

In cooperation with Northern Arizona University

The Ecology of the Southwestern Willow Flycatcher in Central Arizona—a 10-year Synthesis Report

By Eben H. Paxton¹, Mark K. Sogge¹, Scott L. Durst¹, Tad C. Theimer², and James R. Hatten³

¹U.S. Geological Survey, Southwest Biological Science Center, Colorado Plateau Research Station, Flagstaff, Ariz.; ²Department of Biological Sciences, Northern Arizona University, Flagstaff, Ariz.; ³U.S. Geological Survey, Western Fisheries Research Center, Columbia River Research Laboratory, Cook, Wash.



Open-File Report 2007-1381

This page intentionally left blank

The Ecology of the Southwestern Willow Flycatcher in Central Arizona—a 10-year Synthesis Report

By Eben H. Paxton, Mark K. Sogge, Scott L. Durst, Tad C. Theimer, and James R. Hatten

In cooperation with Northern Arizona University

Open-File Report 2007–1381

2007

U.S. Department of the Interior
DIRK KEMPTHORNE, Secretary

U.S. Geological Survey
Mark Myers, Director

U.S. Geological Survey, Reston, Virginia: 2007

For product and ordering information:

World Wide Web: <http://www.usgs.gov/pubprod>

Telephone: 1-888-ASK-USGS

For more information on the USGS—the Federal source for science about the Earth, its natural and living resources, natural hazards, and the environment:

World Wide Web: <http://www.usgs.gov>

Telephone: 1-888-ASK-USGS

Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Although this report is in the public domain, permission must be secured from the individual copyright owners to reproduce any copyrighted materials contained within this report.

Suggested citation:

Paxton, E.H., Sogge, M.K., Durst, S.L., Theimer, T.C., and Hatten, J.R., 2007, The ecology of the southwestern willow flycatcher in central Arizona—a 10-year synthesis report: U.S. Geological Survey Open-File Report 2007-1381, 143 p.

Contents

Executive Summary	1
Chapter 1—Introduction	5
Introduction.....	5
Report Structure.....	5
Project Objectives.....	5
Southwestern Willow Flycatcher	7
History and Recent Operations of Roosevelt Lake.....	9
Description of Roosevelt Lake and San Pedro/Gila Study Sites	11
Acknowledgements.....	14
References.....	15
Chapter 2—Survivorship	19
Introduction.....	19
Methods.....	19
Results	26
Discussion.....	36
Management Considerations	39
References.....	39
Chapter 3—Productivity	43
Introduction.....	43
Methods.....	43
Banding and Resighting.....	45
Nest Monitoring	45
Statistical Analysis	46
Results	47
Discussion.....	53
Management and Research Considerations	54
References.....	55
Chapter 4—Movement.....	59
Introduction.....	59
Methods	59
Banding and Resighting.....	62
Statistical Analysis	63
Results	64
Discussion.....	74
Management and Research Considerations	77
References.....	78

Chapter 5—Demographic Modeling	81
Introduction.....	81
Methods	81
Vital Rates	83
Demographic Models.....	84
Results	84
Discussion.....	89
Management and Research Considerations	93
References.....	94
Chapter 6—Spatial Modeling	97
Introduction.....	97
Methods.....	98
Surveys and Monitoring.....	98
Spatially Explicit Modeling	102
Demographic Analysis	105
Results	105
San Pedro/Gila Models	107
Flycatcher Habitat: 1985–2005	113
Demographic Relationships to Spatial Characteristics	118
Discussion.....	118
Management and Research Considerations	121
References.....	122
Chapter 7—Non-territorial Floaters	125
Introduction.....	125
Methods.....	126
Results	128
Discussion.....	129
References.....	133
Chapter 8—Conclusions.....	137

Executive Summary

Background

From 1996 to 2005, the U.S. Geological Survey (USGS) conducted a demographic study of the Southwestern Willow Flycatcher (*Empidonax traillii extimus*) in Arizona in collaboration with the Arizona Game and Fish Department (AGFD). The study was begun the year following the listing of the Southwestern Willow Flycatcher as an endangered species. At the time of the listing, very little was known about the biology and threats to the flycatcher, and one of the main objectives of the study was to gather detailed long-term information on the biology of the flycatcher.

This report is organized into eight chapters. Following the introductory chapter, we deal with specific aspects of flycatcher ecology and habitat use in each of six separate chapters. We end with a concluding chapter that synthesizes information into broad topical themes that address key management issues. Each of the core chapters (chapters 2 through 7) conclude with a list of management considerations derived from the findings of the respective chapter.

Chapter 1—Introduction

The Willow Flycatcher is a small Neotropical migrant that breeds across much of the United States and southern portions of Canada, and winters from central Mexico south to northern South America. There are four commonly recognized subspecies, with the southwestern subspecies breeding in Arizona, western New Mexico, and southern portions of California, Nevada, Utah, and Colorado. The southwestern subspecies is dependent on generally dense riparian habitat, a habitat that has been greatly reduced over the last 100–150 years. In 1995, the Southwestern Willow Flycatcher was declared a federally endangered species because of sharp declines in numbers across its range.

The same year the Southwestern Willow Flycatcher was listed as endangered (1995), the Bureau of Reclamation completed modifications to Roosevelt Lake dam in central Arizona. The purpose was to increase water storage capacity, which would lead to inundation of riparian vegetation adjacent to the reservoir. Because breeding flycatchers occupied much

of the habitat that would be inundated, Reclamation (in consultation with the U.S. Fish and Wildlife Service) proposed to mitigate for the potential habitat destruction, in part, by funding a 10-year research project on flycatchers at Roosevelt Lake, and at the San Pedro/Gila River confluence area. Both study sites (Roosevelt Lake and San Pedro/Gila) are typical of Sonoran Desert Riparian Woodland, and contain multiple patches of varying size and stand age. Additionally, both study sites hosted some of the largest breeding populations of flycatchers across the range throughout the study period. Research was conducted jointly by USGS and AGFD, with AGFD taking lead on surveys and nest monitoring, and USGS taking the lead on banding and tracking of individual flycatchers.

Chapter 2—Survivorship

We used Maximum Likelihood methods to estimate flycatcher survivorship probabilities, based on the banding and tracking of 1,080 adults and 498 nestlings, from 1996 to 2005. Overall, average survivorship was 64% for adults and 34% for juveniles, with considerable yearly variation. For adults, yearly variation was the most important influence on survivorship, with no difference between sites or sex. Mean life expectancy was 1.9 years, but some individuals lived to at least 9 years of age; for those few that lived beyond the average lifespan, there was an increase in survivorship compared to younger adults. For juveniles, the most important predictor of survivorship was fledge date, with nestlings fledging later in the breeding season having lower survivorship than those fledged early in the breeding season. We could not test for site and sex differences in juvenile survivorship.

In addition, we evaluated several other factors that might influence survivorship. Habitat type (native, exotic, or mixed) in which adults bred did not appear to influence survivorship. However, the breeding status of an individual did, with successful breeders having higher survivorship than non-successful breeders, unpaired individuals, and those of unknown status. To understand where mortality occurs (i.e., breeding grounds, wintering grounds, or migration), we combined our breeding ground study with that of a study of wintering flycatchers; the combination of the two studies suggests that most mortality occurs off the breeding grounds, primarily

2 The Ecology of the Southwestern Willow Flycatcher in Central Arizona

during migration. Finally, we evaluated the potential impacts of permanent emigration on our survivorship estimates. To do so, we calculated survivorship at different spatial scales, from individual patches up to the entire study area. We concluded that survivorship would be underestimated if we use data from only small spatial scales, but because we conducted this study at a larger spatial scale we are probably detecting most birds and have robust survivorship estimates.

Chapter 3—Productivity

Using the extensive information derived from the tracking of banded birds over multiple years, we calculated seasonal nest success (percent of nests that successfully fledged at least one young per breeding season), seasonal fecundity (total number of young fledged per breeding season), age-based seasonal fecundity, and Minimum Lifetime Productivity (the total number of young fledged per individual over their estimated lifetime). Seasonal measures of reproductive success varied by site and year, although overall the San Pedro/Gila had higher reproductive success. Average seasonal fecundity for females was 1.6 at Roosevelt Lake and 2.0 at the San Pedro/Gila. Male seasonal fecundity was 0.4 higher than females at Roosevelt Lake and 0.5 higher at San Pedro/Gila. Older females had higher seasonal productivity than second-year females, and there was no difference in productivity by habitat type (native, saltcedar, and mixed habitats). Average Minimum Lifetime Productivity was 3.3 for females and 3.8 for males. Over a third of individuals did not fledge any young that we detected, and over 50% of the young fledged were contributed by just 16% of the breeding adults.

Chapter 4—Movement

Movement of banded birds was observed both within and between years and at multiple scales (between-drainage, between-patches, and within-patch). Natal dispersal was on average 11 km farther than adult movements, and the longest observed movements were from natal dispersal (up to 444 km). Fewer than 1% of banded nestlings returned to their natal patch.

We documented within-season and between-season movement by adults. Within season movements occurred from small scales (within-patch) to large scale (between-drainage), and represented strategies from territory switching to post-breeding non-territorial movements. Between-year movements were far more common, and ranged from 0.1km to 214 km. There was no difference in mean movement distance between males and females, but flycatchers at the San Pedro/Gila study site moved significantly farther within-drainage than those at Roosevelt Lake. This difference primarily reflected differences in the spatial arrangement of breeding patches. The proportion of flycatchers that returned to their previous year territory, moved to another territory in the same patch, or moved to another patch also varied by year and study site. One important factor in whether a flycatcher returned to their previ-

ous year territory was their previous year nest success, with the odds of showing territory fidelity increasing 1.5 for every young fledged. Additionally, the decision to move or show territory fidelity, which is based in part on reproductive performance, has implication on the subsequent year's performance. Successful individuals that returned to their territory tended to do well, while those that did not do well in the previous year and moved tended to do better than in the previous year.

While reproductive success may strongly influence whether an individual returns to the same territory, other factors also appear to influence such decision making. One cause may be habitat selection. Young riparian habitat patches can be quickly colonized by flycatchers, and immigration into the young habitat is the dominant movement pattern.

As the habitat matures, immigration declines while emigration from the patch increases. While territory fidelity also increases as the patch ages, this is by a dwindling number of individuals. Such changes in movement patterns may be a key reason for the often ephemeral pattern of breeding patch occupation observed across the range of the flycatcher.

Chapter 5—Demographic Modeling

Survivorship, productivity, and movement can all influence whether a population increases, decreases, or remains constant in size. However, how each of these vital rates influences a population can only be understood via the simultaneous consideration of all the vital rates synergistically combined. We constructed demographic models that evaluated how these vital rates, considered simultaneously, contributed to the growth potential of the two study site populations. Further, to assess the strength of the model's ability to accurately mimic flycatcher population dynamics, we applied the model retrospectively to the study sites, comparing predicted numbers to those actually observed. In general, the demographic models underestimated the growth potential of the breeding populations when compared to the observed population changes from 1996 to 2005. This was surprising given that the models were based on the robustly-measured vital rates from these populations. The reason for the discrepancy between observed and modeled growth rates is unknown, though it could be because of underestimations of productivity, survivorship, or immigration rates. We suggest development of models that will accurately reflect flycatcher population dynamics.

Chapter 6—Spatial Modeling

The decline of the Southwestern Willow Flycatcher is believed to be tightly linked to the decline in the riparian habitat they depend on for breeding, and the ability to accurately describe and predict suitable flycatcher breeding habitat is an important step in the ultimate recovery of the species. We used spatially explicit models to describe the habitat of flycatchers, taking an important next step in modeling from earlier efforts. Specifically, we expanded upon earlier efforts of modeling

flycatcher habitat by developing models that added additional environmental parameters, modeled specifically for a reservoir and riverine systems, and incorporated a temporal component. The models constructed were then tested against 10 years of territory location data from both study areas to evaluate the temporal robustness of the models. We found that modeling reservoir and riverine systems separately, in contrast to earlier efforts that averaged across the two, provided much better accuracy, especially for the reservoir system. However, the greatest improvement in the models came when temporal change in habitat was incorporated into the models. This highlights the dynamic nature of riparian habitat, and the importance of incorporating such dynamics into habitat models.

Applying the best models to environmental information collected from 20 years at both study sites, the amount of predicted habitat changed substantial over the years at the two systems. Roosevelt Lake varied from a low of 41 ha in 2005 to a high of 483 ha in 2004. The San Pedro/Gila had a low of 406 ha in 2002 and high of 1,392 ha in 1987. Changes in the amount of predicted habitat were driven largely by water. At Roosevelt Lake, the fluctuations in the reservoir level had profound effects on the amounts of predicted habitat, while at the San Pedro/Gila scouring floods could reduce the amount of habitat, as could severe droughts. Matching flycatcher dynamics to the habitat was difficult. At Roosevelt Lake, a general increase in the amount of predicted habitat from 1996 to 2004 coincided with an increase in the breeding population size there. However, at the San Pedro/Gila study site, increasing population sizes did not match changes in the amount of predicted habitat; this may indicate that habitat was not limiting on the San Pedro/Gila during the modeled period. Further, while these models performed very well in predicting where a flycatcher territory may occur, the elements of the spatial models (e.g., NDVI, distance from river) were only weakly related to measure of reproductive success, suggesting that the factors that flycatchers use to locate territories may be different from factors that determine ultimate nesting success.

Chapter 7—Floaters

The prevalence of floaters (non-territorial individuals) in a population is difficult to detect and thus is poorly understood. Based on field work in the first half of this study, we suspected that there was a population of floaters, and that they may constitute a not-insignificant proportion of the population. From 2001 to 2005 we enacted a passive netting operation to detect floaters at Roosevelt Lake. Overall, we detected 134 individuals during this period that were present at the breeding site but which we believed were non-territorial for an entire season. In most years the number of floaters was relatively small (less than 10% of population), but it was high in the one year of severe drought (2002; 25% of population). Most floaters were male (85%) and most were young adults (88% were second-year adults).

To understand why a flycatcher may become non-territorial, and whether they contribute to a breeding population, we evaluated the breeding performance of individuals in pre- and post-floater years. Productivity did not differ pre- or post-floating, suggesting no benefit to floating for a year. Lifetime productivity of birds that floated was lower than individuals that were territorial in every year detected, suggesting a cost to forgoing a year of breeding. There was a negative relationship between the average productivity of a site (all breeding individuals considered) and the prevalence of floaters, suggesting that years with poor productivity had higher numbers of floaters (such as in the year of the severe drought, 2002). Thus, while floaters do form a part of the population at Roosevelt Lake, contributing substantially to numbers in some years, in most years they constitute a small portion of the population.

Chapter 8—Conclusions

Taking the insights into flycatcher ecology and biology derived from the previous chapters, we synthesize findings from across chapters to address a range of management concerns.

Role of Reservoirs

Although reservoirs and their operation can lead to alteration and degradation of riparian systems, in certain situations they can support large tracts of apparently high-quality riparian habitat in their drawdown zones. Roosevelt Lake is one example, and Southwestern Willow Flycatchers bred extensively in the ephemeral riparian habitat that developed within the lakebed during low water years. Given that reservoirs fluctuate over time, they can sometimes create conditions for habitat creation and destruction cycles that can lead to development of a mosaic of different aged riparian woodland stands. Even if the habitat patches are periodically destroyed, such mosaics can benefit Southwestern Willow Flycatchers and other riparian obligate species.

Response to Reservoir Rise

While the drawdown of Roosevelt Lake created hundreds of hectares of riparian vegetation between 1996 and 2004, the high lake levels in 2005 wholly or partially inundated most of the previously occupied flycatcher habitat. Flycatchers responded by using partially inundated habitat or by shifting to new patches above the lake level. We did not observe large-scale dispersal to other breeding locations in the Southwest. Thus, the existence of “refuge” habitat near current breeding populations may be important for the long-term sustainability of flycatchers in an area. This may be particular important for reservoirs, where high water levels and associated habitat loss can be expected to regularly reoccur.

Scale of Management

Flycatchers showed a high degree of movement from 1996 to 2005, with movements common among sites that were 30–40 km apart and within the same drainage. Therefore, our perception of what constituted a biologically meaningful site has shifted from considering every patch as a distinct site, to considering a network of patches within the same drainage as a site. At a larger geographic scale, infrequent movements that connect different drainages allow for metapopulation-scale processes to occur. Thus, management of the flycatcher will be most effective if conducted at drainage and regional scales, with a consideration of patch connectivity.

Dynamic Species and Dynamic Habitats

Flycatchers showed high variability in most of their life history traits, which may reflect their adaptation for the dynamic riparian habitats in which they evolved and upon which they depend. Riparian habitat can establish rapidly, and be colonized by flycatchers when the structure becomes suitable. Therefore potential breeding habitat can be developed quickly, under the right conditions. Flycatchers appear to leave habitat as it matures, at least if there is younger alternative habitat nearby. Riparian habitat can disappear rapidly through scouring floods, inundation, fire, or other disturbances. When riparian habitat is lost, flycatchers appear to be able to shift to new breeding locations, if suitable habitat is present. Recognizing the dynamic nature of riparian habitat is one key to successful long-term management of the flycatcher.

Habitat Use

Southwestern Willow Flycatchers depend on typically dense riparian habitat, but the exact structure and species composition can be variable within and between sites. This use of diverse plant species suggests that vegetation structure, not species composition, is the most important feature of flycatcher habitat. Flycatchers appear to prefer young habitat, and bred in some riparian patches that were only 3 years of age. However, they will occupy older habitat, perhaps as refugia until younger habitat becomes available. At Roosevelt Lake and the San Pedro/Gila, flycatchers bred in exotic saltcedar, with no apparent negative effects.

Riparian Restoration

Despite the many challenges to successful riparian restoration activities, it is possible to create riparian habitat relatively quickly and for it to be rapidly colonized by Southwestern Willow Flycatchers. Newly created habitat can be colonized by flycatchers within as little as 3 years, especially if within 30–40 km of extant breeding locations. GIS models developed as part of this study can be used as tools for planning and assessing riparian habitat restoration.

Monitoring Implications

Local flycatcher population sizes can change rapidly, and flycatchers can quickly colonize new habitat. Therefore, periodic monitoring is needed in order to have high confidence about the status of local Southwestern Willow Flycatcher populations. Similarly, riparian habitat can also develop, change structure, or be lost quickly. Accordingly, periodic habitat monitoring is important to be certain of the current distribution of potential flycatcher breeding habitat.

Drought Impacts

Drought has negative effects on breeding flycatchers and their habitat. The extreme drought of 2002 caused near complete reproductive failure of flycatchers at Roosevelt Lake, and caused a dramatic rise in the prevalence of non-breeding floaters. More frequent or more sustained droughts—as predicted by many climate change models—could have long-term negative effects on the sustainability of flycatchers. Thus, long-term management of the flycatcher will be more effective if it takes into account, and investigates possible ways to ameliorate, the negative effects of future droughts.

Future Research Needs and Directions

While we have learned much about the flycatcher over this 10-year study, there are still many important areas for future research. These include: whether small populations have different population dynamics than the large populations we studied; development of improved or new demographic models to help guide complex management decisions; development of spatial models that link key determinants of flycatcher habitat (e.g., groundwater, stream flow) to the characteristics of suitable habitat (as identified by our models); development of decision tools to conduct scenario planning and address management issues; the role and impact that emerging disease threats may have on flycatcher populations; and a better understanding of the migration ecology of flycatchers.

Chapter 1—Introduction

Introduction

This project was funded by the Bureau of Reclamation, as a result of a Section 7 Biological Opinion on the effects of raising Roosevelt Dam, located in central Arizona. An increase in the height of the dam structure provided additional water conservation space (as well as flood control and dam safety improvements), but also increased the amount of Southwestern Willow Flycatcher habitat that would be periodically inundated. The Biological Opinion issued by the U.S. Fish and Wildlife Service (USFWS 1996) identified a Reasonable and Prudent Alternative (RPA) that would avoid “jeopardy” to the species. As part of the RPA, the Opinion required that Reclamation fund a comprehensive Southwestern Willow Flycatcher research program. As outlined in RPA 1.e.2, Reclamation was required to collect flycatcher demographic data through color-banding and monitoring studies at Roosevelt Lake and at select locations along the lower San Pedro/Gila River confluence area (hereafter referred to as the San Pedro/Gila site; fig. 1). Roosevelt Lake was the focal area because of potential dam-related impacts to the flycatchers breeding there. However, when the Opinion was written it was anticipated that the lake might rise to the new capacity level before the 10-year research period ended. Therefore, areas along the San Pedro and Gila Rivers were included as research locations because they were not subject to reservoir inundation, and birds dispersing as a result of Roosevelt Dam operations might move to or from these areas.

Reclamation contracted with both the U.S. Geological Survey (USGS) Southwest Biological Science Center and the Arizona Game and Fish Department (AGFD) to collect data on various aspects of Southwestern Willow Flycatcher demography. A series of USGS annual reports summarized the results of our efforts each year (Paxton and Sogge 1996, Paxton et al. 1997, Netter et al. 1998, English et al. 1999, Luff et al. 2000, Kenwood and Paxton 2001, Koronkiewicz et al. 2002, Newell et al. 2003, Newell et al. 2005, Causey et al. 2005); AGFD produced a similar series detailing their project components. Summary data compilation, database integration, and analysis occurred in 2006 and 2007. This synthesis report is intended to (1) summarize the 10 years of research activity; (2) analyze and model the data to provide insight into the flycatcher population and habitat dynamics; and (3) provide interpreta-

tions of the data that can inform management and conservation of the Southwestern Willow Flycatcher at Roosevelt Lake, and potentially elsewhere in its range.

Report Structure

This final report consists of an Introduction, six stand-alone chapters, and a Conclusion chapter. The Introduction (chapter 1) provides the background necessary to understand the overall research project: a general description of the origin and scope of the project, an overview of the natural history of the Southwestern Willow Flycatcher, a brief summary of the history and operations of Roosevelt Lake, and descriptions of the Roosevelt Lake and San Pedro/Gila study sites. The next three chapters cover the topics of Survivorship (chapter 2), Productivity (chapter 3), and Movement (chapter 4). These are key drivers of how a population functions and changes over time and space; it is crucial to understand how and why they vary to understand why a population grows, remains steady, or declines. The next two chapters, Demographic Modeling (chapter 5) and Spatial Modeling (chapter 6), bring together the previous population parameters to explore how they interact with one another in a spatial and temporal context. Chapter 6 also evaluates refined models of predicted flycatcher habitat and changes in predicted habitat over time. Floaters (chapter 7) describes the nature and extent of non-territorial flycatchers at Roosevelt Lake, to determine what factors influence territoriality and non-territoriality, and whether floaters are an important component of the population. Chapters 2 through 7 each include introductory material, methods, results, conclusions, and management considerations specific to each topic. The Conclusion (chapter 8) summarizes key data and management considerations contained in previous chapters.

