United States and Canada are not well-known. Bond (1979) listed the willow flycatcher as a vagrant in Cuba, Isle of Pines, and Jamaica in September and October, and Sturgis (1928) reported it as a spring migrant through the Panama Canal Zone (a semi-Caribbean locale). On the other hand, willow flycatchers were not recorded on Grand Bahama Island (Emlen 1977), Cuba (Barbour 1923, Davis 1941), Haiti and the Dominican Republic (Whitmore and Sales 1931), British Guyana (Blake 1950), or the islands off Venezuela (Voous 1957).

McCabe (1991) suggested a circum-Gulf migration pattern, in which the alder flycatcher leap-frogged the willow flycatcher in establishing winter range, based on studies by Gorski (1969, 1971) and a range map by Fitzpatrick (1980) that showed the wintering distribution of alder flycatchers as disjunct from that of willow flycatchers and lying more to the south. Miller *et al.* (1957) recorded *E. t. traillii*, in spring from the Mexican east coast states of Oaxaca, Tamaulipas and Veracruz, and from Guerrero, Michoacan, Chiapas and Baja California on the west coast in fall. Rappole *et al.* (1979) proposed two different routes for willow and alder flycatchers based on captures of 181 migrant willow-alder flycatchers in Texas (48 km north of Corpus Christi) and 113 in Los Tuxtlas, Veracruz in fall, and 14 willow-alder flycatchers in Texas and 136 in Veracruz in spring migration. They suggested that spring migration is a westerly inland route following the western coastal plain and mid-elevations of the Sierra Madre Oriental of Mexico northward, whereas fall migration followed a western Gulf coast route.

In the Southwest, mist-netting studies and flycatcher surveys show than many willow flycatchers use riparian habitats along rivers and tributaries during migration. Greater effort is needed to survey non-riparian areas to determine extent of willow flycatcher migration and stopover use of other habitats. According to William Haas (pers. comm.), “many willow flycatchers in southern California migrate through scrub (including coastal sage scrub), agricultural valleys that are minimally riparian, and other open woodlands (especially where Mexican elderberry is common)”. Willow flycatchers sing during spring migration making spring migrants easier to distinguish from other *Empidonax* flycatchers than fall migrants. Major drainages where migrating willow flycatchers have been regularly recorded in spring include the Colorado River (Rosenberg *et al.* 1991, Sogge *et al.* 1997; McKernan and Braden 1999), the San Juan River (Johnson and Sogge 1997, Johnson and O’Brien 1998), and the Green River (M. Johnson unpubl. data). In New Mexico, the willow flycatcher is known to migrate regularly in spring and fall along the Rio Grande (Yong and Finch 1997, Finch and Kelly 1999) and the Pecos River (Hubbard 1987), and occurs regularly as a migrant in the southwestern-most desert region and the eastern-most plains region of the state (Hubbard 1987).

Arrival and Departure Dates

Other subspecies of the willow flycatcher migrate through the breeding range of the southwestern subspecies, making accurate identification of arrival and departure dates of *extimus* difficult (Unitt 1987, Yong and Finch 1997, Hubbard 1999). In addition to subspecies differences in migration timing, variation in age, sex, body condition, and point of departure can influence migration arrival and departure dates (Yong and Finch 1997). Male willow flycatchers are reported to arrive on the breeding grounds before females (Bent 1942, Walkinshaw 1966). In the middle Rio Grande valley of New Mexico, adult willow flycatchers migrated through a week earlier (August 26) on average than hatching-year birds (September 2) (Yong and Finch 1997). In addition, spring and fall migration dates of willow flycatchers can vary greatly from year to year (e.g., by as many as 29 days for spring arrivals in Wisconsin (McCabe 1991), further complicating interpretations of subspecies migration periods.

Arrival and departure dates of willow flycatchers vary in relation to the latitude where the birds are recorded. Based on literature records, McCabe (1991) concluded that earliest and latest spring arrival dates of the willow flycatchers at 30-35 degrees north latitude were April 27 and May 11, respectively, whereas at 46-50 degrees north latitude, earliest and latest dates were May 26 and June 14, respectively. Earliest and latest fall departure dates were August 25 and October 8, respectively at 30-35 degrees north latitude and August 27 and September 30 at 46-50 degrees (McCabe 1991).

In Big Bend National Park, Texas, the willow flycatcher is an uncommon spring migrant from May 11-May 28 (Wauer 1985). Hubbard (1987) reported that May 5 was the earliest verified date that willow flycatcher arrived in New Mexico. Southwestern willow flycatchers usually arrive on breeding grounds between early May and early June (Muiznieks *et al.* 1994, Maynard 1995). The typical arrival date of *extimus* in southern California and southern Arizona is the first week of May (Phillips *et al.* 1964, Unitt 1987), but breeding *extimus* has been detected at Prado Reservoir as early as late April (William Haas pers. comm. citing Loren Hays pers. comm.). In the Grand Canyon, Arizona, the earliest record of a male *extimus* on a breeding territory was May 8, although most resident breeding males were detected the third week of May (Sogge *et al.* 1997). In south-central Arizona, some *extimus* arrive as early as the third week in April (Paradzick *et al.* 1999). Yong and Finch (1997) reported that the dates of first and last captures of spring-migrating willow flycatchers netted in the central Rio Grande valley of New Mexico were May 13 and June 8, respectively. We found that spring migration (all subspecies) on the middle Rio Grande peaked in the first week of June, although flycatcher numbers and migration schedules varied by year (1994 to 1997) and by site (Figure 7-2a, b).

The spring migration of *extimus* is earlier than that of the more numerous *brewsteri* (Unitt 1987). *Brewsteri* migrants typically appear 10-15 May (Garrett and Dunn 1981), peaking in numbers through southern California around 1 June (Unitt 1987) and are still migrating north until about 20 June, depending on weather patterns (Garrett and Dunn 1981). Northbound migrants of *brewsteri* as well as other subspecies travel through areas where *extimus* has already begun breeding. To prevent mistaking other subspecies as resident *extimus* breeders, repeated surveys should be conducted from June 20-July 15 (Unitt 1987).

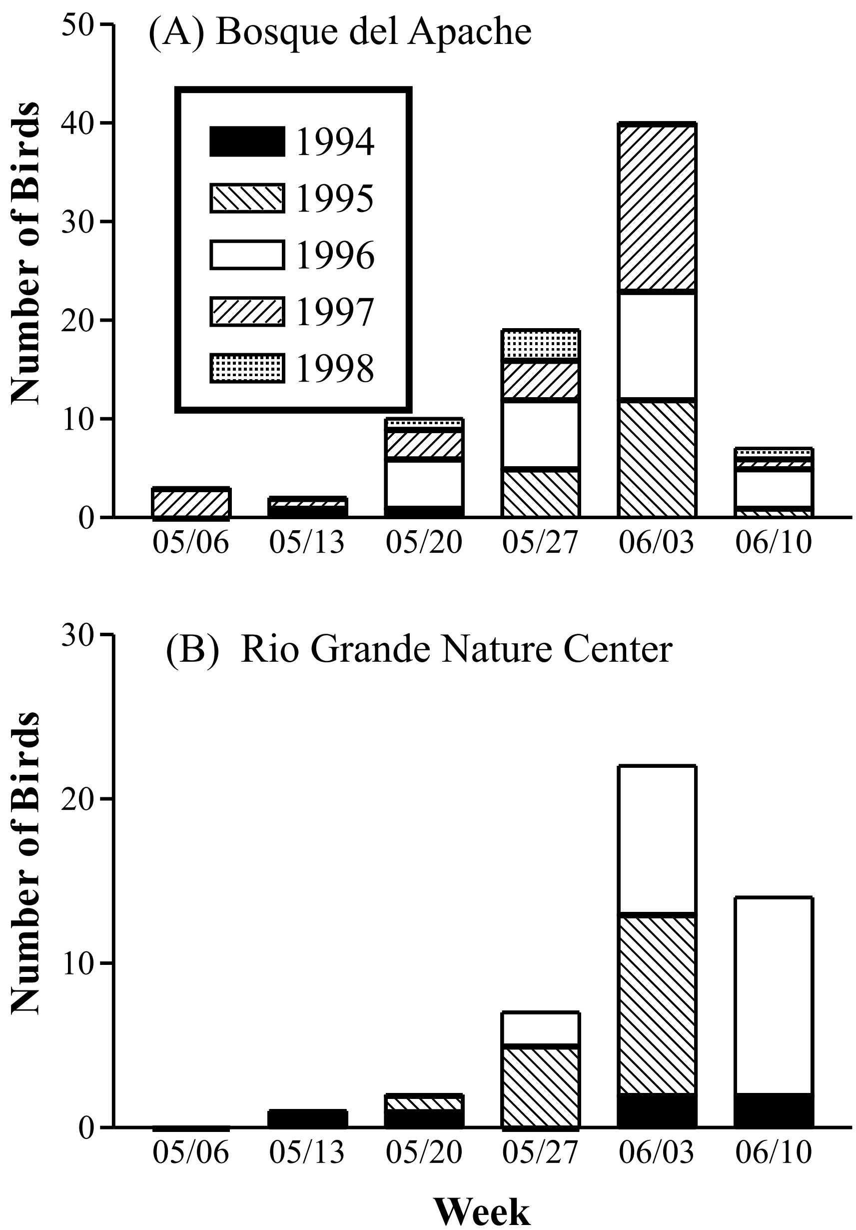

Figure 7-2. Number of willow flycatchers captured by date and year at (A) the Bosque del Apache National Wildlife Refuge (1994-1998) and (B) Rio Grande Nature Center (1994-1996), New Mexico during spring migration (data from Finch and Kelly 1999 and unpublished).

Wauer (1985) reported that the willow flycatcher was a fairly common fall migrant from July 21-September 24 each year at Big Bend National Park, Texas. Fall *brewsteri* migrants arrive in southern California by July 18 (Unitt 1987) when resident *extimus* pairs are still breeding. Earliest records reviewed by Hubbard (1987) for autumn migrants in New Mexico were July 27 (Ft. Bayard), July 29 (Cedar Crest) and July 30 (Hachita). Along the middle Rio Grande, the latest fall capture date for willow flycatchers was September 16 (Yong and Finch 1997). Our observations suggest that fall numbers of willow flycatchers, at least in the middle Rio Grande valley, can vary greatly by year and site (Figure 7-3a, b). Variation in fall numbers from year to year may be related to yearly differences in nesting success, fledgling survival, weather patterns, predation rates, or a combination of factors. Yong and Finch (1997) suggest that habitat differences among sites in the same drainage are most likely to explain site-to-site variation in migration volume. Habitat probably does not explain individual differences in migration timing within each season (Figure 7-2 *in* Finch and Kelly 1999).

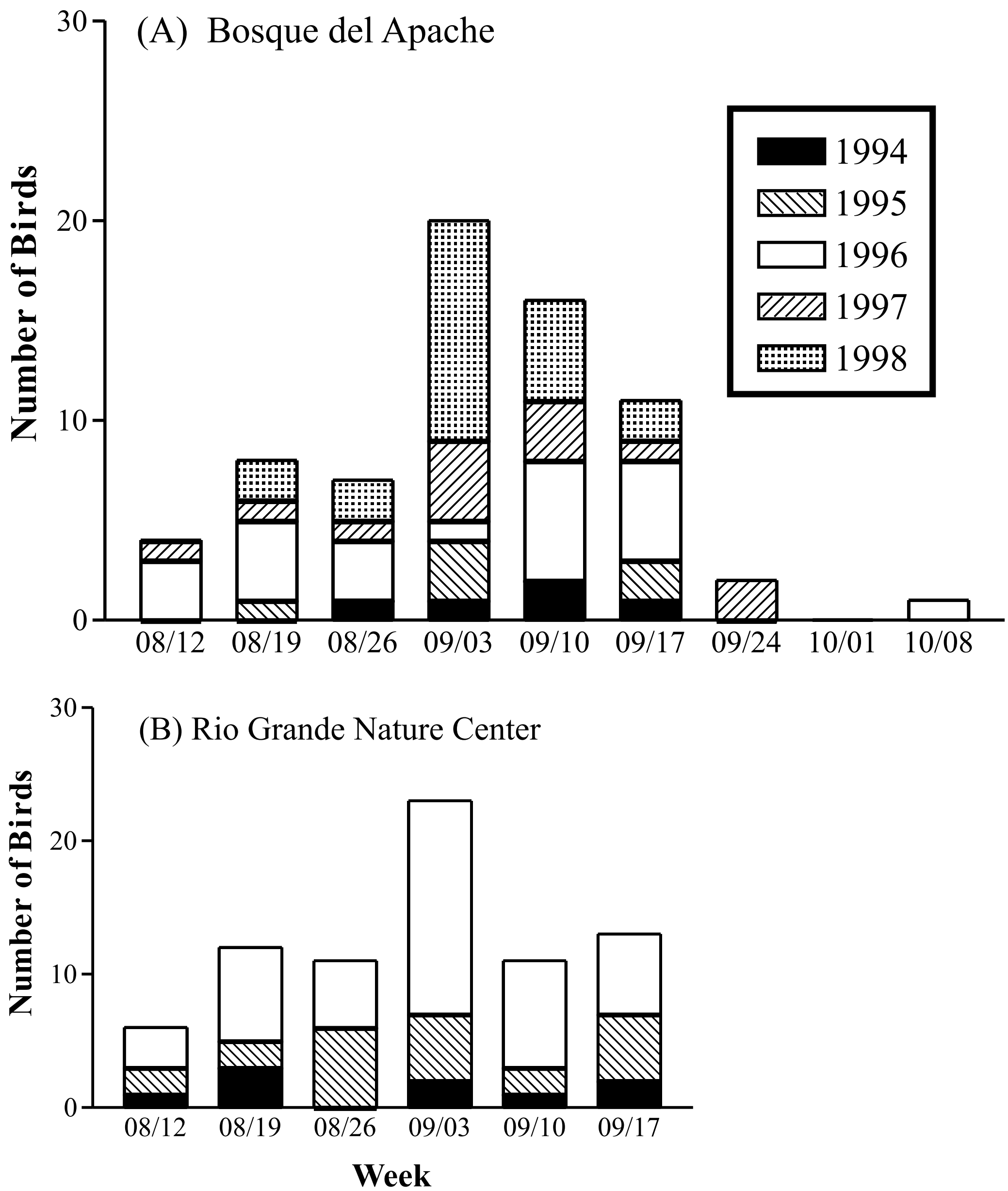

Figure 7-3. Number of willow flycatchers captured by date and year at (A) the Bosque del Apache National Wildlife Refuge (1994-1998) and (B) Rio Grande Nature Center(1994-1996), New Mexico during fall migration (data from Finch and Kelly 1999 and unpublished).

Fat Storage and Body Condition During Migration

Small landbird migrants deposit fat stores before their long-distance flights to prepare for the high energy demands of migration. Migratory birds can deposit fat stores of up to 30-50% of lean body mass (Berthold 1975). However, small landbird migrants, especially Neotropical long-distance migrants such as the willow flycatcher, generally do not deposit enough fat to fly nonstop between breeding and wintering areas. In their study of stopover migrants along the middle Rio Grande, Yong and Finch (1997) reported that 50% of the 84 willow flycatchers sampled in spring and fall had no observable subcutaneous fat stores. Average body mass of migrant willow flycatchers on the middle Rio Grande was 12.7 g and ranged from 10.3 to 15.9 g. Body mass significantly differed among fat classes. Using Pennycuick's (1989) estimator, Yong and Finch computed that average potential flight ranges for all willow flycatchers captured at their study sites was 225 km, but flight ranges were estimated at 257 km to 404 km or higher for flycatchers having fat stores.

Low fat stores could be caused by depletion of fat during nocturnal migration, which according to Moore and Kerlinger (1987), can vary in relation to wind direction and precipitation. Alerstam and Lindstrom (1990) proposed that stopover migrants may maintain low fat stores to minimize the energetic costs of flying with unnecessary weight. Owing to low fat stores, willow flycatchers may be constrained to feed at stopover sites to make progress toward their breeding or wintering destination. Based on low recapture rate (8% of total captures) and the short duration (within one day) between capture and recapture, Yong and Finch (1997) concluded that stopover length of willow flycatchers was relatively brief compared to many other species. About 70% of willow flycatchers were captured between 0700 and 0900 (spring and fall combined) along the middle Rio Grande. Average body mass of recaptures in the middle Rio Grande valley was 12.4 g at initial capture and 12.6 g at last capture, or an average change of 1.6% body mass/day. Body mass tended to be positively associated with daily time of capture in spring and fall.

Average body mass of willow flycatchers captured in spring was significantly higher than that of fall captures along the middle Rio Grande (Yong and Finch 1997). If hatching-year birds weighed less then adults, then age may explain differences in body mass between fall and spring captures. However, adults and hatching-year birds did not differ in body mass in fall. Although body mass did not vary by capture date within spring and fall migration periods, declines in wing length through spring and fall and increases in condition index (mass/wing length-3) during spring migration suggested that flycatcher condition and wing size may be related to departure times (and travel distances) of different groups or subspecies of flycatchers. Differences in departure times of sexes, and influences of interactions between sex, age, and subspecies, may also partially explain variation in body condition and wing length during spring and fall migrations.

Habitat Use During Migration

Karr (1976) recorded willow flycatchers in two shrub habitats of Panama in September, October, January and April. In Veracruz, Mexico, fall and spring willow flycatcher migrants were commonly captured in tall, evergreen tropical forest of various seral stages (Rappole *et al.* 1979). Further north near Corpus Christi, Texas, fall migrants were common in Aransas River floodplain forest but spring migrants used this forest type and/or route less frequently (Rappole *et al.* 1979). At Big Bend National Park, Texas, specimens of the willow flycatcher were taken at sites with water present during spring migration (Wauer 1985).

In New Mexico, migrating willow flycatchers have been recorded in a diversity of habitats. In the Cliff-Gila valley of southwestern New Mexico, migrants use broadleafed riparian forests with canopies composed of box-elder (*Acer negundo*), Fremont cottonwood (*Populus fremontii*), Arizona sycamore (*Platanus wrightii*), and Goodding's willow (*Salix gooddingii*), and understories of mostly native species such as *Rhus trilobata*, *Amorpha fruticosa*, shrub willow (*Salix* spp.), seep willow (*Baccharis glutinosa*), Arizona alder (*Alnus oblongifolia*) (Stoleson and Finch pers. obs.). Along the middle Rio Grande, migrating willow flycatchers use cottonwood woodlands with understories composed of native and/or exotic shrubs such as Russian olive (*Elaeagnus angustifolia*), saltcedar (*Tamarix ramosissima*), New Mexico olive (*Floresteria neomexicana*), willow (*Salix* spp.), and saltbush (*Atriplex* spp.); monotypic saltcedar habitats; irrigation ditches; and agricultural fields (Yong and Finch 1997). Migrant flycatchers have been captured in mist nets along mowed and unmowed water-conveyance channels dominated by coyote willow (*Salix exigua*) and seep willow (Finch *et al.* 1998, Finch and Kelly 1999). Hubbard (1987) reported migrant use of a desert grassland/shrubland site in the southwestern part of the state, and lake and drier sites in the eastern plains grasslands (Hubbard 1987).

A greater variety and distribution of habitats, including non-riparian vegetation, are used by willow flycatchers during migration than during breeding. Migration habitats may lack key components important for breeding birds such as the presence of standing water or moist soils and suitable patch size and structure.

Where native and non-native riparian habitats are present together, some evidence suggests that migrating flycatchers favor native vegetation, especially willow (Yong and Finch 1997, Finch *et al.* 1998, Finch and Kelly 1999). Yong and Finch (1997) reported that willow flycatcher capture rates varied substantially among riparian habitat types during spring migration as well as in fall. In a study comparing stopover use among five habitats along the middle Rio Grande, Finch and Kelly (1999) reported that capture rates of willow flycatchers were higher in unmowed coyote willow than in cottonwood, saltcedar, agricultural edge, and disturbed (previously-mowed) channel willow. A greater number of willow flycatchers were captured in disturbed willow along channels than in other habitats owing in part to greater banding effort in channel willow. Comparing relative habitat use by willow flycatchers to net hours of effort, Finch *et al.* (1998) and Finch and Kelly (1999) found that generally greater percentages were captured in disturbed and undisturbed willow along channels than expected based on the percent effort devoted to banding in that habitat. In contrast, fewer willow flycatchers were captured in agricultural edge and cottonwood habitats than that expected by netting effort expended.

Capture rates of migrant willow flycatchers may vary among habitats in relation to inter-habitat differences in food supplies within and among seasons. DeLay *et al.* (1999) found a positive association between the relative abundance of migrant willow flycatchers and the relative abundance of aerial insects in one year of a two-year study. No relationship was detected between foliage insects (beetles, plant bugs) and flycatcher abundance in either year. Arthropod abundance varied by year, season, and habitat. Habitat differences in arthropod abundance were evident during the period of spring migration but not in fall. In spring, mean numbers of arthropods per trap were highest in willow, intermediate in cottonwood, and lowest in saltcedar. The results of this study suggest that spring migration schedules and stopover habitat-use patterns by willow flycatchers may be influenced by food availability or by cues such as weather that predict *en-route* food supplies.

If food supply varies among habitats during migration periods, fat condition and body mass may depend on how successfully migrants select foraging habitats with plentiful food during stopover. Yong and Finch (1997) reported that body mass and fat condition of stopover willow flycatchers tended to differ by habitat, with heaviest birds captured in willow. However, Finch and Kelly (1999) reported that fat scores and body masses of willow flycatchers did not differ among native and non-native habitats, nor between disturbed (mowed) and undisturbed coyote willow during spring and fall migrations along the middle Rio Grande. Because sample sizes of flycatchers in these studies were small, we suggest that the relationships among habitat, food supply, and body condition during migration be investigated further.

Wintering Ecology

Distribution

Little information is known about the wintering habits of the willow flycatcher, let alone of the subspecies *extimus*. Early accounts did not distinguish between this species and the alder flycatcher. Instead, the two species were collectively described as wintering from south Mexico south through northern Argentina (Meyer de Schauensee and Phelps 1978). More recently, however, it has been recognized that the alder flycatcher alone reaches mid-South America (Howell and Webb 1995), wintering in Brazil, Bolivia, Ecuador, Peru, and northern Argentina (Stotz *et al.* 1996). In Central America, *E. alnorum* occurs only as a transient during migration (Ridgely 1976, Howell and Webb 1995). In contrast, *E. traillii*'s primary wintering grounds are Mexico from the state of Nayarit south and all of Central America (Peterson and Chalif 1973, Stiles and Skutch 1989, Howell and Webb 1995).

In Mexico and northern Central America, the willow flycatcher appears to be restricted to the Pacific Slope (Howell and Webb 1995). From Honduras south, its distribution is less known, but it appears to be present on both the Atlantic and Pacific slopes (see Stiles and Skutch 1989, Howell and Webb 1995). In Costa Rica, the willow flycatcher winters primarily on the Pacific Slope, but it may be found on the Caribbean Slope as well (Stiles and Skutch 1989). Its occurrence as far south as Panama has been well documented by Gorski (1969). Whether the willow flycatcher reaches northern South America has been debated (Gorski 1971, Stotz *et al.* 1996). Hilty and Brown (1986) do not exclude the possibility that in extreme northwest Columbia the wintering resident is *traillii* rather than *alnorum*. Everywhere else in Columbia, however, *alnorum* may replace *traillii*. Unitt (pers. com.) somewhat disagrees with this view, suggesting that the wintering distribution of the willow flycatcher includes instead all of Columbia and northwestern Venezuela while the wintering distribution of the alder flycatcher is disjunct and lies to the south, mainly in Bolivia and Peru.

On its wintering grounds in southwestern Mexico, northern Central America, and Panama, the willow flycatcher is described as fairly common to common (Ridgely 1976, Howell and Webb 1995). In Costa Rica, however, it appears to be generally uncommon as a winter resident (Stiles and Skutch 1989), except perhaps in the northwestern region of Guanacaste (see Koronkiewicz *et al.* 1998).

Based on a recent evaluation of flycatcher museum skins collected on the wintering grounds, Unitt (1997) suggested that the different subspecies co-occur rather than segregate during the winter. The relative proportions of each subspecies to the total population in a wintering area is likely to vary (Sogge pers. comm.). In addition, information is needed on whether males and females winter separately or together.

Habitat

Although varied, the primary wintering habitats for *E. traillii* indicate a preference for semi-open brushy areas often near water. Both Ridgely (1976) and Hilty and Brown (1986) contrast the habitat preference of the willow and alder flycatchers with that of other *Empidonax* spp. such as the Acadian flycatcher (*E. virescens*), the latter group being more strongly associated with woodlands and forests. The list of habitats where wintering *E. traillii* has been recorded includes thickets, shrubby clearings, second-growth scrub, woodland and forest edges, coastal lowlands, and riparian woodlands (Land 1970, Edwards 1972, Peterson and Chalif 1973, Hilty and Brown 1986, Stiles and Skutch 1989, Stotz *et al.* 1996). Habitats used by wintering flycatchers range from humid to semi-arid sites.

In Mexico, wintering flycatchers were found chiefly in coastal lowlands comprised of edge, open woodland, or scrubby habitats (Edwards 1972). A strong association between willow flycatchers and standing water has been described in Panama (Gorski 1969) and Costa Rica (Koronkiewicz *et al.* 1998). In Panama, Gorski (1969) found them in transitional and edge areas, typically near a wetland. In Costa Rica and Panama, willow flycatchers were recorded in lagunas and freshwater wetlands, muddy seeps, wet pastures, slow or meandering rivers, and oxbows, which were often bordered by fields, dense shrubby vegetation, and small groves (Koronkiewicz *et al.* 1998; Koronkiewicz and Whitfield 1999). Specific habitat elements of flycatcher wintering habitat were standing or sluggish water, patches of dense shrubs, stringers or patches of trees, and open to semi-open areas. Dense woody shrubs 1-2 m in height (e.g., *Mimosa* sp. and *Cassi*a sp.) that bordered wetlands were commonly used by willow flycatchers in winter.

Deforestation has been recognized as an important threat for many Neotropical migratory species (Finch 1991, Sherry and Holmes 1993). In light of its habitat associations, however, the susceptibility of the willow flycatcher to deforestation *per se* remains to be established. In Costa Rica, threats to this bird and its habitat may instead consist of livestock grazing, chemical use, and alteration of wetlands due to water diversion and encroachment by plantations (Koronkiewicz *et al.* 1998).

Behavior

Willow flycatchers defend winter territories for foraging, with winter and breeding territories measuring approximately the same size (Gorski 1969). Winter territories may remain relatively constant over the winter (Koronkiewicz and Whitfield 1999). With the onset of the dry season in Panama, however, individuals move to another area and establish new territories (Gorski 1969). Koronkiewicz *et al.* (1998) noted that in northwestern Costa Rica, surface waters are more widespread in the early part of the winter. As the dry season progresses, the availability of standing water diminishes, and the distribution of willow flycatchers may become more restricted.

Further research is needed to determine whether individual flycatchers return each winter to the same site or territory. Territoriality suggests that winter resource(s) may be limiting, at least some of the time, and therefore, territorial flycatchers may be defending one or more resources such as food, water, or perch sites. In Costa Rica, willow flycatchers forage within the dense foliage of woody shrubs (Koronkiewicz *et al.* 1998). Winter diet consists primarily of small insects, which they capture after a short aerial pursuit, or a sally down to the ground, or upward in the foliage (Koronkiewicz *et al.* 1998).

In general, the *fitz-bew* song is rarely heard spontaneously on the wintering grounds (Hilty and Brown 1986, but see Koronkiewicz *et al.* 1998). The *kit* or *whit* note is the call usually observed (Ridgely 1976). Willow flycatchers are apparently more aggressive in winter than alder flycatchers when confronted with playback recordings of their own songs (Gorski 1969, 1971).

Possible Threats

Landbird migrants face a variety of obstacles and threats during migration including inclement weather, landscape barriers, predators, limited food and water, and discontinuity of stopover habitat (see Moore 2000). The probability of a successful migration is likely to be increased when stopover habitats are managed with distances between stopovers in mind. Assuming flycatchers can fly nonstop about 225 km on average (up to 404 km using fat reserves) (estimated by Yong and Finch 1997), then distances between stopover habitats that exceed 225 km may be difficult for many flycatchers to negotiate. Fragmentation of stopover habitats along migration routes may therefore be a potential threat to successful migration and survival of willow flycatchers. Finch *et al.* (1998) and Finch and Kelly (1999) suggest that increasing cycle length of vegetation mowing or eliminating mowing and clearing activities along channels and ditches may improve stopover habitats for migrating flycatchers.

In some habitats, fragmentation that results in smaller habitat patches can increase predation risk at songbird nests. It is possible that predation risk for adult songbird migrants also increases with patch size although data specific to willow flycatchers during any part of their annual cycle are lacking. Given that southwestern riparian habitats are naturally discontinuous, the relationship between predation probability and habitat patch size may be weaker than in habitats naturally occurring as large blocks.

Invasion of exotic shrubs such as saltcedar and Russian olive may affect migration success and habitat use patterns if stopover habitat quality is reduced (Finch and Yong 2000). Although some evidence suggests that migrating willow flycatchers use native habitats such as willow and cottonwood more frequently than introduced habitats such as saltcedar and agricultural fields (Finch *et al.* 1998, Finch and Kelly 1999), habitats dominated by woody exotics supply more structural continuity and food resources for migration than open habitats dominated by grasses and forbs, or man-made sites of riprap banks and urban lots (Kelly and Finch 1999).

Birds eliminate water during migration, and stopovers provide the opportunity to replenish lost body fluids. The presence or absence of available water may influence migration routes, stopover probabilities, and time spent in stopovers. Willow flycatchers are commonly reported in migration near water sources. Water limitations caused by drought, irrigation, and water management activities may pose a problem for migrating flycatchers, and ensuring that water is always present in habitats used by flycatchers may be the best management solution.

Koronkiewicz and Whitfield (1999) reported that the primary threat to flycatcher wintering habitat is loss related to agricultural activities. Winter flycatcher habitats are susceptible to conversion to man-made landscapes used as livestock pastures, clearings, and agricultural plantations. Draining of wetlands used by wintering willow flycatchers will accelerate conversion to habitats associated with drier conditions. Given that wintering flycatchers frequently use habitats associated with standing or slow-moving water, reduction of water and wetlands through irrigation, draining, damming, and habitat conversion may impact survival of willow flycatchers in winter.

Wintering flycatchers forage in wetlands adjacent to, or near agricultural areas that are treated with chemicals (Koronkiewicz *et al.* 1998). They are therefore potentially exposed to these chemicals through the food they eat. Willow flycatcher deformities (Paxton *et al.* 1997) recorded on the breeding grounds may be linked to toxins ingested during any period of the annual cycle. Deformities are not reported from all southwestern willow flycatchers suggesting that deformities may be associated with site-specific effects.

Protection of riparian habitats where the flycatcher winters and migrates needs to be increased (Finch and Yong 2000). Increased research and awareness of the flycatcher's habitat requirements in winter and migration will improve management efforts. Loss and degradation of known wintering sites used by flycatchers should be avoided. Discussions with local managers and landowners may help to prevent serious habitat losses on the wintering grounds, but increased funds and incentives are needed before these concerns are likely to be addressed in a serious way. Cooperative international ventures involving governments of multiple countries and coalitions and nongovernment organizations such as Partners in Flight, Audubon Society, and World Wildlife Fund should be pursued to protect and restore wintering habitats. Along migration routes, denuded river and ditch banks and wetland edges can be substantially improved by allowing them to grow riparian vegetation in place of riprap or cement (Finch *et al.* 1998). Maintaining or adding water in or adjacent to winter and stopover riparian habitats is desirable. The presence of water can influence local arthropod abundance. Arthropods are food through the winter and supply energy for replenishing fat stores during migration.

Further research on migration routes used by flycatchers is needed to improve efforts to protect and restore habitats and recover flycatcher populations. A better understanding of wintering distribution and habitat use patterns by flycatchers is also needed for conserving winter habitats. Increased emphasis on conservation and protection of winter and migration habitats should not supplant habitat management goals and activities on the breeding grounds.

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Chapter 8:

Demographic Characteristics and Population Modeling

An understanding of the basic demography of a species is necessary to estimate and evaluate population trends. The relative impact of different demographic parameters on growth rates can be assessed through a sensitivity analysis, in which different parameters are altered singly to assess the effect on population growth. Identification of critical parameters can allow managers to focus their efforts on factors most likely to increase populations.

In this chapter, we describe the demography of the southwestern willow flycatcher. Our objectives are to (1) describe basic population characteristics of the subspecies, (2) summarize and estimate vital demographic parameters of the flycatcher, (3) use those parameters in a life table and population projection model, and (4) use an elasticity analysis to determine which parameters have the greatest impact on population growth rates, and therefore offer the greatest potential for management. Much of these data come from the only two well-studied populations of *E.t. extimus*, in the Kern River Preserve in California (data from Whitfield 1990, Whitfield and Strong 1995, Whitfield and Enos 1996, and Whitfield unpublished) and the Grand Canyon in Arizona (data from Sogge et al. 1997 and Sogge unpublished). Information from the Kern River Preserve that lacks a citation represents previously unpublished data of M. Whitfield. To provide perspective, we present additional data from other willow flycatcher subspecies as well as other *Empidonax* flycatchers.

Populations Characteristics

Age Classes

Because of the lack of age-specific plumages, there are only two discernible age classes for the willow flycatcher: hatching year (HY) and after hatch-year (AHY).

Sex Ratio

There is no sexual dimorphism in this species; therefore inferences about sex ratios are necessarily circumstantial. Fledgling sex ratios are likely to be 1:1, as is true for almost all birds (Clutton-Brock 1986, Breitwisch 1989). Although facultatively monogamous, the sex ratio of adults in some populations of this subspecies appears to be male-biased, as suggested by the substantial proportion of unmated males observed. However, the proportion of unmated males, and therefore the sex ratio, varies greatly among sites. For example, in the Grand Canyon from 1993-1996, 44% of territorial males were unpaired (Sogge et al. 1997). In contrast, at the Kern River Preserve, generally 2-4 of 28-35 males (6-14%) are unpaired in any year, while in the upper Gila Valley, New Mexico, a maximum of 8 of

195 singing males (4.1%) may have been unpaired in 1997 (Parker 1997; S. Stoleson and D. Finch, unpublished data). The apparent skewed sex ratio in some populations may be due to higher mortality among females (see Survivorship section below). Alternatively, in very small populations, such as the Grand Canyon, sex ratios skewed in either direction can result from demographic stochasticity (Burgman et al. 1993). Polygyny has been recorded in this species, which may result from an excess of females in a population (Sedgwick & Knopf 1989, M. Whitfield unpublished data). However, mating systems in this species may be more complex than previously thought, as both unmated and polygynous males can occur in the same population (M. Whitfield, unpublished data).

Population Growth Rates

Few, if any, populations of *E.t. extimus* have been monitored for a sufficient time to quantify long-term population trends. Former populations in Arizona on the lower Salt River, Santa Cruz River, and lower Colorado River near Yuma are believed to have been extirpated. In California, a large population on the Santa Ana River in San Bernadino County mentioned by Hanna (1928) is gone although some suitable habitat remains (R. McKernan, personal communication). Similarly, a population at the mouth of the Santa Clara river appears to have been extirpated (M. C. Badger, cited in Unitt 1987).

In the short term, most monitored populations of the southwestern willow flycatcher have declined or shown no trend. For example, between 1993 and 1997, two small populations (3 to 4 pairs) in the Verde Valley, Arizona, have disappeared. Two small populations in the White Mountains of Arizona have decreased steadily over the past five years (Langridge and Sogge 1997). Between 1989 and 1993, the population in the Kern River Valley, California, dropped from 44 to 27 pairs (Whitfield 1993), but since then has remained relatively stable at about 32 to 34 pairs (Whitfield et al., in review). Similarly, the overall population in the Grand Canyon has not shown any consistent trend in the years 1982 to 1997, although there have been local extirpations and recolonizations at all the small breeding patches (Brown 1988, Sogge et al. 1997). Surveys conducted from 1994 to 1999 along the upper Gila River in New Mexico suggest that flycatcher numbers there may be increasing (Parker 1997, Stoleson & Finch unpublished data).

Fecundity

Fecundity is the measure of rate of reproduction in a population. Seasonal (or annual) fecundity is difficult to quantify in the field, especially for species that can attempt multiple nests in a season (Clobert & Lebreton 1991). In bird populations, average seasonal fecundity is the product of the average probability of an individual breeding in a given season, the average number of eggs produced per clutch, the average number of nesting attempts per season, and the overall hatching and fledging success rates of nesting attempts within a season. We address these components individually below.

Probability of Breeding

Willow flycatchers apparently begin to breed in their second calendar year, i.e., on their first return to the breeding grounds (M. Whitfield, unpublished data, Paxton et al. 1997). At the Kern River, all females of all age classes appear to breed every year, perhaps as a result of a skewed adult sex ratio. The same is likely to be true for other populations as well. As noted above, in many populations a significant portion of territorial males may remain unpaired. Whether or not a male remains unmated during a season appears to be independent of age (M. Whitfield, unpublished data).

Clutch Size

The modal clutch size is three eggs throughout most of the range of *E.t. extimus*, and varies from 1 to 5 (although one-egg clutches are likely the result of predation or disturbance). Clutch sizes at the Kern River appear to be larger than in Arizona or New Mexico (Table 8-1). Four-egg clutches are common among first nesting attempts of a season at the Kern ($\bar{x}$ = 3.64 ± 0.68 eggs [mean ± SD], n = 96). Elsewhere in the southwest, clutches of four eggs are rare (Sferra et al. 1997, Sogge et al. 1997, S. Stoleson and D. Finch, unpublished data). Among other subspecies of the willow flycatcher, clutches of four are not uncommon, and mean clutch size is generally larger than that of *E.t. extimus* (Table 8-1).

In general, clutch sizes of other flycatchers in the genus *Empidonax* tend to be larger than those of *E.t. extimus* (Table 8-1). Clutches of four eggs are common, and clutches of five eggs occur in several species (e.g., Briskie & Sealy 1989, Sedgwick 1993, Bowers & Dunning 1994). This difference may be related to habitat or latitude. Unlike the shrub and riparian woodland inhabiting willow flycatcher, several of the other *Empidonax* listed in Table 8-1 occupy closed forest habitats (Bent 1942). Forest interior birds may experience lower predation rates, and consequently may have evolved relatively larger clutch sizes than sister taxa in more open habitats or edges (Martin 1993, 1995). In general, clutch sizes of birds increase with increasing latitude (Lack 1968, Klomp 1970). The southwestern willow flycatcher breeds further south than any other subspecies of *E. traillii* (Unitt

Table 8-1. Clutch sizes of willow flycatchers and other *Empidonax* species.

Taxon[a]	Site	Mean	*N*	Range	Source
E.t. extimus	Kern River, CA (1987)	NA	16	1-4[b]	Harris 1991
	Kern River, CA (1989-97)	3.33	154	1-5[b]	M. Whitfield unpub. data
	Grand Canyon, AZ	3	3	3	Sogge et al. 1997
	Arizona, statewide	2.34	67	1-4[b]	Sferra et al. 1997
	San Luis Rey, CA	2.69	29	1-4[b]	W. Haas pers. comm.
	Cliff-Gila Valley, NM	2.67	21	2-4	Skaggs 1996, Stoleson and Finch unpub. data
E.t. adastus	WA	3.42	33	3-4	King 1955
E.t. brewsteri	Truckee R., CA	2.82	11	2-3	Flett & Sanders 1987
E.t. traillii	MI	3.28	92	3-5	Walkinshaw 1966
	OH, NE	3.41	91	2-5	Holcomb 1972, 1974
	WI	3.59	415	3-5	McCabe 1991
E. difficilis	Monterey, CA	4.00	23	NA	Davis et al. 1963
E. fulvifrons	AZ	3.37	12	2-5	Bowers & Dunning 1994
E. minimus	MI	3.95	46	3-5	Walkinshaw 1961
	Manitoba	3.92	192	2-5	Briskie & Sealy 1989
E. oberholseri	MT	4.00	21	2-5	Sedgwick 1993
E. virescens	MI	2.54	66	NA	Walkinshaw 1961
	MI	2.92	25	2-4	Mumford 1964

[a] *E. traillii* = willow flycatcher, *E. difficilis* = Pacific-slope flycatcher, *E. fulvifrons* = buff-breasted flycatcher, *E. minimus* = least flycatcher, *E. oberholseri* = dusky flycatcher, *E. virescens* = acadian flycatcher.
[b] Clutch sizes of one are likely the result of disturbance or predation.

1987), and further south than most of the other species listed in Table 8-1. Therefore, *E.t. extimus* may be expected to have smaller clutches, on average, than other subspecies or other *Empidonax* species. It may be noteworthy that the Kern River population is further north than populations in Arizona and New Mexico and tends to have larger clutch sizes. The Acadian Flycatcher (*E. virescens*), whose breeding range extends further south in the United States than any other *Empidonax* (Bent 1942), also tends to have smaller clutch sizes than its congeners (Table 8-1).

Clutch size in the southwestern willow flycatcher does not increase or decrease as a function of age (M. Whitfield, unpublished data). However, clutch size does tend to decrease with successive nesting attempts within a year (Holcomb 1974, M. Whitfield, unpublished data). For example, at the Kern River, mean clutch size declined from 3.64 for first attempts to 2.87 for second and 2.67 for third attempts. Least Flycatchers (*E. minimus*) show a similar pattern of decreasing clutch size in successive nesting attempts (Briskie & Sealy 1989), as do many other passerines (Rowe et al. 1994, Young 1994).

Number of Nesting Attempts per Season

Willow flycatchers often respond to cowbird parasitism, nest destruction, or other severe disturbance by abandoning their nests and renesting. Consequently, females will frequently attempt several nests per season following the failure of earlier nests (Holcomb 1974, Whitfield 1990, Harris 1991). At the Kern River, females averaged 1.82 ± 0.89 nesting attempts per season from 1989 to 1997. Some females in Arizona and New Mexico have been suspected of initiating up to four clutches in a season, although this is uncertain because the birds were unbanded (T. McCarthey, S. Stoleson and D. Finch, unpublished data). The highest documented number of nesting attempts within a season occurred at the Kern River during a year of intense cowbird parasitism, where one pair built six nests (Harris 1991). In general, a high incidence of cowbird parasitism leads to an increased number of nesting attempts per season because many flycatchers will quickly abandon and renest. For example, at the Kern River, females averaged 2.04 ± 0.99 (n=82) attempts per year prior to cowbird trapping, and only 1.66 ± 0.78 (n=118) attempts afterwards.

Other than renesting after nest failure or parasitism, multiple nesting attempts within a season are rare. McCabe (1991) considered willow flycatchers to be single-brooded. However, double brooding (raising a second brood after successfully fledging the first) has been documented or suspected at several sites in the southwest (Whitfield 1990, Griffith & Griffith 1995, Sferra et al. 1997, S. Stoleson and D. Finch, unpublished data). For example, at the Kern River, 3.8% of successful females attempted to raise second broods. Double brooding is relatively rare in other *Empidonax* flycatchers as well, although reported at least occasionally in most species (e.g., Walkinshaw 1961, Davis et al. 1963, Sedgwick 1993, Bowers & Dunning 1994, Briskie 1994). Briskie and Sealy (1987) suggested that the Least Flycatcher may double brood infrequently because delaying fall migration to raise a second brood may prevent birds from establishing and maintaining winter territories. This may apply to willow flycatchers as well: females seem to double brood only when the young from their first brood have fledged by late June or very early July.

Hatching Success

Hatching success of southwestern willow flycatcher eggs varies among populations. The overall hatching rate in unparasitized nests for all monitored sites in Arizona in 1996 was 66% (Sferra et al. 1997). At the Kern River and San Luis Rey River populations in California, 63% and 86% of eggs hatched in unparasitized nests, respectively (Whitfield and Sogge 1999, W. Haas personal communication). Hatching rates for other subspecies vary widely among populations, from a low of 54.8% (*n*=272) in Ohio and Nebraska (Holcomb 1972) to a high of 92.6% (*n*=67) in Washington (King 1953). Thus, populations at the Kern River and in Arizona appear to experience relatively low hatching success, although comparable rates have been reported for both Acadian (Walkinshaw 1961) and Dusky Flycatchers (*E. oberholseri*; Sedgwick 1993).

Nesting Success

Nesting success for the southwestern willow flycatcher varies greatly among sites (Table 8-2). Areas with high levels of cowbird parasitism exhibit very low success (e.g., the Grand Canyon, the Kern River prior to cowbird trapping). In contrast, other sites experience relatively high levels of nesting success. For example, at some sites in Arizona and in the Gila Valley of New Mexico, 50 to 55% of nests successfully fledged one or more young (Sferra et al. 1997, Skaggs 1996, S. Stoleson and D. Finch, 1999). At the San Luis Rey River in California, nesting success has reached 70% in an area of intensive cowbird trapping (W. Haas, personal communication). In general, nesting success rates for cup-nesting passerines in North America range from about 38 to 70%, with a median value of 52% (Nice 1957, Martin 1993). Thus, some populations of *E.t. extimus* (listed in Table 8-2) experience poor nesting success compared to other cup-nesting songbirds.

Nesting success in Tyrannid flycatchers tends to be relatively high for the size of the bird, perhaps because of their aggressive nature (Murphy 1983). Studies of other willow flycatcher subspecies have generally indicated higher nesting success rates than are typical for *E.t. extimus*, from lows of about 40% to almost 70%

Table 8-2. Measures of nesting success in willow flycatchers and other *Empidonax* species.