Project Objectives

At a broad scale, our goal was to understand important demographic parameters and their potential drivers, and to develop models that can provide useful information to resource managers who are responsible for long-term per-

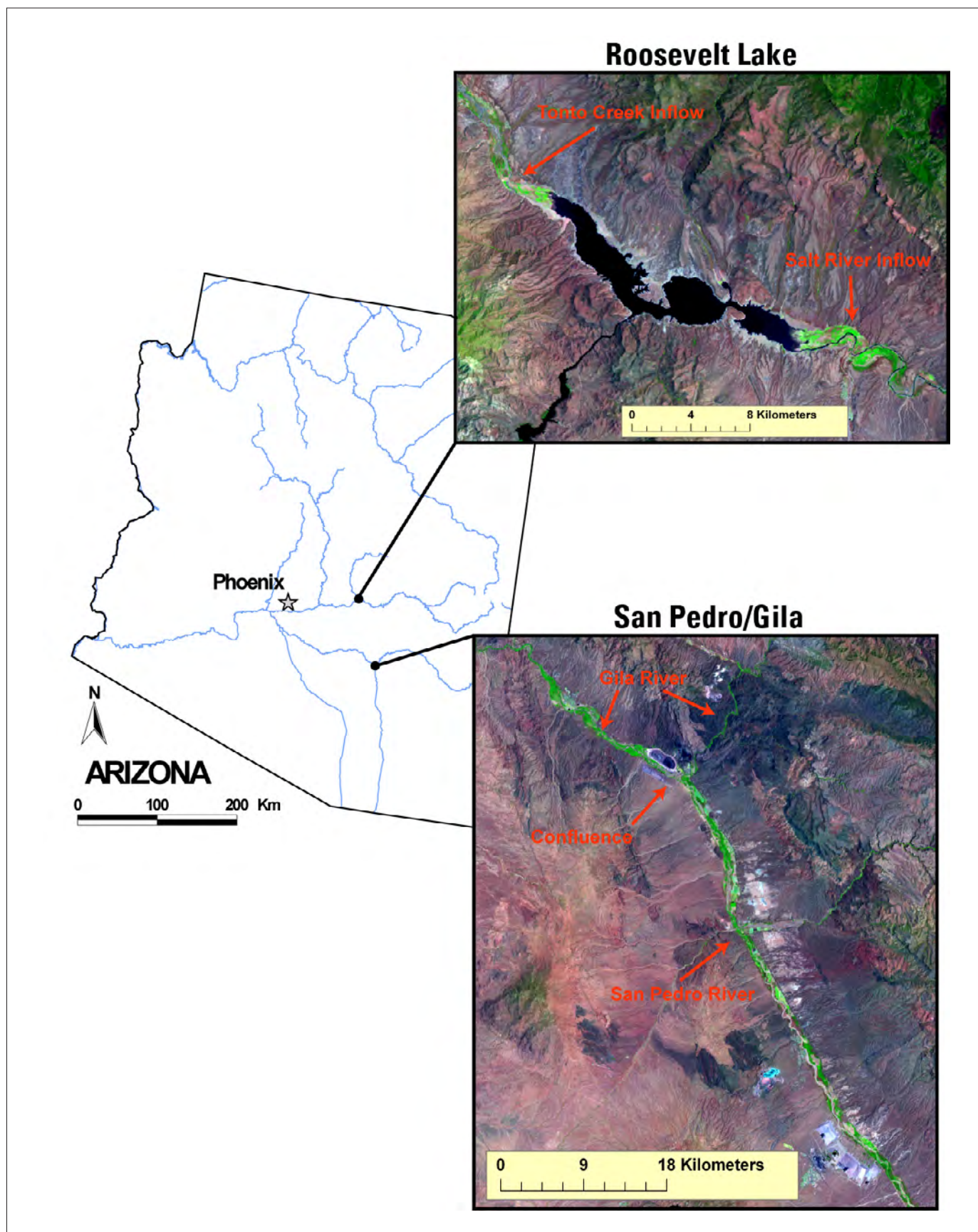


Figure 1. Location of the Roosevelt Lake and San Pedro/Gila study areas in central Arizona.

sistence of Southwestern Willow Flycatchers in Arizona. In particular, this information was anticipated to be of use in the recovery of the flycatcher. The interim data produced during this study were widely used in the development of the Southwestern Willow Flycatcher recovery plan (USFWS 2002), critical habitat designation (USFWS 2005), and other recovery planning.

Each year, we color-banded and resighted as many Southwestern Willow Flycatchers as possible within our study sites in order to gather detailed demographic information about the populations. Over the course of this study (1996–2005), USGS captured and banded 1,080 adult and 498 nestling/fledgling willow flycatchers. The presence of banded birds at each site also contributed to on-going flycatcher studies by AGFD, providing a more accurate assessment of the number of breeding birds and the ability to document breeding activities (e.g., pairing, nesting attempts, reproductive success) of individuals within and between years. Specific objectives of the USGS-based demography study were to collect data on:

1. between-year survivorship and mortality of adults and young;
2. immigration, emigration, site and patch fidelity, and movement between patches and sites; and
3. sex and age structure of flycatcher population.

In addition to directly addressing the research objectives of the Roosevelt Dam Biological Opinion, our activities at Roosevelt Lake provided an opportunity to conduct supplemental studies on topics such as morphology (Paxton et al. 2005), home range and habitat use (Cardinal et al. 2006, Sogge et al. 2006), physiology (Owen et al. 2005), genetic variation and structuring (Sogge et al. 1998, Busch et al. 2000, Paxton 2000), nestling sex ratio (Paxton et al. 2002b), and food habits (Drost et al. 2003, Durst 2004). These studies provided valuable context in which to better understand the ecology of the Southwestern Willow Flycatcher at Roosevelt Lake, and elsewhere in the bird's range. Furthermore, during this project we developed or refined several new field techniques, including targeted mist-net capture (Sogge et al. 2001), a floating mist-net technique for flooded habitats (Pollock and Paxton 2006), low-impact aluminum color bands (Koronkiewicz et al. 2005), radio telemetry (Paxton et al. 2002a), and a nestling aging guide (Paxton and Owen 2002). Each of these new techniques proved valuable in meeting our project objectives, and many have been adopted by other flycatcher research projects.

Coordination with Arizona Game and Fish Department

Throughout this research effort, project leaders and field staff of the USGS and AGFD worked cooperatively to collect the data upon which this report and other related science products are based. AGFD and USGS had concurrent field crews working within the same study sites at Roosevelt Lake and

the San Pedro/Gila from 1996 to 2000. Generally, AGFD had lead responsibility for surveying and locating flycatcher territories, and monitoring nests; USGS conducted flycatcher capture and banding efforts, and focused on resighting of banded individuals. However, both groups collected information on flycatcher locations, nests, and band identifications, and shared all field data accordingly. Beginning in 2001, USGS focused field work totally on the flycatchers at Roosevelt Lake, and AGFD took over responsibility for all field efforts on the San Pedro/Gila while also remaining at Roosevelt Lake. This collaborative approach allowed the collection of more and better field data than would have otherwise been possible. A separate 10-year synthesis report by AGFD (Ellis et al. 2008) details their components of the overall project, including an evaluation of how the flycatchers responded to rising reservoir levels and habitat inundation at Roosevelt Lake during the 2005 season.

Southwestern Willow Flycatcher

The following is a brief summary of the natural history, distribution and abundance, and conservation status of the Southwestern Willow Flycatcher; it does not include the new information from our 10-year study that is reported in later chapters. We focus here on the breeding season, as that is the time during which we conducted our flycatcher research at Roosevelt Lake. For more detailed overviews of flycatcher biology and habitat use (including images of breeding habitats throughout the Southwest), and migration and winter ecology, see Sogge et al. (1997), Sogge (2000), Finch and Stoleson (2000), Koronkiewicz (2002), USFWS (2002), Sogge et al. (2003a), USFWS (2005), and Koronkiewicz et al. (2006).

Breeding Ecology

The Willow Flycatcher (*Empidonax traillii*) is a widespread species, breeding across much of the conterminous United States. There are four widely recognized subspecies (Unitt 1987), all of which are Neotropical migrants that winter in Central and South America, coming to North America for only 4–5 months each year to breed (Sedgwick 2000). The Southwestern Willow Flycatcher (*E.t. extimus*) is a distinct subspecies. It is generally paler than other Willow Flycatcher subspecies, although this difference is subtle and requires considerable experience and taxonomic training to detect, and the use of known subspecies study skins as comparative reference material (Unitt 1987). Despite the subtle morphological differences, the taxonomic validity of *E.t. extimus* has been critically reviewed and confirmed multiple times (Hubbard 1987, Unitt 1987, Browning 1993, Paxton 2000). The known breeding range of the southwestern subspecies includes southern California, Arizona, New Mexico, southwestern Colorado, and extreme southern portions of Nevada and Utah (USFWS 2002).

Willow Flycatchers generally depart their wintering grounds in April and May (USGS unpub. data). They will frequently sing during migration, perhaps to establish temporary territories for short-term defense of food resources. Southwestern Willow Flycatchers generally arrive at their breeding sites from late April through May, earlier than is true for the more northern subspecies. Therefore, from May through mid-June, northbound migrant Willow Flycatchers of other subspecies are passing through the Southwest, which can make it challenging to determine local breeders from migrants (Sogge et al. 1997). In the same manner, southbound migrants can appear in late July and August, when some Southwestern Willow Flycatchers are still tending nests or young. USFWS (2002) presents a generalized migration and breeding chronology for Southwestern Willow Flycatchers.

Breeding Southwestern Willow Flycatchers are riparian obligates; they typically establish territories and nest in relatively dense riparian vegetation where surface water is present or soil moisture is high enough to maintain the appropriate vegetation characteristics (Sogge and Marshall 2000). However, because hydrological conditions in the Southwest can be highly variable within a season and between years, water availability at a site may change dramatically (ranging from flooded to dry) over the course of a breeding season or from year to year. Vegetation characteristics of Southwestern Willow Flycatcher breeding habitat generally include high canopy or midstory cover, dense twig structure, and high levels of live green foliage (Allison et al. 2003); dense midstory vegetation in the 2–5-m range is common. Beyond these generalities, the flycatcher shows adaptability in habitat selection, as the dominant plant species (both native and exotic), size and shape of breeding patch, and canopy height and structure can be variable (USFWS 2002). Unlike breeders, migrating Willow Flycatchers are regularly found in riparian habitats that would not be suitable for breeding, as well as in some non-riparian habitats (Sogge et al. 1997).

Overall, male Southwestern Willow Flycatchers arrive on the breeding grounds before females, with older males generally arriving before younger ones. Although females usually arrive a few weeks after males, some older females are present on territories before late-arriving males. Flycatchers will sometimes travel extensively through large areas of the Roosevelt Lake study site before and after breeding, possibly as a way to evaluate potential breeding habitat (Cardinal et al. 2006). Males establish territories and exclude other males through singing and aggressive interactions. Male song rate is very high early in the season, then declines after pairing (Yard and Brown 2003). Territory size tends to be larger when a male first arrives, then gets smaller after a female pairs with the male. At Roosevelt Lake, average territory size (after pairing) was approximately 1 ha; however, estimated territory sizes can vary widely and range from 0.06 ha to 2.3 ha (Sogge 1995, Sogge et al. 1995, Whitfield and Enos 1996). Although the Willow Flycatcher as a species is considered predominantly monogamous during the breeding season (Sedgwick 2000), some Southwestern Willow Flycatcher populations

have a relatively high degree of polygyny whereby one male's territory can include more than one breeding female (generally two, but up to four have been recorded; Davidson and Allison 2003).

Females generally begin nest construction within a week or two of pair formation; males play little or no role in nest building. The nests are built as open cups, typically woven in place on the branch of a tree or shrub where several small-diameter stems can provide support. Nest height is highly variable and depends on the available plant structure within the territory; nests have been found from 0.6 m to 18 m above ground. Southwestern Willow Flycatchers will commonly place their nests in native plants such as willows (*Salix* spp.) and box elder (*Acer negundo*; in the Gila-Cliff Valley, NM only), and in exotics such as saltcedar (*Tamarix* spp.) and Russian olive (*Elaeagnus angustifolia*; Sogge and Marshall 2000, Stoleson and Finch 2003, Durst et al. 2006). In Arizona, most nests are in tamarisk or willows (Paradzick and Woodward 2003, McLeod et al. 2007). Flycatcher nest location appears to be driven more by plant structure than by species composition.

Egg laying generally begins in early June, but a few early clutches occur by mid-May (Sogge et al. 1997). Clutch size averages 3–4 eggs for first nests, with one egg laid per day. Only the female develops a brood patch and incubates the eggs. The incubation period is typically 12–13 days from the date the last egg is laid, and all eggs generally hatch within 24–28 hrs of each other.

Flycatcher chicks are altricial and weigh only about 1–2 g at hatching, but grow rapidly and are ready to leave the nest at 12–15 days of age (Sedgwick 2000, Paxton and Owen 2002). The female initially provides most care for the young, but the male will help with feeding, especially as the chicks grow and their food needs increase. Both adults will defend the nest and nestlings from intruders and predators, using distraction behavior (trying to draw attention away from the nest) and physical aggression. After young fledge, they generally stay together and close to the nest for 3–5 days, then travel increasingly farther distances from the nest and, eventually, their natal territory. The adults continue feeding the fledged young for approximately 2 weeks.

Southwestern Willow Flycatchers readily re-nest, especially after a nest is unsuccessful; they will also sometimes nest again after a successful nesting attempt. Clutch size generally decreases with each successive nesting attempt (Whitfield and Strong 1995). Second nests are often built very close to the first (sometimes in the same tree), but can be placed anywhere within the same territory. Reuse of old nests is uncommon, but does occur (Yard and Brown 1999, D. Ahlers, personal commun.). Pairs may even attempt a third nest if the second one fails.

Based on studies of banded birds, most Southwestern Willow Flycatchers that survive from one year to the next will return generally to the same river drainage, often in proximity to the same breeding site, though some long-distance movements within and between drainages have been observed (USFWS 2002, Causey et al. 2006, McLeod et al. 2007).

Between-year survivorship of adults appears to be similar to that of most small passerine birds studied, generally ranging from approximately 40% to 60% (Stoleson et al. 2000, McLeod et al. 2007). Survivorship of young has been studied at only a few sites, but appears generally to be lower than adult survivorship (Stoleson et al. 2000, McLeod et al. 2007). However, first-year birds (i.e., returning nestlings) may be more prone to dispersal to new sites, which would artificially increase estimates of first-year mortality. Overall, the flycatcher population in the Southwest appears to persist as one or more widely dispersed metapopulations. There is movement of individuals, and thus genetic exchange, across the landscape, but the amount of interchange is smaller among more distant sites.

During the breeding season, Southwestern Willow Flycatchers are exclusively insectivorous, and consume a wide range of prey taxa (Drost et al. 2003, Durst 2004) ranging in size from small leafhoppers (Homoptera) to large dragonflies (Odonata). Major prey taxa include bugs (Hemiptera), bees and wasps (Hymenoptera), flies (Diptera), and leafhoppers; however, diet can vary widely between years and among different habitat types. Owen et al. (2005) investigated the effects of habitat-based diet differences on Southwestern Willow Flycatchers breeding in native-dominated and saltcedar-dominated habitats, and found no negative physiological or immunological impacts from breeding in saltcedar.

Conservation Status

Conservation attention was first focused on the Southwestern Willow Flycatcher at a rangewide scale by Unitt (1987), who described declines in flycatcher abundance and distribution throughout the Southwest. *E.t. extimus* populations have declined during the twentieth-century, primarily because of habitat loss and modification from activities such as dam construction and operation, groundwater pumping, water diversions, and flood control. In 1991 the U.S. Fish and Wildlife Service designated the Southwestern Willow Flycatcher as a candidate category 1 species (USFWS 1991). In July 1993, the USFWS proposed to list *E.t. extimus* as an endangered species and to designate critical habitat (USFWS 1993). A final ruling listing *E.t. extimus* as endangered was published in February 1995 (USFWS 1995); critical habitat was designated in 1997 (USFWS 1997) and re-designated in 2005 (USFWS 2005). Both the Roosevelt Lake and San Pedro/Gila study sites are included within the designated critical habitat. The Southwestern Willow Flycatcher is also listed as an endangered species or species of concern in Arizona (AGFD 1998), New Mexico (New Mexico Department of Game and Fish 1996), California (California Department of Fish and Game 1991), and Utah (Utah Division of Wildlife Resources 1997). Riparian habitat loss and alteration continues to occur, with potential negative effects to the flycatcher in some areas (Marshall and Stoleson 2000, USFWS 2002).

When proposed for listing in 1993, there were only 30 known Southwestern Willow Flycatcher breeding sites and

111 estimated territories rangewide (Sogge et al. 2003b). As a result of extensive survey efforts since 1995, following its listing as endangered, Southwestern Willow Flycatchers have now been recorded breeding at 275 sites, with an estimated total of 1,214 territories in 2005 (Durst et al. 2006). Arizona, New Mexico, and California account for approximately 90% of territories. Within Arizona, Roosevelt Lake and the San Pedro/Gila sites supported the majority of known flycatcher territories during our study period (Paradzick and Woodward 2003; Durst et al. 2006).

History and Recent Operations of Roosevelt Lake

Roosevelt Dam was constructed at the confluence of the Salt River and Tonto Creek, approximately 75 km (50 miles) northeast of Phoenix. Standing 85 m (280 ft) high, the first stone was laid in 1906, and the dam completed in 1911 (<http://www.srpnet.com/water/dams/roosevelt.aspx>). Named after then-President Theodore Roosevelt, it was the largest masonry dam in the world and created a reservoir capacity of 526,875 acre-feet. An 8-year, \$430 million project to increase the dam height was completed in 1996 (fig. 2). Raising the dam by approximately 25 m (77 ft), to a height of roughly 115 m (357 ft), provided for a total 2.9 million acre-feet of water storage at full capacity.

Although the dam modification project was completed in 1996, lake levels did not approach capacity for almost a decade. Low rainfall in the mid- and late-1990s led to very low water levels from 1998 through 2004 (fig. 3), during which time substantial amounts of new riparian habitat developed in the exposed reservoir bottom. In 2005, much of the riparian habitat was inundated (fig. 4) when the new conservation space at Roosevelt Lake filled to 95 percent capacity for the first time. Roosevelt Lake exceeded 2,136 ft from February to September 2005 and filled to elevation 2,148 ft in April and May 2005.

Southwestern Willow Flycatchers were first detected at Roosevelt Lake in 1993 (Sferra et al. 1995). As lake levels subsequently dropped and riparian vegetation expanded, the flycatcher population expanded from 48 territories in 1998 to 140 territories in 2001 (Smith et al. 2002), moving into newly created habitat within the exposed lakebed. The number of flycatchers continued to increase through 2004, with a high of 209 territories (Munzer et al. 2005). As riparian habitat was lost or altered through inundation, the Southwestern Willow Flycatcher population declined to 153 territories in 2005 and 111 territories in 2006 (English et al. 2006, Graber et al. 2007).

The Bureau of Reclamation owns Roosevelt Dam, but it is operated and maintained by the Salt River Project (SRP) pursuant to a 1917 agreement between the two agencies, in conjunction with the downstream dams on the Salt River. Lake levels are generally lowest in the winter and early spring, rise in late spring due to the capture of winter runoff, and then



Figure 2. The modified Roosevelt Dam, now 115 m (357 ft) high and providing a storage capacity of 2.9 million acre-feet for Roosevelt Lake (in background).

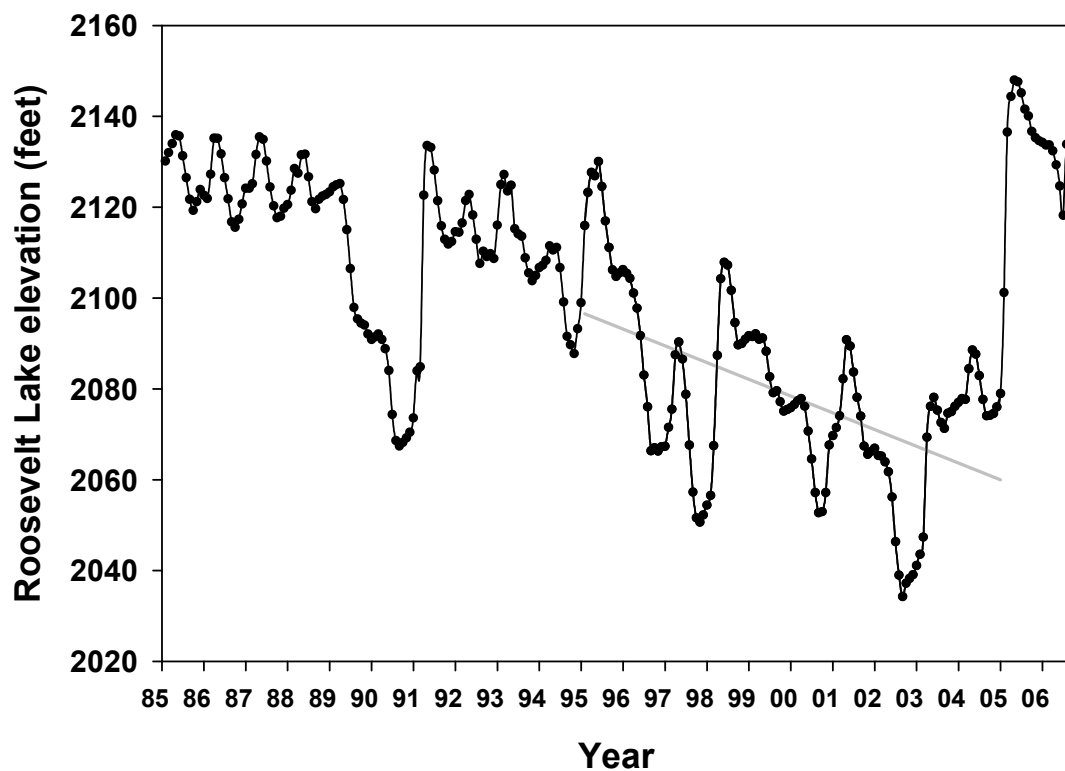


Figure 3. Lake level fluctuations at Roosevelt Lake reservoir from 1985 to 2005, with 1995–2004 regression line of general trend toward lower lake levels. Each solid circle is a mean monthly value of lake level elevation. Data are from the Bureau of Reclamation.



Figure 4. Panoramic views of the Orange-peel Campground site at Roosevelt Lake, in April 2004 (A) and April 2005 (B). The extensive Southwestern Willow Flycatcher breeding habitat in mid-photograph (2004) was completely inundated during the 2005 breeding season. This is one example of the loss of flycatcher breeding habitat that occurred when lake levels rose dramatically during the winter/spring of 2005.

decline over the summer and fall as releases are made from the dam. The Bureau's Section 7 Biological Opinion (USFWS 1996) addressed only the Federal action of raising the dam, and the corresponding new conservation and flood control space above 2,136 ft (689-m) elevation—not the operation of Roosevelt Dam. SRP received authorization to “take” Southwestern Willow Flycatchers below 2,136-ft level, by developing a Habitat Conservation Plan (HCP) as authorized in Section 10 of the Endangered Species Act (ESA). The resulting HCP (SRP 2002) includes all impacts associated with SRP's storage of water, both in the new and existing conservation space. The Bureau of Reclamation continues to be responsible for implementation of its 1996 Biological Opinion requirements.

Description of Roosevelt Lake and San Pedro/Gila Study Sites

Our two focal study sites (fig. 1) were breeding populations at Roosevelt Lake (33°39'N, 110°58'W) and the San Pedro and Gila Rivers confluence (hereafter San Pedro/Gila; 32°59'N, 110°46'W). Roosevelt Lake was the area subject to potential reservoir inundation impacts because of the operation of Roosevelt Dam; the San Pedro/Gila site provided a com-

parison area that was not subject to possible reservoir effects. We conducted our demographic research in cooperation with AGFD from 1996 to 2005 (Causey et al. 2005, English et al. 2006). We defined sites as a collection of riparian woodland patches, occupied by breeding flycatchers, which are collectively closer to one another than to other breeding patches, and are found within the same drainage (or along the same lake). Exact definitions of a site are difficult, and the definition of a site differs regionally (Durst et al. 2006). Likewise, we defined a breeding patch as a distinct patch of riparian vegetation which breeding flycatchers occupied, that is separated from other riparian vegetation by non-riparian habitat (e.g., open ground, scrub, river). We delineated breeding habitat patches by projecting territory locations for all years onto rectified aerial photographs, and used natural breaks or distribution of territories to estimate their approximate boundaries manually in ArcView 3.0 (ESRI, Inc).

Our two study sites were among the largest known Southwestern Willow Flycatcher breeding populations throughout the period of this study, with mean population sizes of 201 and 239 individuals at Roosevelt Lake and San Pedro/Gila, respectively. At each site, extensive survey efforts were conducted at least three times in the breeding season to detect all territorial flycatchers within the immediate and surrounding areas. In addition, other breeding sites in Arizona and throughout the Southwest (49–444 km away) were periodically visited, which

along with cooperative efforts of other researchers, allowed detection of dispersing or moving flycatchers.

The breeding habitat at the Roosevelt Lake and San Pedro/Gila study sites consisted of a heterogeneous mosaic of discrete riparian forest patches of varying ages and vegetation composition, ranging from 0.2 ha to 43 ha in size. At both study sites, we characterized habitat at both the territory and patch level based on vegetation composition as: (1) native ($\geq 90\%$ native vegetation), (2) mixed native (50%–89% native vegetation), (3) mixed exotic (50%–89% exotic vegetation),

and (4) exotic ($\geq 90\%$ exotic vegetation). Native habitat was characterized by Goodding's willow (*Salix gooddingii*) and Fremont cottonwood (*Populus fremontii*). Exotic habitat was dominated by saltcedar. The understory vegetation consisted of a variety of grasses, forbs, and shrubs (mesquite [*Prosopis* spp.], coyote willow [*S. exigua*], tamarisk, *Baccharis* spp., and cocklebur [*Xanthium strumarium*]). Adjacent and surrounding non-riparian vegetation was primarily composed of Sonoran Desert Uplands (Brown 1994), and in some cases agricultural lands.

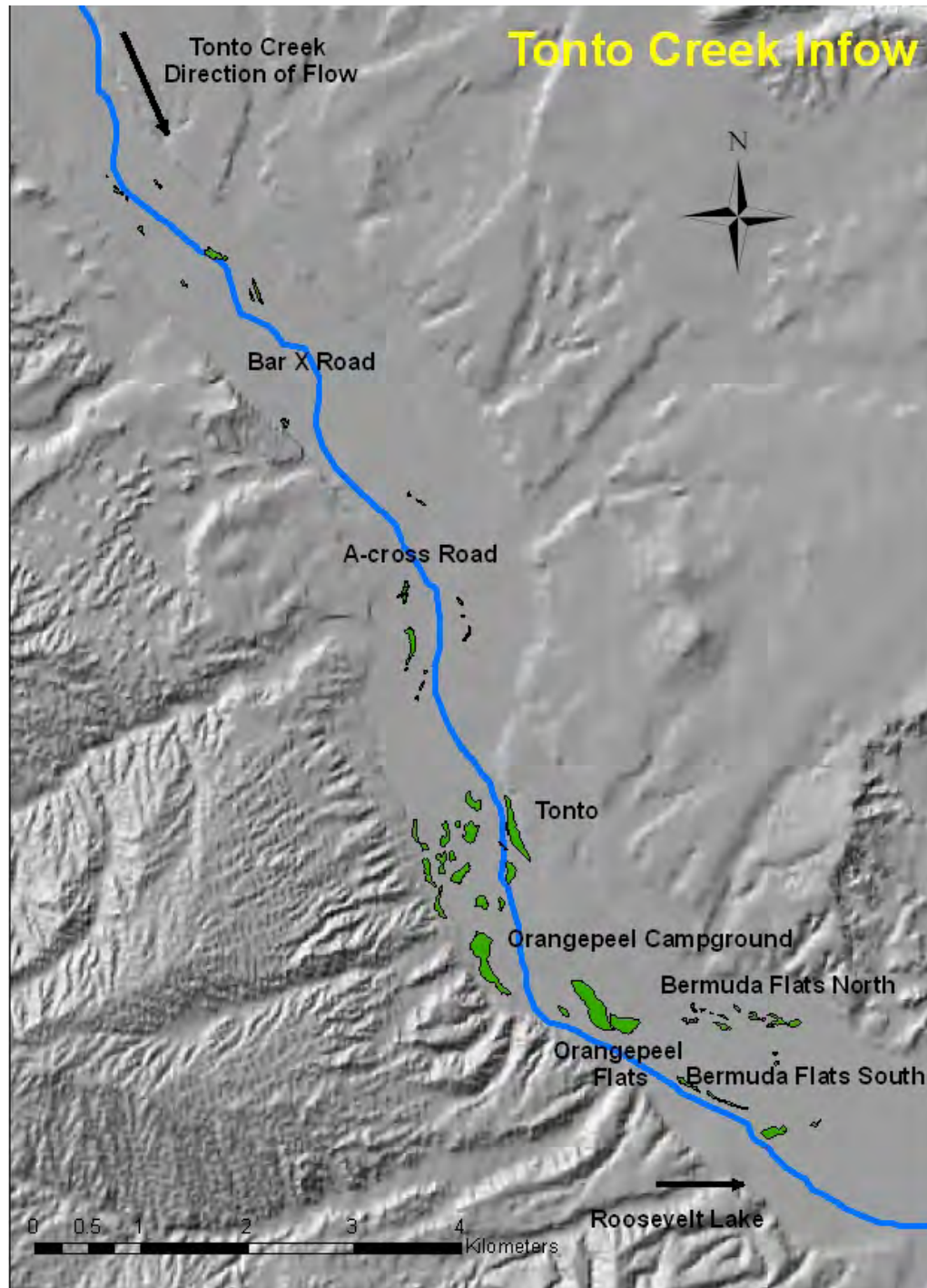


Figure 5. Location and names of habitat patches occupied in at least one year by Southwestern Willow Flycatchers at the Tonto Creek inflow at Roosevelt Lake, 1996–2005. Because of changes in lake levels and riparian habitat, not all sites were present or occupied by flycatchers in all years.

Roosevelt Lake Study Site

The Roosevelt Lake study site consisted of two sub-sites approximately 30 km apart at the inflows of Tonto Creek (fig. 5) and the Salt River (fig. 6). Breeding was documented as far as 12 km upstream on Tonto Creek and 9 km on the Salt River. The number of riparian patches in which breeding was documented varied over time as a result of colonization or desertion of patches, in many cases driven by fluctuating lake levels. Over the 10-year period, we documented breeding occurring in a maximum of 23 patches encompassing approximately 242 ha of riparian habitat.

San Pedro/Gila Study Site

The San Pedro/Gila study site encompassed 101 km of the San Pedro River and Gila River systems, centered at the confluence. On the free-flowing San Pedro River, flycatcher breeding patches extended from just south of Aravaipa Creek downstream to CB Crossing (fig. 7). Along the regulated Gila River (fig. 8), occupied patches were located between the San Pedro River confluence downstream to the Kelvin Bridge. As with Roosevelt Lake, the number of patches changed over the 10 years, with as many as 29 habitat patches documented as

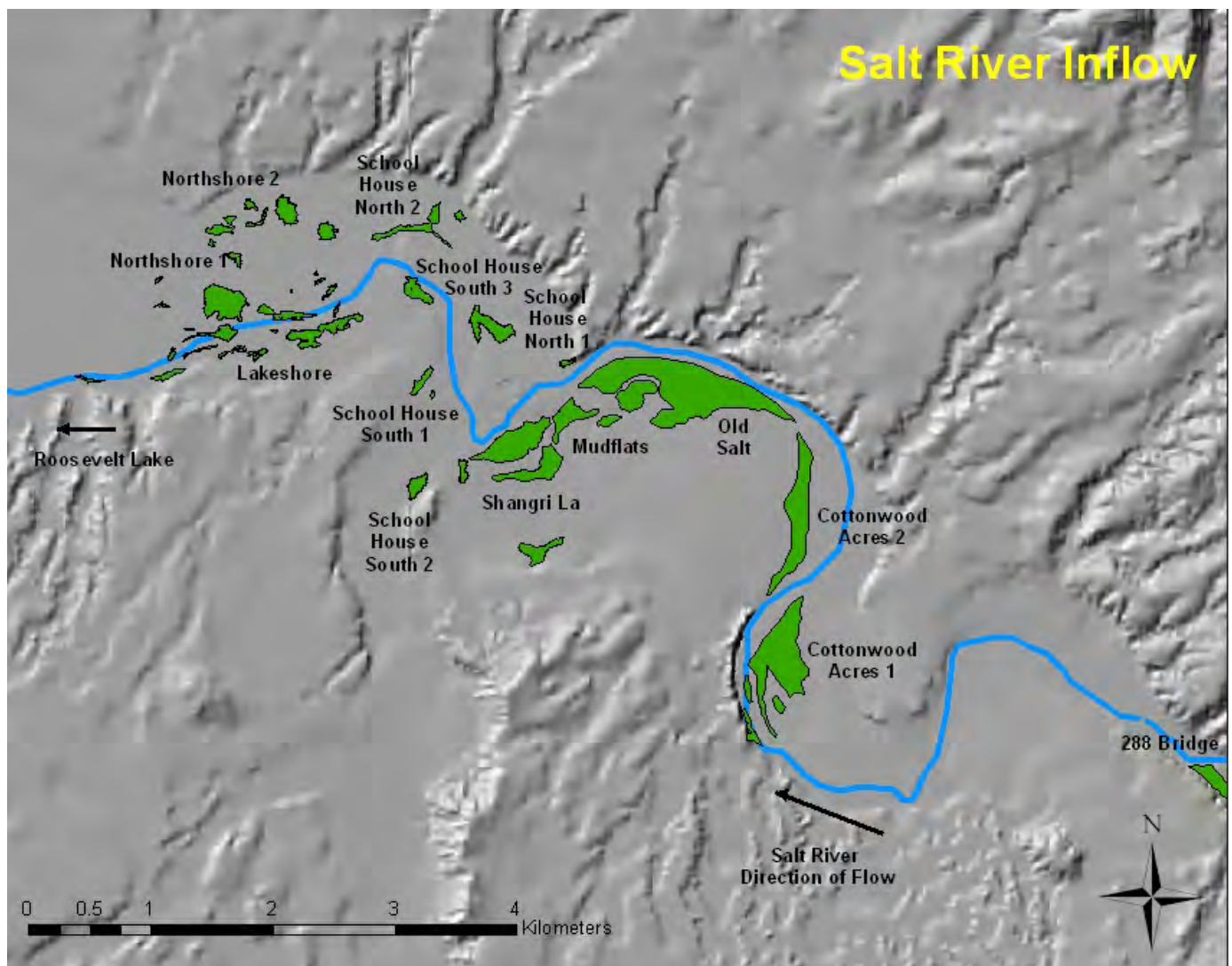


Figure 6. Location and names of habitat patches occupied in at least one year by Southwestern Willow Flycatchers at the Salt River inflow at Roosevelt Lake, 1996–2005. Because of changes in lake levels and riparian habitat, not all sites were present or occupied by flycatchers in all years.

supporting breeding efforts, comprising approximately 222 ha of riparian forest along this stretch.

Acknowledgements

This project was made possible by the support and cooperation of many persons, agencies, and private organizations and companies. Funding was provided by the Bureau of Reclamation (Reclamation) Phoenix Area Office, the USGS Southwest Biological Science Center, and Northern Arizona

University. The coordination, sharing of information, and/or land access permission from the AGFD, EcoPlan Associates, Inc., the U.S. Forest Service (USFS) Tonto Ranger District, The Salt River Project (SRP), SWCA Environmental Consultants, Inc., and Westland Resources, Inc. was of particular importance. We truly appreciate the AGFD's outstanding contributions to this project, through logistical assistance, planning and coordination, resighting and information sharing, collegiality, and good humor; our thanks especially to Rebecca Davidson, Lisa Ellis, Heather English, Tracy McCarthey, Olivia Munzer, Chuck Paradzick, Jay Rourke, Alex Smith, Mike Summner, and April Woodward. Special thanks also to

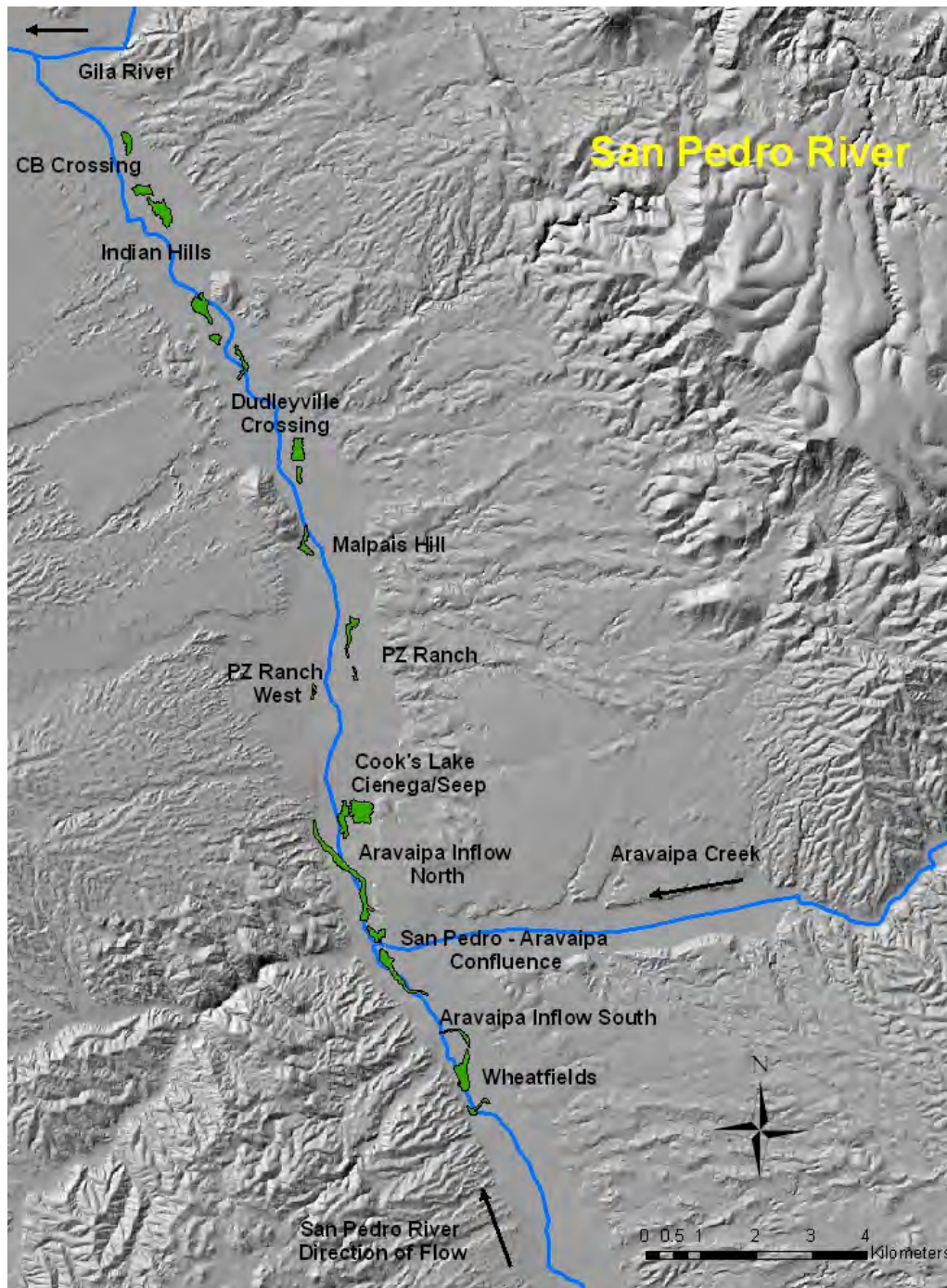


Figure 7. Location and names of habitat patches occupied in at least 1 year by Southwestern Willow Flycatchers within the San Pedro River portion of the San Pedro/Gila study area, 1996–2005. Because of changes in river flows and riparian habitat, not all sites were present or occupied by flycatchers in all years.

Susan Sferra and Henry Messing (Reclamation), and Gary Smith, Craig Woods, and Heidi Plank (USFS) for their essential help in this project. The success of our project is ultimately due to the efforts of the field personnel on the USGS banding crew: Amanda Bakian, Nathan Banfield, Suzanne Cardinal, Michelle Davis, Noel Dodge, Robert Emerson, Lisa Fitzgerald, Mark Gillilan, Phil Heavin, Patty Hodgets, Joanna Hubbard, Katie Kauffman, Kerry Kenwood, Jessie Knowlton, Tom Koronkiewicz, Suzanne Langridge, Therese Littlefeather, Yen Luc, Jen Luff, Andy McIntyre, Michael Moore, Tawna Morgan, Jessica Murray, Renee Netter, Jen Owen, Amy Porter, Casey Richart, Justin Schoefer, J.D. Semones, Valerie Steen, Valerie Stein, and Jocelyn Tutak. We are grateful to the peer reviewers who provided excellent feedback that greatly improved this report: Terry Arundel, Greg Beatty, Lisa Ellis, Barbara Kus, Jeff Lovich, Tom Koronkiewicz, Scott Stoleson, Charles van Riper, and Mary

Whitfield. Editorial and other assistance from Linda Sogge, Kristina Paxton, Lara Schmit also contributed greatly to this report. Our thanks also to Susan Sferra and Henry Messing for their thorough and insightful reviews of each chapter.

References

- Allison, L.J., C.E. Paradzick, J.W. Rourke, and T.C. McCarthy. 2003. A characterization of vegetation in nesting and non-nesting plots for Southwestern Willow Flycatchers in central Arizona. *Studies in Avian Biology* 26:81–90.
- Arizona Game and Fish Department. 1998. Threatened native wildlife in Arizona. Arizona Game and Fish Department, Phoenix, Arizona.

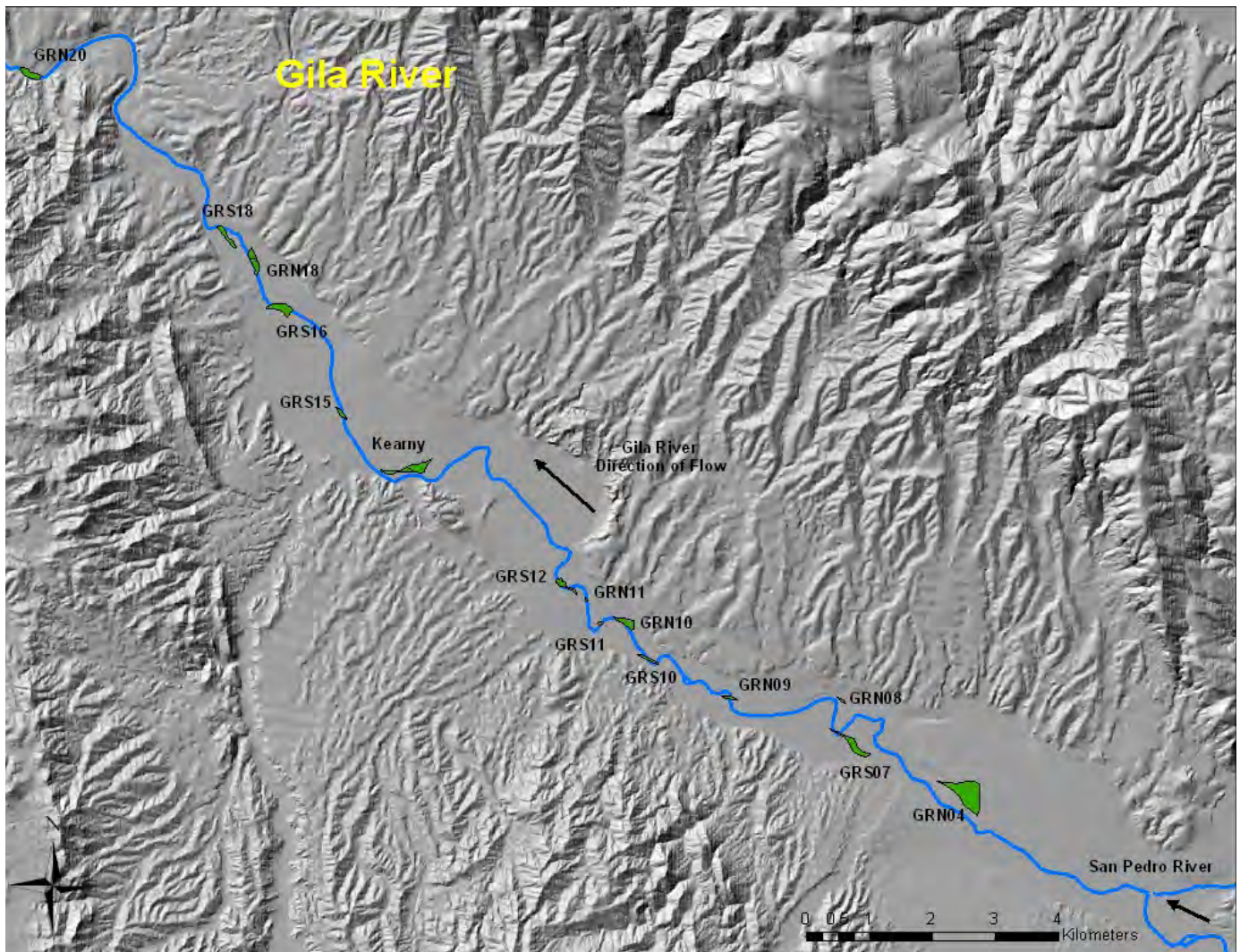


Figure 8. Location and names of habitat patches occupied in at least one year by Southwestern Willow Flycatchers within the Gila River confluence section of the San Pedro/Gila study site, 1996–2005. Because of changes in river flows and riparian habitat, not all sites were present or occupied by flycatchers in all years.

- Brown, D.E. (ed.). 1994. Tropical-subtropical desertlands. Pages 180–221 in *Biotic communities: Southwestern United States and northwestern Mexico*. University of Utah Press, Salt Lake City, Utah.
- Browning M.R. 1993. Comments on the taxonomy of *Empidonax traillii* (Willow Flycatcher). *Western Birds* 24:241–257.
- Busch, J.D., M.P. Miller, E.H. Paxton, M.K. Sogge and P. Keim. 2000. Genetic variation in the endangered Southwestern Willow Flycatcher. *Auk* 117: 586–595.
- California Department of Fish and Game. 1991. Endangered and threatened animals of California. State of California, The Resources Agency, Department of Fish and Game. Sacramento, California. 5 pp.
- Cardinal, S.N., E.H. Paxton, and S.L. Durst. 2006. Home range, movement, and habitat use of the Southwestern Willow Flycatcher, Roosevelt Lake, AZ—2005. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix, AZ. 21 pp.
- Causey, C.F., M.G. Pollock, S.L. Durst, P.J. Newell, E.H. Paxton, and M.K. Sogge. 2005. Survivorship and movements of Southwestern Willow Flycatchers at Roosevelt Lake, Arizona—2005. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix, AZ. 59 pp.
- Davidson, R.F., and L.J. Allison. 2003. Effects of monogamy and polygyny on reproductive success in Southwestern Willow Flycatchers (*Empidonax traillii eximius*) in Arizona. *Studies in Avian Biology* 26:118–124.
- Drost, C.A., E.H. Paxton, M.K. Sogge, and M.J. Whitfield. 2003. Food habits of the Southwestern Willow Flycatcher during the nesting season. *Studies in Avian Biology* 26:96–103.
- Durst, S.L. 2004. Southwestern Willow Flycatcher potential prey base and diet in native and exotic habitats. M.S. Thesis. Northern Arizona University, Flagstaff, Arizona.
- Durst, S.L., M.K. Sogge, H.C. English, S.O. Williams III, B.E. Kus, and S.J. Sferra. 2006. Southwestern Willow Flycatcher breeding site and territory summary—2005. U.S. Geological Survey, Southwest Biological Science Center report to Bureau of Reclamation, Flagstaff, Arizona.
- Ellis, L.A., D.M. Weddle, S.D. Stump, H.C. English, and A.E. Graber. 2008. Southwestern Willow Flycatcher final survey and monitoring report. Arizona Game and Fish Department, Research Technical Guidance Bulletin #10, Phoenix, Arizona, USA.
- English, H.C., A.E. Graber, S.D. Stump, H.E. Telle, and L.A. Ellis. 2006. Southwestern Willow Flycatcher 2005 survey and nest monitoring report. Nongame and Endangered Wildlife Program Technical Report 248. Arizona Game and Fish Department, Phoenix, Arizona.
- English, H.C., E.H. Paxton and M.K. Sogge. 1999. Survivorship and movements of Southwestern Willow Flycatchers in Arizona—1999. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix, AZ.
- Finch, D.M., and S.H. Stoleson (eds.). 2000. Status, Ecology, and Conservation of the Southwestern Willow Flycatcher. USDA Forest Service Rocky Mountain Research Station General Technical Report RMRS-GTR-60. 131 pp
- Graber, A.E., D.M. Weddle, H.C. English, S.D. Stump, H.E. Telle, and L.A. Ellis. 2007. Southwestern willow flycatcher 2005 survey and nest monitoring report. Nongame and Endangered Wildlife Program Technical Report 249. Arizona Game and Fish Department, Phoenix, Arizona.
- Hubbard J.P. 1987. The status of the Willow Flycatcher in New Mexico. Report to the New Mexico Department of Game and Fish. 29 pp.
- Luff, J.A., E.H. Paxton, K.E. Kenwood and M.K. Sogge. 2000. Survivorship and movements of Southwestern Willow Flycatchers in Arizona—2000. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix. 46 pp.
- Kenwood, K.E., and E.H. Paxton. 2001. Survivorship and movements of Southwestern Willow Flycatchers in Arizona—2001. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix, AZ.
- Koronkiewicz, T.J., S.N. Cardinal, M.K. Sogge and E.H. Paxton. 2002. Survivorship and movements of Southwestern Willow Flycatchers in Arizona—2002. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix, AZ.
- Koronkiewicz, T.J., E.H. Paxton, and M.K. Sogge. 2005. A technique to produce aluminum color bands for avian research. *Journal of Field Ornithology* 76: 94–97.
- Koronkiewicz, T.J., M.K. Sogge, C. van Riper III, and E.H. Paxton. 2006. Territoriality, site fidelity, and survivorship of Willow Flycatchers wintering in Costa Rica. *Condor* 108:558–570.
- Marshall, R.M., and S.H. Stoleson. 2000. Threats. Pages 13–24 in *Status, ecology, and conservation of the Southwestern Willow Flycatcher*. (D.M. Finch and S.H. Stoleson, eds.) USFS Rocky Mountain Research Station, Gen. Tech. Rep. RMRS-GTR-60.
- McLeod, M.A., T.J. Koronkiewicz, B.T. Brown, and S.W. Carothers. 2007. Southwestern Willow Flycatcher surveys, demography, and ecology along the lower Colorado River and tributaries, 2006. Annual report submitted to Bureau of Reclamation, Boulder City, Nevada by SWCA Environmental Consultants, Flagstaff, AZ. 194 pp.