Taxon[a]	Site	% nest success[b]	No. of nests	Fledglings per nest	Fledglings per female	Source
E.t. extimus	Kern River, CA (1987)	15.8	19	0.62	1.25	Harris 1991
	Kern River, CA (1989-1997)	36.4	324	1.27	1.44	Whitfield unpub. data
	Grand Canyon, AZ	18.0	17	NA	0.70	Sogge et al. 1997
	statewide ave., AZ	42.9	163	0.93	0.99[c]	Sferra et al. 1997
	Cliff-Gila Valley, NM	55.2	97	NA	NA	Skaggs 1996; Stoleson & Finch unpub. data
	San Luis Rey R., CA (1994)	64.0	11	2.09	NA	Griffith & Griffith 1995
	San Luis Rey R., CA (1995-97)	66.0	70	1.54	2.45	Haas pers. comm.
E.t. adastus	North Park, CO	40.7	27	0.89	NA	Sedgwick & Knopf 1988
	Malheur N.W.R., OR	NA	876	NA	1.81	Sedgwick & Iko 1999
E.t. brewsteri	Truckee R., CA	54.5	11	1.27-1.36	1.40-1.50	Flett & Sanders 1987
E.t. traillii	MI	69.5	209	NA	NA	Berger 1967
	MI	65.2	92	2.15	NA	Walkinshaw 1966
	OH, NE	39.5	91	1.11	1.88	Holcomb 1972
	WI	68.6	459	2.13	NA	McCabe 1991
E. difficilis	Monterey, CA	73.9	43	1.92	NA	Davis et al. 1963
E. fulvifrons	AZ	NA	12	2.08	NA	Bowers & Dunning 1994
E. minimus	MI	56.3	16	3.80	NA	Walkinshaw 1961
	Manitoba	58.6	273	1.25	NA	Briskie & Sealy 1989
E. oberholseri	MT	58.3	24	1.60	1.90	Sedgwick 1993
E. virescens	MI	59.1	66	1.36	NA	Walkinshaw 1961

[a] See Table 8-1 for common names of taxa.
[b] Percentage of nests of known outcome that produced at least one flycatcher fledgling; not Mayfield estimates (Mayfield 1975).
[c] *n* = 102 females

(Table 8-2). Nesting success among other *Empidonax* species tends to be somewhat higher yet, usually well over 55% (Table 8-2). Willow flycatchers may have somewhat lower success than their congeners because their riparian habitats tend to be patchy, fragmented, linear, and with a high proportion of edge, especially in the Southwest. Birds in such habitats are likely to be more vulnerable to predation or parasitism than in more contiguous wooded habitats (Robinson et al. 1995). As mentioned above, most of the other species in Table 8-2 are species of contiguous forest, which tend to have higher rates of nesting success than species that nest in more open or fragmented habitats (Martin 1993). In addition, most forests in the west are higher in elevation and further from concentrations of livestock than are floodplain riparian woodlands, so there may be an elevational component to the difference in nest success as well.

Seasonal Fecundity

Fecundity can be measured as the number of young fledged on a per nest or per pair basis. The number of fledglings produced per nest is much more easily determined. At most sites where data are available, southwestern willow flycatchers fledge less than one chick per nest, including nests that fail or are abandoned (Table 8-2). In contrast, studies of other willow flycatcher subspecies have usually reported more fledglings per nesting attempt, ranging from 1.11 to over 2 (Table 8-2). One exception was in North Park, Colorado, where heavy cowbird parasitism on *E.t. adastus* reduced per-nest productivity to 0.89 fledglings (Sedgwick & Knopf 1988). Because cowbird parasitism often provokes nest abandonment, it can greatly reduce the average nest productivity. For example, at the Kern River, an intensive cowbird control program increased the average per-nest productivity from 1.04 fledglings to 1.72 fledglings (Whitfield et al., in review). The effects of cowbird parasitism on productivity are discussed in depth in the following chapter. Other *Empidonax* show higher per-nest productivity than *E.t. extimus* as well (Table 8-2).

Because flycatchers may renest multiple times during a breeding season, per-nest productivity does not necessarily equate with seasonal fecundity. Rather, the best measure is the number of chicks fledged per pair per year (Clobert & Lebreton 1991). Recent evidence suggests low levels of mate fidelity in the willow flycatcher, even within a season (Paxton et al. 1997). Because female fecundity is much easier to assess accurately than male fecundity, we will use the number of fledglings per female per year as the measure of seasonal fecundity. Unfortunately, this rate has been calculated in very few studies, in part because it requires having color-banded birds, and because of the difficulty of following individual females through the course of an entire breeding season (Pease & Grzybowski 1995).

Seasonal fecundity of *E.t. extimus* ranges from a low of 0.7 fledglings per female in the Grand Canyon to 2.45 fledglings per female (3 year average) at the San Luis Rey River (Table 8-2). The low rate of reproduction in the Grand Canyon suggests a sink population. In contrast, the fecundity of the San Luis Rey population, where cowbirds are controlled, exceeds that of most populations of other subspecies and other *Empidonax* species (Table 8-2).

Survivorship

Data on survivorship for willow flycatchers are sparse. Information that does exist comes from return rates of banded birds. Estimates of survivorship based on resighting or recapture of banded individuals are necessarily conservative because they do not discriminate between mortality and emigration (Lebreton et al. 1992, Noon & Sauer 1992). Individuals of *E.t. extimus* have been color-banded systematically for more than three years only at the Kern River Preserve, although in 1996 the Colorado Plateau Field Station began a statewide banding effort in Arizona (Paxton et al. 1997).

Return Rates of Banded Birds

Return rates of banded adult flycatchers from the two color-marked populations of *extimus* were very similar: about 52% for males and 35% for females (Table 8-3). In contrast, studies of other subspecies

Table 8-3. Return rates of color-banded willow flycatchers in four areas.

Site	HY[a]	AHY:male[a]	AHY:female[a]	Source
Kern River, CA	34.2% (38)	51.7% (29)	33.8% (207)	Whitfield unpub. data
Arizona	8% (12)	52.0% (50)	34.0% (48)	Paxton et al. 1997
Michigan	1.4% (147)	40.9% (22)	22.6% (31)	Walkinshaw 1966
Malheur NWR, OR	13.2% (214)	43.3% (192)	46.8% (211)	Sedgwick & Klus 1997

[a] HY = hatch year (from fledging through first breeding season), AHY = after hatch year.

showed lower return rates. Whether this represents lower survival rates or greater dispersal due to more available habitat is unclear. In general, return rates of female flycatchers were lower than those of males. Because adult female willow flycatchers are thought to show high site fidelity (Walkinshaw 1966, Sedgwick & Knopf 1989, but see Paxton et al. 1997), lower return rates probably indicate lower survival rates than for males. Male-biased survival rates are common among passerines (Breitwisch 1989). The population at Malheur National Wildlife Refuge, Oregon, is exceptional in that females returned to the site at about the same rate as males (Sedgwick & Klus 1997). In general, annual survival rates for small migratory passerines range from 0.3 to 0.6 (Dobson 1990, Karr et al. 1990), so the estimates based on resighting probabilities presented in Table 8-3 seem reasonable for birds the size of willow flycatchers.

Estimates of survivorship for first year birds based on return rates to their natal region are usually biased because first year birds normally disperse from their natal area, and it is impossible to differentiate mortality from permanent emigration (Clobert & Lebreton 1991, Noon & Sauer 1992). Relatively low return rates for Michigan and Oregon populations (Table 8-3) almost certainly reflect high rates of natal dispersal. A relatively high proportion of first year birds returned to the Kern River Preserve (Table 8-3), perhaps because very little suitable riparian habitat exists in that region into which birds can disperse, so more return to their natal area and are detected. For that reason, return rates of first year birds to the Kern may be our best estimate of first year survival. The situation is likely to be similar in Arizona, but small sample sizes (1 of 12 individuals banded in 1996 returned in 1997) make the reported 8% figure suspect (Paxton et al. 1997). Data are equally scant for related species. Of 410 fledgling Least Flycatchers banded in Manitoba, only 4.2% were ever recaptured (Briskie 1994).

The between-season survival rate of fledglings appears to decline as the breeding season progresses. Whitfield and Strong (1995) found significantly higher return rates for young fledged before July 21 than for young fledged afterwards. This pattern has been reported in numerous other avian species as well (e.g., Hochachka 1990, Verhulst et al. 1995, Brinkhof et al. 1997). Therefore, there are two reasons why cowbird parasitism can affect seasonal fecundity even when birds are successful after abandoning early parasitized nests. Second (or later) clutches will be smaller, and fledglings from later attempts will be less likely to survive to breeding age. At the Kern River, observed return rates for fledglings were greater following the initiation of cowbird control in 1992, exceeding 0.50 in 1996 and 1997, although this may reflect increased resighting effort in those years (see Chapter 8).

Lifespan

Apart from a few anecdotal accounts, there is little information available on the longevity of willow flycatchers. In Oregon, one of 537 birds banded as adults survived at least eleven years after its first capture (J. Sedgwick, personal communication). One of 22 males banded as adults survived at least five years in Michigan (Walkinshaw 1966). For *E.t. extimus*, one male survived at least six years after banding, and three females and a male were still alive five years after banding at the Kern River (Whitfield and Enos 1996). Similarly, little is known of lifespans of other *Empidonax* flycatchers. The maximum known age for any other species, based on banding recoveries, is 8 years for a Dusky Flycatcher (Sedgwick 1993).

The average life span of a bird can be estimated from mortality rates using the formula:

$$L = \frac{2 - m}{2m}$$

where L = average lifespan and m = the average annual mortality rate (Gill 1990). Substituting 0.66 for m (based on minimum annual survival = 0.34, see Table 8-3) yields an average lifespan of 1.02 years; using 0.47 for m (based on maximum annual survival = 0.53, see Table 8-3) gives a lifespan of 1.63 years. Thus, the average lifespan of southwestern willow flycatchers is likely to be somewhere between 1.02 and 1.63 years.

Lifetime Reproductive Success

Lifetime reproductive success (LRS) has been estimated for very few passerines, in part because of the logistical difficulties in following individual females through the course of their lifetimes. Long term studies of *E.t. adastus* in Oregon have revealed that females reared, on average, 3.60 young over their lifespans (Sedgwick and Iko 1999). LRS varied with whether or not females were parasitized in their first breeding year, but was not affected by parasitism in subsequent years.

Immigration and Emigration

To date, what little is known of movement among populations of *E.t. extimus* comes from recent work in Arizona (Paxton et al. 1997). Rates of immigration and emigration varied considerably among populations, perhaps based on the relative degree of isolation of the population. Overall, of 48 birds that bred in 1996 and were resighted in 1997, 13 (27%) returned to a different site. It is likely that immigration rates are lower where available breeding sites are limited, such as at the Kern River (Paxton et al. 1997). Also, site fidelity tended to be lower for sites with lower overall nesting success, suggesting higher emigration rates (Paxton et al. 1997). Information on sex-biased dispersal is sparse, but recent data from color-banded birds in Arizona suggest that males emigrate more frequently than females, contrary to the normal pattern among passerine birds (Greenwood & Harvey 1982). It is yet unclear whether females disperse further than males, as in other birds.

Life Table Analyses

A life table summarizes the vital rates of age-specific survivorship and fecundity for a population. As mentioned above, because of the difficulty in determining fecundity rates for males, life tables are normally female-based. Observed rates of fecundity are divided in half to indicate the rate of production of female fledglings, and assume an equal sex ratio at fledging (Noon & Sauer 1992).

It is evident from previous sections of this chapter that estimates of demographic parameters for the southwestern willow flycatcher are available from very few sites, and that estimates vary considerably, both among sites, and within sites depending on year and management practices. For no population (with the possible exception of the Kern River) is there sufficient knowledge of demographic parameters to create a complete life table. Therefore we present two composite life tables, using estimates of parameters from various populations. One table is conservative, and uses minimum estimates of survival and fecundity. It may be thought of as a worst case scenario. The second table is more optimistic, uses the highest recorded parameter estimates, and represents a best case scenario. The two tables bracket the likely range of demographic parameters for the majority of willow flycatcher populations.

Life Table Parameters

In the conservative life table, we used 0.34 as the survival rate (p_x) for both the HY age class, based on the observed return rate of HY birds at the Kern River, and for the AHY age class, based on observed return rates for adult females in Arizona (Table 8-3; Paxton et al. 1997). The fecundity rate, or maternity function m_x, denotes the expected number of female fledglings produced by a female of age x. We used the observed rate of 0.7 fledglings per female per season from the Grand Canyon (Sogge et al. 1997), divided by two to account for female offspring only. In the optimistic life table, HY birds were assigned a survival rate of 0.50 (M. Whitfield, unpublished data), and AHY birds a rate of 0.47 (Sedgwick & Klus 1997). We used an optimistic fecundity rate of 1.28 female fledglings per female per season, based on 1997 data from San Luis Rey, California (W. Haas, personal communication).

Other parameters in both life tables are x, which denotes age class expressed in years; p_x, the probability of survival from age class x to age class x+1; l_x, the probability that an individual aged 0 will survive to enter age class x; and $l_x m_x$, the age-specific reproductive rate. The latter term multiplied by age x is used for calculating population parameters (see below). Life tables assumed no reproductive senescence, but were truncated at eight years, the maximum recorded lifespan for willow flycatchers. Fecundity and survival were assumed to be constant after the hatching year.

Life tables are presented as tables 8-4 and 8-5. They show that for either scenario, a very small proportion

Table 8-4. Life table of the southwestern willow flycatcher based on conservative[a] parameter values[b].

x	p_x	l_x	m_x	$l_x m_x$	$x l_x m_x$
0	0.340	1.000	0.00	0.000	0.000
1	0.340	0.340	0.35	0.119	0.119
2	0.340	0.116	0.35	0.040	0.081
3	0.340	0.039	0.35	0.014	0.041
4	0.340	0.013	0.35	0.005	0.019
5	0.340	0.005	0.35	0.002	0.008
6	0.340	0.002	0.35	0.001	0.003
7	0.340	0.001	0.35	0.000	0.001
8	0.340	0.000	0.35	0.000	0.000
			SUM:	0.180	0.272

[a] Conservative scenario uses the lowest value recorded among all willow flycatcher populations for each parameter.
[b] Table parameters are: x = age class in years; p_x = probability of survival from age class x to x+1; l_x = probability that an individual aged 0 will survive to enter age class x; m_x = average number of female offspring by a female of age x; $l_x m_x$ = product of l_x and m_x, the age-specific reproductive rate; and $x l_x m_x$ = product of $l_x m_x$ and x (used for calculation of population parameters).

Table 8-5. Life table for the southwestern willow flycatcher based on optimistic[a] parameter values[b].

x	p_x	l_x	m_x	$l_x m_x$	$x l_x m_x$
0	0.500	1.000	0.00	0.000	0.000
1	0.470	0.500	1.28	0.640	0.640
2	0.470	0.235	1.28	0.301	0.602
3	0.470	0.110	1.28	0.141	0.424
4	0.470	0.052	1.28	0.066	0.266
5	0.470	0.024	1.28	0.031	0.156
6	0.470	0.011	1.28	0.015	0.088
7	0.470	0.005	1.28	0.007	0.048
8	0.470	0.003	1.28	0.003	0.026
			SUM:	1.205	2.250

[a] Optimistic scenario uses the highest value recorded among all willow flycatcher populations for each parameter.
[b] Refer to Table 8-4 for definitions of parameters.

of any cohort will survive beyond 3 years of age. Consequently, females in the 1 and 2 year age classes make the greatest contribution to reproduction (as indicated by the $l_x m_x$ terms).

Population Parameters Calculated from the Life Table

The life table enables calculation of R_0, the net reproductive rate, and generation time T. The net reproductive rate is calculated as the sum of the $l_x m_x$ terms, and measures the expected production of female fledglings by a female during the course of its lifetime. Table 8-4 indicates that in the worst-case scenario, a female willow flycatcher will produce, on average, 0.18 female fledglings in its lifetime, or 0.36 fledglings of both sexes assuming an equal sex ratio. This rate is clearly well below the replacement rate of 1 female fledgling per female, and indicates a rapidly declining population. The best case scenario suggests a net reproductive rate of 1.21 female fledglings per female, and indicates a population growing at a relatively rapid rate.

Generation time T is a measure of the mean interval between the birth of a female and the birth of her offspring (Caughley 1977). T is calculated as

$$T = \frac{\sum x(l_x m_x)}{R_0}$$

Generation time calculated from the conservative life table is 1.51 years, and from the optimistic life table 1.87 years. The life table based on optimistic values yields a longer generation time because the expected reproductive lifespan of females is greater due to higher survival rates. In either case, the very short generation time suggests considerable potential for rapid population growth as well as considerable vulnerability to rapid population decline.

Population Projection Model

Effective management and recovery of a threatened or endangered species depend on identifying and correcting the factors that limit population growth. Demographic modeling can indicate probable population trends under current or future conditions if model parameters are well known. Sensitivity analyses can be used to indicate which life history components are the most likely to affect population growth rates, and hence provide the most potential for management. Because the southwestern willow flycatcher occurs in assemblages of local breeding populations that occupy dynamic habitat patches scattered across the landscape, it would be an ideal candidate for a metapopulation or spatially-explicit model (Hanski 1998). However, these types of models are data-intensive, and require reasonable estimates of dispersal and patch-specific demographic rates, among other data, to produce meaningful results (Beissinger and Westphal 1998). Those data do not yet exist; therefore the use of a spatially structured demographic model would be premature at this time.

Instead, we present a simple stage-based matrix projection model for the southwestern willow flycatcher (Caswell 1989, McDonald & Caswell 1993). As with the life tables, we use estimates of demographic parameters from various populations. Accordingly, the model will not represent the dynamics of any particular population of willow flycatchers, but rather will provide a crude measure of range-wide population dynamics. The model was used to estimate lambda (λ), the finite rate of population growth, which indicates the factor by which a population grows over the projection interval. A lambda less than one indicates a declining population, and a lambda greater than one a growing population.

Model Structure

In the absence of age-specific vital rates (see Life Table Analyses above), a simple model was created based on the two life stages that are identifiable in the field: hatching year and after-hatch year. The population life cycle diagram is presented in Figure 8-1, and is based on post-breeding censuses and a one-year projection interval. This life cycle is typical of many birds (McDonald & Caswell 1993). Post-breeding censuses are used for the model because parameters are

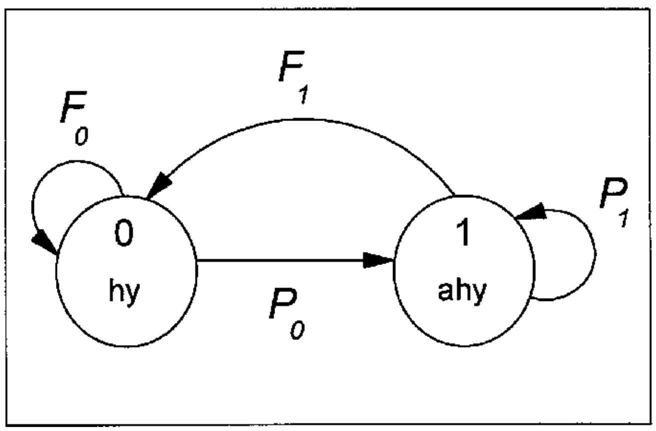

Figure 8-1. A simple life cycle diagram for the southwestern willow flycatcher used to create a stage-based population model. P_0 = probability of a fledgling surviving through the following breeding season; P_1 = annual survival probability for adults; F_0 = fecundity (i.e., the number of fledglings produced per female per breeding season) of birds in their first year of life; F_1 = annual fecundity of birds one or more years old; hy = hatch year; ahy = after hatch year.

more easily estimated from field data than is true for pre-breeding censuses. Pre-breeding censuses also confound estimates of fecundity and first year survival (Noon and Sauer 1992). Note that the timing of the census for the purposes of this model is not meant to address questions of field methodology.

In the model, P_0 is the probability that a fledgling will survive to the next breeding season. P_1 is the annual survivorship of adults. The annual fecundity (number of female fledglings per female per year) is given as F_0 for hatch-year birds and F_1 for adults. Note that because this is a post-breeding model, the fecundity value for HY birds indicates the productivity of birds in their first breeding attempt, after their return to the breeding grounds but before the census. The flow of events in the model is (1) birds are censused at the close of the breeding season, (2) birds survive to the next season, (3) individuals are aged one year, (4) survivors breed, and (5) birds are censused again. The model is completely deterministic, as there are no data available on the variance of parameters within a population. Because in this model birds must survive to the next season before breeding, F values are the product of the maternity rate (m_x) from the life tables and the stage-specific survival rates P.

The model assumes that: (1) males do not affect survival and reproduction of females, (2) rates of survival and fecundity are constant among individuals within a stage class and among years, (3) breeding occurs in a single birth-pulse, (4) the population is near a stable age distribution, and (5) parameters are not density dependent (Noon & Sauer 1992). None of these assumptions are likely to be strictly true for a passerine bird. In particular, both survival and fecundity can vary greatly among years at some sites. However, slight violations of these assumptions are unlikely to affect the qualitative results of the model (Noon & Sauer 1992). As with the life tables, we examined the model using both optimistic and conservative parameters. We also added an intermediate set of values as perhaps more typical of most populations. Because data are available for very few populations, we used simple means of the extreme parameter values in the intermediate scenario. The vital rates used for the conservative and optimistic models were the same as in the life tables (Table 8-6).

Populations were projected over a 25 year time span, arbitrarily starting with 100 pairs of flycatchers. Lambda was calculated for each scenario analytically as N_t / N_{t-1} at t=25 years, where N is the total population size. For all three scenarios, lambda had stabilized after 20 years.

Population Projection Results

Under the optimistic scenario, the hypothetical population grew exponentially (Figure 8-2). Lambda was calculated to be 1.11, which indicates an annual increase of 11%. This rapid population growth is based on actual rates measured in the field, and illustrates that under optimal conditions, willow flycatchers have the potential for rapid recovery. In contrast, populations declined to extinction under both the intermediate and conservative scenarios. In the worst-case scenario, lambda was 0.46, which indicates a precipitous population decline of 54% per year. The population still declined at an annual rate of 22% under the intermediate scenario. Estimates of lambda derived from this model should not be considered as representing the growth rate of any population of willow flycatcher, nor should they be used to predict future population sizes. However, if the parameter values used are considered to be representative of the extremes found in flycatcher populations, then the trajectory of any particular population is likely to be

Table 8-6. Values used for demographic parameters[a] in a conservative, an intermediate and an optimistic population projection model[b].

Model	P_0	P_1	m_x	F_0	F_1
Conservative	0.34	0.34	0.35	0.12	0.12
Intermediate	0.42	0.41	—	0.38	0.36
Optimistic	0.50	0.47	1.28	0.64	0.60

[a] See Figure 8-1 for definitions of parameters; maternity function, mx = number of female fledglings per female (see Tables 8-4, 8-5).
[b] Conservative and optimistic models defined as in Table 8-4; intermediate model uses means of extreme values.