- Munzer, O.M., H.C. English, A.B. Smith, and A.A. Tudor. 2005. Southwestern Willow Flycatcher 2004 survey and nest monitoring report. Nongame and Endangered Wildlife Program Technical Report 244. Arizona Game and Fish Department, Phoenix, Arizona.
- Netter, M.R., E.H. Paxton, and M.K. Sogge. 1998. Banding and movements of the Southwestern Willow Flycatcher at Roosevelt Lake and San Pedro River/Gila River confluence, Arizona—1998. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix, AZ.
- New Mexico Department of Game and Fish. 1996. List of threatened and endangered. Amendment No. 1, NMAC 33.1; 31 January 1996. New Mexico Department of Game and Fish, Santa Fe, New Mexico.
- Newell, P.J., C. Causey, M. Pollock, E.H. Paxton, and M.K. Sogge. 2005. Survivorship and movements of Southwestern Willow Flycatchers at Roosevelt Lake, Arizona—2004. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix.
- Newell, P.J., E.H. Paxton, and M.K. Sogge. 2003. Survivorship and movements of Southwestern Flycatchers at Roosevelt Lake, Arizona—2003. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix. 53pp.
- Owen, J.C., M.K. Sogge, and M.D. Kern. 2005. Habitat and gender differences in the physiological condition of breeding Southwestern Willow Flycatchers. *Auk* 122:1261–1270.
- Paradzick, C.E., and A.A. Woodward. 2003. Distribution, abundance, and habitat characteristics of Southwestern Willow Flycatchers (*Empidonax traillii extimus*) in Arizona, 1993–2000. *Studies in Avian Biology* 26:22–29.
- Paxton, E.H. 2000. Molecular genetic structuring and demographic history of the Willow Flycatcher. MS thesis. Northern Arizona University. 43 pp.
- Paxton, E.H., S.N. Cardinal, and T.J. Koronkiewicz. 2002. Evaluating the feasibility of radio-telemetry research on the Southwestern Willow Flycatcher: a pilot study. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix, AZ. 24 pp.
- Paxton, E.H., C. Causey, T.K. Koronkiewicz, M. Johnson, M.A. McLeod, P. Unitt, and M. Whitfield. 2005. Assessing variation of plumage coloration within the Willow Flycatcher: A preliminary Analysis. U.S. Geological Survey report. 13 pp.
- Paxton, E.H., S. Langridge, and M.K. Sogge. 1997. Banding and population genetics of Southwestern Willow Flycatchers in Arizona—1997 Summary Report. U.S. Geological Survey / Northern Arizona University report. 63 pp.
- Paxton, E.H., and J.C. Owen. 2002. An aging guide for Willow Flycatcher nestlings. Colorado Plateau Field Station, Northern Arizona University, Flagstaff, AZ. 18 pp.
- Paxton, E.H., and M.K. Sogge. 1996. Banding and population genetics of Southwestern Willow Flycatchers in Arizona—1996 summary report. U.S. Geological Survey/Northern Arizona University report. 25 pp.
- Paxton, E.H., M.K. Sogge, T.D. McCarthey, and P. Keim. 2002b. Nestling sex ratio in the Southwestern Willow Flycatcher. *Condor* 104:877–881.
- Pollock, M.G., and E.H. Paxton. 2006. Floating mist nests: a technique for capturing birds in flooded habitat. *Journal of Field Ornithology* 77:335–338.
- Salt River Project. 2002. Roosevelt Habitat Conservation Plan, Gila and Maricopa counties, Arizona. Salt River Project, Phoenix, Arizona.
- Sedgwick, J. A. 2000. Willow Flycatcher (*Empidonax traillii*). In *The Birds of North America*, No. 533 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, Pennsylvania.
- Sferra, S.J., R.A. Meyer, and T.E. Corman. 1995. Arizona Partners in Flight 1994 Southwestern Willow Flycatcher survey. Nongame and Endangered Wildlife Program Technical Report 69. Arizona Game and Fish Department, Phoenix, Arizona.
- Smith, A.B., C.E. Paradzick, A.A. Woodward, P.E.T. Dockens, and T.D. McCarthey. 2002. Southwestern Willow Flycatcher 2001 survey and nest monitoring report. Nongame and Endangered Wildlife Program Technical Report 191. Arizona Game and Fish Department, Phoenix, Arizona.
- Sogge, M.K. 1995. Southwestern Willow Flycatcher (*Empidonax traillii extimus*) monitoring at Tuzigoot National Monument. 1995 progress report to the National Park Service. National Biological Service Colorado Plateau Research Station/Northern Arizona University report. 20 pp.
- Sogge, M.K. 2000. Breeding season ecology. Pages 57–70 in *Status, Ecology, and Conservation of the Southwestern Willow Flycatcher*. Finch, D.M. and S.H. Stoleson (eds.). USDA Forest Service Rocky Mountain Research Station General Technical Report RMRS-GTR-60. 131 pp.
- Sogge, M.K., J. Busch, E. Paxton, M. Miller, and P. Keim. 1998. Population genetic analysis of the Southwestern Willow Flycatcher: 1996–1997. Report to Arizona Game and Fish Department Heritage fund. Heritage fund project 196049.
- Sogge, M.K., B.E. Kus, S.J. Sferra, and M.J. Whitfield. 2003a. Ecology and Conservation of the Willow Flycatcher. *Studies in Avian Biology* 26. Cooper Ornithological Society, Camarillo, California.

- Sogge, M.K., and R.M. Marshall. 2000. A survey of current breeding habitats. Pages 43–56 in *Status, Ecology, and Conservation of the Southwestern Willow Flycatcher*. Finch, D.M. and S.H. Stoleson (eds). USDA Forest Service Rocky Mountain Research Station General Technical Report RMRS-GTR-60. 131 pp.
- Sogge, M.K., R.M. Marshall, T.J. Tibbitts and S.J. Sferra. 1997. A Southwestern Willow Flycatcher Natural History Summary and Survey Protocol. National Park Service Technical Report NPS/NAUCPRS/NRTR-97/12. 37 pp.
- Sogge, M.K., J.C. Owen, E.H. Paxton and S.M. Langridge. 2001. A targeted mist net capture technique for the Willow Flycatcher. *Western Birds* 32:167–172.
- Sogge, M. K., E. H. Paxton, and A. A. Tudor. 2006. Saltcedar and Southwestern Willow Flycatchers: lessons from long-term studies in central Arizona. Pages 238–241 in C. Aguirre-Bravo, P. J. Pellicane, D. P. Burns, and S. Draggan, eds. *Monitoring science and technology symposium: unifying knowledge for sustainability in the Western Hemisphere*. 2004 September 20–24; Denver, Colorado. Proceedings RMRS-P-42CD. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.
- Sogge, M.K., S.J. Sferra, T.D. McCarthey, S.O. Williams, and B.E. Kus. 2003b. Distribution and characteristics of Southwestern Willow Flycatcher breeding sites and territories: 1993–2001. *Studies in Avian Biology* 26:5–11.
- Sogge, M.K., T.J. Tibbitts, C. van Riper III, and T. May. 1995. Status of the Southwestern Willow Flycatcher along the Colorado River in Grand Canyon National Park—1995. Summary report. National Biological Service Colorado Plateau Research Station/Northern Arizona University. 26 pp.
- Stoleson, S.H., and D.M. Finch. 2003. Microhabitat use by breeding Southwestern Willow Flycatchers on the Gila River in New Mexico. *Studies in Avian Biology* 26:91–95.
- Stoleson, S.H., M.J. Whitfield, and M.K. Sogge. 2000. Demographic characteristics and population modeling. Pages 83–94 in *Status, Ecology, and Conservation of the Southwestern Willow Flycatcher*. Finch, D.M. and S.H. Stoleson (eds). USDA Forest Service Rocky Mountain Research Station General Technical Report RMRS-GTR-60. 131 pp
- Unitt, P. 1987. *Empidonax traillii extimus*: an endangered subspecies. *Western Birds* 18:137–162.
- U.S. Fish and Wildlife Service. 1991. Notice of review: animal candidate review for listing as endangered or threatened species. Federal Register 56:58804–58836 (November 21, 1991).
- U.S. Fish and Wildlife Service. 1993. Proposal to list the Southwestern Willow Flycatcher as an endangered species and to designate critical habitat. Federal Register 58:39495–39522 (July 23, 1993).
- U.S. Fish and Wildlife Service. 1995. Final rule determining endangered status for the Southwestern Willow Flycatcher. Federal Register 60:10694–10715 (February 27, 1995).
- U.S. Fish and Wildlife Service. 1996. Biological opinion on the operation of the modified Roosevelt Dam. Arizona Ecological Services Office, Phoenix, Arizona.
- U.S. Fish and Wildlife Service. 1997. Final determination of critical habitat for the Southwestern Willow Flycatcher (*Empidonax traillii extimus*). Federal Register 62:39129–39147 (July 22, 1997).
- U.S. Fish and Wildlife Service. 2002. Southwestern Willow Flycatcher (*Empidonax traillii extimus*) final recovery plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico.
- U.S. Fish and Wildlife Service. 2005. Designation of critical habitat for the Southwestern Willow Flycatcher (*Empidonax traillii extimus*), Final Rule. Federal Register 70:60886–61009 (October 19, 2005).
- Utah Division of Wildlife Resources. 1997. Utah Sensitive Species List—March 1997. Utah Division of Wildlife Resources, Salt Lake City, Utah. 28 pp.
- Whitfield, M.J., and K.M. Enos. 1996. A Brown-headed Cowbird control program and monitoring for the Southwestern Willow Flycatcher, South Fork Kern River, California—1996. California Department of Fish and Game Report, Sacramento, California. 14 pp.
- Whitfield, M.J., and C.M. Strong. 1995. A Brown-headed Cowbird control program and monitoring for the Southwestern Willow Flycatcher, South Fork Kern River, California. California Department of Fish and Game, Bird and Mammal Conservation Program Report 95-4, Sacramento, California. 17 pp.
- Yard, H.K., and B.T. Brown. 1999. Willow Flycatcher nest reuse in Arizona. *Journal of Field Ornithology* 70:211–213.
- Yard, H.K., and B.T. Brown. 2003. Singing behavior of the Southwestern Willow Flycatchers in Arizona. *Studies in Avian Biology* 26:125–130.

Chapter 2—Survivorship

Introduction

Survival of individuals between successive time periods determines a population's survivorship rate, which both influences and results from fitness, life history characteristics, and population dynamics (Williams et al. 2002). Survivorship is a key parameter in demographic studies (Lebreton et al. 1993, Beissinger et al. 2000), and is a crucial determinant of population trends (Lebreton et al. 1993). For threatened and endangered species, understanding survivorship rates is necessary for making decisions regarding competing management alternatives and for effective recovery planning (Lebreton et al. 1993, Forsman et al. 1996). Within species, survivorship may vary between years (Brownie et al. 1986, Lebreton et al. 1992, Lebreton et al. 1993), within years (Sillett and Holmes 2002), among different locations (Lebreton et al. 1992, Lebreton et al. 1993), and in response to demographic factors such as sex and age (Lebreton et al. 1992). Thus, understanding how and where survivorship varies within and among populations is a crucial step in understanding population trajectories.

Although accurate population survivorship estimates are essential for many purposes, they can be difficult to obtain because they often are limited by field effort, spatial scale, and duration of a study. Robust estimates of survivorship require an "adequate" (typically large) number of marked individuals that are intensively tracked over time to ensure a high detection probability (White and Burnham 1999). Because of the inherent difficulty of detecting all living individuals over time, maximum likelihood methods of estimating survivorship (Cormack 1964, Jolly 1965, Seber 1965) were developed and are used to take into account the uncertainty of individual birds being detected within a given period. Even with maximum likelihood methods, higher detection rates lead to better survivorship estimates; therefore, survivorship studies need to be conducted with intensive efforts to detect all marked individuals. However, because maximum likelihood estimates cannot distinguish between true mortality and permanent emigration from a study area, survivorship studies should also be conducted over as large a spatial area as possible to maximize the probability of detecting individuals that move from core study areas. Finally, stochastic events can have large impacts on yearly survivorship, such that long-term studies are needed to more fully capture the range of variation in yearly survivorship (Pollock et al. 1990, Lebreton et al. 1992, Martin et al. 1995).

The Southwestern Willow Flycatcher (*Empidonax traillii extimus*) is a small, migratory passerine that breeds exclusively

in riparian habitats scattered throughout portions of the southwestern U.S. (Unitt 1987, Marshall 2000), and winters from central Mexico south to northern South America (Sedgwick 2000). Flycatcher numbers have declined precipitously as riparian habitats on the breeding grounds have been lost or modified (USFWS 1993, Marshall and Stoleson 2000), and *E. t. extimus* was listed as a federally endangered species in 1995 (USFWS 1995). At the time of listing, most aspects of the flycatcher's biology, and threats to the species' persistence, were poorly understood (Marshall and Stoleson 2000, Stoleson et al. 2000).

From 1996 to 2005, we collaborated with the Arizona Game and Fish Department (AGFD) to conduct a large-scale demographic study of flycatchers at two large breeding sites in central Arizona. Additionally, collaborative banding and monitoring efforts at many other breeding sites across the Southwest allowed for the detection of dispersing individuals. This field effort allowed us to document long-term variation in both adult and juvenile flycatcher survivorship and to evaluate factors that might affect survivorship, as well as to determine mean life expectancy. Factors that we believed may influence juvenile and/or adult flycatcher survivorship, and therefore evaluated, were breeding site, habitat type, sex, age, breeding status, and fledge date. Because estimates of annual survivorship in the flycatchers are the product of survivorship across the 12-month calendar year, we estimated flycatcher survivorship for each portion of their annual cycle (i.e., breeding, wintering, migration) to evaluate whether survivorship was constant across these periods. We accomplished this by linking data from our breeding ground study sites in Arizona to data collected on the wintering grounds in Costa Rica (Koronkiewicz et al. 2006). Lastly, we examined survival estimates at multiple spatial scales to determine the appropriate spatial scale necessary for robust survival estimates and to evaluate how reliable our survivorship estimates were to the confounding effects of permanent emigration.

Methods

Study Site

Our two focal study sites (fig. 1) were breeding populations at Roosevelt Lake (33°39'N, 110°58'W) and the San Pedro/Gila River confluence (hereafter San Pedro/Gila; 32°59'N, 110°46'W) from 1996 to 2005, where we conducted

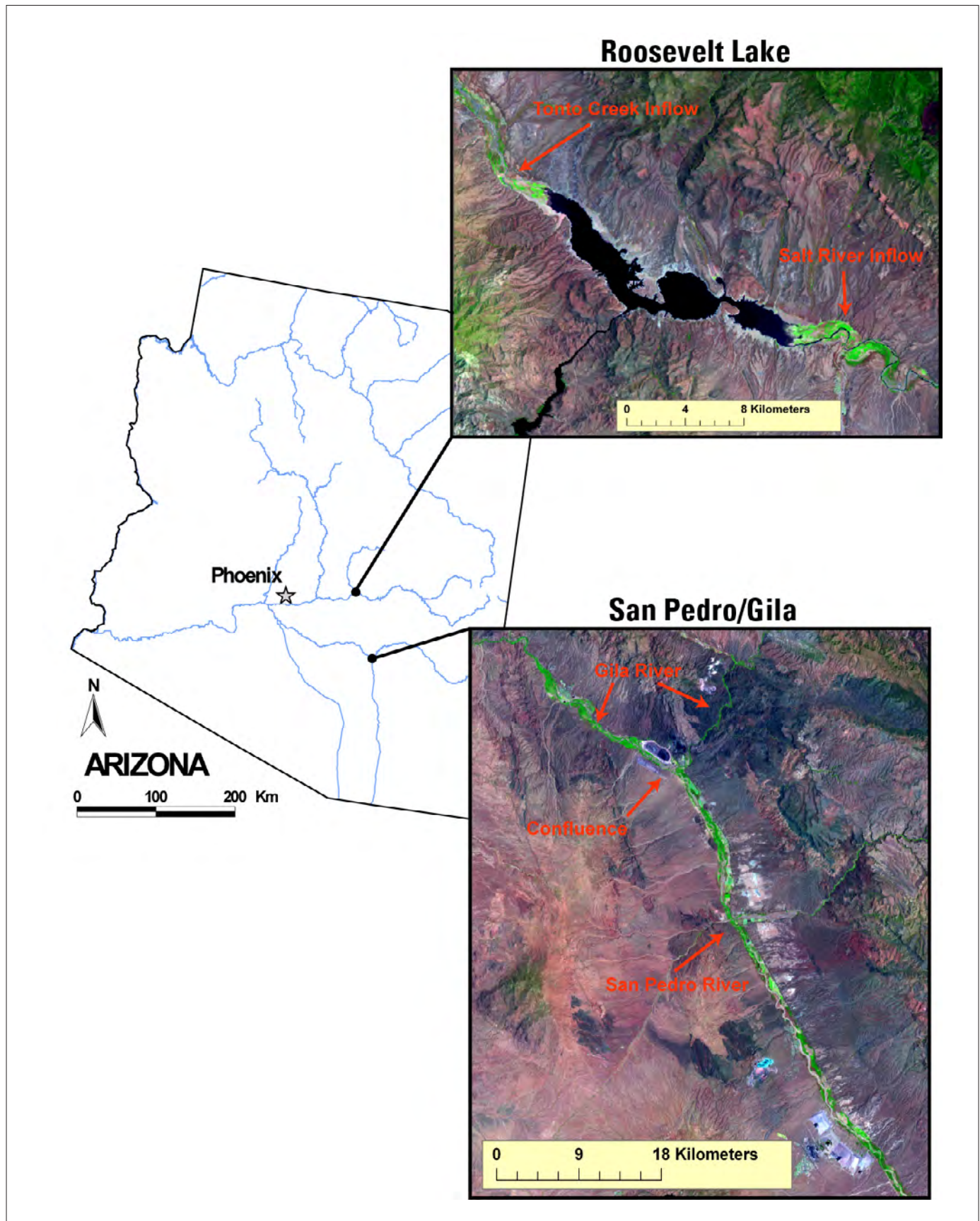


Figure 1. Location of the Roosevelt Lake and San Pedro/Gila study areas in central Arizona.

demographic research in cooperation with AGFD (English et al. 2006). These two sites supported among the largest known Southwestern Willow Flycatcher breeding populations throughout the period of this study (Durst et al. 2005), with mean population sizes of 201 and 239 individuals at Roosevelt Lake and the San Pedro/Gila, respectively. At each site, extensive survey efforts were conducted at least three times in the breeding season to detect territorial flycatchers within the immediate and surrounding areas. In addition, multiple other breeding sites in Arizona and throughout the Southwest (49–444 km away) were periodically visited, which along with cooperative efforts of other researchers allowed detection of dispersing or moving flycatchers (see chapter 4).

The breeding habitat at Roosevelt Lake and the San Pedro/Gila consisted of a heterogeneous mosaic of discrete riparian forest patches of varying ages and vegetation composition, ranging from 0.2 ha to 43 ha in size. At both study sites, we characterized habitat at both the territory and patch level based on vegetation composition as: (1) native ($\geq 90\%$ native vegetation), (2) mixed native (50%–89% native vegetation), (3) mixed exotic (50%–89% exotic vegetation), and (4) exotic ($\geq 90\%$ exotic vegetation). Native habitat was characterized by Goodding's willow (*Salix gooddingii*) and Fremont cottonwood (*Populus fremontii*). Exotic habitat was dominated by tamarisk (saltcedar; *Tamarix* spp.). The understory vegetation consisted of a variety of grasses, forbs, and shrubs (mesquite [*Prosopis* spp.], coyote willow [*S. exigua*], tamarisk, *Baccharis* spp., and cocklebur [*Xanthium strumarium*]). Adjacent and surrounding non-riparian habitats were primarily composed of Sonoran Desert Uplands (Brown 1994), and in some cases agricultural lands.

Roosevelt Lake Study Site

The Roosevelt Lake study site consisted of two sub-sites each concentrated at the confluence of the reservoir and the inflows of the Salt River and Tonto Creek, with breeding documented as far as 12 km upstream on Tonto Creek. The number of riparian patches in which breeding was documented varied over time as a result of colonization or desertion of patches, in many cases driven by fluctuating lake levels. We defined habitat patches as contiguous riparian patches distinct from other patches, with their boundaries estimated manually in ArcView 3.0 (ESRI, Inc) using rectified aerial photographs. Over the 10-year period, we documented breeding occurring in a maximum of 23 patches encompassing approximately 242 ha of riparian habitat. The Tonto Creek inflow sub-site contained as many as seven habitat patches covering a maximum of 49 ha of riparian habitat in which breeding was documented. The Salt River inflow sub-site supported as many as 16 breeding patches covering a maximum of 193 ha. Long-term persistent drought conditions between 1996 and 2005 in the Southwest (McCabe et al. 2004) resulted in reservoir levels dropping to a low of 10% capacity in 2002; the exposed lakebed was colonized by riparian vegetation, which was subsequently colonized by breeding flycatchers (see chapter 6). In 2005,

following unusually high winter precipitation, Roosevelt Lake filled to near capacity, inundating much of the breeding habitat that was occupied in 2004 (see chapter 6).

San Pedro/Gila Study Site

The San Pedro/Gila study site encompassed 101 km of river system, centered at the confluence of the free-flowing San Pedro River and the regulated Gila River, and extending upstream of the San Pedro to San Manuel Crossing and downstream of the Gila River to Kelvin Bridge. As with Roosevelt Lake, the number of patches changed over the 10 years, with as many as 29 habitat patches documented as supporting breeding efforts, comprising approximately 222 ha of riparian forest along this stretch. The San Pedro River sub-site included approximately 77 km of the river, containing 13 habitat patches covering a maximum of 173 ha of riparian forest. The Gila River sub-site supported 16 breeding patches containing as much as 49 ha of riparian forest along a 24-km stretch of the river.

We shared data with researchers at other study sites, effectively creating a broader study area. Other sites included Greer and Alpine in the White Mountains, AZ; Camp Verde, AZ; Gila River near Safford, AZ; Horseshoe Reservoir, AZ; Browns crossing near Alamo Lake, AZ; and several sites along the Colorado River including the Grand Canyon, Lake Mead, and Topock Marsh, AZ; and Mesquite and Mormon Mesa, NV (see Durst et al. 2005).

Banding and Resighting

To provide robust survivorship estimates, our objective was to band as many adults and nestlings as possible over the period of this study. Nestlings and adults were banded at both Roosevelt Lake and the San Pedro/Gila from 1996 to 2005, with the exception that nestling banding at the San Pedro/Gila ceased after 2000. Each nestling was banded at 7–10 days of age (as determined via Paxton and Owen 2002) with a color-anodized, numbered federal bird band; banded nestlings detected and recaptured as adults in subsequent years were given an additional color band to produce a unique color combination to assist in resight tracking (Koronkiewicz et al. 2005). A drop of blood was taken at the time of banding for genetic gender determination (Paxton et al. 2002). Each adult captured was banded with a color-anodized, numbered federal bird band and a second color band (Koronkiewicz et al. 2005) to create a unique color combination for each individual. Adults were primarily target-netted (Sogge et al. 2001, Pollock and Paxton 2006) to allow for efficient, focused capture effort. From 2001 to 2005, we also conducted extensive passive netting operations (see Ralph et al. 1993) aimed at capturing non-territorial flycatchers that were not readily detectable with conventional survey techniques (i.e., tape-playback; Sogge et al. 1997). Overall, the combination of targeted and passive

netting resulted in an average of 74% (range: 68%–88%) of detected flycatchers being banded in a given year. To determine gender of adult flycatchers, we used a combination of physical characteristics (presence of a cloacal protuberance for males or brood patch for females), behavioral cues, and/or genetic sexing methods (Paxton et al. 2002). Adult flycatchers were aged as “known,” if the individual was first banded as either a nestling or a second-year (SY: based on retained rectrices; Pyle 1998), or “unknown” (2 or more calendar years of age).

We tracked banded flycatchers over the 10 years primarily through resighting, supplemented by occasional recaptures. Resighting consisted of using binoculars to determine the unique color band combination on a flycatcher’s legs. This is minimally intrusive method of “recapture,” and the most reliable method for establishing the particular territory a flycatcher belongs to because playback capture techniques can lure adults in from neighboring territories. To ensure high accuracy in the identification of resighted individuals, only multiple high-confidence resights from at least two different observers on different days were used to confirm the identity and territory of individual banded flycatchers. Computer databases were updated and queried daily to prioritize resighting efforts, allowing us to track as many as 393 uniquely color banded individuals in a given year. Field crew sizes of up to 35 personnel (USGS and AGFD combined) allowed for intensive detection and resighting of banded individuals, resulting in nearly all territorial flycatchers detected at the study sites being positively identified multiple times in each year. Recaptures, especially via passive netting, provided additional detection resolution, especially for non-territorial birds.