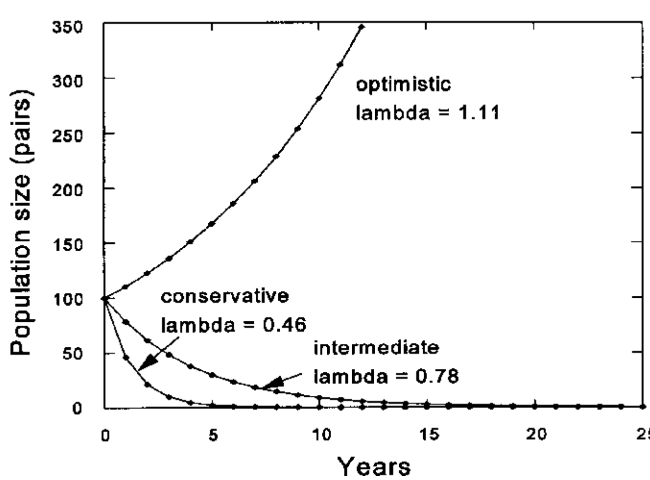

Figure 8-2. Hypothetical population trajectories for the southwestern willow flycatcher using conservative (lowest values among all populations), optimistic (highest values among all populations), and intermediate (mean of conservative and optimistic values) parameters for fecundity and survival. Initial population size was 100 pairs. See text for details of model.

Table 8-7. Elasticity of lambda to changes in demographic parameters for three different scenarios. See Table 8-6 for parameter definitions and values used in each of the scenarios.

Model	P_0	P_1	F_0	F_1
Conservative	0.19	0.56	0.07	0.19
Intermediate	0.24	0.28	0.24	0.24
Optimistic	0.24	0.21	0.31	0.24

within the extremes presented. Further, if the intermediate values used are indeed typical of most flycatcher populations, then the prospect for all but a few populations is bleak.

Elasticity of Demographic Parameters

Elasticity is a measure of the proportionate effect of a parameter on lambda. Parameters showed different elasticity among the three scenarios (Table 8-7). Under the conservative scenario, lambda was most strongly affected by adult survival (P_1), and little affected by other parameters. This suggests that prolonging the reproductive lifespan of breeding females would have a greater effect on population growth than would increasing seasonal fecundity, perhaps since fecundity is low. In contrast, under the optimistic scenario, lambda was most strongly affected by HY fecundity (F_0), and moderately affected by the other parameters about equally. From Table 8-5 it is evident that first time breeders make the largest contribution to reproduction (as indicated by the $l_x m_x$ term), and increasing their fecundity would have a disproportionate effect on population growth. Under the intermediate scenario, the effect of all parameters on lambda was similar.

Implications for Management

The effectiveness of management actions can be maximized by concentrating efforts on those demographic components that have the greatest effect on population growth rates. However, which demographic component to manage depends on which scenario is used. With the conservative scenario, increasing the population growth rate would be best accomplished by increasing adult survivorship. Better data are needed on the causes and timing of adult mortality to accomplish this task. On the other hand, the optimistic scenario suggests increasing fecundity may be the best strategy. This might be accomplished by reducing cowbird parasitism or nest predation. In reality, it is probably much easier to improve fecundity through management than it would be to increase survival rates, in part because this species is a neotropical migrant with overwinter survival constrained by factors outside of the United States, and therefore difficult to manage. In addition, demographic rates, and hence the best management strategies, are likely to be site-specific.

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Chapter 9:

The Ecology of Brown-Headed Cowbirds and Their Effects on Southwestern Willow Flycatchers

Brown-headed cowbirds (*Molothrus ater*) are obligate brood-parasites, that is, female cowbirds lay their eggs in nests of other species. If the cowbird eggs are accepted, the host pair may raise the young cowbird, often at a reduction of the hosts' reproductive success. Cowbird females are also known to remove host eggs and nestlings from nests, which may also affect the reproductive success of the hosts (Smith 1981, Scott et al. 1992, Sealy 1992). It is difficult to assess the impact of parasitism both because reproductive success operates at many levels and because the hosts have defenses against parasitism or cowbird intrusion. In this chapter, we review the data on the effects of brood parasitism on reproductive success of the southwestern willow flycatchers (WIFL). We estimate the effects of brood parasitism on populations of WIFLs and the degree to which parasitism is a factor in their recovery. For most of the analyses, we use data from one population along the South Fork Kern River, Kern County, California.

Cowbird Ecology

In this section, we review the ecology of cowbirds and point out how the ecological and life history considerations may affect various management decisions regarding WIFLs. Because cowbirds are a wide-ranging species, we have focussed our literature review on studies conducted in the southwest, within the historic range of the Southwestern Willow Flycatcher.

Breeding Biology

The breeding season of cowbirds overlaps with the initial period of breeding for southwestern willow flycatchers. In mid-April to early May, female cowbirds arrive on their breeding grounds (Fleischer et al. 1987, Braden et al. 1997), although in some years, females may arrive earlier (Darley 1983). Cowbirds begin laying eggs at the end of April and end in mid-July throughout much of the cowbirds' range (e.g., Payne 1976, Yokel 1987, Brown 1994, Braden et al. 1997, Schweitzer et al. 1998). In some areas, cowbirds may lay in late July (Whitfield, unpub. data). The length of the breeding season for an individual female may depend on weather conditions (e.g., Scott and Ankney 1979), age of the female (Fleischer et al. 1987) or location. Typically, however, most female cowbirds are laying eggs in May and June. As the breeding season progresses, fewer cowbirds are laying eggs

(Scott and Ankney 1979, Yokel 1987, Holford and Roby 1993). Because WIFLs generally begin nesting at the end of May, with the highest number of nests initiated in June, and with some nesting into August (Sogge et al. 1997), the early nests of WIFLs are at a higher risk of parasitism than later nests.

During the breeding season, female cowbirds are egg-laying machines with the maximum number of eggs laid dependent on the laying rate and breeding season length. The laying rate of cowbirds may vary by age and region, but studies show that cowbirds lay eggs at rates of 0.5 to 0.8 eggs per day (Scott and Ankney 1979 and 1980; Fleischer et al. 1987, Jackson and Roby 1992, Holford and Roby 1993).

Female cowbirds are extreme generalists, having been documented to parasitize over 200 species in North America (Friedmann and Kiff 1985). Variability in host preference by cowbirds is observed in individual females and between regions. Individual females lay eggs in nests of many hosts (Fleischer 1985 and 1986). Between regions of North America, the primary hosts of cowbirds differ, i.e., hosts that are parasitized heavily in one region may not be the preferred host in another region (Hoover and Brittingham 1993). Thus, the relationship of cowbird parasitism to an endangered host is not a simple relationship of cowbird abundance to endangered host number . So, although cowbirds may be present in an area with WIFLs or endangered populations of hosts, the actual parasitism levels of the endangered species depend on other factors as well.

During the breeding season, cowbird females likely have two limiting resources: forage and host nests to parasitize. Because cowbirds are not confined by parental care duties, cowbirds can use one area for breeding and another for feeding. Throughout the southwest, host-rich areas tend to be riparian habitat (cf. Knopf and Samson 1994) and this may be where female cowbirds concentrate their nest searching activities. In some areas with apparently high densities of both hosts and food, individual females stay in a relatively compact home range for a few days or throughout the season (Table 9-1). Examples of use of small home ranges are found in prairie habitats in the Midwest (Elliott 1980), with ephemeral abundant food along a riparian strip in desert (Yokel 1987), and alpine meadows with cattle (Verner, cited in Rothstein et al. 1987).

When the two resources of host and forage are spatially separated, female cowbirds split their time between host-rich areas and concentrated food sources. Females generally stay in their breeding areas or host-rich areas in the morning before 1100 hrs and then commute to feeding areas (Raim 1978, Smith 1981, Dufty 1982a, Rothstein et al. 1984, Yokel 1987, Thompson 1994, Gates and Evans 1998, Farmer 1999). Depending on the landscape, the feeding areas may be adjacent to the breeding areas or disjunct from the breeding areas. Feeding areas favored by cowbirds have short-grass and high invertebrate densities or grain seeds. Feeding areas are often associated with anthropogenic factors, e.g., livestock-grazed pastures, feedlots, dairy farming, golf courses, bird feeders, and camping grounds (Rothstein et al. 1984, Rothstein et al. 1987, Thompson 1994, Morris and Thompson 1998, Goguen and Matthews 1999, Farmer 1999) but generally, cowbirds feed near livestock (Morris and Thompson 1998).

The distances that cowbirds commute vary across landscapes (Table 9-1). Feeding sites tend to attract cowbirds from a great distance, but will tend to have proportionately lower numbers of female cowbirds (Rothstein et al. 1984, Rothstein et al. 1987). Recent research indicates a gradient of cowbird abundance and parasitism rates from feeding sites. In studies where cowbirds were feeding near cattle and the cattle were subsequently moved further from breeding areas, cowbird density or parasitism rates of hosts decreased (Goguen and Matthews 1997, Cook et al. 1997). Therefore, if potential feeding sites are distant from breeding areas, parasitism rates of riparian-nesting species may be lowered.

Later in the day, female cowbirds either roost with other blackbirds and cowbirds in the evening (e.g., Thompson 1994) or return to their breeding areas (Rothstein et al. 1984) by dusk. Shortly before sunrise, female cowbirds generally fly straight to a host's nest to lay their egg (Scott 1991) and presumably begin the cycle again. Rarely do females lay an egg later than 30 minutes past sunrise (Scott 1991).

Female Cowbird Range and Densities

In historic times, cowbirds were found in Arizona, New Mexico, and California (Perriman and Kelly, this vol.). By the 1920s, cowbirds were considered abundant along the Colorado and Gila River valleys and the rivers' tributaries in Arizona (Wyman and Burnell 1925). In New Mexico in the same time period, cowbirds were considered "fairly common" in the southern parts of New Mexico (Bailey 1928, cited in Schweitzer et al. 1998). In southern California, cowbirds expanded their range from the southeastern areas to the northwest throughout the early 1900s (Laymon 1987, Rothstein 1994).

In more recent decades, cowbird abundance throughout the southwest has shown no consistent trend, based on Breeding Bird Survey data (Wiedenfeld, in press). During 1966-1996, the mean abundances range from the lowest density category of 0.01-1 birds/survey to intermediate density category, 4-10 birds/survey (Sauer et al. 1997).

Table 9-1. The habitats which female cowbirds used for breeding and feeding sometimes differred. The area which female cowbirds used primarily for breeding or feeding is listed in parentheses along with the sample size of banded or radiotracked females. The mean or range of distances that female cowbirds commuted between the breeding and feeding areas are listed, when given.

Breeding (ha, sample size)	Feeding	Distance between breeding/feeding	Reference
		(km)	
riparian in desert (2.64 ha, n=25)	corrals, bird feeders, grazed pastures	0.6-3.3	from Yokel, 1987
woodland, open woodland, shrub, swamp (9.6 ha, n=7)	bird feeders, lawns cattle pastures, woodland, swamp		Teather and Robertson, 1985
campus/creek (4.5 ha, n=39)	open lawn areas		Darley 1983
montane forest, riparian (78 ha, n=5)	bird feeders, corrals	2.1-6.7	Rothstein et al., 1984
campus, New York (21.2 ha, n =13)		ca. 0.4	Dufty 1982a
riparian	pastures, golf course urban, dairy	2.8-13.6	Farmer, in press
forest/shrub sapling (*, n=84)	short-grass, crops, feedlots	mean=1.3	Thompson 1994
grassy meadows, shrubs/trees	not on island	1.3-7 km	Smith 1981
prairie pastures	cattle-grazed pastures	0	Elliott 1980
deciduous forest with brush (ca 8.8, n=19)	mainly grazed pastures	mean = 2.27 (0.3-6.14)	Gates and Evans, 1998
oak/juniper oak/savannah (99 ha,n=28)	cattle-grazed pastures, (0-18.1)	mean=1.7	Koloszar, in prep

Cowbirds tend to concentrate in specific habitats within a landscape, in the 'edges' of forest or in larger open areas within forests (Gates and Gysel 1978, Brittingham and Temple 1983 and 1996, Coker and Capen 1995, Annand and Thompson 1997, Niemuth and Boyce 1997, Evan and Gates 1997, Miller et al. 1998). The size of the opening within forests or the distance to feeding sites may affect cowbird abundance (Germaine et al. 1997), but the relationship of cowbird abundance with 'edge' transitions in landscapes is not always found throughout North America (Hahn and Hatfield 1995, Suarez et al. 1997, Bielefeldt and Rosenfield 1997, Miller et al. 1998). Generally, cowbirds are found in the highest densities near riparian zones and agricultural-use fields (Anderson et al. 1984, Chase 1997, Cook et al. 1997, Evan and Gates 1997, Farmer 1998). Cowbirds are found in low densities in desert (Sauer et al. 1997), coastal sage scrub (Farmer 1999 a,b, Braden et al. 1997), and in the interior of forests with small openings and low anthropogenic influences (Verner and Ritter 1983, Germaine et al. 1997 but see Hahn and Hatfield 1995). Cowbird densities in riparian areas traversing deserts can have low abundances, e.g., Lower San Pedro, Hunter, unpub data), although if there are anthropogenic factors nearby then densities can be high, e.g., Owens River near Bishop, California (Yokel 1987; pers obs). Because southwestern willow flycatchers nest in riparian habitats (e.g., Miller 1951), and because riparian habitat tends to be fragmented or linear throughout the southwest (Johnson and Haight 1984), cowbirds tend to occupy the same breeding habitat as do WIFLs.

Parasitism rates and effects are hypothesized to be correlated with abundance of cowbirds. This correlation is the rationale for many cowbird trapping programs. Obviously, with no cowbirds present, there is no parasitism. With varying densities of cowbirds, however, the effects on specific hosts depends on many factors, such as the relative abundance of cowbirds to hosts (e.g., May and Robinson 1985), the host preferences of cowbirds between areas (Hahn and Hatfield 1995, Hoover and Brittingham 1993), proximity of other nests near nests of an endangered species (Barber and Martin 1997), overall nest availability (e.g., Sedgwick and Knopf 1988), surrounding landscape use and bird community (e.g., Strausberger and Ashley 1997) and the efficacy of host responses (e.g., Uyehara and Narins 1995). The regional host preferences of cowbirds and the parasitism levels of WIFLs within different host assemblages needs to be researched.

Factors Affecting Cowbird Surveys

Given the sex-specific and temporal aspects of cowbird movements, surveying both breeding areas and (potential) feeding sites yields different information. Cowbirds are opportunistic feeders and use ephemeral sources of food, e.g., outbreaks of cicadas (Yokel 1987) within the breeding areas. But if insect or seed availability is low within a breeding area, cowbirds commute to feeding sites by afternoon (Yokel 1987; Thompson 1994). Therefore, censusing cowbirds in breeding areas before 1100 hrs will yield a more accurate number of breeding females in an area. Because females spend part of the morning concealed within the vegetation or under the canopy, (Norman and Robertson 1975, Payne 1973, Lowther 1979, Uyehara 1996), detection of female cowbirds is enhanced with playbacks of the female 'chatter' call (e.g., Dufty 1982b, Rothstein et al., in press).

Throughout its range, male cowbirds tend to outnumber females. This sex bias could be due to the higher mortality rate of females (Darley 1971), although in one California study, female cowbirds did not have higher mortality rates than males (Yokel 1987). In the western US, female cowbirds are actively monogamous (Yokel 1986) and breeding males tend to be older (Yokel and Rothstein 1991). The breeding males have consistent morning ranges within which copulations occur (Yokel 1989). Younger, presumably unmated, males tend to visit more feeding sites and travel further than females (Darley 1983, Rothstein et al. 1987). This difference suggests that trapping males at feeding sites is not as effective at controlling parasitism as trapping on the breeding grounds (Rothstein et al. 1987), although more studies are needed.

Cowbird Management Practices

The effect of parasitism or cowbird management practices on particular hosts has been difficult to assess. If parasitism is affecting a species, then high parasitism rates and low nesting success would be correlated with declining populations (e.g., Trail and Baptista 1993). However, high parasitism rates and low nesting success have been reported for species with relatively stable populations (e.g., Robinson 1992) and low parasitism rates have been reported for fluctuating populations (McCabe 1991). Thus, the effect of cowbirds on hosts needs to be assessed for each species or assemblage of species (e.g., Barber and Martin 1997), host density (e.g., Spautz 1999), and site-specific vegetation characteristics.

For long-term benefits to hosts, increasing suitable habitat has been advocated (Laymon 1987). Decreased parasitism levels have been associated with dense vegetative cover around the nesting heights (e.g., Spautz 1999, Farmer 1999b, Uyehara and Whitfield *in press*). Decreased parasitism has also been associated with fewer perch sites from which presumably, female cowbirds use to scan the adjacent area (e.g., Uyehara 1996, Brittingham and Temple 1996, Averill-Murray et al. 1999).

To control parasitism in specific host populations, cowbirds have often been removed, either selectively (Stutchbury 1997) or through intensive trapping efforts using decoy traps. Selective removal is likely most effective at low densities of cowbirds (e.g., Stutchbury 1997). Intensive trapping can be highly effective at decreasing cowbird numbers at sites with a concomitant increase in host numbers (Griffith and Griffith, in press). However, cowbird removal programs have not always led to increases in nesting success or host numbers (e.g., Kelly and DeCapita 1982, Braden et al. 1997, Whitfield et al. 1999, Winter and McKelvey 1999). For WIFL, cowbird trapping programs have not resulted in an increase in populations at two sites in California (Whitfield et al. 1999, Winter and McKelvey 1999) In addition, cowbird traps can cause mortality of nontarget species (Terpening 1999).

To minimize the effects of parasitism, cowbird eggs in nests have been addled or removed. Because cowbirds also remove host eggs from nests, this strategy does not eliminate the effects of parasitism.

We present information on parasitism rates at different sites and reproductive success with different management regimes. In one population in Kern County, CA, cowbirds were not removed from 1989-1990. Selective removal of 23 female cowbirds was used in 1991. Cowbird trapping was instituted in 1993 with increasing number of traps in subsequent years. In addition, cowbird eggs found in WIFL nests were shaken to prevent hatching from 1992.

Effects of Parasitism on WIFL

Cowbird Abundance and Parasitism Rates

McCabe (1991) hypothesized that, in the case of linear habitats with low availability of hosts, the parasitism rates of WIFLs may be higher than in areas with less fragmentation and higher densities of other hosts. This hypothesis is supported by two studies of WIFLs. Of nine parasitized hosts in a coastal central Californian community, WIFLs are parasitized more often than expected given the overall parasitism rate found within the community (Farmer 1999b).

WIFLs occupy territories with structural heterogeneity (Sedgwick and Knopf 1992, Uyehara and Whitfield in press). Pairs of WIFLs which occupied territories with more open canopy and less dense vegetation at the horizontal level around the nest were more likely to be parasitized than were pairs with more continuous canopy and dense vegetation around the nest (Uyehara and Whitfield, *in press*). The association of parasitism with nests located in more open areas has been found with other species (Brittingham and Temple 1996, Burhans 1997, Larison et al. 1998).

The parasitism rates of southwestern willow flycatchers tends to be high throughout their range (cf. Whitfield and Sogge 1999). Of nine sites where 10 or more nests were checked, the annual parasitism rates ranged from 3% at the San Pedro River in Arizona to a high of 66% at the South Fork Kern River in California. In other parts of the west, high parasitism rates occur (Sedgwick and Knopf 1988). Also, at Kern, the relative abundance of cowbirds surveyed in June is significantly correlated with the parasitism rates of the population among years (Fig. 9-1), indicating that a positive relationship exists for this population.

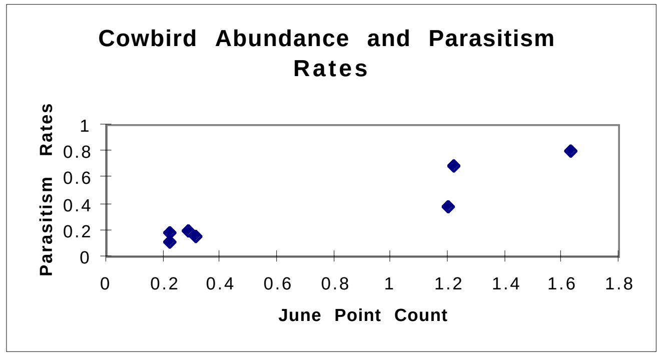

Figure 9-1. Parasitism rates of southwestern willow flycatchers in a central California population are correlated with female cowbird abundance (r=0.94, p=0.002). Sites for point counts (n=60-75 pts/yr) were located 200 m apart along the edge of riparian habitat near the South Fork Kern River.

Nest Level

The effects of parasitism at a WIFL nest depend on the response and subsequent events at that nest (e.g., Whitfield 1990). Even in areas with high densities of cowbirds and relatively low numbers of willow flycatchers, some nests are not parasitized. The WIFLs at unparasitized nests may present fewer cues near the nest, or aggressively distract female cowbirds when cowbirds are further from the nest (Uyehara and Narins 1995).

Female cowbirds sometimes remove host eggs before 1230 hrs or after 1700 hrs (Scott et al. 1991, Sealy 1992), usually before parasitizing a nest. For first clutches of flycatchers from Kern County, CA (Table 9-2), 52 parasitized nests had a significantly

Table 9-2. Possible effects of parasitism at the nest level are listed and tested with data from Kern County, CA. A parasitized nest contained at least one cowbird egg.

Effect	Data from Kern County, CA, 1989-1991
a) Reduced clutch size	Mean number of eggs/clutch: parasitized nests = 3.17 unparasitized nests = 3.60 eggs,
b) Reduced hatching success	% Flycatcher eggs hatched parasitized nests = 22% unparasitized nests = 63%
c) Reduced fledging rates	28/73 parasitized nests hatched cowbirds, 3/73 parasitized nests fledged flycatchers
d) Overall nesting success	% nests fledged one flycatcher For unparasitized nests only = 54.8%. All nests, par and unpar = 28.9%.

lower mean number of eggs than did 97 unparasitized nests (t-test, $t = -2.94$, $p = 0.004$).

The presence of a cowbird egg in the nest is associated with decreased hatchability of flycatcher eggs (Table 9-2). The reduced hatchability of flycatcher eggs in parasitized nests may be due to insufficient incubation by the host if there is a larger egg in the nest, due to cracking of the flycatcher egg, or due to desertion of the nest. We have documented the effect of reduced hatchability at Kern but have no data on the mechanism leading to the reduced hatching rate.

If a cowbird hatches in a flycatcher nest, WIFLs rarely are able to successfully raise both their own young with the cowbird. There is also some evidence that cowbirds eat or remove all eggs or nestlings from a nest (e.g., Scott et al. 1992, Sealy 1992, Scott and McKinney 1994, Arcese et al. 1996, Sheppard 1996), perhaps to initiate renesting by the host. To our knowledge, there are no observations of nestling predation by cowbirds in WIFL nests.