Statistical Analysis

Estimating Survivorship and Detection Probability

We used Program MARK (White and Burnham 1999) to estimate survivorship (Φ) and detection (p) probabilities. Program MARK uses encounter history files (detections or non-detections per individual per year) to produce maximum likelihood estimates of survivorship. Survivorship is the probability of an individual being alive from one period to the next, and detection probability is the probability of an individual being detected, conditional on being alive and present at the study area. Because some individuals are not detected in a given year, yet are detected in subsequent years, a simple return rate (i.e., the percentage of individuals in year A that are detected in year A+1) underestimates true survival. Thus, survivorship estimates use both the return rate and the detection probability. Permanent emigration cannot be distinguished from mortality, thus reported estimates are often referred to as apparent survivorship (i.e., minimum survivorship). When reporting annual estimates of survivorship, we fixed the detec-

tion probability (p) for the first and last encounter periods (study years) at the overall mean detection probability, because the binomial model underlying the survivorship estimates cannot separate survivorship and detection probability for the first and last periods (White and Burnham 1999); however, we did not fix parameters for the purposes of model selection, and all other detection probabilities were not fixed.

For each question, we evaluated multiple models in Program MARK, with each model consisting of different combinations of explanatory variables (e.g., age, sex, site). To choose between models based on their relative strengths, we used the Akaike Information Criteria (AIC) model selection framework to rank multiple models (Burnham and Anderson 2002), with the best AIC model typically used to conduct our interpretation of the data and to select the parameter estimates for survivorship and detection probability. The AIC model selection framework is rooted in the Principle of Parsimony, where the best model is that which explains as much variation as possible with the least amount of information (the least number of parameters). Thus, AIC weights the contribution of each parameter (i.e., how much variation it can explain) against the cost of adding it. While AIC is a commonly used model selection tool, it cannot differentiate between statistical and biological significance; therefore all of our models were chosen *a priori* to reduce Type I statistical error and model selection results were accepted or rejected based on their apparent biological significance. Because AIC might reject a parameter that is nonetheless biologically important, we reported parameter estimates from weakly supported models in cases where we were interested in exploring a particular facet of flycatcher biology.

Several values listed in the AIC tables help interpret the weight of evidence for selecting one, or multiple, competing models. The AIC (QAIC, AICc) value is used to rank the models, with the lowest value ranked first. The AIC number is the product of the amount of variation unexplained by the variables included (deviance) weighted by the number of parameters (variables; K). Thus, a model that explains much of the variation in the data (low deviance) with just a few variables will have a lower AIC value than an alternative model that explains an equal amount of variation but with more variables (K). Likewise, a model that explains more variation (lower deviance) but with more variables (higher K) compared to another model may have a higher AIC score, and thus be ranked lower. Typically, global (fully parameterized) models explain the most variation but are rarely ranked as the best models because they have the largest number of parameters and therefore higher AIC values. The delta AIC is the difference in that AIC score of a particular model compared to the best AIC model; thus, the delta AIC value for the top model is always zero. Models with delta AIC values ≤ 2.0 are considered to have strong support, given the data and the models considered, while those with delta AIC values > 10.0 are considered to have essentially no support, given the data and the models considered (Burnham and Anderson 2002). The AIC weight is another approach to comparing the relative

strength of multiple models considered. It can be interpreted as the weight of evidence that a specific model is the best of all those considered. AIC values are relative to one another for the particular analysis, but are not comparable to AIC values from other analyses. When appropriate, we corrected for small sample sizes in our AIC model selection (AICc; Burnham and Anderson 2002).

Goodness-of-fit Testing

Goodness-of-fit tests are used to ensure that the survivorship data conforms to the underlying binomial model distribution, tested on the most parameterized (global) models for each distinct dataset. Failure of goodness-of-fit could be caused by violation of assumptions of the Cormack-Jolly-Seber (CJS) model or from the failure of the model to accurately describe the data (Cormack 1964, Jolly 1965, Seber 1965). These assumptions are: (1) survivorship and detection probability are equal for all individuals, within a given group; (2) no bands are lost from the flycatchers; and (3) the time intervals considered are the same for all individuals. In general, evidence of a poor fit is believed to be derived from a violation of the first assumption, which is usually caused by not identifying all the important groups. For example, if males and females in some population had very different survivorship and detection probabilities, but an analysis of survivorship did not group individuals by sex, then the assumptions would be violated and the data may fit the underlying model poorly. When this occurs in a binomial model, the data are said to be overdispersed. Overdispersion does not affect the maximum likelihood estimates, just the estimate of error, which can be corrected. Depending on the goodness-of-fit measures available for different model structures, we used Program RELEASE (Test 2 + Test 3) (Burnham et al. 1987), bootstrap goodness-of-fit, or median \hat{c} values (where $\hat{c} = 1$ equates to perfect model fit). In cases of deviation from goodness-of-fit, we attempted to identify the source of deviation or adjusted median \hat{c} values (which measure overdispersion) to obtain adjusted QAIC values for model selection and estimates.

Survivorship Models

We ran separate analyses in Program MARK for different datasets, questions, and/or modeling strategies. The specifics of each of these analyses, including factors in the models, along with results of goodness-of-fit testing, are detailed below. Each dataset has a global (fully parameterized) model, and a number of nested models which present different subsets of the variables in the global model. To describe the combination of variables in different models succinctly, we used the format proposed by Lebreton et al. (1992). This model description convention includes: “*” to indicate interactions among two variables, “+” to separate variables and treat them as main effects, and “.” to indicate the value for the parameter (e.g., Φ , p) is the average value (i.e., not considering any factors).

Juvenile Survivorship

Juvenile survivorship is the probability that a banded nestling will survive from the time it fledges to the following breeding season in its second calendar year of life. Although approximately 40% of returning juveniles are not detected in their second calendar year of life as SY adults, but rather as TY or older adults, it is only this first year that is calculated as juvenile survivorship. To evaluate sources of variation in juvenile survivorship, we assessed the contribution of the following factors:

- YEAR: annual variation of between-year juvenile survivorship, 1996–2005;
- HABITAT: plant composition of the natal territory (native, exotic, mixed native, or mixed exotic) derived from AGFD nest measurements of habitat; and
- FDATE: The exact fledge date was not always known, so we used banding date as a surrogate to fledge date, which is 2–5 days before fledging is estimated to occur. Nestlings from nests that failed prior to fledging were excluded. The variable FDATE was used as a continuous covariate in Program MARK.

Our global (fully parameterized) model for juvenile survivorship and detection probability was $\Phi(\text{habitat} \cdot \text{year} + \text{Fdate}) p(\text{habitat} \cdot \text{year} + \text{Fdate})$. We did not evaluate study site differences, as no nestlings were banded at San Pedro/Gila after 2000, and few were banded before, and thus we could not separate site differences from year differences. The model had a median $\hat{c} = 2.13$, indicating moderate overdispersion, and we used a QAIC with the adjusted \hat{c} value for model selection and variance estimates.

Adult Survivorship

Adult survivorship is the probability of annual survivorship, breeding season to breeding season, beginning with flycatchers in their first year as an adult (i.e., second-year adults or after-hatch-year adults). As with juveniles, we predicted that yearly differences would contribute to survivorship rates over the 10 years of this study. We also believed that the following factors could contribute to variation in adult survivorship:

- STUDY SITE: differences between the two study sites, Roosevelt Lake and San Pedro/Gila;
- SEX: differences between males and females.

Thus the global model for adult survivorship and detection probability was $\Phi(\text{sex} \cdot \text{year} + \text{site} \cdot \text{year}) p(\text{sex} \cdot \text{year} + \text{site} \cdot \text{year})$; other factors, such as habitat, are more complex for adults and are evaluated separately, below. The goodness-of-fit tests for the global model of adult survivorship and detection probability revealed mixed results. Program RELEASE indicated lack of fit with the global model ($\chi^2 = 149.4$, $df = 86$, $p < 0.01$), but we found no systematic bias in the Program RELEASE subtests (Program RELEASE tests: Test3.SR, Test3.Sm, or Test2C), indicating that the CJS model

was adequate but the lack of fit was due to overdispersion of the data. However, median $\hat{c} = 1.14$, suggesting negligible overdispersion, and on the weight of \hat{c} evidence we accepted the model as adequate, did not adjust the \hat{c} value, and used a non-corrected AIC for model selection.

Breeding Habitat and Adult Survivorship

Adults may occupy multiple riparian habitat types on the breeding grounds over the course of their lifetimes. To evaluate potential effects of breeding habitat on adult survivorship, we needed to account for this adult movement into different habitats over multiple years tracked. To do this, we used a multistate model in Program MARK to model adult flycatcher survivorship and detection probabilities among native, mixed native, mixed exotic, and exotic habitats, as characterized at the patch level. The multistate models not only provide estimates of survivorship (Φ) and detection (p) probabilities based on the habitat occupied, but also account for the probability of moving from one habitat to another, or transitions (Ψ). We used a multinomial logit (Mlogit) link to constrain the model to ensure that the transition probabilities among the four different habitats all summed to 1. In other words, since there are only four habitat types in which we detected banded flycatchers at our study sites (native, mixed native, mixed exotic, exotic), the sum of probabilities of returning to the same habitat as occupied in the previous year (e.g., exotic to exotic), or moving to another habitat (e.g., native to mixed exotic) must equal 100%. The survivorship estimate is the probability that an adult detected in a particular habitat in year “ t ” survives to year “ $t+1$ ” regardless of which habitat it returns to, and the detection probability is the probability that it is detected in year “ t ” at the habitat type specified.

Breeding Status and Adult Survivorship

We also used a multistate model to estimate the survivorship and detection probabilities among individuals classified into four breeding statuses per season: (1) successful breeders, consisting of individuals that fledged at least one young; (2) unsuccessful breeders, consisting of individuals that attempted to breed, but did not fledge any young; (3) territorial but non-nesting, consisting of individuals that were territorial but did not attempt to breed; and (4) non-territorial and non-nesting, consisting of individuals that were thought to be floaters (see chapter 7). Flycatchers shift between these breeding statuses over their lives, and the multistate model accounts for the probability of transitions (Ψ) among these different breeding statuses while providing an estimate for adult survivorship (Φ) and detection probability (p) for each group. We used the Mlogit link to constrain the sum of transition probabilities for all breeding status over a single time period to one.

Age-class and Adult Survivorship

To evaluate changes in survivorship by age, we used a subset of our data to look at known-age adults only ($n = 266$;

25% of banded adults). These birds were either initially banded as nestlings or captured as SY adults. Because of small sample sizes, we pooled estimates of age-specific survivorship for sixth-year and older birds. While bootstrap results suggested a good fit of the data to the model, a $\hat{c} = 1.4$ indicated slight overdispersion and we used the median \hat{c} value to rank models by QAIC.

Adult Survivorship Throughout the Annual Cycle

The annual cycle of migratory birds includes breeding, wintering, and two migration periods (spring and fall), and each may have a different rate of survivorship. True partitioning of survivorship across these annual periods would require tracking the same individuals continuously throughout the year, something nearly impossible to do. Instead, we partitioned survivorship among the four periods using the methods of Sillett and Holmes (2002) by combining our breeding-ground survivorship estimates (this study) with similar data from a wintering study in Costa Rica (Koronkiewicz et al. 2006), with the understanding that the strength of the comparison is dependent on the strength of the connectivity between the two populations. We believe there is at least moderate connectivity between these populations, because (1) Southwestern Willow Flycatchers appear to winter primarily, perhaps exclusively, in Mexico and Central America (Unitt 1997); and (2) two individuals detected at the Costa Rica study areas were initially banded in the Southwest, one of them at Roosevelt Lake and the other at Ash Meadows NWR, Nevada (Koronkiewicz and Sogge 2001). While we believe that more than one subspecies wintered at the Costa Rica sites (Koronkiewicz et al. 2006), the evidence for regional connectivity is sufficient to combine the two studies.

We calculated within-season survivorship (i.e., estimates of survivorship during the breeding and wintering stationary periods) separately for the two studies. We estimated within-season survivorship on the breeding grounds by grouping all resight and recapture encounters of banded flycatchers throughout the breeding season into two equal periods: May 1 to June 15 and June 16 to early-August. The average interval between these periods, 1 month, was used to estimate the average survivorship in a 1-month period. We estimated monthly winter survivorship from the 3-month interval between the mid-winter (December/January) and late-winter (March/April) research periods. The within-season monthly survival estimates obtained from Program MARK were used to obtain seasonal estimates for the 3-month average breeding period and the 6-month average wintering period by raising the monthly estimates to the third and sixth power, respectively.

Between-season estimates for the breeding and wintering populations are needed to estimate survivorship during the migratory period (Sillett and Holmes 2002). We define between-season survivorship for a population at any one period as the product of the survivorship during the other two periods. For example, between-season survivorship for the

breeding population is the product of survivorship during the migration and wintering periods. Average between-season survivorship estimates for each period are derived by dividing their average annual survivorship by their respective average within-season survivorship; e.g., for breeding grounds:

$$\Phi_{\text{between-season (non-breeding)}} = \frac{\Phi_{\text{annual (breeding)}}}{\Phi_{\text{within-season (breeding)}}}.$$

To estimate survivorship during the migratory periods, we combined the mean survivorship estimates from both the breeding and wintering studies (Sillett and Holmes 2002). Separately, between-season survivorship estimates from both stationary periods were divided by the within-season survivorship of the opposite stationary period to estimate survivorship during the migratory period; e.g., for breeding grounds:

$$\Phi_{\text{spring/fall migration survivorship}} = \frac{\Phi_{\text{between-season (non-breeding)}}}{\Phi_{\text{within-season (wintering)}}}.$$

The estimates for survivorship during migration are for both spring and fall migration combined, which are estimated to be 3-months long on average. To estimate survivorship separately for the spring and fall migratory periods we assumed equal survivorship and took the square-root of the migratory period estimate, and the cubed-root of the migratory period survivorship estimate to obtain monthly migration survivorship. We used a reduced portion of the breeding season data, corresponding to the time period of the Costa Rica study (1999–2002) to estimate survival for this procedure. Percentages of mortality were calculated by applying the different survival rates to a hypothetical group of individuals and calculating the proportion that died in each period of interest.

Adult Survivorship by Spatial Scale

We evaluated detection data at multiple spatial scales to better understand how the scale of a study influences survivorship estimates through its effect on the ability to distinguish between mortality and undetected permanent emigration. The spatial scales, described more fully in the Study Site section, were:

- PATCH: a distinct area of riparian vegetation, spatially separated from other nearby riparian patches by non-riparian vegetation;
- SUB-SITE: comprised of all patches found within each distinct drainage (i.e., Tonto Creek inflow, Salt River inflow, Gila River, and San Pedro River);

- SITE: a combination of the two sub-sites (i.e., both of Roosevelt Lake sub-sites and the entire San Pedro/Gila Rivers confluence area); and
- STUDY AREA: comprising the Roosevelt Lake and San Pedro/Gila study sites, plus breeding sites throughout the Southwest from where we or collaborative researchers collected resight and recapture information from.

We ran separate analyses for each spatial scale to determine average survivorship. At the patch scale, individual flycatchers were coded as alive and returning as long as they returned to the patch in which they were originally banded. If the flycatcher was not subsequently detected within the same patch, the model considered it a non-survivor (either permanently emigrated or dead). In a similar manner, survivorship estimates were calculated at increasingly larger spatial scales for the sub-site, site, and study area scales. Average apparent survivorship estimates for each of these spatial scales were plotted to evaluate changes by scale. We predicted that if the survivorship estimates increased and quickly converged as we moved from the smallest to the larger scales, then the survivorship estimates based on a geographically large study area, such as ours, would not be substantially biased by undetected emigration even though there is certain to be some level of missed emigration. If the estimates did not converge with increasing scale, but continued to increase with each larger spatial scale considered, we would conclude that permanent and undetected emigration might have a major influence on our survivorship estimates, biasing them downward. At the patch, sub-site, and site level, resight effort was similar. Beyond these scales, the likelihood of detecting an emigrating flycatcher decreases as they could disperse to an unknown or unstudied site, or to a site in which resight efforts are not as thorough; either scenario would have the same effect of biasing downward the true survival estimate due to undetected emigrants. In each case, we averaged across years as we were only interested in the overall effect of different spatial scales on survivorship and detection probabilities.

Influence of Global Climate Patterns on Survivorship

Recent studies have indicated that global climate patterns may impact demographic characteristics of migratory songbirds (Sillett et al. 2000, Nott et al. 2002). We suspected that changes in the Southern Oscillation/El Niño weather pattern (as measured by the Southern Oscillation Index, SOI) might impact Southwestern Willow Flycatcher survivorship because of the strong climatic effects of El Niño at both the breeding grounds in the southwestern United States and on wintering grounds in Central America (Kiladis and Diaz 1989, Ropelewski and Halbert 1987, Ropelewski and Halbert 1989, Ropelewski and Halbert 1996). We calculated a single SOI value per year as the average monthly SOI value between arrival on the breeding grounds (May) in the previous year

to the end of spring migration in the current year (April). We used a Pearson's correlation of both mean juvenile and adult survivorship to these yearly mean SOI values to examine relationships between survivorship and this measure of global climate.

Flycatcher Mean Life Expectancy

Mean life expectancy (MLE) uses both average adult and juvenile survivorship values to obtain an average life expectancy estimate (Brownie et al. 1986), where Φ_a and Φ_j refer to adult and juvenile survivorship, respectively:

$$MLE = \{1 / -\ln(\Phi_j) + \Phi_a / (-\ln(\Phi_a) + \Phi_j / (-\ln(\Phi_j))\}$$

In addition, we calculated the observed distribution of the maximum ages of banded individuals, based on the frequency of the ages of known-age and minimum-age birds when last detected.

Results

Juvenile Survivorship

From 1996 to 2004, we banded 498 nestlings from 223 nests at the Roosevelt Lake and San Pedro/Gila study sites. Of these, we recaptured 122 from 1997 to 2005, resulting in a juvenile return rate of 24% (table 1). Most (69%) were first detected as second-year adults (SY: the year following their natal year), 26% as third-year adults (TY: in the second year following their natal year), and the remaining 5% at 3–4 years after they were banded as nestlings. While 59% of returning nestlings exhibited territorial behavior in the first year they were detected, 41% did not do so and were primarily detected via passive netting operations that were conducted at Roosevelt Lake from 2001 to 2005.

Overall, juvenile survivorship estimates averaged 34% (range = 13%–57%; table 1). We evaluated the effects of natal habitat, fledge date, and year on juvenile survivorship, and found the strongest support for the model with fledge date only, and weak support for the model that also included effects of year (table 2). Survivorship estimates were virtually identical (26%–27%) for native, mixed native, and exotic habitats, but higher (42%) for mixed exotic habitat; however, widely overlapping confidence intervals and poor support from model selection suggests that any habitat-based differences in the estimated values are not important for understanding juvenile survival. Fledge date, however, had a strong effect on survivorship. For each day progressively further into the breeding season (mid-June to mid-August) that a nestling was banded, and thus fledged, its odds of survivorship decreased by 2% (beta = -0.01998). Thus, the odds that a nestling fledged

around July 15 would survive and be detected the following year were only 55% that of a nestling fledging around June 15. Overall, first-year survivorship declined from an early season high of 44% to a low of 19% by the end of the season (fig. 2). This relationship was linear, indicating the effect was constant throughout the season.

Adult Survivorship

We tracked 1,080 adult Southwestern Willow Flycatchers that were either newly captured as adults, or recaptured as returning nestlings and subsequently tracked as adults. From 1996 to 2005, the overall return rate for adult flycatchers was 55% (range = 43%–61%; table 3). Evaluating the influence of year, sex, and site on survivorship suggested that only year affected survivorship and detection probabilities in the most parsimonious model (table 4), producing an annual survivorship estimate of 64% (range = 53%–73%; table 3). Consistent with model selection results, average point estimates of survivorship between the sites and sexes were identical to one another and to the overall mean of 64%.

Influence of Global Climate Patterns on Survivorship

We suspected that global climate patterns, especially the El Niño Southern Oscillation, could explain some of the variation in adult annual survivorship. Over the period of our study, the Southern Oscillation Index varied substantially (fig. 3); however, we found no correlation between yearly mean SOI values and juvenile or adult survivorship (juveniles: $r = 0.3$, $df = 1$, $p = 0.43$; adult: $r = 0.2$, $df = 1$, $p = 0.61$).

Breeding Habitat and Adult Survivorship

Because adults may occupy different habitats in different years over the course of their lives, we used a multistate model to test for a relationship between the habitat an individual occupies during the breeding season and their subsequent survival probability. The best AIC model indicated that habitat (interacting with year) did appear to influence survivorship, detection, and transition probabilities (table 5). However, models including the effects of habitat but excluding a year interaction fared poorly (table 5), suggesting weak effects of habitat alone. Furthermore, the differences in survivorship by habitat were slight, with the largest differences found in detection and transition probabilities (table 6).

Breeding Status and Adult Survivorship

A multistate model was used to examine the relationship between a flycatcher's breeding status and the probability of its survival and detection the following year. The best model suggested that breeding status (interacting with year) influ-

Table 1. Apparent annual survivorship of juvenile Southwestern Willow Flycatchers in Arizona, 1996–2005. N is the number of nestlings banded in the first year, and return rate is the percentage returning in a subsequent year. Survivorship estimates were calculated using maximum likelihood estimates in Program MARK. Survivorship probabilities are from the model $\Phi(\text{year}+\text{Fdate})p(\text{year}+\text{Fdate})$.

Year	n	Return rate (%)	Apparent survivorship (%)	95% confidence interval (%)	Detection probability (%)	95% confidence interval (%)
1996–97	4	25	38	4–89	51*	N/A*
1997–98	21	10	13	3–43	35	3–90
1998–99	24	21	21	8–42	100	0–100
1999–2000	62	16	26	14–44	35	13–65
2000–01	71	27	31	20–45	85	55–96
2001–02	107	20	41	28–54	41	24–60
2002–03	2	50	57	7–96	100	100–100
2003–04	121	28	41	27–56	37	21–56
2004–05	86	16	32	19–50	51*	N/A*
Average	498	24	34	27–40	51	40–62

* Detection probability fixed at 10-year average (0.510) to allow for estimation of first and last year survivorship

Table 2. Program MARK QAIC model selection results for Southwestern Willow Flycatcher juvenile survivorship (Φ) and detection probability (p), considering year, natal habitat type, and nestling banding date as a proxy for nestling fledging date (Fdate). The top five models are presented along with the global model. QAIC model selection was used to account for overdispersion ($\hat{c} = 2.13$).

Model	QAICc	Delta QAICc	QAICc weights	K	QDeviance
$\Phi(\text{Fdate})p(\text{Fdate})$	954.16	0.00	0.84011	4	946.12
$\Phi(.)p(.)$	958.78	4.63	0.08311	4	950.75
$\Phi(\text{year}+\text{Fdate})p(\text{year}+\text{Fdate})$	959.91	5.75	0.04741	18	923.37
$\Phi(\text{year})p(\text{year})$	960.86	6.71	0.02937	18	924.33
$\Phi(\text{Fdate})p(.)$	1051.27	97.11	0.0000	3	1045.25
$\Phi(\text{habitat}*\text{year}+\text{Fdate})p(\text{habitat}*\text{year}+\text{Fdate})$	1148.83	194.67	0.0000	108	912.89

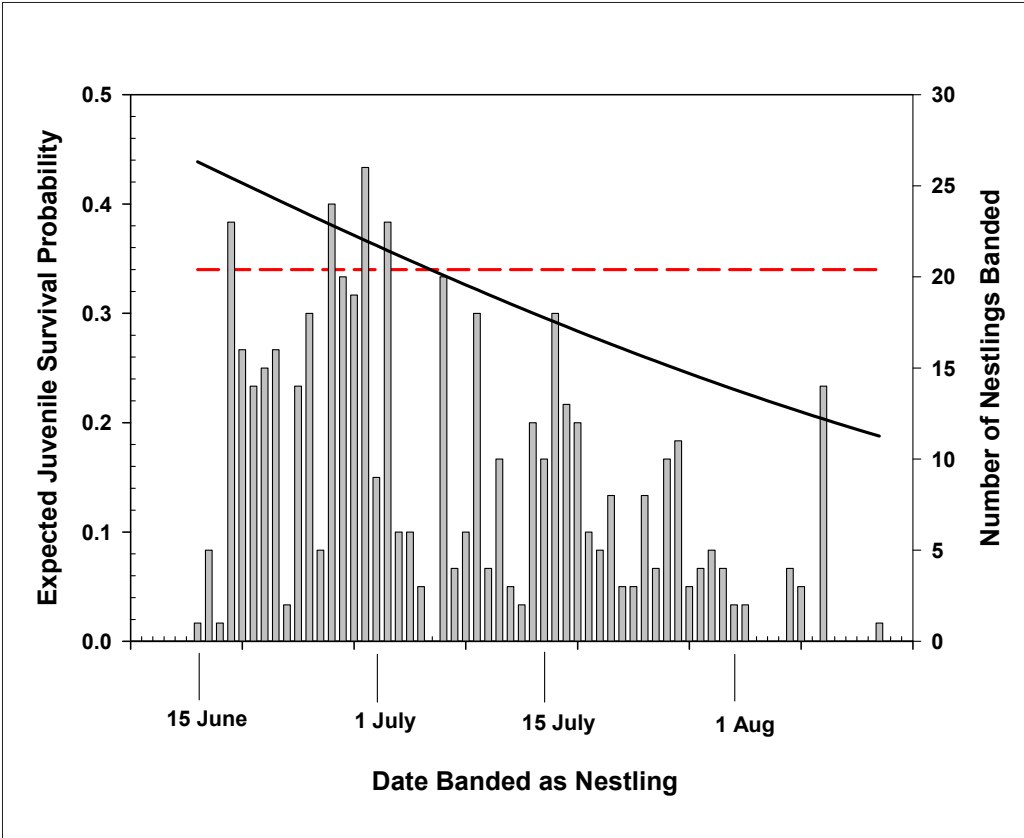


Figure 2. Estimated juvenile survivorship (solid line) of Southwestern Willow Flycatchers declined as fledging date progressed through the breeding season. The X-axis date is banding date, a proxy for fledge date (generally 2 to 5 days prior to fledging). The average date nestlings were banded was July 7, and mean survival probability was 34% (dashed line). The number of nestlings banded (y-axis, vertical bars) by date are shown for all nestlings, 1996–2004.