The low success at fledging WIFLs in parasitized nests does not mean that the WIFLs are necessarily fledging cowbirds successfully. The actual proportion of cowbird eggs that hatch and subsequently fledge young in flycatcher nests is low (Fig. 9-2 and Table 9-2). This low success rate is due partially to the responses of flycatchers, which can reject the cowbird egg by burying the cowbird egg (which prevents hatching) or abandoning the nest. At Kern, of a total of 73 parasitized nests in 1989-1991, 11 eggs were buried within the nest floor. In 47 parasitized nests, WIFLs initially accepted the cowbird egg, but of those, 26 nests were eventually abandoned, probably as a response to some

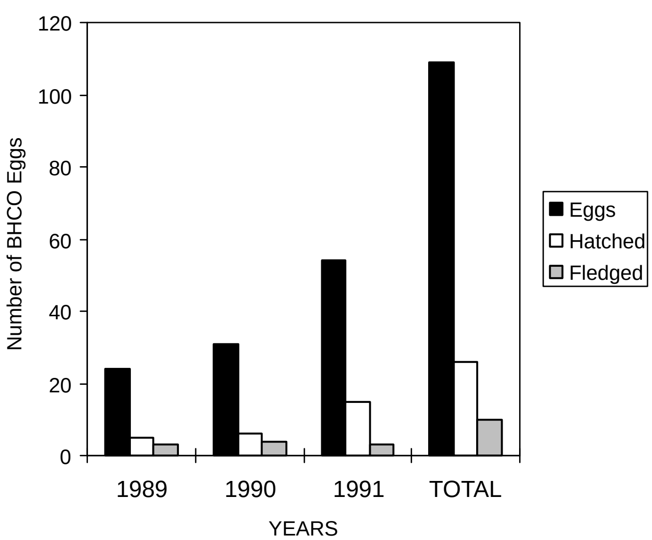

Figure 9-2. Of the cowbird eggs laid in southwestern willow flycatcher nests, only a small proportion hatched or fledged.

aspect of parasitism. Overall, for about half of the parasitized nests, the flycatchers responded so that the cowbird egg never hatched. Of 28 nests in which cowbirds hatched, three successfully fledged flycatchers. These nests were likely successful because the cowbird egg was laid late during incubation.

Nesting success is defined as the percentage of nests that fledge at least one flycatcher young. Parasitized nests rarely fledge flycatcher young. Of 28 nests in which cowbirds hatched, two nests fledged the flycatcher and the cowbird nestling died. One nest fledged one flycatcher and cowbird each.

Parasitism can reduce reproductive success at all nesting stages for flycatchers. For other populations of WIFLs, (not the southwestern willow flycatcher), the composite nest success is 83% across five studies (summarized in McCabe 1991, p 114). Thus, the nesting success at Kern is low relative to that of other subspecies (McCabe 1991, Stoleson et al., this vol).

Paradoxically, if a parasitized nest is subsequently depredated the flycatcher may renest, which may increase the flycatchers' nesting success. Thus, to better assess the effects of parasitism, we examined parasitism effects at the level of female reproductive success per season.

Annual Reproductive Success Per Female

Sedgwick and Knopf (1988) noted that parasitism rates of nests may not be the best measure of the effects of parasitism. Willow flycatchers can still nest after the cowbirds stop laying eggs in mid-July, or a parasitized female may exhibit rejection behavior and produce flycatcher fledglings during a season. Rejection behaviors by the flycatchers have the effect of delaying nesting. At the Kern River Preserve in central California, parasitism followed by rejection of cowbird eggs caused a delay of about 13 days in the first egg dates at parasitized nests relative to unparasitized nests (Whitfield and Sogge 1999).

We tested whether the number of fledglings in a season differed between parasitized and unparasitized females in the Kern population. Over all years, parasitized females raised about 1.05 yg annually whereas unparasitized females fledged 1.93 yg annually. There was considerable variation in the annual reproductive success per female among years (Fig. 9-3), so we also examined the differences for individual seasons. In 1989, parasitized females fledged significantly fewer young than did unparasitized females, (Mann-Whitney U test, $U=16.50$, $p=0.007$). However, in 1990, there was no difference in the number of fledglings produced by 18 parasitized and 6 unparasitized females (Mann-Whitney U test, $U=55.0$, $p=0.94$). For 1991, there were only 2 unparasitized females, so the data are not amenable to statistical testing. Starting in

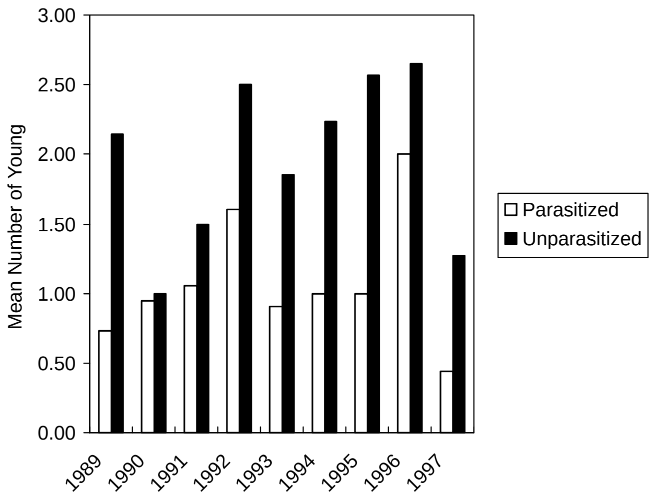

Figure 9-3. The mean number of flycatcher young fledged in parasitized and unparasitized nests. The numbers represent the number of females in the population that were parasitized or unparasitized. Beginning in 1993, management practices designed to minimize parasitism effects were instituted. (See text for additional details.)

1993, we hypothesized that more active management of cowbirds would increase productivity of WIFL females. Despite increased cowbird trapping efforts, the number of fledglings per female were not significantly different between parasitized and unparasitized females for any year between 1993-1997 (Fig. 9-3). To a certain extent, cowbird management practices increased the reproductive success per individual female, although the main effect may have been to reduce parasitism rates so that a smaller proportion of females in the total population were affected by parasitism.

The difference in significance levels between years with and without cowbird management (1989-1991) suggests that other factors besides parasitism are important in determining annual reproductive success per female. This hypothesis is further supported by the variation in reproductive success for unparasitized females over all years (Fig. 9-3) and by studies on other species (Braden et al. 1997). Logically, to assess the effect of parasitism, one has to combine the information of parasitism rates with its subsequent effect on productivity. The productivity of females is the sum of the number of young fledged in a season multiplied by the number of seasons that they reproduce. We do not have the data to assess the impact of parasitism on the survival of females and their lifetime reproductive success. On the other hand, we do have data to examine the effects of parasitism on changes in population size and the year-to-year variation in population growth.

Population Level

We have presented summaries and data that indicate parasitism reduces productivity when measured on the level of the nest and on a per-female basis. Arguably, the most important analysis of the effects of brood parasitism should be conducted at the population level (e.g., Trail and Baptista 1993, Rogers et al. 1997). If brood parasitism is significantly decreasing the population growth rate (λ) below the level of a self-sustaining population, then active management may increase its probability of persistence.

We can test whether the effects of parasitism have been mitigated by management practices at Kern County. We analyzed the correlation between parasitism rates and the annual population growth rates for the Kern population of WIFLs. If parasitism is reducing population growth, we would predict a significant negative relationship between parasitism rates and population growth rates.

We used a standard demographic model to calculate population growth rates. The model makes the following assumptions:

1. Female reproduction is not limited by the availability of males, so it suffices to count only females (Caswell 1989).
2. There is no immigration or emigration of birds outside of the study area.
3. Mortality rates can be calculated as the return rates of banded birds.

We chose a pre-breeding model to include any possible effects of parasitism on (winter) adult survivorship within the same time step as the (summer) parasitism events. Heuristically, the model starts with the survey of adults at the end of May. In reality, some adult females do not arrive until mid-June (Whitfield, unpub data), but for the purposes of the model, all adults are treated as arriving by 1 June. Adults are categorized into two age groups: yearlings (Second-Year or SY) and older adults (After Second-Year or ASY). Both groups nest and raise young. At the end of the breeding season, the juveniles, yearlings, and adults migrate to their wintering sites. Those individuals that survive return as yearlings (SY) and older adults (ASY). The yearlings are those birds hatched the previous year at Kern. The older adults are now the returning SYs and ASYs of the previous year.

In this standard demographic model, there are four parameters that contribute to the population growth rates (Table 9-3):

(a) the reproductive rate of SY adults, or equivalently, the number of fledglings produced by SY adults multiplied by the return rate of the fledglings the next spring;

(b) the reproductive rate of ASY adults, or equivalently, the number of fledglings produced by ASY adults multiplied by the return rate of the fledglings the next spring;
(c) the survival rate of SY adults
(d) the survival rate of ASY adults

Banding data from 1990 to 1997 indicated that the average number of young fledged did not differ by parental age: SY fledged 1.65 yg (n=20) and ASY fledged 1.66 yg (n=29). We also assumed that the survivorship of fledglings to yearlings was the same regardless of parental age, thus simplifying the model so that a = b. We also did not distinguish between the survival rates of SY and ASY adults, so that c = d.

Note that our prebreeding model differs from postbreeding models (e.g., Stoleson et al., this vol). In our calculation of reproductive rates, the fledglings produced by adults must survive to the following June. In a postbreeding model, the reproductive rate of hatching-year birds (HY) is calculated. This reproductive rate is the product of two factors: a) fledgling survival to SY and (b) the mean number of fledglings produced during the following breeding season. In our prebreeding model, we never calculate a reproductive rate for hatching year birds because they do not reproduce until the time step in which they are adults. Instead, a reproductive rate is calculated for all adults (Table 9-3).

The overwinter survival of juveniles and adults were estimated from the data on banded birds, which yields minimum estimates of survival. The numbers of banded birds varied across years as did the field effort to resight birds. In general, the numbers and proportions of banded adults were higher for more recent years than at the beginning of the study. There was an increased field effort to resight and mark adult birds from 1994.

We used the survival and reproductive rates of females to calculate the annual population growth rate, λ. The simplification of a = b and c = d, we were able to calculate the population growth rate, λ, directly as λ = a + c.

We looked at the relationship between λ for each year (June to June) and the parasitism level of the breeding season (Jun-Aug). We used data from all years, including the six years of cowbird management. Cowbird management practices at Kern may reduce parasitism effects on individual basis, but may not eliminate all effects. A significant negative relationship between λ and the parasitism rate means that parasitism is affecting the population growth rate at Kern.

The growth rates of this WIFL population do tend to decrease with increasing parasitism rates (Fig. 9-4; linear regression analysis, $r^2 = 0.44$, $p=0.073$). Although the p value is slightly above 0.05, parasitism rates explain 44% of the variation in the annual population growth rates. This effect of parasitism rates on λ seems strong, especially considering that cowbird management occurred in 5 of 8 breeding seasons and that the statistical power of our analyses is low due to the small number of years. The slope of the best-fit line gives an indication of the benefit of reducing parasitism rates. For every drop of 0.10 (10%) in parasitism rates, lambda increases by 0.076 for this population.

Table 9-3. Life history parameters of one population of SWFLs in Kern County, California. Banding and nesting biology of SWFLs were used to calculate the population growth rate, Lambda. Rates are calculated for females only. We assumed that half of the banded fledglings were female. This number is parenthetically noted after juvenile survival rates. Rates for adult survival are calculated as the number of banded female adults which were resighted or recaught the following year. The means for all years and for years with cowbird trapping (1993-1996) are calculated separately.

Breeding Year	Female Fledglings per adult	Juvenile Survival Rate (banded female nestlings)	Female Adult Survival (banded adult females)	Reproductive Rate	λ
1989	0.57	0.38(8)	0.00(2)*	0.25	0.63
1990	0.48	0.09(11.5)	0.43(7)	0.05	0.47
1991	0.60	0.00 (4.5)	0.63(8)	0.00	0.63
1992	0.89	0.20 (10)	0.38(8)	0.17	0.55
1993	0.56	0.36(14)	0.54(13)	0.24	0.74
1994	1.00	0.27(17.5)	0.35(20)	0.25	0.62
1995	1.00	0.50(14)	0.42(19)	0.50	0.92
1996	1.27	0.59(19.5)	0.63(19)	0.74	1.39
Mean (All yrs)	0.67	0.30	0.42	0.28	0.74
Mean (Trap yrs)	0.96	0.43	0.49	0.41	0.90

*Neither of the two adult females banded in 1989 returned in 1990. Because of the low number of banded birds for 1989, we used the overall mean of 0.42 for adult survival rate to calculate lambda for 1989-1990.

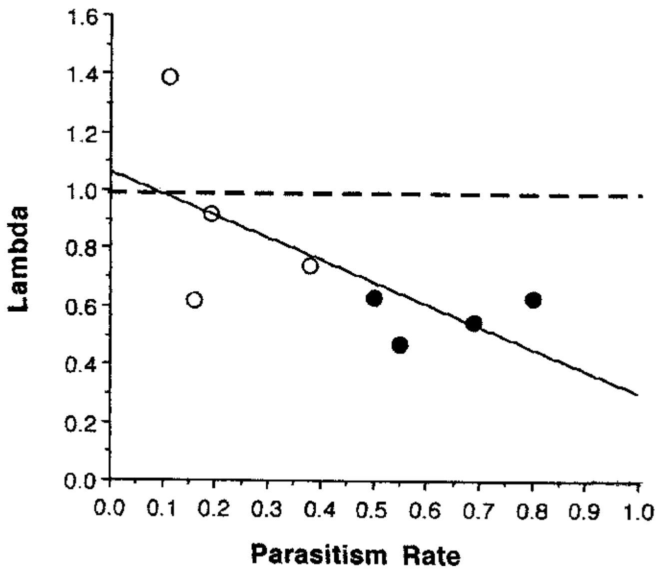

Figure 9-4. The population growth rates of the Kern population is significantly associated with parasitism rates. Solid circles represent years with no cowbird management (1989-1991) and open circles represent years with cowbird management (1993-1996).

The regression analysis suggests that the recovery of the Kern population ($\lambda \geq 1$) necessitates a very low parasitism level. The best-fit line for the data reaches a self-sustaining population ($\lambda = 1$) at the low parasitism rate of 8.4%, with population growth likely only to increase if parasitism levels are maintained below 8.4%. Note that the 8.4% parasitism rate is only a guideline, as it is based on data from a relatively small number of years.

Using this regression analysis, we produced guidelines for parasitism levels for a self-sustaining or recovering Kern population, assuming that the range of rates remain within the parameters for 1989-1997. For the years without cowbird management (1989-1991), the high levels of parasitism and subsequent low λ values indicate that the Kern population was not a self-sustaining population for those years.

The guidelines we have produced are applicable to the Kern population or a population with similar rates for survival and nesting success. Populations with different parameters of nesting success and overwinter survival will have different population growth rates for the same parasitism levels. We cannot compare survival rates because we are unaware of any data on survival rates in other WIFL populations. However, the range of nesting success of the Kern population appears comparable to other populations (cf. Stoleson et al., this volume). The nesting success for the Kern population from 1989-1997 ranges from 0.48 to 1.27 female fledglings per female (Table 9-3) or 0.96 to 2.5 fledglings per female. Stoleson et al. (this vol) report comparable values of 1.25-2.45 fledglings per female for other WIFL populations. One final analysis may indicate how responsive the Kern population would be to continued cowbird management.

Elasticity Analyses and Cowbird Management

The biology and data for rates of survival, reproduction, and parasitism show a pattern that warrants further analysis in planning the recovery of an endangered species. At Kern, parasitism rates have been lowered with cowbird management. Is continued management of cowbirds likely to contribute significantly to population recovery? An indirect answer to this question can be obtained using elasticity analysis of the data (e.g., Stoleson et al., this vol.). Elasticity values predict how a change in each parameter of our prebreeding model would affect the population growth rate.

Cowbird management may directly affect reproductive rates (along with other factors), but have less or no effect on the survival rates of adults. If survival rates are predicted to have a major effect on the population growth then continued cowbird management will have small effects on population growth. Conversely, if changes in reproductive rates of SY or ASY adults have large effects on population growth, then cowbird management as a means of enhancing reproductive success is an efficient option for recovery.

The results of the elasticity analyses support the findings by Stoleson et al. (this vol.) and the efficacy of cowbird management practices (Table 9-4). With no cowbird management, the reproductive rates were low (Table 9-3), and the strongest effect to a change in population growth rate was survival of adults. For example, from Jun 1989-Jun 1990, a 0.01 increase in population growth rates could be accomplished if ASY survival rates increased by 0.025. The elasticity measurements for 1991 show that with poor reproductive success, the population growth rate is most responsive to an increase in adult survivorship. In 1996, the elasticities were more evenly divided. An increase in any one parameter will have about the same effect on the population growth rate, although increasing reproductive success of SY adults will have the most beneficial effect on population growth.

However, cowbird management practices will likely affect reproductive rates of both age-classes simultaneously. When reproductive success is equivalent for females of both age-classes, then we can calculate the reproductive success necessary to produce a self-sustaining population using the mean values during active cowbird management (1993-1996). The overall lambda is 0.90 for the years with active cowbird

Table 9-4. Elasticities of the demographic parameters. From 1989-1991, no cowbird management was attempted. In 1992, selective cowbird shooting at the nest eliminated 21 female cowbirds. From 1993, cowbird traps were placed throughout the breeding and feeding areas.

Year	Parasitism Rate	Lambda	E(a)	E(b)	E(c)	E(d)
1989	0.50	0.67	0.11	0.22	0.22	0.44
1990	0.55	0.48	0.01	0.09	0.09	0.80
1991	0.80	0.63	0.00	0.00	0.00	1.00
1992	0.69	0.55	0.10	0.22	0.22	0.47
1993	0.38	0.78	0.09	0.21	0.21	0.48
1994	0.16	0.59	0.17	0.24	0.24	0.35
1995	0.19	0.92	0.30	0.25	0.25	0.21
1996	0.11	1.37	0.29	0.25	0.25	0.21

management (Table 9-3). This indicates that even with the high survival and reproductive rates recorded for these years, this population needs to increase either productivity or overwinter survival to persist over the long term. A self-sustaining population with cowbird trapping requires a 10% increase in λ or assuming adult survival rates remain constant, then the overall reproductive rate of 0.51 will allow this population to become self-sustaining. Because reproductive rates are the product of nesting success and return rates of fledglings of the previous season and assuming that return rates of fledglings are not amenable to cowbird management, then, on average, a self-sustaining population at Kern requires 1.18 female fledglings per female or an average nest success of 2.36 yg per female. On average, any increase over 2.36 yg per female will contribute to population recovery.

Summary

The brown-headed cowbird parasitizes nests of the southwestern willow flycatcher (*Empidonax traillii extimus*). The main breeding season of cowbirds (May to mid-July) overlaps with the initial nesting period of southwestern willow flycatchers (Jun-Aug). Parasitism rates of willow flycatchers tends to be high, possibly because of the forest structure and landscape influences in current nesting areas. Parasitism rates vary with cowbird abundance, across years, and at different sites. The effect of parasitism on willow flycatchers can depend on many factors: cowbird abundance, the overall parasitism rate of nests, the timing of cowbird parasitism, and the events subsequent to parasitism, e.g., cowbird egg burial, nest desertion, renesting, and predation.

For one central California population of southwestern willow flycatchers, we have documented the effects of cowbird parasitism on a per nest, per female, and population basis. About 1/3 of parasitized nests reached the stage where cowbirds hatched, the stage which is considered to lead to the highest reproductive loss for flycatchers. Of the nests in which cowbirds hatched, 41% fledged cowbirds. Flycatcher response to parasitism, however, ameliorated the effects of parasitism in about half of all parasitized nests.

Per individual female, the major effects of parasitism were to delay nesting, decrease hatchability of flycatcher eggs in parasitized nests and decrease clutch size either because of removal by cowbirds or later clutches tend to be smaller. Except for decreased hatchability, these effects have been documented throughout the range of willow flycatchers. Due to the small but cumulative effects of parasitism, the annual reproductive success of females is influenced by parasitism, if parasitism is the major cause of nest failure for that year.

For one population in Kern County, California, increasing parasitism rates decreases population growth rates. Parasitism can explain 44% of the variation in population growth rates. Our analysis shows that parasitism rates must be low for this population to persist or increase. Given the life history parameters at Kern, population growth may be dependent on active cowbird management to decrease the effects of parasitism. In order for this population to become self-sustaining or increase, females need to fledge an average of 2.4 young. We provide evidence of the detrimental effects of parasitism on southwestern willow flycatcher recovery and document the extent of the benefits of cowbird management. Although our conclusions are based mainly on one population of WIFL, this population appears to be similar enough to others that our conclusions may apply to other populations as well.

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Chapter 10:

Management Recommendations

This chapter was developed over a series of meetings using a group-consensus process. Our recommendations are based on published results, on information compiled in the previous chapters, on expert opinion, and on unpublished data of conservation team members. This chapter is available as temporary guidance until the Recovery Plan for the southwestern willow flycatcher is published in the Federal Register. A draft Recovery Plan has been prepared by the Technical Subgroup of the Recovery Team and is under current review by the U.S. Fish and Wildlife Service and by Implementation Subgroup Members of the Recovery Team. The Technical Subgroup reviewed this Assessment management chapter to aid in drafting the Recovery Plan. Several members of the temporary Conservation Assessment Team were also members of the ongoing Recovery Team. Given that the draft plan was assembled over a 2-year period requiring more than 20 Recovery Team meetings, its guidance will be much more exhaustive and up-to-date than the recommendations identified herein. Upon publication of the final Recovery Plan, this chapter will be obsolete and should not be used in place of, or to contradict, the Plan.

To initiate discussion for this chapter, we first listed actual and potential threats to the survival and reproduction of the southwestern willow flycatcher, then listed potential ways to mitigate or eliminate threats. In some cases, insufficient research limited our understanding of how perceived threats actually harmed flycatchers or their habitats, or what steps to take to mitigate the threat. For example, lack of published knowledge of the range and habitats used by flycatchers on the wintering grounds constrained our discussion of management recommendations on this topic. We also describe methods to improve and restore willow flycatcher habitats as well as ways to distribute information and educate people about how to protect and recover flycatcher populations. We include specific sections addressing potential threats to willow flycatchers from biological factors, invasive exotic plants, catastrophic fire and management activities, as well as methods for habitat and watershed restoration and improvement. Many of our recommendations may also be of use in conserving and protecting populations of other sensitive bird species that occupy riparian ecosystems, such as the Yellow-billed Cuckoo (*Coccyzus americanus*) or the endangered Least Bell's Vireo (*Vireo bellii pusillus*).

Throughout the chapter, we refer to WIFL habitats as potential, suitable, or occupied. Potential habitats are defined as sites that lack one or more habitat component(s) that WIFLs require but that can be manipulated to make the site suitable for occupancy. Potential habitat types include those that are naturally regenerating and close to suitable, and those that need more time or active improvement before suitability is achieved. Unoccupied suitable habitats are defined as unoccupied sites that are or appear suitable for WIFL occupancy without manipulation. Unoccupied suitable habitats are similar to occupied habitats except that they lack WIFLs. Occupied habitats are suitable without saying and are those where evidence of WIFL breeding, such as observations of territorial males, breeding pairs, mating behavior, carrying of twigs and food items, nests, and fledglings, have been recorded and verified.

Reducing the Probability of Biological Threats

Brown-headed Cowbird Parasitism

Brown-headed cowbirds frequently lay eggs in willow flycatcher nests; cowbird parasitism substantially reduces the nesting success of flycatchers and is often a significant biological threat to flycatcher productivity. Adult cowbirds can reduce host nesting success by stimulating nest desertion, and removing, piercing, or depredating host eggs. Cowbird nestlings frequently outcompete host nestlings and fledglings for food, causing host chick starvation, and occasionally nudge host nestlings out of the nest. To prevent loss of host eggs and nestlings caused by cowbirds, a series of preventative steps are strongly recommended.