Table 3. Apparent annual survivorship of adult Southwestern Willow Flycatchers in Arizona, 1996–2005. N is the number of adults banded in a given year year, and return rate is the percentage returning in a subsequent year. Survivorship estimates and detection probabilities were calculated using maximum likelihood estimates in Program MARK. The survivorship estimates are based on the best AIC model for adult survivorship, $\Phi(\text{year})p(\text{year})$. Note, sample sizes from each year include individuals detected in multiple years, and thus do not sum to the overall sample size of the study.

Year	n	Return rate (%)	Survivorship estimate (%)	95% Confidence interval (%)	Detection probability (%)	95% Confidence interval (%)
1996–97	87	51	53	41–65	78*	N/A*
1997–98	120	52	53	45–62	90	78–96
1998–99	137	56	63	54–71	84	72–91
1999–2000	197	55	56	50–63	93	86–97
2000–01	241	61	66	59–72	84	76–89
2001–02	264	59	73	66–80	62	54–69
2002–03	282	57	67	61–73	77	70–83
2003–04	301	59	68	61–74	78	70–84
2004–05	393	43	57	51–63	78*	N/A*
Average	1080	55	64	62–66	78	75–80

* Detection probability fixed at 10-year average (0.775) to allow for first- and last-year estimations of survivorship

Table 4. AIC model selection results for adult Southwestern Willow Flycatcher survivorship by sex, study site, and year, 1996–2005, calculated in Program MARK. The top five models that we analyzed are presented including the global model.

Model	AIC	Delta AIC	AIC weight	K	Deviance
$\Phi(\text{year})p(\text{year})$	7083.56	0.00	1.00000	17	741.09
$\Phi(\text{site}*\text{year})p(\text{year})$	7118.99	39.08	0.00000	28	754.07
$\Phi(\text{sex}*\text{year}+\text{site}*\text{year})p(\text{sex}*\text{year}+\text{site}*\text{year})$	7122.21	42.30	0.00000	68	675.32
$\Phi(\text{sex}+\text{site})p(\text{year})$	7124.10	44.19	0.00000	13	789.50
$\Phi(\text{sex}*\text{year})p(\text{year})$	7125.84	45.92	0.00000	28	760.92

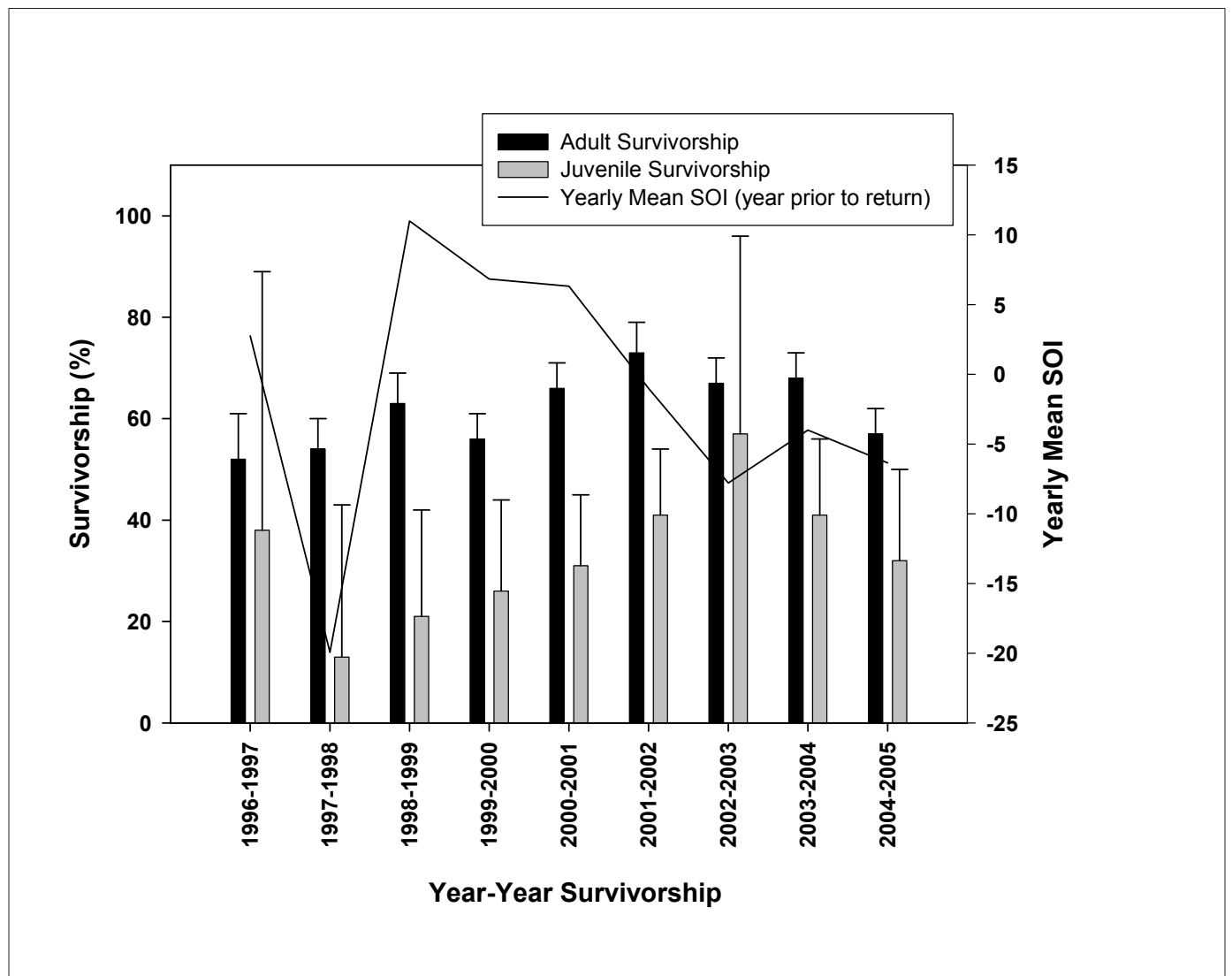


Figure 3. Relationship between adult and juvenile Southwestern Willow Flycatcher survivorship (vertical bars) and the yearly mean Southern Oscillation Index (SOI) values (solid line), 1996–2005. SOI values overlaid for a particular year refer to the SOI values averaged for the previous 12 months prior to the return date. Error bars represent the upper 95% confidence interval for each bar.

Table 5. AIC model selection results for the multistate model of Southwestern Willow Flycatcher breeding habitat characterized at the patch-level. Habitat was characterized at the patch-level as native, mixed native, mixed exotic, and exotic. The top five models are presented.

Model	AICc	Delta AICc	AICc weight	K	Deviance
$\Phi(\text{habitat} \times \text{year})p(\text{habitat} \times \text{year})\Psi(\text{habitat} \times \text{year})$	5434.81	0.00	1.00000	122	1348.74
$\Phi(.)p(\text{habitat})\Psi(\text{habitat})$	5523.18	88.37	0.00000	17	1662.73
$\Phi(\text{habitat})p(\text{habitat})\Psi(\text{habitat})$	5528.90	94.10	0.00000	20	1662.34
$\Phi(.)p(.)\Psi(\text{habitat})$	5535.47	100.66	0.00000	14	1681.11
$\Phi(\text{habitat})p(.)\Psi(\text{habitat})$	5539.84	105.04	0.00000	17	1679.39

Table 6. Survival, detection, and transition probabilities among different types of breeding habitats for adult Southwestern Willow Flycatchers, 1996–2005. Fidelity represents flycatchers that returned to the same habitat type between years, while emigration and immigration represent between-year movements among different habitat types. Percent fidelity and emigration sum to 1.0. Values shown are averaged over all years, although yearly variation was influential on these probabilities.

Habitat type	Survival (%)	Survivorship 95% confidence interval (%)	Detection (%)	Fidelity (%)	Emigrate (%)	Immigrate (%)
Native	67	58–75	60	88	12	11
Mixed native	64	58–71	60	52	48	15
Mixed exotic	64	60–67	83	74	26	48
Exotic	64	60–68	83	73	27	39

ences survivorship and detection probabilities, but only breeding status (no interactions with year) influences the transition probabilities (table 7). Averaging across years, successful breeders had higher survivorship (73%) than birds in the other three status groups (59%–60%; fig. 4). While the average detection probability for all adults combined was 78% (table 3), the detection probabilities for the three territorial groups were nearly 100%, while the probability of detection for birds in the non-territorial group was only 13% (fig. 4). This suggests that within a given year, a territorial flycatcher at our main study areas was nearly always detected. The transition probabilities among the groups indicate that flycatchers frequently move between these different states (fig. 4). For example, 45% of successful breeders bred successfully again in the following year, but 25% became non-territorial. Similarly, 44% of non-territorial flycatchers remained so in the following year, but 35% of those returning became successful breeders.

Mean Life Expectancy and Differential Adult Survivorship

We calculated the mean life expectancy of flycatchers by combining the average survivorship estimates for juveniles (34%) and adults (64%) to yield a mean life expectancy of 1.9 years following fledging. The distribution of observed maximum ages (the age of a flycatcher in the last year it was detected) of birds in our populations was consistent with this estimate (table 8, fig. 5), as most individuals were detected for only 1–2 adult years, but some individuals lived much longer. The pattern for minimum-age adults was similar to that of known age birds (fig. 5). There was no significant difference in the frequency of maximum ages for known-age and minimum-age flycatchers ($\chi^2 = 3.1$, $df = 7$, $p = 0.88$), suggesting that a large component of unknown age birds assigned to the AHY (after-hatch-year) category were in fact SY individuals.

Table 7. AIC model selection results for the multistate model of adult Southwestern Willow Flycatcher breeding status survivorship and transitions. Breeding status groups are successful breeder, unsuccessful breeder, territorial but non-nesting, and non-territorial. The top five models are presented along with the global model.

Model	AIC	Delta AIC	AIC Weight	K	Deviance
$\Phi(\text{status} \times \text{year})p(\text{status} \times \text{year})\Psi(\text{status})$	5850.74	0.00	0.99975	69	1663.02
$\Phi(\text{status} \times \text{year})p(\text{status} \times \text{year})\Psi(\text{status} \times \text{year})$	5867.35	16.61	0.00025	135	1533.62
$\Phi(\text{status} \times \text{year})p(\text{status})\Psi(\text{status})$	6036.21	185.47	0.00000	47	1895.06
$\Phi(\text{status})p(\text{status})\Psi(\text{status})$	6045.91	195.17	0.00000	20	1960.57
$\Phi(\text{status})p(.)\Psi(\text{status})$	6059.82	209.08	0.00000	17	1980.59
$\Phi(.)p(\text{status})\Psi(\text{status})$	6064.25	213.51	0.00000	17	1985.01

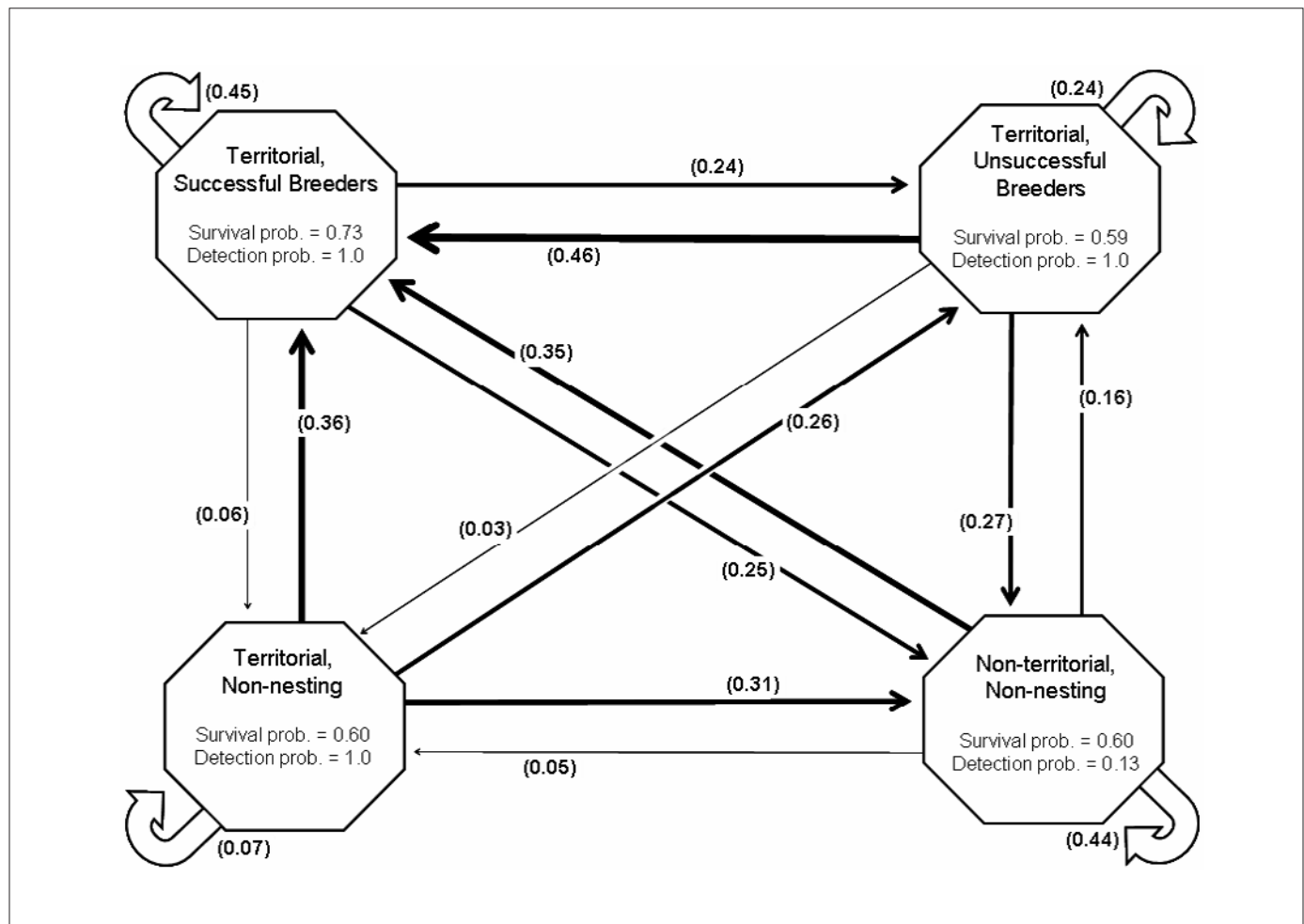


Figure 4. Adult Southwestern Willow Flycatcher survivorship, detection probability, and transition rates as a function of breeding status, 1996–2005. Breeding status categories were successful breeders, unsuccessful breeders, territorial but non-nesting, and non-territorial. Each group is graphically represented by an appropriately labeled box, with its associated survival and detection probabilities. Directional lines between octagons refer to transition probabilities among the four breeding statuses; line width is proportional to the transition probability. Curved arrows (returning to each octagon) refer to probability of remaining in that breeding status between years.

Table 8. Numbers and proportions of the age when adult Southwestern Willow Flycatchers were last detected over the course of the study, and are presumed to be the age that they died. Ages (in calendar years) are SY=second year, TY=third year, 4Y=fourth year, 5Y=fifth year, 6Y=sixth year, 7Y=seventh year, 8Y=eighth year, 9Y=ninth year, AHY≥ second year, ASY≥ third year, ATY≥ fourth year, A4Y≥ fifth year, A5Y≥ sixth year, A6Y≥ seventh year, A7Y≥ eighth year, and A8Y≥ ninth year.

Known age	n	Proportion	Minimum age	n	Proportion
SY	165	0.52	AHY	463	0.50
TY	79	0.25	ASY	199	0.21
4Y	28	0.09	ATY	119	0.13
5Y	22	0.07	A4Y	61	0.07
6Y	13	0.04	A5Y	43	0.05
7Y	8	0.03	A6Y	22	0.02
8Y	1	<0.01	A7Y	13	0.01
9Y	1	<0.01	A8Y	12	0.01



Figure 5. Distributions of the age when adult Southwestern Willow Flycatchers were last detected (maximum age) over the course of the study, and are presumed to be the age that they died. Ages (in calendar years) are SY=second year, TY=third year, 4Y=fourth year, 5Y=fifth year, 6Y=sixth year, 7Y=seventh year, 8Y=eighth year, 9Y=ninth year, AHY≥ second year, ASY≥ third year, ATY≥ fourth year, A4Y≥ fifth year, A5Y≥ sixth year, A6Y≥ seventh year, A7Y≥ eighth year, and A8Y≥ ninth year.

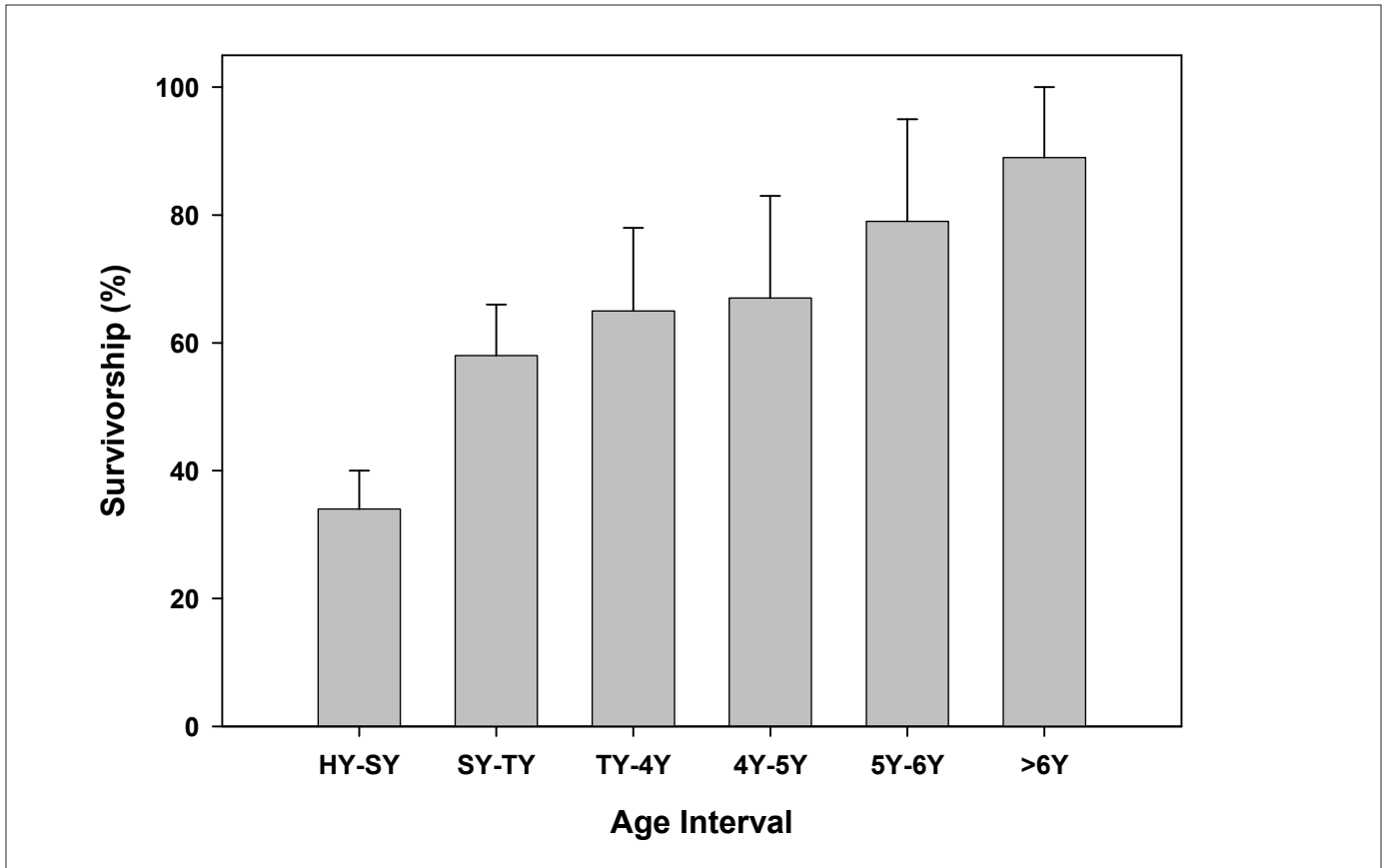


Figure 6. Apparent survival probability of Southwestern Willow Flycatchers as a function of age. The X-axis represents the age interval from one year to the next, with some individuals tracked over multiple age intervals as they survived successive years. The last age interval (>6Y) represents all the age intervals of known age birds older than 6Y (6Y-9Y). The Y-axis represents the percent survivorship estimate for each age class. Error bars represent the upper 95% C.I. Estimates for HY-SY survivorship are based on $\Phi(\text{age}+\text{Fdate})p(\text{age}+\text{Fdate})$ from table 3 and survivorship estimates for all older age classes are from the $\Phi(\text{age})p(.)$ model from table 9.

Table 9. QAIC model selection results for effects of adult age on Southwestern Willow Flycatcher survivorship probabilities, using Program MARK. We used QAIC to correct for slight overdispersion ($\hat{c} = 1.401$). The table displays all the models we analyzed for survivorship by age.

Model	QAIC	Delta QAIC	QAIC Weight	K	QDeviance
$\Phi(\text{year})p(\text{year})$	555.56	0.00	0.66696	14	62.66
$\Phi(\text{age})p(.)$	557.22	1.67	0.28938	6	81.13
$\Phi(\text{age})p(\text{age})$	560.96	5.40	0.04466	10	76.54
$\Phi(\text{age}+\text{year})p(\text{age}+\text{year})$	625.09	69.53	0.00000	49	50.49
$\Phi(\text{age}*\text{year})p(\text{age}*\text{year})$	626.72	71.17	0.00000	50	49.58

However, survivorship of adults was not constant; it increased in older individuals (fig. 6). Based on known age birds (n = 266), we found moderate support for an effect of age on adult survivorship (table 9). Thus, while most flycatchers live for just 1–2 years as adults, those that live beyond the mean life expectancy experience increasingly lower annual mortality probabilities, though occurring in decreasing numbers (fig. 6).

Adult Survivorship Throughout the Annual Cycle

Breeding Season Survivorship

Within-breeding season survivorship was estimated at 100% for most years, with an average breeding season (May to August) survivorship of 97% (95% C.I.: 88%–99%; table 10). Therefore, given the mean annual adult survivorship estimate of 64%, most (92%) adult flycatcher mortality must occur outside of the breeding grounds.

Non-breeding Season Survivorship

Within-season winter survivorship averaged 88% (95% C.I.: 77%–94%) during the 6-month wintering period from 1999 to 2002 (table 10). While the average monthly estimate for winter season survival was 98%, approximately the same as the monthly survival on the breeding grounds (99%), the longer time period spent on the wintering grounds (twice the average time period) resulted in an overall 10% lower seasonal survivorship estimate on the wintering grounds. The average annual survivorship of the Costa Rican wintering flycatchers was 65% (95% C.I.: 59%–70%; Koronkiewicz et al. 2006), nearly identical to our breeding ground annual survivorship estimate of 64% (95% C.I.: 62%–66%). Thus, much of the flycatcher’s annual mortality did not appear to occur during the stationary periods (winter and breeding grounds), and thus probably occurred during migration.