Monitoring—We recommend that the potential for threat to the southwestern willow flycatcher from cowbird parasitism be monitored at all occupied sites. Monitoring consists of determining cowbird presence or abundance via surveys, population counts, or radio-tracking (Verner and Ritter 1983, Beezley and Rieger 1987, Rothstein et al. 1987, Whitfield in press); surveying flycatcher nests for presence of cowbird eggs and nestlings (Harris 1991, Whitfield 1995); and determining cowbird parasitism rates at WIFL nests (Whitfield 1990, Whitfield in press). If parasitism rates exceed the threshold of 10% (Whitfield in press), then cowbird trapping should be initiated along with an analysis of WIFL productivity. Because parasitism rates vary with site, year, patch size, and population size of flycatchers and cowbirds (Robinson et al. 1993, 1995), sites should be monitored for more than one season. It is possible that the trapping threshold may vary in relation to site conditions and host nesting success. If cowbird parasitism does not exceed the predefined threshold (10% threshold being conservative), continue monitoring.

If sites have not been monitored for cowbird parasitism, trap cowbirds if more than three willow flycatcher territories are present. If cowbirds are not present at WIFL-occupied sites, continue surveying for both flycatchers and cowbirds in subsequent years.

Control Program—There are short-term and long-term aspects to a cowbird control program (Schweitzer et al. 1996). Cowbirds are known to be attracted to riparian habitats that have been fragmented into smaller patches, narrow, linear corridors, and edge habitats (Robinson et al. 1993, 1995). Management practices over the long term should emphasize:

- Reducing phreatophyte removal, wildfire, water loss, and exotic plant invasion.
- Increasing habitat patch sizes and migration corridors, and reducing the extent of edge.
- Educating human communities about cowbird attractants, including types of birdfeeder seed (e.g., millet) that attract cowbirds.

Over the short term, we recommend implementation of the Griffith Brown-headed Cowbird Trapping Protocol (Griffith and Griffith 1996) to control cowbird numbers. During the trapping effort, cowbirds and parasitism rates should be monitored over multiple years to determine if trapping is having the desired effect of reducing parasitism rates (Robinson et al. 1993, Whitfield in press). For trap-shy birds, other methods of cowbird removal such as shooting may be needed (Schweitzer et al. 1996). In addition to trapping, cowbird attractants such as livestock should be removed from WIFL breeding sites. Other attractants include trash, food, agricultural fields, bird feeders, plowed fields, livestock feedlots, dairies, and pack stations. Possible actions to reduce the probability of attracting cowbirds include removing attractants, covering trash, and scheduling more frequent trash pickups. If attractant removal is not possible, use attractants as sites for trapping. Removing attractants from lands adjacent to occupied sites is also worthwhile, although the feasibility of attractant removal will need to be evaluated on a site-specific basis. Attractants that are feasible to move include cows, trash, and bird-feeders; non-feasible removal may include stationary attractants such as cropfields and feedlots.

At trap sites, space traps according to habitat size and landscape features, distribution of WIFLs and cowbirds, and available finances (refer to Griffith and Griffith 1996, in press). Where cowbirds are concentrated in known feeding sites in close proximity to WIFL sites, consider trapping off site and in conjunction with on-site trapping. We do not define a distance for off-site trapping because of site-specific variation in cowbird commuting distances, habitat use, and landscape pattern (Stephen Rothstein, pers. comm., Frank Thompson pers. comm.). Note that permission to trap on private lands will be needed. Federal landmanagers adjacent to private lands having WIFL sites will need to work with private landowners to trap cowbirds. Initiating cooperative efforts to trap cowbirds in mixed-ownership lands is a responsibility of the federal, state, or municipal agency.

Multiple years of trapping are recommended. Trapping efforts may be reduced or stopped if all of the following are observed:

- Significant reduction of cowbird numbers based on cowbird trapping rates.
- Significant reduction of parasitism rate on WIFL nests.
- WIFL population shows a significant upward trends at the site(s).

Trapping should be renewed at previously-trapped sites if parasitism rates ≥10%. A depiction of the feedback loop for initiating trapping is given in Figure 10-1.

To trap cowbirds, we recommend using the Griffith trap design, trap size, and protocol. Trap size can be reduced by half when finances are limiting, at remote sites, or when cowbird densities are low. Use the recommended trap size when cowbird densities are high and/or at feeding lots where cowbirds are concentrated. Alternatives for trap materials include PVC to reduce trap weight; shadecloth to reduce heat stress; or plywood for shading when windy. Predator control mechanisms may need to be added to the trap design to deter raccoons, weasels, snakes, and other predators. Traps placed in or adjacent to livestock-occupied pastures generally have good success in trapping cowbirds, but they need to be protected from livestock damage.

When to stop cowbird trapping depends on site-specific conditions and whether WIFL populations are recovering at each site. Maintenance trapping may be needed over prolonged periods of time even when increased WIFL nesting success is detected. WIFL populations should show significant increases before they can be considered locally recovered.

Predators

Willow flycatchers, like most songbirds, have open-cup nests that can be readily accessed by a variety of natural predators. These can include small mammals such as raccoons, skunks, squirrels, and packrats; birds such as hawks, owls, roadrunners, and corvids; tree-climbing snakes such as racers; lizards; and domesticated and feral cats and dogs. Nest predation usually explains the greatest proportion of nest failure in local flycatcher populations (Whitfield 1990). Adult flycatchers can be captured on the wing by many raptors such as falcons, accipiters, and possibly owls. Other predators can catch adult flycatchers at their nests or at their singing and foraging perches. To reduce predation rates, the following steps are recommended:

- Control presence of predator attractants such as trash and food.
- Use sensitive techniques (e.g., avoid tree-climbing, minimize time at nest, avoid touching or moving nest and young) when conducting nest monitoring.
- Educate public about cats and dogs as predators of birds.

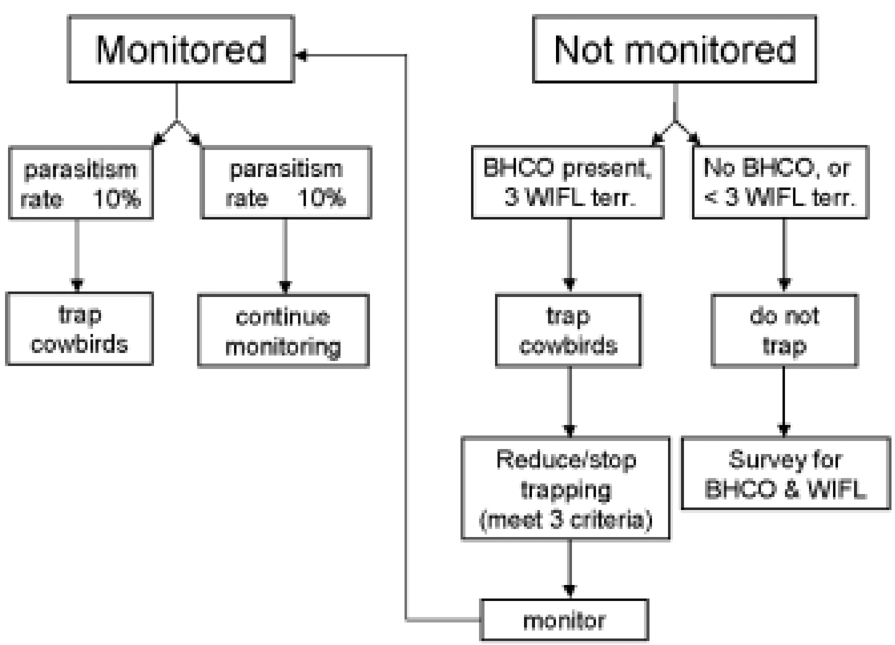

Figure 10-1. Cowbird trapping feedback loop.

- Trap domestic feral cats, when they are perceived as a problem.
- Reduce predator intrusion into flycatcher habitat at edges and along trails by increasing habitat patch size, reducing patch isolation, and closing trails.
- If possible, identify predators during nest monitoring.
- If monitored nests have high predation rates, develop and implement feasible predator control measures in the local area.

Evaluate nest predation signs to determine kinds of predators. Identity of nest predators is valuable information for deciding how to reduce predation levels, if necessary. However, effective control measures and strategies still need to be designed for many identified predators. Nest observers should be careful to avoid attracting mammalian predators to the nest. Such predators are known to follow humans or their scent trails. To mitigate this problem, nest observers should vary their pathways to nests and take steps to eliminate human scent using napthalene or other scent removers.

Beaver

If beaver are present at occupied, suitable, or potential WIFL sites, managers should determine if they are benefiting WIFLs (e.g., beaver dams may be creating backwater, a habitat condition associated with WIFL occupancy) or damaging habitat by removing vegetation. Beaver damage is more likely to be a problem at sites where riparian habitat is linear and habitat patches are small or where their dams cause habitats to become inundated (e.g., high elevation sites). If beavers are determined to be beneficial to WIFLs, beavers should be left in place and the site should be monitored to assess future conditions. If beavers are determined to be detrimental to WIFLs (e.g., by removing essential WIFL habitat), consider active reduction or removal of the beaver population. Site-specific analyses are needed to make determinations.

As part of a habitat restoration program, beaver reintroduction may be a useful tool to enhance a site, creating conditions such as still water that encourage colonization by flycatchers.

Parasites and Disease

There is little evidence that southwestern willow flycatchers have problems with parasites or disease. In addition, management capability to address such problems may be limited. Determining whether parasites or disease are a significant problem is the first step in deciding how to address them. In cases where other bird species are being studied in an area occupied by willow flycatchers, we suggest that they be intensively examined for evidence of parasitism or disease. Any evidence of parasitism detected by WIFL nest surveyors should always be recorded. Field forms should be modified to include space for documenting evidence of parasites or disease. If flycatchers are found dead at nests or elsewhere, their carcasses should be collected and analyzed for parasites or disease. To evaluate incidence of botfly larvae, we recommend that nests be collected and analyzed by investigators having permits to do so.

Genetics

Southwestern willow flycatchers may be facing problems typically associated with small populations such as genetic isolation and inbreeding. To evaluate presence of genetic problems, the incidence of deformities will need to be documented through the collection of tissue samples. This should be conducted by qualified scientists. Reports of possible genetic problems and specimens should be sent to the U.S. Fish and Wildlife Service. Tissue analyses can be referred to the U.S. Fish and Wildlife Service's Disease Lab in Madison, WI. The best approach to reducing the probability of genetic isolation and inbreeding is to apply habitat restoration and population recovery methods to increase WIFL abundance and expand its distribution.

Mitigating Loss of Native Habitat Due to Invasion by Exotic Plants

Invasive exotic plants such as salt cedar (*Tamarix ramosissima*, *T. chinensis*), Russian olive (*Elaeagnus angustifolia*), Siberian elm (*Ulmus pumila*), tree-of-heaven (*Ailanthus altissima*), white mulberry (*Morus alba*) and giant reed (*Arundo donax*) are replacing native vegetation along many rivers and streams in the Southwest (Campbell and Dick-Peddie 1964, Robinson 1965, Ohmart et al. 1977, Dick-Peddie 1993, Crawford et al. 1993, Ohmart 1994). Habitat changes resulting from the spread of salt cedar can influence bird species composition and use (Hunter et al. 1987, 1988). Whether encroachment of riparian habitats by exotics has had a negative effect on willow flycatchers is debatable. At some monotypic and mixed salt cedar sites, for example, WIFL nests have been found and many of these nests have successfully fledged WIFLs. At higher elevations, salt cedar thickets are often the only habitat with suitable structure available for the WIFL to nest in. Yet, effects of salt cedar invasion of riparian zones, particularly at lower elevations occupied by cottonwoods, may be more negative than positive owing to increased fuel loading, increased frequency of catastrophic fires related to salt cedar flammability, loss of native plant communities to type conversion, and loss of flycatcher habitat to wildfire. Anderson et al. (1977) noted that 21 of the 25 tamarisk stands they studied had burned in the prior 15 years. When dense tamarisk thickets burns, the fires are typically fast moving and intense. For example, during just 3 years, recent fires totaled 1,000 ha of riparian habitat along the Lower Colorado River—a substantial amount considering only about 6,200 ha of suitable bird habitat currently exists along this river (U.S. Bureau of Reclamation 1999).

With emphasis on salt cedar, we recommend the following steps be initiated to avert catastrophic fire risk and prevent further loss of native plants due to exotic plant invasion while maintaining WIFL breeding sites where exotics are already present:

- Justify the need for exotic plant control at a particular site prior to taking action.
- Develop a watch list of exotic plant species in riparian ecosystems with focus on rate of spread, WIFL use, and effects on native plant species and ecosystems.
- In occupied sites, leave exotics as is, unless exotics are significantly increasing and detrimentally altering habitats.
- If exotics are encroaching on previously occupied sites, consider removing exotics and restoring sites.
- If exotics encroach on occupied sites that were exotic-free, eradicate exotics without disturbance (i.e., during the non-breeding season). Evaluate symptoms and address causes of exotic encroachment. If conditions are not appropriate for restoration of native plants, then remove of exotics may not be of strong benefit.
- Monitor effects of increasing presence of exotics at occupied sites. If signs of negative effects on WIFL numbers or nesting success are detected, then remove invasive exotics. For example, type conversion and structural alterations of habitat may signal a decline in habitat quality that could potentially influence WIFL populations or productivity.
- In suitable and potential habitats dominated by native plants, suppress encroachment of exotics.
- In suitable habitats dominated by exotics, survey for WIFL at least 3 years prior to removal of exotics. Removal should be conducted in incremental blocks of no more than 25% annually at surveyed sites.
- Evaluate potential for restoration success by investigating measures of watertable depth, salinity, geomorphology, and hydrology. If sites are amenable for restoration, exotics may be removed. If not amenable, management of exotics is not cost-effective and may be detrimental to other animal species.
- Several aspects should be considered with respect to biological control of exotics (*sensu* DeLoach 1997):
  - — Removal of exotics may be detrimental if the site is not capable of replacing salt cedar with natives or if erosion is increased as a consequence of removal.
  - — A more comprehensive approach that includes restoration is needed before implementing biological control.
  - — Adequate field testing is needed before evaluations of biocontrol agents can be considered completed.
  - — Managers must first evaluate whether or not exotics should be removed from WIFL habitat; once the decision is made to remove exotics, managers need to decide what method of control is most appropriate.
  - — If biocontrol is considered to be the best method of control, then adequate laboratory tests and isolated field experiments are needed prior to full release.
  - — State of knowledge of biotechnology is currently inadequate to recommend full release.

In addition to salt cedar, the following exotic species should be considered when designing removal programs:

- ***Giant Reed***—Removal is beneficial because native vegetation will replace it and because WIFLs have not been documented to use reed for nesting.
- ***Russian Olive***—The distribution of Russian Olive is limited to New Mexico, Colorado, and northeastern Arizona. This exotic can provide habitat structure and nest trees for WIFLs, and WIFLs are known to nest in it. Detrimental effects of this exotic to WIFLs are unknown.
- ***Tree of Heaven***—This exotic occurs locally in Arizona, California, and New Mexico. Very little is known about the relationship between WIFLs and Tree of Heaven. This exotic is not highly concentrated in riparian habitats and detrimental effects to WIFLs, if any, are unknown. We recommend that it be included on a watch list.
- ***Siberian Elm and White Mulberry***—Concern about these exotics are similar to that reported for Tree of Heaven. Detrimental effects to WIFLs, if any, are unknown. We recommend that they be included on a watch list.

Reducing the Threat of Catastrophic Fire

In 1997, six WIFL sites in Arizona were destroyed by fires. This catastrophe alerted managers to the need to have better plans in place for preventing and responding to unexpected wildfire events. Before a fire occurs, we urge the following steps be taken for all occupied breeding WIFL sites:

- Prepare a site-by-site fire management plan for each occupied site in coordination with local fire-fighters. These plans should include steps for preventing fires, as well as methods for protecting willow flycatchers and their habitats if a fire occurs.
- Refer to the White Canyon Fire Biological Opinion (U.S. Fish and Wildlife Service, Ecological Services, Phoenix, AZ) as an example of a responsible fire management plan.
- Identify water sources that are not near or in occupied WIFL habitat in the fire plan.
- Erect fire prevention signs.
- Restrict use of campfires and camping in high risk areas.
- Reduce fuels adjacent to occupied sites using tools such as fuel breaks, mechanical clearing, prescribed burning except in salt cedar, herbicides.
- Host training sessions and implement other measures to educate fire-fighters about WIFL resource values and locations. This will ensure that flycatcher protection is included in the fire plan.
- Identify who needs to be trained.
- Seasonal grazing is not recommended as a fuel reduction method in occupied WIFL sites because predominant fuels are woody materials, i.e., not primary livestock forage (also see livestock management criteria). But livestock grazing may be appropriate in adjacent uplands where fuel loads can lead to fire spread to riparian zones.

When a fire event does occur in habitat occupied by willow flycatchers, the "fire management plan" should immediately be implemented. Emergency consultation with U.S. Fish and Wildlife Service should be initiated to ensure that destruction of WIFL habitat is avoided. Care should be taken when establishing fuel breaks during the fire. The potential costs of using fuel breaks are: fragmentation of WIFL habitat, increased erosion, establishment of a potential travel corridor for predators or access point for recreationists, destruction of potential or suitable habitat, and invasion by exotic or undesirable plants. Alternatively, the benefits of fuel breaks include the installation of a fire barrier that limits fire spread, the creation of a fire-fighting attack point, and the minimization of direct fire threats to WIFL-occupied habitats.

After a fire event, habitats may need to be restored. If WIFL habitats have been destroyed, fire rehabilitation efforts should be implemented with WIFL habitat requirements in mind. Emergency consultation can be included after post-fire rehabilitation plans have been initiated.

Reducing Potential Threats Caused by Management Activities

Pesticides

Pesticide use by landowners and agencies in areas near occupied WIFL habitats should be evaluated periodically. Water quality tests can be conducted to determine if pesticides are entering the ecosystem. Visible pesticide effects (e.g., plant or arthropod responses) at WIFL and adjacent sites should be documented. Any deformities or abnormal behavior of WIFLs or co-existing birds should be reported by nest surveyors and migration banders to the U.S. Fish and Wildlife Service. Deformities in California WIFLs have been documented with photographs, suggesting that pesticides may pose a threat to WIFLs as well as other associated fauna. If pesticides are perceived to be a problem, a pesticide reduction plan and public education efforts should be implemented. To verify pesticide contamination, abandoned WIFL eggs and individuals of surrogate species can be tested further. Pesticide use in a region can possibly be inferred based on distribution of sales.

Livestock and Other Ungulates

In potential and suitable but unoccupied WIFL habitats, site conditions should be evaluated prior to exclusion of livestock. Changes in livestock rotation schedules and the timing and period of pasture use can go a long way toward restoring riparian habitats to benefit WIFLs. If site conditions are suitable (see criteria below), controlled grazing can be permitted during the dormant season of woody species. When grazing is allowed, vegetation should be monitored to determine if the site is undergoing unusual damage from grazing. To allow regeneration of habitat, we recommend that ungulates be excluded during the growing season (at minimum) of woody species. To restore degraded or overgrazed riparian habitats, it may be desirable to exclude cattle altogether. To allow potential habitat to progress to a stage that is suitable for WIFL occupancy, livestock removal is appropriate. However, if priorities for livestock exclusion from potential habitats must be established, then those habitats adjacent to or near occupied WIFL habitats are higher priorities for protection from grazing than potential habitats that are at a great distance from WIFL occupied sites.

If breeding WIFLs occur at the site, we recommend complete exclosure to all livestock and other ungulates year-round. For all excluded sites, managers should conduct frequent inspections to identify trespass livestock. In occupied sites, remove trespass livestock by drawing them out using attractants (hay, mineral blocks) rather than herding. If livestock cannot be attracted out of the occupied area, wait until September 1 (post-WIFL breeding season) before driving livestock out.

Under proper management, livestock presence may sometimes be compatible with habitat quality. Therefore, exceptions to year-round livestock removal from occupied habitats on public lands should be available if the livestock owner can demonstrate to the permitting agency that grazing during the nongrowing season of woody species at a specific site does not adversely affect WIFL habitat structure and composition. The following documentation should be supplied to justify exceptions:

- Dated pictures of habitat conditions before and after grazing at specified photo points repeated at the same time each year.
- On-site demonstration visits.
- Data of measured vegetation before and after grazing. Measurements should be taken of stem densities, foliage height diversity, canopy cover, plant species composition, and aerial extent (patch size) of habitat.

The timing, duration, and intensity of grazing should not preclude recruitment or adversely affect existing regeneration of riparian plants. If time is not available to monitor vegetation, then grazing should not be permitted. These criteria for excepting livestock exclusion apply to all 3 habitat levels (occupied, suitable, potential). Managers and stockraisers alike must maintain an open mind when working together and avoid being influenced by biased information or unsubstantiated opinions. By building trust and cooperation, effective and honest decisions can be made.

Recreation

We recommend that recreational impacts at occupied, suitable, and potential sites be evaluated regularly to detect any habitat damage, cowbird presence, or other factors that may impact WIFL. Activities such as camping, hiking, fishing, boating, biking, photography, and driving vehicles are known to have varying impacts on nesting birds, depending on the intensity, timing, location, noise level, predictability, and type of disturbance as well as the species, abundance, and habituation level of birds (Knight and Gutzwiller 1994). The following preventative steps are recommended to mitigate negative effects of recreational activities:

- Close areas to off-road vehicles year round in potential, suitable, and occupied habitats.
- Exclude human access from occupied sites; use “Area Closed” signs.
- Fence off occupied habitat; do not allow entry during breeding season.
- If area closures are implemented, ensure that closure orders are written to allow entry by authorized personnel (e.g., researchers, surveyors, etc.)
- Occupied habitats that are closed during the breeding season should be open for day use only in the non-breeding season. Campfires should not be permitted at any time.
- Avoid construction of new campground or day use facilities in occupied, suitable, or potential sites.
- Evaluate if recreational impacts are occurring to habitat during the non-breeding season. Limit use with permits if needed. Implement year-round closure to recreation if warranted based on analysis of impacts.
- No product harvest within occupied or suitable habitat during the breeding season. The demand for willow and cottonwood seedlings may be met, but permit product harvest only outside of the breeding season and only where it will have beneficial results (e.g., increased vigor and resprouting in decadent stands).
- To avoid attracting predators and cowbirds, provide adequate trash receptacles and frequent trash pick-up in developed campgrounds and dispersed campsites adjacent to or near WIFL occupied sites.
- Use interpretive signs with a message such as “prevent fires to avoid destruction of wildlife habitat”.
- Prohibit construction of new roads or trails in or adjacent to occupied, suitable, or potential WIFL habitat.
- For WIFL habitats accessible by boats, use speed limits, buoys, and closures to restrict boating use and access. Nests located close to water level can be disturbed by waves from boats. Also, fishing lines and lures may disturb nests and/or birds.
- Work with the local community to find alternative recreation areas away from occupied, suitable, or potential areas.

Water Management

Southwestern willow flycatchers occupy breeding habitats associated with water. Breeding sites are typically found near still or slow-moving water. Managing for the presence of water is a critical factor in sustaining occupied flycatcher habitats and in encouraging recolonization of potential and suitable habitats. Regulated stream flow from dams, levees, and channelization is thought to be one of the most important factors explaining the decline of cottonwood and willow woodlands in riparian ecosystems (Rood and Heinze-Milne 1989, Fenner et al. 1985, Rood and Mahoney 1990). Given that such water manipulation and demand can be extreme in the

Southwest (Brown et al. 1977, Fenner et al. 1985, Crawford et al. 1993), close monitoring of in-stream flow is critical to ensure sufficient water for sustaining and regenerating willow flycatcher habitat. To protect water resources, implementation of a water-management strategy that accounts for habitat needs of flycatchers is urged. Components of such a strategy are outlined as follows:

- Enforce existing laws to minimize illegal water withdrawal.
- Evaluate effects of goundwater withdrawal and pumping on riparian habitat. If a problem exists, work with water users to mitigate water loss by using financial incentives, public education, etc.
- Where applicable or possible, maintain or acquire instream flow water rights or work with water rights holders to increase instream flow.
- Evaluate alternative methods to diverting water from riparian areas. Although it has its own drawbacks, pumping may be a worthy compromise if it results in greater instream flow.
- Work with users to maintain, increase, and create WIFL habitat.
- Eliminate phreatophyte control at occupied sites and minimize control at suitable and potential sites.
- Along established earthen ditches, encourage vegetative growth by avoiding mowing and clearing. Evaluate mowing cycles.
- Work with agencies engaged in phreatophyte control to minimize disturbance to suitable and potential habitat.
- Evaluate dredging plans for waterways, including rivers, streams, ditches, ponds, and lakes to minimize habitat damage. Work with flood control agencies to minimize habitat damage and evaluate management plans.
- Develop public education on water uses (e.g., switching to drip systems rather than flood or sprinkler irrigation).
- Develop plans to minimize destructive effects of catastrophic floods, including those caused by poor riparian conditions. Do this by emphasizing improvement or restoration of healthy riparian habitat (refer to habitat restoration section). Small-scale flood events may be desirable to create backwater habitat for WIFL and to control salinity. Identify what can be done to recover habitat after destruction occurs. Remember that healthy riparian systems are capable of sustaining high runoff events.
- Develop plans to minimize impacts to WIFL habitat at dams and impoundments.
- Avoid dam construction and operations that will inundate WIFL habitat.
- Evaluate potential for creating WIFL habitat below dams by releasing water to mimic natural hydrology and water conditions conducive to WIFL use.

Mining

Proposed mining (e.g., sand, gravel) sites in riparian areas of public lands should be surveyed for WIFLs and habitat suitability and potentiality prior to mine development. If habitat is occupied, suitable, or potential, alternative sites should be selected, whenever possible. Where mining is ongoing, managers should develop a mitigation plan to minimize disturbance to WIFL habitat during mining operations. After mining is completed, a reclamation plan that requires restoration of WIFL habitat should be developed and implemented.

Direct Disturbance by Management

Construction and maintenance of man-made structures in the vicinity of WIFL habitats is likely to disturb birds while they are nesting, and steps should be taken to minimize or eliminate this disturbance. Habitat maintenance or maintenance of fences, powerlines, dams, roads, trails, facilities, and houses that occur in or adjacent to occupied sites should preferably be scheduled during the non-breeding season with minimal damage to habitats. If damage occurs, habitats should be restored. If emergency repairs are needed, disturbance to nesting birds should be minimized.

Upland management activities such as grazing, mining, development, wood-cutting, offroad vehicle use, prescribed fires, and road construction may sometimes have a downslope effect on riparian zones, through increased soil erosion, increased runoff, runoff of contaminated water, and reduced vegetation protection. Effects of upland management activities on riparian habitats in watersheds that have occupied, suitable, or potential WIFL habitat should be evaluated periodically. A plan to minimize effects on riparian habitats prior to implementation of upland management or while management activities are ongoing should be developed.

Working with Private Landowners

Lands owned privately play an important role in maintaining WIFL populations. The largest known population of the southwestern willow flycatcher, for example, is on a private ranch leased from Pacific Western Corporation in the Cliff-Gila Valley of New Mexico. Working cooperatively with private landowners to maintain and enhance riparian habitats, especially but not exclusively those occupied by WIFL, is a high priority. To assist landowners in making informed decisions about WIFL habitat, agency representatives should provide oral and written information to them about methods and goals for improving riparian systems to healthy states. Walking tours to riparian sites on private properties provide time for establishing a relationship with the landowner. Developing mutual trust is an important goal in establishing a cooperative relationship. The collaborative development of conservation agreements and plans to prevent damage to WIFL habitats on private lands while maintaining landowner livelihoods should be an objective. The establishment of conservation easements is also a worthy investment.

Acquiring lands with WIFL habitats using a similar land base for exchange should be a high priority for land-managing agencies or conservation groups such as The Nature Conservancy. Large parcel ownerships are more desirable than small parcel ownerships. Land transactions that result in subdivisions should be avoided.

Habitat and Watershed Restoration and Improvement

Unhealthy or damaged riparian areas can be improved using a variety of restoration techniques. We emphasize, however, that protection of existing habitat is the soundest, most cost-effective management approach. In areas managed for livestock, a high degree of flexibility in livestock operations is beneficial. Changes in livestock rotation schedules, timing and period of pasture use, method of herding, and type of livestock can go a long way toward restoring riparian habitats.

Replanting lost vegetation is not a substitute for habitat protection. In addition, conditions may not be suitable for revegetation efforts if the site has been irreparably damaged, if nonnegotiable factors limit the extent of restoration possible, or if the site was never conducive to vegetation growth in the first place. We discourage revegetation (plantings) if other kinds of positive management (e.g., stock removal) are available and appropriate. Plantings, however, may be appropriate when the following conditions are met:

- The seed sources are native.
- Revegetation is necessary to control water.
- Plantings are used to jump-start habitat restoration (e.g., by creating multi-layered structures or accelerating natural processes).
- Plantings are used to control exotic plants and prevent them from returning.
- Plantings are needed to prevent erosion and stabilize stream banks.

If the decision is made that revegetation is desirable but the area is not initially suitable because of the presence of exotics, it may be appropriate to supplement with more water, provided this will allow the site to support WIFLs.

Sites need to be evaluated for conditions appropriate for WIFL habitat restoration based on factors such as soils, watertable, water quality, geomorphology, elevation, genetic stock of vegetation, floodplain characteristics, lower gradients, and historical records. Conditions are suitable for habitat restoration when:

- Adequate surface water and ground water are present (i.e., surface water is present until the end of May). Suitable conditions can include moist areas with potential to restore surface flow.
- A natural or simulated flooding regime exists.
- The site is in close proximity to occupied or historically-used WIFL habitat.
- There is commitment to long-term management at the site.
- The site can become relatively self-sustaining over time.

Approaches for creating suitable conditions for WIFL colonization and occupancy include:

- Creation of slow water conditions (through Section 7 consultation) by excavating to groundwater (e.g., Gila National Forest; Kern River Preserve); by controlled inundation (e.g., Bosque del Apache National Wildlife Refuge); or by using beavers to dam small pools of water where appropriate.
- Appropriating instream flow.
- Acquiring habitat with water rights.
- Establishing farming landbanks to discourage use of flood control structures and enable meander patterns of stream.
- Working with private landowners to establish crop rest-rotation areas.
- Establishing conservation easements.
- Maintaining vegetation along stream banks to distribute flood flows across floodplain and to slow water velocity. This will help to re-hydrate the floodplain and enhance further plant germination and growth.

Wintering and Migration Habitats

The dearth of information on where and what habitats WIFLs use in winter and migration limits our ability to make recommendations. When more information is available on the wintering range and habitats of WIFLs, it will be easier to identify threats and solutions on the wintering grounds. Information can be solicited from investigators who study birds in Latin America by posting requests on web sites and newsletters published by organizations such as the Ornithological Society of North America, the National Audubon Society, and The Nature Conservancy. Partnerships with Latin American organizations should be encouraged to survey habitats for the presence of wintering flycatchers, and to gain new information on threats and habitat use. Involving Partners in Flight, the international, interagency coalition for conserving Neotropical migratory birds, in winter surveys would also be beneficial.

A bird survey program administered by Mexican agencies is needed, and North American organizations can assist Mexican biologists in developing this. Possible breeding sites in northern Mexico also need to be inventoried (e.g., Rio Santa Tomas; Santa Cruz; San Pedro), and more information is needed on migration routes and habitats through Mexico.

Rivers known to be used by migrating willow flycatchers include the Colorado River, the Gila River, and the Rio Grande. The time needed for migration consumes more than a quarter of the annual cycle of willow flycatchers. Individuals must stop periodically to refuel their energy reserves, and therefore, habitats that sustain an abundant food supply of arthropods may represent higher quality habitat to migrating flycatchers than habitats with depauperate arthropod faunas. Habitats in close proximity to water may enable flycatchers to replenish water that was lost during flight. Exposure to inclement weather and predators can also be mitigated during migration if suitable habitat is available for cover. Habitat protection along major migration routes should be emphasized more than it has been in the past. For example, practices such as mowing phreatophytes to improve stream channels and water flow is likely to reduce quantities of WIFL migration habitat. We recommend that mowing cycles be modified to allow a longer growing period of channel vegetation and to retain some vegetation at intervals along each channel. Rather than mowing every year, consider mowing every 3 years.

Length of stopover time, body fat condition, and captures rates are thought to be relevant measures of quality of migration habitats. According to Yong and Finch (1997) unmowed coyote willow along the middle Rio Grande was used more frequently and by fatter willow flycatchers during migration than mowed willow, cottonwood, agricultural fields, or Russian olive. To ensure successful migration by willow flycatchers, we recommend that steps be taken to protect and enhance willow thickets along southwestern drainages used by migrating willow flycatchers.

Information and Education

We recommend that Partners In Flight (PIF) state working groups take the lead on developing information and education (I&E) materials about the southwestern willow flycatcher. PIF state working groups have I&E committees already in place that can do this work. In addition, individual agencies and conservation organizations are encouraged to develop I&E materials on the willow flycatcher. Some ideas for I&E materials include slideshows and scripts that are duplicated and sold at cost; videos of WIFL, their habitats, and interviews with WIFL experts; brochures; posters; newspaper and magazine articles; interpretation signs at campsites; interpretive talks; and a paragraph on WIFL at the PIF web site. Funding sources need to be developed for I&E materials and for research reports.

Scientists are encouraged to promptly publish WIFL results and distribute reports and reprints to their constituencies. Progress reports and updates prepared by agencies and conservation groups should be widely circulated to other organizations and interested parties. A list-server for WIFL discussions and news updates can be established on the Internet. New publications such as this Conservation Assessment should be marketed and distributed to pre-established mail lists. Drawings and photos help to make technical documents more user-friendly. Information-sharing sessions should be held periodically to keep interested parties updated on new developments in the WIFL arena. We also recommend that a symposium devoted to the WIFL (or endangered riparian bird species in general) be sponsored by agencies or professional societies and a proceedings of the symposium be published and circulated to WIFL mail lists.

Managers need more research and technical information to effectively manage WIFLs and their habitats. Technical information can be supplied through consultations, publications, WIFL training sessions, and "show-me" tours. One of the most significant publications that managers could apply on the ground is a recovery plan for the southwestern willow flycatcher (now in progress). Finally, new knowledge and methods to protect and recover WIFL are needed; more specifics are identified in the next chapter.

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Chapter 11: Research Needs

Until the southwestern willow flycatcher was proposed for listing as an endangered species in 1993, it was subject to relatively little scientific scrutiny, in part because it is drab, prone to inhabiting dense, wet thickets, and difficult to identify and observe. Consequently, it remained one of the lesser-known of North American birds. Since that time, it has become clear that significant gaps exist in our understanding of its status, distribution, ecology, and management. Recently, many questions about the subspecies have arisen due to controversy over management actions and resulting litigation. New information that addresses these specific questions is essential to effect recovery of the bird. In this chapter we present, in annotated outline form, what we consider to be important areas for further research. This list of research needs is not intended to be exhaustive, and has not been prioritized. Refer to the southwestern willow flycatcher Recovery Plan for research priorities.

Historical and Current Status of Habitat

The greatest threat to the continued existence of the southwestern willow flycatcher is the loss and degradation of its riparian habitat throughout the Southwest (Chapter 4). A better understanding of the patterns and changes of distribution of riparian habitats will enable a greater understanding of the causes and patterns of population declines in the flycatcher.

- Review historical and archival records (e.g., historical photos, agency management records, military records, journals and diaries) and other literature to assess the historical extent and condition of riparian areas in the Southwest, especially where willow flycatcher populations were known to have existed.
- Document and map the temporal and spatial patterns of habitat loss in the Southwest, and determine the causes of historical habitat loss. Cross-check historical records with paleobotanical data (e.g., pollen, phytolith, macrobotanical analyses, packrat middens).
- Correlate changes in willow flycatcher numbers and distribution to changes in riparian habitats over time.
- Research and document the current distribution and extent of riparian vegetation in the Southwest, to determine (1) the location and amount of currently available habitat, and (2) the types and condition of extant riparian habitat, including micro and macroclimatic condition and landscape context.

Status on the Breeding Ground

Although there is a concensus that population levels of the southwestern willow flycatcher have declined in this century, questions remain about its historical range and distribution. The geographic extent of the breeding range of *E. t. extimus* is unclear, particularly where it intergrades with the ranges of *E. t. brewsteri* and *E. t. adastus* (see Fig. 7-1). Sound management and recovery require a better understanding of both the historical and current breeding range as well as the current status of the southwestern subspecies to ensure that efforts target the correct subspecies.

- Analyze museum specimens using morphometric methods to assess (1) species level limits (alder vs. willow flycatchers) among populations, and (2) sub-specific level limits among populations. In particular, efforts should be made to determine whether birds breeding in western Texas, northern New Mexico, southern Colorado, Utah, and Nevada, and at higher elevations in Arizona and New Mexico, are *E. t. extimus*.
- Analyze museum specimens and field captures using genetic methods to assess (1) species level limits among populations, and (2) sub-specific level limits among populations. In particular, efforts should be made to determine whether birds breeding in western Texas, northern New Mexico, southern Colorado, Utah, and Nevada, and at higher elevations in Arizona and New Mexico, are *E. t. extimus*.
- Identify transitional areas between the ranges of *E. traillii* subspecies, using genetics, morphology, and vocalizations.
- Review historical and archival records to document the historical distribution and abundance of willow flycatchers in the Southwest.
- Refine our knowledge of the current distribution and abundance of *E. t. extimus* throughout the Southwest.
- Determine the breeding status of *E. t. extimus* in Mexico using information from surveys.
- Identify and locate suitable riparian habitat not currently occupied by flycatchers, in order to determine the degree of habitat saturation by flycatchers.

Threats to the Southwestern Willow Flycatcher

The various threats to the southwestern willow flycatcher, described in Chapter 4, are imperfectly understood. Many must be considered merely potential threats because their actual impacts on flycatchers or their habitats are unknown at this time. A better understanding of those threats and their interactions with flycatchers and human activities is required to mitigate for the threats effectively. Also, it is critical to understand that many of these threats are interrelated.

Effects of Small Population Size

Populations composed of few individuals are vulnerable to genetic problems, particularly when they exist as fragmented subpopulations. Small populations tend to lose much of their genetic variability through drift, making them less able to adapt to changing environments. In the extreme case, very small populations may be prone to inbreeding depression. Recently, a study of population genetics in southwestern willow flycatchers in Arizona was initiated by the USGS Colorado Plateau Field Station (Paxton et al. 1997). This program should be expanded to the whole range of the flycatcher to address the following genetic questions. Considering the very small size and fragmented distribution of southwestern willow flycatchers, these topics should be considered high priority.

- Characterize the genetic variability and relationships within and among breeding populations.
- Assess the extent of gene flow among populations.
- Determine if inbreeding depression occurs in flycatchers.
- Determine the effective population size (N_e) of *E.t. extimus*.
- Determine whether the 2% observed rate of physical deformity in southwestern willow flycatchers is genetically based, by examining pedigrees of marked birds.
- If warranted, explore tools or techniques to increase genetic variability, e.g., cross-fostering.

Habitat Threats and Considerations

- Quantify habitat characteristics of Willow flycatcher breeding sites across entire range, in terms of (1) patch area and shape, (2) proximity to water, (3) stand age and successional status, (4) vertical structure, (5) plant species composition, (6) landscape matrix, (7) climate and microclimate variables, and (8) topography.
- Characterize 'suitable' breeding habitat and qualitatively describe variation in 'suitable' habitat across range (in more detail than in Sogge et al. 1997).
- Assess why willow flycatchers are absent from potentially suitable native habitats, especially with respect to microclimate.
- Compare placement of nest sites in relationship to substrate availability and in association with other habitat features, such as patch size and stand characteristics.

- Evaluate the impacts of phreatophyte mowing regimes on willow flycatcher habitat suitability.
- Evaluate the direct and downstream effects of sand and gravel operations on hydrology and habitat, using results from the literature or by conducting field studies.
- Evaluate the impacts of beaver on willow flycatcher habitat in the southwest, through a compilation of historical records and an assessment of current beaver distribution in different drainages.

Water Management—Water is a scarce resource in the southwest, and the health of riparian habitats is directly impacted by water management practices. Much remains to be learned about how water management affects riparian vegetation, and how water management can be altered to benefit riparian habitat and the willow flycatcher.

- Compile information on the effects of water management (e.g., dams, diversions, impoundments) on riparian habitat, using sources such as aerial photos and previous studies.
- Compare dammed and undammed drainages with respect to habitat features.
- Evaluate the effects of groundwater withdrawal or pumping on riparian habitat.
- Evaluate the effects of surface water movement (e.g., ditching, irrigation) on riparian habitat.
- Identify management regimes that favor native plant species and natural patterns of succession.
- Evaluate the impacts of dredging and channel bed alterations on riparian habitat.
- Determine how willow flycatchers respond to catastrophic habitat loss (e.g., flooding of Roosevelt Lake, Lake Mead).

Livestock Grazing—Livestock grazing in riparian areas and adjacent uplands has been identified as a major cause of the loss and degradation of riparian habitats. However, because grazing practices can vary considerably in terms of timing, location, and intensity, the effects of different grazing regimes on vegetation and flycatchers are also likely to vary. Livestock grazing remains one of the principle uses of public and private lands within the range of *E. t. extimus*. As a result, management policies that affect grazing are likely to have severe economic and political implications. Robust data on the effects of different grazing regimes on flycatchers and their habitats is essential for effective, intelligent, and defensible management of flycatcher habitat.

- Evaluate the impact of different grazing regimes (timing, livestock density, duration of grazing) on flycatcher ecology, e.g., reproductive success, population size, nest placement, productivity, predator assemblage, cowbird parasitism rates.
- Evaluate the direct and indirect effects of grazing on or adjacent to riparian habitats both occupied and unoccupied by flycatchers.
- Evaluate the effects of livestock grazing in upland habitats adjacent to riparian breeding habitat on flycatchers and their habitat.
- Evaluate the effects of livestock grazing upstream from riparian breeding habitat on flycatchers and their habitat.
- Compare the impact of different grazing regimes on plant community structure, particularly the incidence of native vs. exotic species.
- Determine the effects of livestock grazing on fuel load, and whether such effects impact flycatchers either positively or negatively.
- Use artificial nests to quantify the impacts of trampling and direct disturbance by livestock.

Recreation—Recreational activities tend to be concentrated in riparian areas in the Southwest, and therefore are likely to create significant conflicts with flycatcher conservation (Johnson and Carothers 1982). We currently know little about the direct or indirect effects of recreation on flycatchers.

- Assess the effects of human activity in and around riparian habitats on habitat quality, e.g., effects on vegetation structure, erosion, and introduction of exotics.
- Assess the impacts of human activity in and around riparian habitats on the settlement and productivity of flycatchers, e.g., possible changes in rates of nest abandonment.
- Assess the impacts of the presence and density of roads on flycatcher habitat use and productivity.

Fire—Fire has become an issue of concern in southwestern riparian systems, especially with the recent loss of some occupied willow flycatcher sites. Research on fire may help in the development of management strategies that minimize future losses to burning.

- Summarize the historical role of fire in riparian systems.
- Characterize fire sources and risks.
- Compare fire risks in exotic vs. native stands.
- Determine whether fuel loads present a fire hazard, and if so, determine what tools can be used to effectively reduce fuel loads.
- Determine the short- and long-term response of flycatchers to different types of fire, e.g., catastrophic, prescribed burnings, and patchy fires.
- Determine the effectiveness and ecological ramifications of fire breaks, e.g., do breaks significantly increase fragmentation of riparian habitats.

Exotic Vegetation—Much riparian habitat in the southwest has been invaded by exotic plants, particularly tamarisk. At the same time, many extant populations of the southwestern willow flycatcher nest in pure or mixed stands of tamarisk, while others breed in other exotic species, such as Russian-olive. A better understanding is needed of the relative quality of exotic plants as willow flycatcher habitat and nest substrate, as well as the potential for restoring native vegetation.

- Compare willow flycatcher nesting success in exotic vs. native plant communities (e.g., tamarisk, Russian-olive, willow, box-elder, oak).
- Compare insect prey abundance and flycatcher foraging efficiency in exotic vs. native plant communities, and in relation to site-specific nesting success and flycatcher abundance.
- Evaluate quality of tamarisk habitat in relation to structure, density, canopy cover, and presence of native species.
- Identify water and land management options that favor native vegetation.
- Evaluate biocontrol of tamarisk in terms of (1) likelihood that native species will return to treated sites, (2) rate of movement of biocontrol insects, (3) responses of target and nontarget plants to biocontrol, (4) control mechanisms and containment procedures for biocontrol insects, and (5) responses of willow flycatchers to vegetation changes resulting from biocontrol.

Habitat Restoration—Because habitat loss constitutes the major threat to the flycatcher, riparian habitat restoration should prove to be a vital tool for recovery efforts. However, riparian restoration efforts have differed in their goals, methodologies, and levels of success. Very few have been conducted specifically to restore wildlife habitat for a particular species. Recently, restored riparian sites in California were colonized by least Bell's vireos (*Vireo bellii pusillus;* Kus 1998), although it remains to be seen whether the sites can persist without management (B. Kus, personal communication). As noted in the discussion on habitat (Chapter 9), not all riparian areas provide suitable habitat for the willow flycatcher. Thus, research is urgently needed to assess the appropriateness and efficacy of restoration techniques for flycatcher recovery.