We estimated survival over the migratory period using the within-season survival estimates from the breeding and wintering grounds, and the opposite season’s annual survival

Table 10. Willow Flycatcher within-season monthly and seasonal estimates for survivorship and detection probabilities for breeding grounds (central Arizona, 1997–2005), and wintering grounds (Costa Rica, 1999–2003). Seasonal estimates were calculated based on an average of 3 months on the breeding grounds and 6 months on the wintering grounds. (* Detection probability fixed at 10–year average (0.775) to allow for estimation of survivorship in last year.)

Source	Time period	Monthly estimates		Seasonal estimates			
		Survivorship estimate (%)	95% Confidence interval	Survivorship estimate (%)	95% Confidence interval	Detection probability (%)	95% Confidence interval
Breeding Grounds	1997	100	100–100	100	100–100	76	69–81
	1998	97	89–99	91	70–97	92	86–96
	1999	100	96–100	100	88–100	86	80–90
	2000	99	85–100	97	61–100	89	85–92
	2001	97	91–99	91	75–97	84	79–88
	2002	100	100–100	100	100–100	60	56–65
	2003	100	100–100	100	100–100	79	76–82
	2004	100	100–100	100	100–100	74	71–78
	2005	100	100–100	100	100–100	78*	N/A*
Winter	1999/2000	96	93–98	81	65–90	100	100–100
	2000/2001	100	98–100	100	94–100	82	68–97
	2001/2002	98	93–100	89	63–97	91	78–96
Breeding Grounds Average		99	96–100	97	89–99	78	77–80
Wintering Grounds Average		98	95–99	88	77–94	97	92–99

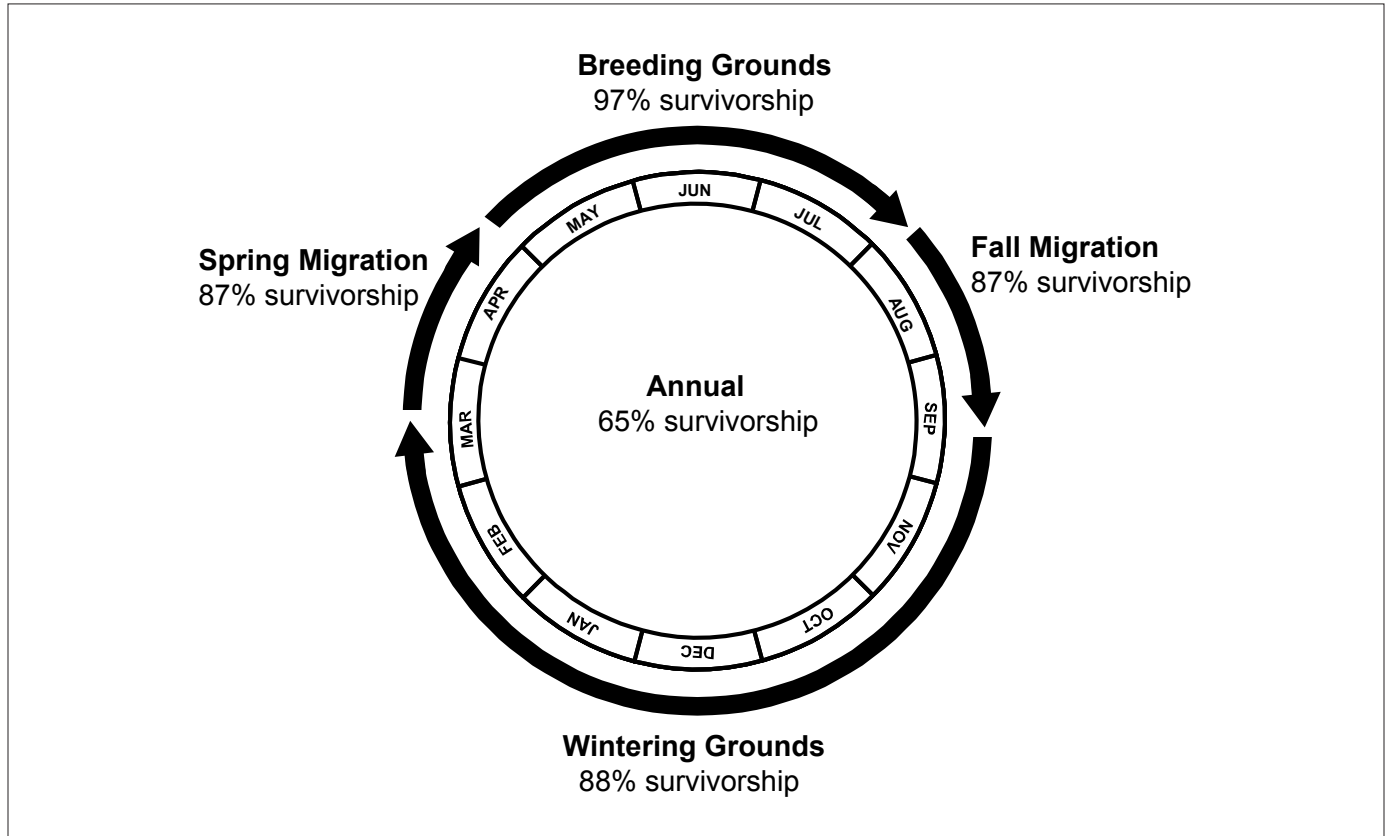


Figure 7. Estimated survival probabilities for Willow Flycatchers, partitioned over the major periods of the annual cycle based on breeding season and wintering season data from 1999 to 2003. Shown are the months (represented by a three letter month code), and approximate time periods for each period are represented by the curved arrows with their associated seasonal survival values. The estimates for the breeding season cover the period of 1999–2003, rather than the entire 1996–2005 Roosevelt Lake/San Pedro dataset, in order to match the Costa Rica winter season dataset (Koronkiewicz et al. 2006); thus, estimate for the breeding ground survivorship is different than the mean values for the entire 10-year study. Migration survivorship rates were assumed to be equal for the spring and fall periods.

Table 11. Survivorship and detection estimates for Southwestern Willow Flycatchers in Arizona increase as the spatial scale of study is increased, from a single patch to the entire study of over 52 patches. See Methods section for description of scale categories.

Spatial scale	Estimated survivorship (%)	95% Confidence interval (%)	Estimated detection (%)	95% Confidence interval (%)	Number of patches	Amount of occupied habitat (ha)
Patch	41	38–44	71	64–76	1	0.2–43
Sub-site	60	57–62	74	70–77	7–16	49–193
Site	63	61–65	78	74–81	23–29	222–242
All sites	64	62–66	78	75–80	52*	444*

* Additional sites where emigrating flycatchers were detected are not included in this estimate.

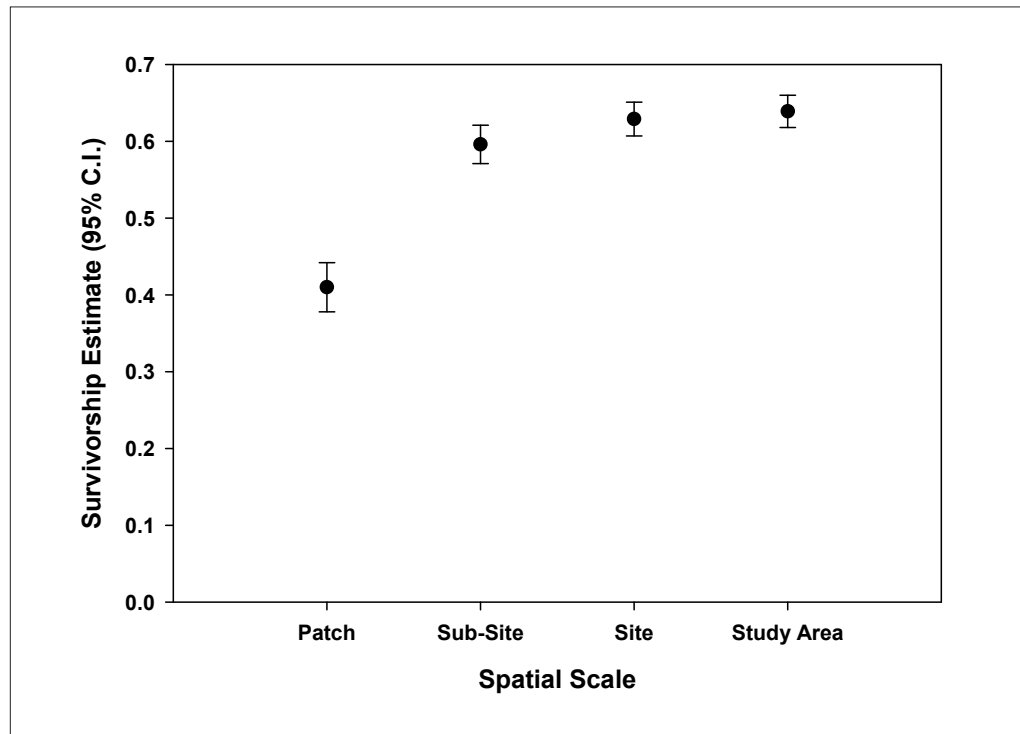


Figure 8. Average survivorship probability estimates for Southwestern Willow Flycatchers as a function of the spatial scale of capture/recapture. As spatial scales increased, survivorship estimates quickly converged on the largest spatial scale estimate. Spatial scales ranged from patch to the entire study area (x-axis), with the corresponding survivorship estimate (filled circle) and 95% C.I. error bars. Refer to the Methods section for detailed description of the different spatial scales.

estimate. Survival during each migratory period (spring and fall migration, equal time periods assumed), calculated separately from breeding and wintering ground data, was estimated by both datasets at 87% (95% C.I.: 83%–96% and 84%–97%, wintering and breeding data, respectively; fig. 7). Monthly survivorship rate during the migratory period (approximately 3 months of the year, spring and fall combined) was estimated at 91%, substantially lower than the monthly estimates of the breeding (99%) and wintering (98%) grounds. Thus, although the migratory period comprises only one quarter of a flycatcher's year, it contributes 64% of the estimated annual mortality that occurs.

Adult Survivorship by Spatial Scale

At the smallest scale (patch), annual survivorship estimates were only 41%. At increasingly larger spatial scales, survivorship estimates increased to 60% (sub-site), 63% (site), and ultimately to 64% for the overall study area (table 11, fig. 8). Detection probability also increased, though less rapidly, from 71% to 78% with increasing spatial scale.

Discussion

Juvenile Survivorship

Estimating juvenile survivorship can be difficult (Newton 1998), as the detection probability of surviving second-year adults is often less than that for adults (Gryzybowski 2005).

In addition, juveniles in most species disperse away from their natal area, often outside of a researcher's study area (Marshall et al. 2004). Such is the case for Willow Flycatchers. Mean detection probability of second-year adults (51%) was lower than for older adults (78%), with 31% of returning birds banded as nestlings first detected in their third to fifth years of life. Furthermore, 41% of SY adults detected (via passive netting efforts) were never observed exhibiting territorial behavior in that year, and would have been undetected using standard survey methods. This may be a major reason why our average juvenile survivorship estimates increased from 19% prior to passive netting (1997–2000) to 37% in the years with passive netting (2001–05). Other reasons for this increase may include yearly differences in the number of nestlings banded, with higher sample sizes in later years; unfortunately, the changing sample sizes cannot be isolated from the effects of year. Nonetheless, the higher juvenile survivorship in the latter half of the study may more accurately reflect true juvenile survivorship, and is closer to the 46% maximum likelihood survivorship estimate from the Kern River Preserve (M. Whitfield, personal commun.) Juvenile dispersal also influenced detection rates; almost no SY adults returned to their natal patches, mean juvenile dispersal distance was greater than adult between-year movement, and the longest distance movements detected were all made by juveniles (see chapter 4). However, the large spatial scale and intensive field efforts of this study allowed us to better understand and document how these difficulties influenced our data and interpretations.

Despite the inherent difficulties, we believe our juvenile survivorship estimates are robust, with the mean survival rate for juveniles (34%) averaging nearly one-half that of adults (64%). Although annual survivorship ranged from 13% to

57%, year received weak support ($\Delta \text{QAICc} = 6.7$) as an important explanatory factor. This lack of importance may be the result of highly variable annual sample sizes, which resulted from changing population sizes, productivity, and shifts in breeding patches (with some patches more difficult to access nests than others). Nonetheless, the wide range of annual survivorship rates suggest, as with adults, that survivorship is not constant through time.

Survivorship estimates for Willow Flycatchers are sparse, and all published information is in terms of return rates, not maximum likelihood estimates (Stoleson et al. 2000). The lack of maximum likelihood estimates makes comparisons between studies difficult, as return rates are very sensitive to detection efforts, a difference that likelihood estimates adjusts for. Nonetheless, return rates may be roughly comparable for studies of equivalent field effort, as our average return rate of 24% is lower than the 34% juvenile return rate observed at the Kern River Preserve, just as our survivorship estimate (34%) is lower than at the Kern River (46%; M. Whitfield, personal commun.). Comparatively, our return rate is higher than the 1% reported from Michigan (Walkinshaw 1966) and the 13% from Oregon (Sedgwick and Klus 1997). Estimates of juvenile return rates for other species range from 15% in Common House-martins (*Delichon urbica*; Stokke et al. 2005), 25% in Swainson's Thrushes (*Catharus ustulatus*; Gardali et al. 2003), and 26% in Western Bluebirds (*Sialia mexicana*; Keyser et al. 2004).

The most important factor that influenced juvenile survivorship in our study was the negative relationship between survivorship and fledge date. For every increase in fledge date by one day, the odds of surviving decreased by 2%, such that flycatchers fledging in mid-June had a 44% probability of surviving versus 19% for flycatchers fledging in mid-August. Flycatchers frequently renest following a failed nesting attempt, which can help to increase their chances of fledging young. However, there is a hidden cost to renesting as each successive nesting attempt has a lower probability of producing young that survive to adulthood. Thus, early flycatcher nests are likely to be the most successful in having young survive and return in subsequent years. This pattern of decreasing survivorship with fledge date has been documented in other species (Great Tit [*Parus major*], Monros et al. 2002 and Smith et al. 1989; European Starlings [*Sturnus vulgaris*], Kremenz et al. 1989), as well as Willow Flycatchers. Studies at both the Kern River (M. Whitfield, personal commun.) and Malheur NWR (Sedgwick and Iko 1999) also found similar relationships with return rates and fledge dates. Explanations for higher apparent survivorship by earlier fledging flycatchers vary, and are not mutually exclusive. There may be greater arthropod food resources earlier in the breeding season, although Durst (2004) found no seasonal difference in total arthropod biomass at Roosevelt Lake. Birds that fledge earlier may reach a further developmental maturity prior to their first fall migration (Westmoreland and Best 1987, Kremenz et al. 1989). Earlier fledging birds may in turn arrive on the wintering grounds earlier and be better able to attain higher quality

wintering habitats (Nilsson 1989, Smith 1994). Finally, it is important to remember that estimated mortality is true mortality plus permanent emigration, and an alternative explanation to the decreasing survivorship linked with later fledging is that late fledglings are more likely to disperse away from our study sites and not be detected again. Additional research exploring the reasons for increased survivorship of early-fledged young will yield useful management and scientific insights.

Our model suggests that juvenile survival is not influenced by the habitat in which a nestling is hatched and raised; the 95% confidence intervals of survivorship estimates for different habitats overlap considerably, even though the point estimate for survival in mixed exotic habitat was much greater than those for other habitat types (42% versus 26%–27%). An important consideration in this comparison is that we could reach and band relatively few nestlings in native habitats (because of high nest placement), which led to unbalanced sample sizes (e.g., only 13 nestlings from native habitats compared to 89 from mixed native habitats). Therefore, although we believe that any influence of natal habitat type on juvenile survivorship is weak, additional research with larger and more balanced sample sizes may be useful in verifying these results.

Adult Survivorship

Apparent adult survivorship averaged across the 10 years was 64% (range = 53%–73%), with yearly variation being the most important explanatory factor. This (along with juvenile survivorship estimates) yielded a mean life expectancy of 1.9 years, meaning most flycatchers do not live for more than 2 years as adults. As adults age, their survivorship probability increases, suggesting that they may learn optimal strategies for foraging, predator avoidance, and migrating, and have presumably found high-quality wintering grounds. Thus the relatively small percentage of flycatchers that survive through their first few years of life have high probabilities of returning each successive year, although annual variation is still an important effect. Our longevity record of a flycatcher of at least 9 years is exceeded by one of ≥ 10 years in Oregon (Sedgwick 2000) and another in California (M. Whitfield, personal commun.). Although a few individuals will realize lifespans exceeding the period of time of this study, this 10-year study is 5-times the expected lifespan of the average flycatcher and thus captures many generations of flycatchers.

Our estimated average adult survival probability of 64% exceeds that of other passerine studies, likely because of the duration and geographic extent of our study. Our survivorship estimate is higher than the estimate of 58% for the Kern River site (M. Whitfield, personal commun.), which is the only other maximum likelihood estimates of survivorship available for the Willow Flycatcher. Our average adult flycatcher return rate (55%) is higher than reported in Oregon (~45%; Sedgwick and Klus 1997) and in Michigan (41% male, 23% female; Walkinshaw 1966). Additionally, our maximum likelihood survivorship estimates are higher than those from other passerine

species, such as 51% and 40% for male and female Black-throated Blue Warblers (*Dendroica caerulescens*), respectively (Silleet and Holmes 2002), 52% in Male Florida Grasshopper Sparrows (*Ammodramus savannarum*; Perkins and Vickery 2001), and 56% in Swainson's Thrush (Gardali et al. 2003). More studies are needed of species similar to the flycatcher before we can put the survivorship estimates from this study fully in context.

The most apparent difference between other survivorship studies and ours is the large spatial extent of this study. Because birds can easily move long distances, and permanent emigration from a study site cannot be distinguished from mortality, studies conducted over small areas may underestimate survivorship. We examined how survivorship estimates derived from different spatial scales affected our estimates, and attempted to better understand the contribution of permanent emigration. As expected, as the spatial extent increased, survivorship estimates also increased from a low of 41% for the patch scale and quickly converged asymptotically to our overall value of 64% as the spatial scale approached the full extent of the entire study area. An important consideration in this analysis is whether tracking efforts are similar at all spatial scales; for our study, tracking effort was equivalent for all scales through the site level, but this is certainly not true for the last category, study area (all sites). There are breeding sites both known and unknown where there are minimal or no resighting activities and where banded flycatchers could go undetected, reducing our estimate of true survivorship. However, because the estimates converged so rapidly on the most inclusive number, we believe that the unknown numbers of undetected dispersing flycatchers were not large enough to significantly influence our survivorship estimates. Thus, we believe further increases in the spatial extent of our study would likely have had a minimal effect on survivorship estimates.

High survivorship within the breeding season (97%) and an annual survivorship rate of 64% (36% mortality) suggests that only 8% of yearly mortality occurs on the breeding grounds; therefore most mortality occurs elsewhere. By linking our study with the Costa Rica wintering study (Koronkiewicz et al. 2006), we estimated that approximately 28% of the flycatcher's annual mortality is occurring on the wintering grounds, while 64% occurred on migration. Silleet and Holmes (2002) found a similar pattern for Black-throated Blue Warblers - lowest mortality on the breeding grounds, slightly higher monthly mortality on the wintering grounds, and greatest monthly and season mortality risk during migration. If migration is a limiting period for flycatchers, as our data suggest, then increasing pressures on their stop-over sites could continue to suppress the population, delaying or hindering recovery efforts. In addition, a shortage of suitable migratory stop-over habitat may increase the time spent on migration, thus possibly increasing mortality during this already perilous time period. More research is needed to understand threats to flycatchers on migration, and whether different wintering and migration stop-over sites have different levels of mortality.

Adult survivorship and detection probabilities were best explained by annual variation. In light of the evidence that little mortality occurs at the breeding grounds, seasonal variation in migration and/or wintering ground mortality may be the drivers of the overall observed annual variation in survivorship. As this study was conducted on the breeding grounds, we were not able to measure the many factors that might contribute to non-breeding season mortality. Some studies have found relationships between yearly survivorship and global climate patterns, such as El Niño and La Niña events as measured by the Southern Oscillation Index (Silleet et al. 2000, Nott et al. 2002). El Niño events, indicated by low negative SOI values, are characterized by heavy winter precipitation in the Southwestern states, leading to high spring and summer run-off, and hot and dry conditions on the wintering grounds. La Niña events are indicated by high positive values and have nearly opposite climatic effects to El Niño. However, while these global patterns clearly have dramatic effects on the landscape (e.g., drought, flooding), we did not detect any relationship with flycatcher survivorship.

We found no support for a sex-bias in adult survivorship, with both females and males having identical survivorship (64%), although detection probability for females (82%) was greater than males (72%). These findings are similar to those from the wintering study (Koronkiewicz et al. 2006) where survivorship differences between the sexes were weak, though these authors found a slight bias in favor of males. Females may have a higher detection probability on the breeding grounds because if they are present they are more likely to engage in breeding activities and thus be detected, while males may be more likely to be present in a non-territorial (i.e., floater) state and more difficult to detect (see chapter 7).

We found weak support for differences in survivorship by habitat type; habitat differences could only be understood in context of yearly variations. Given that the size, length of occupation by breeders, and habitat composition of the 52 breeding patches varied greatly, some of this habitat-based variation could simply be an artifact of the type of suitable habitat that was available to flycatchers at each site, each year, over the course of this study. Factors such as vegetation density, structure and age of patches could also have influenced habitat suitability and associated survivorship, masking patterns evaluated only at the coarse habitat-type level. Mean survivorship values by habitat indicated no effects of breeding habitat on survivorship.

A number of studies have found a relationship between productivity and survivorship, with higher survivorship in those birds that were successful breeders (Koivula et al. 1996, Garamszegi et al. 2004). These results are often interpreted as evidence that superior breeders have superior survival skills. We found that Willow Flycatchers that were successful breeders had higher annual survivorship (73%) compared to birds that were unsuccessful breeders (59%), non-nesting (60%), or non-territorial (60%), indicating a relationship between productivity and survivorship in flycatchers as well. One pos-

sible explanation for this pattern is that adults that are more successful at surviving, possibly through high-quality wintering grounds and better migration strategies, are in better condition upon arrival on the breeding grounds and thus more likely to be successful at reproducing. Alternatively, this relationship may be an artifact of the tendency of successful breeders to return to their previous year's site, and thus be detected, whereas unsuccessful breeders are more likely to emigrate outside of the study area (Sherry 2005). While there is support for the idea that non-productive flycatchers are more likely to move than successful flycatchers (see chapter 4), our ability to detect moving flycatchers over a large area makes this explanation less likely. Moreover, survivorship estimates of flycatchers exhibiting territory-fidelity, patch-fidelity, or between-patch movement were nearly identical (see chapter 4). Age may also be a factor, as second-year adults have lower nest success than older adults (see chapter 3), as well as lower survivorship.

Despite the apparently adequate spatial extent of our study, and intensive field efforts to detect all flycatchers at our two sites, our average adult detection probability was 78%. A major factor explaining why our detection probability was not closer to 100%, despite intensive field effort, was the presence of non-territorial birds, which had a detection probability of only 13% compared to 100% for territorial birds. While we do not believe the actual detection rate for territorial birds was 100% (binomial models have difficulty in estimating numbers close to 1.0, so such an estimate is only approximately 100%), it appears that flycatchers were very likely to be detected if alive, present at our sites, and territorial. It is largely through the use of passive netting efforts started in 2001 that we were able to detect many of the non-territorial flycatchers; 75% of all birds classified as unknown breeding status occurred during the 5-year period after passive netting began. This illustrates the importance of passive netting as a technique to account for birds that would otherwise be undetected. Because flycatchers transition between territorial and non-territorial states during the course of their lives, it is important to track this sometimes "invisible" component of the population (see chapter 7).

Management Considerations

Juvenile and Adult Survivorship

Our survivorship estimates for adults and juveniles are at the high end of estimates for other passerines, and combined with increasing local population numbers, suggest that the flycatchers breeding at Roosevelt Lake and the San Pedro/Gila were not experiencing depressed survivorship during the course of our study. However, survivorship of flycatchers at different breeding sites may not have similar rates, so extrapolating the results of this study to other areas across the range may not be valid. In particular, small populations may be subject to lower or more variable survivorship, especially in response

to stochastic events, which may influence their long-term persistence compared to a large and growing populations such as at our study sites. For example, smaller sites may concentrate predators whereas a larger site would be more likely to disperse them, and larger sites may have more food availability.