- Summarize and evaluate results of past restoration efforts.
- Evaluate restoration techniques in terms of their overall efficacy.
- Compare restoration techniques, e.g., "natural" flooding events vs. managed restoration.
- Monitor colonization by willow flycatchers on restored sites with respect to rate and persistence.
- Determine efficacy of restoration projects with respect to colonization by willow flycatchers or population growth rates of willow flycatchers.
- Compare the efficacy of restoration methods for establishing Willow flycatcher populations as a function of distance to existing flycatcher populations.
- Review success of compliance "mitigation" sites in terms of regeneration and flycatcher use.
- Evaluate the efficacy and feasibility of reinstating "natural" hydrological regimes of disturbance and plant succession to willow flycatcher breeding areas.
- Determine whether successful restoration techniques are compatible with ongoing management regimes.
- Evaluate if modifying management practices can promote habitat restoration; review those modifications that have worked in the past and evaluate those not yet tried.

Factors Directly Threatening Flycatchers

Cowbird Parasitism—Some willow flycatcher populations suffer heavy cowbird parasitism, while for others parasitism appears to be a minor problem. Work is needed to determine which factors of landscape, habitat, avian community structure, or land use affect cowbird abundance and parasitism rates. Cowbird control through trapping has been proven to be effective in reducing rates of parasitism in some willow flycatcher populations (e.g., Whitfield and Strong 1995) as well as in populations of other small passerines. The methodology for trapping cowbirds is well established, but it is a labor-intensive and costly strategy. Questions about when, where, how long, and whether to trap must be answered if we are to maximize its effectiveness as a management tool, and to make the best use of scarce management funds.

- Determine if willow flycatchers are a preferred host of cowbirds at particular sites throughout the Southwest, compared to other host species.
- Determine how parasitism rates on willow flycatchers vary with host assemblage and density.
- Because cowbird abundance has been associated with livestock, characterize the relationships between flycatcher parasitism rates, cowbird abundance in feeding and breeding areas, and grazing regimes (e.g., dispersed vs. congregated, upland vs. riparian).
- Evaluate whether cattle dispersion and grazing characteristics are linked to cowbird travel distances between feeding and breeding sites in the Southwest.
- Quantify cowbird abundance throughout the Southwest (e.g., using Breeding Bird Surveys) to determine where areas of high cowbird density overlap with flycatcher breeding sites.

- Establish scientifically-based criteria to either implement or discontinue cowbird trapping in flycatcher breeding habitat.
- Evaluate the effectiveness of cowbird trapping in different habitats and regions by monitoring its effects on flycatcher productivity and population trends over time.
- Compile a list of sites where Animal and Plant Health Inspection Service blackbird control occurs, and evaluate its effects on cowbird numbers.

Because female cowbirds produce at least 30 to 40 eggs per breeding season and parasitize many species (Rothstein et al. 1986), the availability of alternate hosts in a community may affect the risk of parasitism on flycatchers (e.g., Barber and Martin 1997). Therefore, the following research questions need to be addressed:

- How does the relative timing of nesting phenology among species affect parasitism rates in flycatchers?
- How do cowbirds select hosts to parasitize?
- What management actions can reduce parasitism rates?
- How do landscape and structural features of the habitat (e.g., distance to edge, density of cover, vegetation structure, availability of perches) affect rates of cowbird parasitism?
- Determine the impacts of parasitism on juvenile and adult survival in flycatchers.

Predation—Predation may constitute a major threat to the southwestern willow flycatcher. Nest predation has been identified as a major cause of nest failure in most populations studied. Further, the risk of predation may be increasing as riparian habitats are further fragmented by human activities. Yet, because our knowledge of predators and predation on flycatchers is limited to anecdotal accounts, we lack sufficient data to manage predation effectively.

- Identify potential and documented predators on *E. t. extimus* rangewide.
- Identify the temporal and spatial distribution of predators within riparian habitats.
- Characterize predation rates and types relative to landscape and habitat features.
- Summarize geographic and temporal variation in predation patterns.
- Evaluate methods to minimize predation impacts through management.
- Determine the extent of cowbirds as predators on flycatcher eggs and nestlings.

Parasites and Disease—

- Summarize ectoparasite and disease-related information from netting and banding stations.
- Expand data collection of nest and blood parasites.
- Assess the effects of parasitism on willow flycatcher survival and productivity.

Environmental Toxins—Agricultural development in the southwest tends to be concentrated in floodplain areas, suggesting potential threats to the flycatcher and its habitat from associated pesticides, herbicides, and other toxins.

- Investigate the incidence, range, and prevalence of toxins at flycatcher breeding, stopover, and wintering locations.
- Analyze available specimens and nonviable eggs for toxins.
- Analyze other sympatric riparian birds (specimens and nonviable eggs) for toxins.

Winter and Migration

Willow flycatchers migrate from their summer breeding areas to winter in the tropics. However, little is known about where they go and what they do once they leave their breeding grounds (see Chapter 5). Gathering such information for this endangered subspecies is hampered by difficulties in identifying non-singing *Empidonax* species in the field, let alone subspecies. Such information is essential, however, because conservation measures on the temperate breeding grounds will be futile if the taxon's requirements are not also met during migration and on the wintering grounds.

- Determine the winter range of *E.t. extimus*, through the use of (1) museum specimens from Mexico and Central America, (2) surveys conducted on potential wintering grounds, and (3) information exchange with colleagues in Latin America.

Once the winter range is identified:

- Characterize habitat use and quality.
- Determine if, and how, winter habitat is at risk.
- Identify key areas for protection.
- Develop methods for protecting habitat and birds.
- Identify factors limiting winter survival of flycatchers, e.g., food, weather, contaminants, habitat loss or degradation, catastrophic events, disease, and predation.

Migration is a critical time for migratory songbirds, especially in terms of energy expenditure and physiological stress. However, migration ecology remains poorly known for most species, including the southwestern willow flycatcher.

- Identify migration corridors, if any, by analyzing existing survey data.
- Determine subspecies patterns in migration routes and timing, if possible.
- Determine sex- and age-specific patterns of migration.

- Determine habitat use and influence of exotic vegetation during migration.
- Evaluate stopover time with respect to habitat quality, bird condition, and food supply.
- Examine condition of migrants as a function of age and in relation to stopover time and subsequent probability of survival.
- Examine the relationship between stopover time and bird condition with the size and degree of patchiness of habitats and other landscape features.

Breeding Biology and Demography

Measures of fecundity and mortality are essential for assessing the health of any population. Much more work is needed to develop a better understanding of the factors that affect nesting success, survival, and dispersal. Many aspects of breeding biology and demography can only be determined by observing individual birds, which requires the use of color-banding.

- Expand the current Arizona banding program to create a coordinated, rangewide program.
- Quantify rates of site fidelity, both within and among years.
- Determine rates of recruitment among different populations.
- Determine the age structure of populations.
- Estimate rates of survivorship for different age classes and among different populations.
- Determine the effects of age on nesting success, yearling and adult survival.
- Identify source and sink populations.
- Estimate rates of immigration and emigration, in terms of (1) distances moved, (2) relationship to patch size and isolation, and (3) source and sink populations.
- Characterize the metapopulation structure of *E.t. extimus*.
- Characterize nesting success in terms of (1) number of nesting attempts per season, (2) fledging success over a season, (3) variation among years and among habitats, and (4) seasonal fecundity using the Pease-Grzybowski model (Pease and Grzybowski 1995).
- Determine the relation between nesting success and (1) arrival time on the breeding grounds, (2) movements within and between years, and (3) any habitat or cowbird manipulations.
- Determine the relation between nesting success and habitat or landscape features listed under habitat threats and considerations.
- Assess the relative impacts of predators versus brood parasites on fecundity.
- Determine the rates and causes of nest desertion.

Behavior

Many aspects of willow flycatcher behavior remain poorly known, but have important implications for monitoring, conservation and management. In particular, a better understanding of the flycatcher's mating system would help to answer questions about effective population size and other consequences of small population size in this subspecies.

- Determine the frequency of extra-pair copulations (by sex) to determine mate fidelity, estimates of male fecundity, and genetic relations within and among populations.
- Assess the parentage of family groups to determine the incidence of extra-pair copulations.
- Assess the relative nesting success of polygynous vs. monogamous pairs.
- Correlate mating strategy (floater vs. territorial male) with arrival time on breeding grounds.
- Correlate mating success with patch size, population size, habitat quality, and distance to source population.
- Determine the presence, size, and age of floaters in relation to population size, quality and range of habitats.
- Use data on the genetics of floaters to assess (1) relatedness to nestlings in broods resulting from extra-pair copulations, and (2) the lifetime reproductive success of floaters.
- Characterize nest defense in willow flycatchers, in terms of (1) whether birds actively defend nests, (2) whether nest defense is successful, and (3) how variable nest defense is with respect to age, sex, habitat, nest site, population size of patch, and the type of predator or intruder.

Food Habits

Many of the details of willow flycatcher food habits remain poorly known. A better understanding of the prey choice and foraging behavior is needed because insect prey abundance may be adversely affected by land use and water management practices, and because food has the potential to limit reproductive success and population growth.

- Characterize the diet of southwestern willow flycatchers through (1) fecal analyses, and (2) by direct observations of foraging birds.
- Quantify food delivered to nests, in terms of frequency of food delivery and differences between sexes and among seasons.
- Identify differences between prey eaten by adults and prey delivered to nestlings, in terms of insect size, type, or palatability.
- Assess foraging efficiency in relation to habitat type (exotic vs. native).

- Determine insect availability and type (taxon or size class) in different habitat types, including exotic vegetation. Identify any variation due to the effects of season or weather.
- Assess the existence and degree of diet overlap with other bird species to identify the potential for interspecific competition.
- Determine if willow flycatcher nest success or population trends vary in relation to food availability.
- Determine if food is limiting within or among years. Potential indicators of food limitation include (1) the frequency of nestling starvation, and (2) adult foraging behavior, as measured by the duration of foraging bouts or the percentage of daily activity spent foraging.

Vocalizations

Recent work has documented singing in females and fledglings (Seutin 1987, Sogge 1997), demonstrating that our knowledge of willow flycatcher vocalizations remains incomplete. Increased research on flycatcher song should be considered a high priority for several reasons. Survey protocols, used for assessing numbers and status of birds within populations, are based on singing. At least two current studies report the possibility that song may vary among regions or subspecies (Travis 1996, J. Sedgwick personal communication).

- Characterize the daily and seasonal patterns of song.
- Quantify the frequency, timing, and intensity of female singing.
- Evaluate female territorial defense by singing or chasing behavior.
- Compare singing behavior between sexes in relation to concealment and height of perch.
- Evaluate the role, intensity, and frequency of song in migrating willow flycatchers relative to resident birds.
- Evaluate the relation between song quality and male quality and nesting success.
- Identify and characterize local and regional dialects in vocalizations, and determine if dialects are related to subspecies or geography.
- Characterize variation in song and singing behavior, through the use of sonographs, (1) in relation to social behavior (e.g., floaters, polygyny), (2) between sexes and age classes, (3) among habitats, nest sites, or proximity to edge, and (4) with respect to cowbird abundance and parasitism rates.

Monitoring and Surveying

Most of our knowledge of willow flycatcher status, distribution and reproductive success comes from survey and nest monitoring programs. These methodologies have been developed for this particular taxon only very recently, and are still evolving. Further work is needed to assess and improve the accuracy and reliability of data collected from survey and monitoring efforts.

- Expand rangewide survey efforts to fill gaps in current knowledge of flycatcher distribution.
- Determine the effectiveness of survey protocol in detecting accurate numbers of willow flycatchers, by comparing different census and nest monitoring results to survey results.
- Determine the optimal number of surveys per site.
- Compile and analyze range- and state-wide survey data to address questions about (1) population trends in time and space, and (2) distributional statistics. If there are declines, determine their causes.
- Develop a systematic population monitoring program using surveys repeated annually.
- Develop a standardized nest-monitoring protocol by coordinating the methodologies, reporting, data management and data analysis of state wildlife agencies and the US Fish and Wildlife Service. These data would be used to analyze regionwide trends and patterns in productivity over time.
- Use winter nest searches to document willow flycatcher breeding at unmonitored sites, or where breeding could not be determined during summer monitoring efforts.
- Assess the impacts of human observers on nesting success.
- Assess the impacts of color bands on willow flycatcher survival and mating success.
- Compare and correlate survey trends with trends in nest success and cowbird densities.
- Monitor habitat response to beaver reintroductions.

Population Viability Analysis

In Chapter 7, a population projection model was presented to show possible fates of a hypothetical flycatcher population based on different sets of assumptions about demography. That model was simple and deterministic. The more in-depth process of modeling and analyzing the various deterministic and stochastic forces that determine the fate of a population is called population viability analysis (PVA: Boyce 1992). A PVA can provide quantitative estimates of likely population trajectories under current conditions, as well as test the likely effects of different management actions. Repeated analyses through the species recovery process can provide a gauge of the progress of recovery, and may provide a quantitative criterion for de-listing. However, a PVA model is data-intensive and its results are only as good as the data used to obtain them. Before any attempt can be made to assess the viability of the southwestern willow flycatcher population, many of the research needs outlined in this chapter need to be accomplished.

- Use the data outlined in previous sections to conduct a population viability analysis, taking into account (1) variation in vital rates among and within populations, (2) stochastic events such as fires and floods, and (3) the spatial distribution of flycatcher populations (metapopulation).
- Based on PVA results, prioritize where management efforts should be focused for (1) sustaining current population, and (2) encouraging species recovery.

Multiple Species Considerations

Riparian areas in the Southwest support some of the most diverse and densely populated wildlife communities in North America (Hubbard 1977, Knopf et al. 1988). Many obligate riparian and riverine species in the region are considered threatened, endangered, or sensitive, frequently due to the same factors that have impacted the willow flycatcher. Conservation efforts may be most efficient and cost-effective when they benefit multiple species.

- Identify other sensitive, threatened, or endangered species that share occupancy patterns and distributions with *E.t. extimus* (i.e., a mini-GAP analysis with a riparian focus).
- Evaluate the impacts of flycatcher management on other species, and identify management actions that benefit other sensitive, threatened or endangered species. Develop criteria for rating riparian habitats based on multi-species benefits, or concentrations of threatened or endangered species (to be used to prioritize protection efforts).
- Refer to state Partners in Flight efforts, State Heritage reviews, TNC Bioreserve program, and state-wide GAP analyses, to help prepare sensitive species management plans based on threatened and endangered species priorities.

General Recommendations

- Because many occupied flycatcher sites occur on privately-owned lands, more research should be conducted on private lands in collaborative efforts with landowners.
- Encourage more coordinated efforts in research, monitoring, and data sharing.
- Research to date has revealed that many aspects of flycatcher biology vary considerably among sites. Therefore, interpretation of local research results should take this variation into consideration. Research should be conducted at a broader range of sites to better understand the extent and causes of variation.

Summary

The research needs outlined in this chapter demonstrate extensive gaps in our knowledge of many areas of southwestern willow flycatcher biology. It is unlikely there is enough time or funding to accomplish all of these suggested studies, however. Nor are all of the research needs are of equal importance for recovering the species. The Recovery Plan for the southwestern willow flycatcher suggests that the top priority areas for research are the distribution, abundance, demography, and limiting factors of flycatcher populations. These baseline data are necessary to provide a knowledge base to begin the recovery process. Topics of secondary priority include assessments of flycatcher habitat and factors that affect habitat, such as dam and water management, grazing, and cowbird management, as well as work on migration and wintering distribution and ecology and subspecific taxonomy.

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Appendix:

Author Biosketches and Addresses

Janie Agyagos received her B.S. from Arizona State University in 1993. She is currently the Wildlife Staff Officer for the Beaver Creek/Sedona Ranger District on the Coconino National Forest. In 1997, as part of the Forest Service's Seven Species effort, she led a team that reviewed all Forest Service activities near occupied and suitable southwestern willow flycatcher sites. That team then developed short- and long-term management actions and guidelines to protect the flycatcher and its habitat on National Forest Systems lands throughout Arizona and New Mexico. Janie's duties as District Wildlife officer include managing for and protecting 50 threatened, endangered and sensitive species, including the southwestern willow flycatcher.

Jean-Luc E. Cartron is Director of Research at Hawks Aloft, Inc., and Research Assistant Professor at the University of New Mexico. He received a Ph.D. in Biology from the University of New Mexico. His research experience in Conservation Biology includes a 7-year study on ospreys in the Gulf of California, Mexico; a study on the impact of electrocutions by power poles among raptors in northwestern Chihuahua, Mexico; a study on the distribution and productivity of nesting ferruginous hawks in relation to prairie dogs in central and western New Mexico; and a study of noise disturbance impacts on the distribution and reproductive success of golden eagles in northwestern New Mexico. As a Research Wildlife Biologist at the Rocky Mountain Research Station from 1997 until 2000, he coedited with Deborah M. Finch a conservation assessment for the cactus ferruginous pygmy-owl. His research interests include life history theory, evolutionary biology, and raptor and Threatened and Endangered species conservation.

Deborah M. Finch is a Research Wildlife Biologist and Project Leader with the USDA Forest Service's Rocky Mountain Research Station in Albuquerque. She is also Research Associate Professor in the Department of Biology at University of New Mexico and Adjunct Professor at Northern Arizona's School of Forestry. She received her B.S. in Wildlife Management from Humboldt State University, California, her M.S. in Zoology from Arizona State University, and her Ph.D. in Zoology from the University of Wyoming. Deborah's research interests include Neotropical migratory bird ecology and reproduction, bird migration, endangered species, riparian and grassland ecosystem ecology and conservation, and relationships between commodity use and natural resources. Deborah has published more than 80 articles and journal papers and is an active member of several professional societies. Since 1998, she has served as Leader of the Technical Subgroup of the Recovery Team for the Southwestern Willow Flycatcher.

Lloyd Goldwasser received his A.B. degree in mathematics and music from the University of California, Berkeley, in 1976, and completed a masters degree in mathematics there in 1979. He completed his Ph.D. in zoology at UC Berkeley in 1987. He is currently working on California salmonids for the National Marine Fisheries Service (NOAA) at the Tiburon/Santa Cruz laboratory. He has also modeled the populations dynamics of spotted owls and corals, and has worked on the ecological effects of invasions by non-native species of snails in California estuaries and of plants in California grasslands.

Jeff Kelly is a Research Wildlife Biologist at the Rocky Mountain Research Station in Albuquerque. He received a Ph.D. in Zoology from the Department of Biology at Colorado State University in 1996, a M.S. in Zoology from Oklahoma State University in 1991, and a B.S. in Wildlife Ecology from the University of Maine in 1987. Jeff's research focuses on avian ecology and current projects include: stopover biology of Neotropical migrants, distribution, abundance and habitat use of grassland birds, avian biodiversity of golf courses, and effects of riparian restoration on bird community structure.

Rob Marshall is Conservation Sciences Program Manager for The Nature Conservancy's Arizona Chapter in Tucson. Rob oversees the Chapter's research, monitoring, and restoration programs as well as the Chapter's ecoregional and site conservation planning projects. He is currently leading a binational, interdisciplinary effort to identify conservation priorities and management needs in the Sonoran Desert Ecoregion. Rob received a B.A. in Human Ecology from College of the Atlantic and an M.F.S. in Wildlife Ecology from the School of Forestry at Yale University. His academic training is in avian ecology, wetlands, and wildlife management. Prior to joining the Nature Conservancy Rob worked on endangered species management and research projects for the U.S. Fish and Wildlife Service, U.S. Forest Service Rocky Mountain Forest and Range Experiment Station, Cornell Laboratory of Ornithology, and Manomet Bird Observatory.

Tracy McCarthey received her B.S. degree from Arizona State University in 1990, then completed two years of graduate work at the University of Arkansas. She is currently the Southwestern Willow Flycatcher Project Coordinator at the Arizona Game and Fish Department. Her current responsibilities include: administration of a willow flycatcher survey and nest monitoring project with over 30 hired employees, producing willow flycatcher management recommendations, reviewing critical documents, and synthesizing data from annual, state-wide willow flycatcher surveys.

Richard D. Periman is a Research Archaeologist with Rocky Mountain Research Station's Cultural Heritage Research Unit, where he has worked since 1995. He is currently writing his Ph.D. dissertation in Environment Science and Technology, under the Department of American Studies at the University of New Mexico. His research topic is the development of an interdisciplinary approach for identifying, quantifying, and interpreting long-term landscape history and human-induced environmental change. This study focuses on the nature and extent of human-environmental interaction in order to understand better the socio-ecodynamics of human activities and their possible continuing influence on the landscapes we see today. He received a M.A. in medical anthropology from the University of Montana in 1987 and a B.A. in anthropology from the same university in 1985. From 1987 to 1995, Richard worked as the Heritage Resource Manager and Tribal Governments Coordinator on the Deerlodge National Forest, in the Forest Service's Northern Region. He has conducted research ranging from the socioculture aspects of malaria control to the effects of historic mining on landscape development.

Mark K. Sogge is an Ecologist with the Colorado Plateau Field Station, Flagstaff, Arizona; a unit of the U.S. Geological Survey Forest and Rangeland Ecosystem Science Center. He has worked as a biologist for a variety of federal agencies since 1983. He graduated from San Jose State University, California with a B.A. in Biochemistry, and obtained an M.A. in Zoology from the University of California at Davis. His research interests include avian monitoring programs and protocols, southwestern riparian bird communities, and the ecology of endangered birds. He first studied willow flycatchers in 1988 in the northern Sierra Nevada and southern Cascade Mountains. Since 1992, he has been coordinating and conducting southwestern willow flycatcher studies throughout the southwest, and in portions of its wintering range in Central America. His research emphasis has been on flycatcher demography, breeding ecology, population genetics, and winter ecology and conservation.

Scott H. Stoleson is a Research Wildlife Biologist with the Rocky Mountain Research Station in Albuquerque, New Mexico. He received a B.A. in Biological Science from Dartmouth College, and a Ph.D. in Wildlife Ecology from Yale University. His research interests include breeding biology and demography of birds, parrot biology and conservation, population modeling, riparian conservation, conservation of non-forested tropical habitats, the biology of invasive exotic species, endangered species management, and mycology. He has worked on birds and other wildlife in the western U.S., Costa Rica, Panamá, Ecuador, and Venezuela. His current research examines the breeding biology and habitat associations of southwestern willow flycatchers and other riparian birds in the Gila River Valley of New Mexico.

J.C. "Jamie" Uyehara received her B.S. degree from University of California at Davis in 1981, and then worked in positions involving exotic animal management. Realizing that more information was needed in order to manage and recover endangered birds, she entered the graduate program at UCLA. Her dissertation was "Correlates and field experiments of nest searching behavior in a brood parasite, the brown-headed cowbird" (1996). Currently, she is working as a wildlife biologist with the Los Padres

National Forest in central and southern California. She still believes that research and good analyses are needed when managing for endangered species, but time is a luxury for both the endangered species and the land managers.

Mary J. Whitfield is the research director at the Southern Sierra Research Station. She obtained a B.S. degree in Wildlife and Fisheries Biology from U.C. Davis, and a M.S. degree in Biology from California State University, Chico. Mary has worked on a long-term breeding ecology study of the southwestern willow flycatcher since 1989. In addition, she has studied the effects of a brown-headed cowbird trapping program (started in 1993) on the reproductive success of the southwestern willow flycatcher. For the last two winters, Mary has also worked on a wintering willow flycatcher distribution study in Central America.

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