Because juvenile survivorship is often a major factor in determining a population's growth potential, it can theoretically be manipulated to help increase the growth potential of a population of concern (Beissinger et al. 2000). In our study, the most important factor influencing juvenile survivorship was fledge date, with decreasing survival probabilities as fledge date increased. Therefore, if there were a goal to increase the growth rate of specific flycatcher populations (e.g., sites with declining numbers), managing nesting conditions to reduce early-season nest failures and allow earlier fledging of young would seem to hold promise. Mechanisms to do this are not yet known, but possibilities that could be studied include presence of surface water within territories, timing and manipulation of water levels below nests, density of understory vegetation within a patch, influence of adjacent habitat types, timing of cowbird management activities, and nest predator barriers or management. More study is needed on these and other management methods to determine their feasibility and effectiveness.

Understanding Migration and Wintering Survivorship

Our data suggest that most adult, and presumably juvenile, mortality occurs away from the breeding grounds, and that migration may be the period of greatest mortality. However, we still lack much basic information on habitat needs and threats to migrating flycatchers (Whitfield et al. 2003). Similarly, although our understanding of winter distribution of flycatchers has increased dramatically over the last 6 years, only one study has evaluated survivorship on the wintering grounds (Koronkiewicz et al. 2006). Additional studies of migrating and wintering flycatchers can help identify factors that may be amenable to conservation and management activities aimed at increasing flycatcher survivorship.

Research Design and Field Effort Considerations

Because survivorship estimates are often used as an index of a population's "health", and to compare among different populations, habitat types, or management alternatives, it is important that the estimates be robust. Based on our results, banding and resight efforts at the scale of a single patch will result in survivorship estimates that are biased low. Small, isolated populations may be appropriate for small scale studies, but movement to and from many isolated sites has been documented (see chapter 4). Increasing the scale of a study to include all known breeding patches within at least the contiguous drainage will provide more accurate parameter estimates. Another way to increase detection rates is through the use of

intensive field efforts (e.g., large crews to conduct banding and resighting), and techniques such as passive netting that help detect easily-overlooked segments of a population. Finally, the temporal scale of a survivorship study is an important consideration because many flycatchers are not detected in all years; multiyear studies allow researchers to account for birds that may be absent in some years and to achieve more accurate survivorship estimates, as well as document yearly variation. However, given the intensive banding and resighting effort required, a multifaceted, long-term study covering a large geographic area entails substantial effort and cost. Management and regulatory agencies must ultimately balance the scale, intensity, and duration of study with the cost, timing and importance of the information need.

References

- Beissinger, S.R., J.M. Reed, J.M. Wunderle, Jr., S.K. Robinson, and D.M. Finch. 2000. Report of the AOU Conservation Committee on the Partners in Flight species prioritization plan. *The Auk* 117:549–561.
- Brownie, C., J.E. Hines, and J.D. Nichols. 1986. Constant-parameter capture-recapture models. *Biometrics* 42:561–574.
- Brown, D. E. (Ed.). 1994. *Biotic Communities – Southwestern United States and Northwestern Mexico*. University of Utah Press, Salt Lake City, UT.
- Burnham, K.P., and D.R. Anderson. 2002. *Model selection and multimodel inference*. Springer-Verlag Publishers, New York.
- Burnham, K.P., D.R. Anderson, G.C. White, C. Brownie, and K.H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. *American Fisheries Society Monograph*, no 5.
- Cormack, R.M. 1964. Estimates of survival from sighting of marked animals. *Biometrika* 51:429–438.
- Durst, S.L. 2004. Southwestern Willow Flycatcher potential prey base and diet in native and exotic habitats. MS thesis. Northern Arizona University, Flagstaff, AZ.
- Durst, S.L., M.K. Sogge, H. English, S.O. Williams, B.E. Kus, and S.J. Sferra. 2005. Southwestern Willow Flycatcher breeding site and territory summary – 2004. U.S. Geological Survey report to Bureau of Reclamation, Phoenix, AZ.
- English, H.C., A.E. Graber, S.D. Stump, H.E. Telle, and L.A. Ellis. 2006. Southwestern Willow Flycatcher 2005 survey and nest monitoring report. *Arizona Game and Fish Technical Report* 248.
- Forsman, E.D., S. DeStephano, M.G. Raphael, and R.J. Gutierrez. 1996. Demography of the Northern Spotted Owl. *Studies in Avian Biology* 17.
- Garamszegi, L.Z., J. Torok, G. Michl, A.P. Moller. 2004. Female survival, lifetime reproductive success and mating status in a passerine bird. *Oecologia* 138:48–56.
- Gardali, T., D.C. Barton, J.D. White, and G.R. Geupel. 2003. Juvenile and adult survival of Swainson's Thrush (*Catharus ustulatus*) in coastal California: annual estimates using capture-recapture analyses. *Auk* 120:1188–1194.
- Grzybowski, J.A. 2005. An estimate of juvenile survival in black-capped vireos and its implications to source-sink analyses of songbirds. U S Forest Service General Technical Report PSW 191:810–812.
- Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52:225–247.
- Keyser, A.J., M.T. Keyser, and D.E. Promislow. 2004. Life-history variation and demography in western bluebirds (*Sialia mexicana*) in Oregon. *Auk* 121:118–133.
- Kiladis, G.N. and H.F. Diaz. 1989. Global climatic anomalies associated with extremes of the Southern Oscillation. *Journal of Climate* 2:1029–1090.
- Koivula, K., M. Orell, and S. Rytkoenen. 1996. Winter survival and breeding success of dominant and subordinate Willow Tits *Parus montanus*. *Ibis* 138:624–629.
- Koronkiewicz, T.J., E.H. Paxton, and M.K. Sogge. 2005. A technique for aluminum color-bands for avian research. *Journal of Field Ornithology* 76:94–97.
- Koronkiewicz, T.J., and M.K. Sogge. 2001. Southwestern Willow Flycatchers recaptured at wintering sites in Costa Rica. *North American Bird Bander* 26:161–162.
- Koronkiewicz, T.J., M.K. Sogge, C. van Riper III and E.H. Paxton. 2006. Territoriality, Site Fidelity, and Survivorship of Willow Flycatchers Wintering in Costa Rica. *Condor* 108:558–570.
- Krementz, D.G., J.D. Nichols, and J.E. Hines. 1989. Post-fledging survival of European starlings. *Ecology* 70:646–655.
- Lebreton, J.D., K.P. Burnham, J. Clobert, D.R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Lebreton, J.D., R. Pradel, and J. Clobert. 1993. The statistical analysis of survival in animal populations. *Trends in Ecology and Evolution* 8:91–95.

- Marshall, M.R., D.R. Diefenbach, L.A. Wood, and R.J. Cooper. 2004. Annual survival estimation of migratory songbirds confounded by incomplete breeding site-fidelity: study designs that may help. *Animal Biodiversity and Conservation* 27:59–72.
- Marshall, R.M. 2000. Chapter 2: Population status on breeding grounds. Pages 3–11 in *Status, ecology, and conservation of the Southwestern Willow Flycatcher* (D.M. Finch and S.H. Stoleson, eds.). General Technical Report RMRS-GTR-60. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Marshall, R.M. and S.H. Stoleson. 2000. Chapter 3: Threats. Pages 13–24 in *Status, ecology, and conservation of the Southwestern Willow Flycatcher* (D.M. Finch and S.H. Stoleson, eds.). General Technical Report RMRS-GTR-60. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Martin, T.E., J. Clobert, and D.R. Anderson. 1995. Return rates in studies of life history evolution: are biases large? *Journal of Applied Statistics* 22:863–875.
- McCabe, G.J., M.A. Palecki, and J.L. Bentancourt. 2004. Pacific and Atlantic Ocean influences on multidecadal drought frequency in the United States. *Proceedings of the National Academy of Sciences* 101:4136–4141.
- Monros, J.S., E.J. Belda, and E. Barba. 2002. Post-fledging survival of individual great tits: the effect of hatching date and fledging mass. *Oikos* 99:481–488.
- Newton, I. 1998. *Population limitation in birds*. Academic Press, New York.
- Nilsson, J.A. 1989. Causes and consequences of natal dispersal in the Marsh Tit, *Parus palustris*. *Journal of Animal Ecology* 58:619–636.
- Nott, M.P., D.F. Desante, R.B. Siegel, and P. Pyle. 2002. Influences of the El Niño/Southern Oscillation and the North Atlantic Oscillation on avian productivity in forests of the Pacific Northwest of North America. *Global Ecology and Biogeography* 11:333–342.
- Paxton, E.H., and J.C. Owen. 2002. *An aging guide for Willow Flycatcher nestlings*. Colorado Plateau Field Station, Northern Arizona University.
- Paxton, E.H., M.K. Sogge, T.D. McCarthy, and P. Keim. 2002. Nestling sex ratio in the Southwestern Willow Flycatcher. *Condor* 104:877–881.
- Perkins, D.W. and P.D. Vickery. 2001. Annual survival of an endangered passerine, the Florida Grasshopper Sparrow. *Wilson Bulletin* 113:211–216.
- Pollock, K.H., J.D. Nichols, C. Brownie, and J.E. Hines. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107:1–97.
- Pollock, M.G. and E.H. Paxton. 2006. Floating mist nets: a technique for capturing birds in flooded habitat. *Journal of Field Ornithology* 77:335–338.
- Pyle, P. 1998. Eccentric first-year molt patterns in certain Tyrannid flycatchers. *Western Birds* 29:29–35.
- Ralph, C.J., G.R. Geupel, P. Pyle, T.E. Martin and D.F. DeSante. 1993. *Handbook of field methods for monitoring landbirds*. USFS General Technical Report PSW-GTR-144. Albany, CA; Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture.
- Ropelewski, C.F. and M.S. Halbert. 1987. Global and regional scale precipitation patterns associated with the El Niño/Southern Oscillation (ENSO). *Monthly Weather Review* 115:2352–2362.
- Ropelewski, C.F. and M.S. Halbert. 1989. Precipitation patterns associated with the high-index of the Southern Oscillation. *Journal of Climate* 2:268–284.
- Ropelewski, C.F. and M.S. Halbert. 1996. Quantifying Southern Oscillation-precipitation relationships. *Journal of Climate* 9:1043–1059.
- Seber, G.A. 1965. A note on the multiple recapture census. *Biometrika* 52:249–259.
- Sedgwick, J.A. 2000. Willow Flycatcher (*Empidonax traillii*). In *The Birds of North America*, No 533 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.
- Sedgwick, J.A., and W.M. Iko. 1999. Costs of Brown-headed Cowbird parasitism to Willow Flycatchers. *Studies in Avian Biology* 18:167–181.
- Sedgwick, J.A. and R.J. Klus. 1997. Injury due to leg bands in Willow Flycatchers. *Journal Field Ornithology* 68:622–629.
- Sherry, T.W. 2005. Survival and breeding dispersal estimation in American Redstart in relation to condition-dependent site tenacity: a multi-state capture-resight analysis. 123rd meeting of the American Ornithologists' Union, Santa Barbara.
- Sillett, T.S. and R.T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296–308.
- Sillett, T.S., R.T. Holmes, and T.W. Sherry. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* 288:2040–2042.
- Smith, H.G., H. Kallander, and J.A. Nilsson. 1989. The trade-off between offspring number and quality in the Great Tit *Parus major*. *Journal of Animal Ecology* 58:383–401.

- Smith, S.M. 1994. Social influences on the dynamics of a northeastern Black-capped Chickadee population. *Ecology* 75:2043–2051.
- Sogge, M.K., R.M. Marshall, T.J. Tibbitts, and S.J. Sferra. 1997. A Southwestern Willow Flycatcher Natural History Summary and Survey Protocol. National Park Service Technical Report NPS/NAUCPRS/NRTR-97/12.
- Sogge, M.K., J.C. Owen, E.H. Paxton, S.M. Langridge, and T.J. Koronkiewicz. 2001. A targeted mist net capture technique for the Willow Flycatcher. *Western Birds* 32:167–172.
- Stokke, B.G., A.P. Moller, B.E. Saether, G. Rheinwald, and H. Gutscher. 2005. Weather in the breeding area and during migration affects the demography of a small long-distance passerine migrant. *Auk* 122: 637–647.
- Stoleson, S.H., J. Agyagos, D.M. Finch, T. McCarthey, J. Uyebara, and M.J. Whitfield. 2000. Research needs. Pages 119–127 in Status, ecology, and conservation of the Southwestern Willow Flycatcher. Finch, D.M. and S.H. Stoleson (eds). USDA Forest Service Rocky Mountain Research Station General Technical Report RMRS-GTR-60.
- Unitt, P. 1987. *Empidonax traillii extimus*: an endangered subspecies. *Western Birds* 18:137–162.
- Unitt, P. 1997. Winter range of *Empidonax traillii extimus* as documented by existing museum collections. Report to Bureau of Reclamation, Phoenix, AZ.
- U.S. Fish and Wildlife Service. 1993. Notice of 12-month petition finding/proposal, and to designate critical habitat. *Federal Register* 58:39495–39522.
- U.S. Fish and Wildlife Service. 1995. Final rule determining endangered status for the Southwestern Willow Flycatcher (*Empidonax traillii extimus*). *Federal Register* 60:10694.
- Walkinshaw, L.H. 1966. Summer biology of Trailli's Flycatcher. *Wilson Bulletin* 78:31–46.
- Westmoreland, D. and L.B. Best. 1987. What limits Mourning Doves to a clutch of two eggs? *Condor* 89:486–493.
- White, G.C. and K.P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:s120–s139.
- Whitfield, M.J., M.K. Sogge, S.J. Sferra, and B.E. Kus. 2003. Ecology and Behavior – Introduction. *Studies in Avian Biology* 26:53–55.
- Williams, B.K., J.D. Nichols, and M.J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, CA.

Chapter 3—Productivity

Introduction

The viability and growth of a population is often most directly influenced by the productivity of breeding birds (Perrins et al. 1991, Anders and Marshall 2005, Grzybowski and Pease 2005), and population productivity is often of particular concern for many threatened and endangered species. Multiple factors can have both short- and long-term influences on productivity, including predation, parasitism, and food resources (Rodenhouse and Holmes 1992, Robinson et al. 1995, Arcese et al. 1996, Donovan et al. 1997, Woodworth 1999, Weidinger 2002, Smith and Moore 2003). In arid environments, rainfall can be an important environmental factor, with lack of precipitation negatively affecting productivity (Boag and Grant 1984; Rotenberry and Wiens 1989, 1991; Li and Brown 1999). Additionally, factors may interact to affect productivity; for instance climate can affect nest predation rates, which in turn influences reproductive success (Woolfenden and Fitzpatrick 1984, Grant and Grant 1987). Variations in annual productivity can reveal important sources of environmental influences on the ability of a bird to fledge young, while variation in lifetime productivity highlights individual differences (Clutton-Brock 1988). Ultimately, an understanding of the factors that influence productivity may have critical management implications that could enhance prospects for the viability and sustainability of endangered species.

To adequately characterize the productivity of a population, it is important to measure the reproductive success of individuals over the entire breeding season (Clobert and Lebreton 1991). Most bird species can have multiple nesting events within a breeding season, by renesting following a failed nesting attempt or “double brooding” after a successful nest. Further, to estimate lifetime reproductive success, the seasonal reproductive success of individuals needs to be tracked for their entire lifespan. Measurement of both seasonal and lifetime productivity is therefore challenging, and requires carefully following uniquely marked individuals over multiple seasons and years (Beissinger and McCullough 2002).

The Southwestern Willow Flycatcher (*Empidonax traillii extimus*) is a small, migratory passerine that breeds exclusively in riparian habitats scattered throughout portions of the southwestern United States (Unitt 1987, Marshall 2000), and winters from central Mexico south to northern South America (Sedgwick 2000). Flycatcher numbers have declined precipitously as riparian habitats on the breeding grounds have been lost or modified (USFWS 1993, Marshall and Stoleson 2000), and *E.t. extimus* was listed as a federally endangered species in

1995 (USFWS 1995). At the time of listing, most aspects of the flycatcher’s biology, including variability in productivity and the driving forces responsible for that variability, were poorly understood (Marshall and Stoleson 2000, Stoleson et al. 2000).

From 1996 to 2005, we collaborated with the Arizona Game and Fish Department (AGFD) to conduct a large-scale demographic study of flycatchers at two large breeding sites in central Arizona. A major goal of this project was to document long-term variation in flycatcher productivity by tracking the reproductive success of individual nests and color-banded individuals over the successive breeding seasons and across years.

In this chapter, we focus on three aspects of productivity that required the tracking of banded birds. The first is seasonal nest success, which measures how many nests were successful out of all nesting attempts per individual. A second measure, seasonal fecundity, is the sum of all fledglings produced from all nesting attempts by a given individual in a given season. Lastly, lifetime productivity is the sum of seasonal fecundity over the lifetime of an individual. For each measure, we evaluated several factors which explain variation in the documented estimates. However, most aspects of flycatcher productivity at Roosevelt Lake and the San Pedro River will be analyzed and presented by AGFD in their final project report.

Methods

Study Site

Our two study sites (fig. 1) were breeding populations at Roosevelt Lake (33°39’N, 110°58’W) and the San Pedro/Gila River confluence (hereafter San Pedro/Gila; 32°59’N, 110°46’W), where we conducted demographic research in cooperation with AGFD from 1996 to 2005 (Causey et al. 2006, English et al. 2006). We defined sites as a collection of riparian woodland patches, occupied by breeding flycatchers, which are collectively closer to one another than to other breeding patches, and are found within the same drainage (or along the same lake). Exact definitions of a site are difficult, and the definition of a site differs regionally (Durst et al. 2006). However, based on documented movement patterns, each site has a high degree of movement-based connectivity among patches suggesting a distinct breeding population.

Our two study sites supported some of the largest known Southwestern Willow Flycatcher breeding populations throughout the period of this study (Durst et al. 2006), with mean population sizes of 201 and 239 individuals at Roosevelt

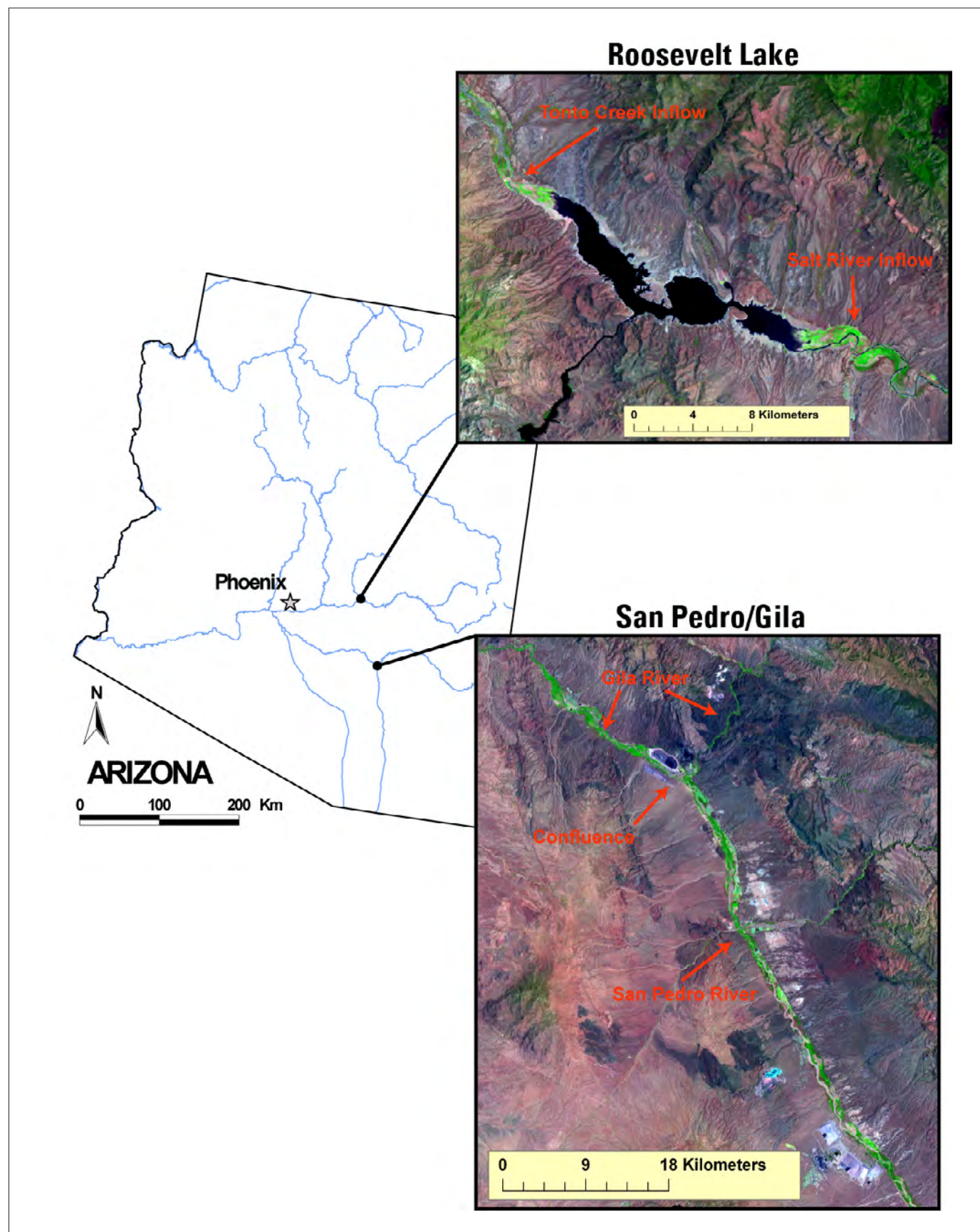


Figure 1. Location of the Roosevelt Lake and San Pedro/Gila study areas in central Arizona.

Lake and San Pedro/Gila, respectively. At each site, extensive surveys were conducted at least three times in the breeding season to detect all territorial flycatchers within the immediate and surrounding areas. In addition, multiple other breeding sites in Arizona and throughout the Southwest (49–444 km away) were periodically visited, which along with cooperative efforts of other researchers allowed detection of dispersing or moving flycatchers (see chapter 4).

The breeding habitat at the Roosevelt Lake and San Pedro/Gila study sites consisted of a heterogeneous mosaic of discrete riparian forest patches of varying ages and vegetation composition, ranging from 0.2 to 43 ha in size. Native habitat was characterized by Goodding's willow (*Salix gooddingii*) and Fremont cottonwood (*Populus fremontii*). Exotic habitat was dominated by tamarisk (saltcedar; *Tamarix spp.*). The understory vegetation consisted of a variety of grasses, forbs, and shrubs (mesquite [*Prosopis spp.*], coyote willow [*S. exigua*], tamarisk, *Baccharis spp.*, and cocklebur [*Xanthium strumarium*]). Adjacent and surrounding non-riparian habitats were primarily composed of Sonoran Desert Uplands (Brown 1994), and in some cases agricultural lands.

Roosevelt Lake Study Site

The Roosevelt Lake study site consisted of two sub-sites, each concentrated at the confluence of the reservoir and the inflows of the Salt River and Tonto Creek, with breeding documented as far as 12 km upstream on Tonto Creek. The number of riparian patches in which breeding was documented varied over time as a result of colonization or desertion of patches, in many cases driven by fluctuating lake levels. Over the 10-year period, we documented breeding occurring in a maximum of 23 patches encompassing approximately 242 ha of riparian habitat. Long-term persistent drought conditions between 1996 and 2005 in the Southwest (McCabe et al. 2004) resulted in reservoir levels dropping to a low of 10% capacity in 2002; the exposed lakebed was colonized by riparian vegetation, which was subsequently colonized by breeding flycatchers (see chapter 5). In 2005, following unusually high winter precipitation, Roosevelt Lake filled to near capacity, inundating much of the breeding habitat that was occupied in 2004 (see chapter 5).

San Pedro/Gila Study Site

The San Pedro/Gila study site encompassed 101 km of river system, centered at the confluence of the free-flowing San Pedro River and the regulated Gila River, and extending upstream of the San Pedro to San Manuel Crossing and downstream of the Gila River to Kelvin Bridge. As with Roosevelt Lake, the number of patches changed over the 10 years, with as many as 29 habitat patches documented as supporting breeding efforts, comprising approximately 222 ha of riparian forest along this stretch.

Banding and Resighting

To measure seasonal and lifetime productivity of individual flycatchers, we banded as many adult and nestling flycatchers as possible, and tracked them throughout the course of this study. Nestlings were banded at 7–10 days of age (Paxton and Owen 2002), from nests that were safely accessible, with a color-anodized, numbered federal bird band. A small drop of blood was taken for genetic gender determination (Paxton et al. 2002). Adults were banded with a color-anodized federal bird band and a second color band to create a unique color combination (Koronkiewicz et al. 2005). Adults were primarily target-netted (Sogge et al. 2001, Pollock and Paxton 2006) to allow for efficient, focused capture effort. From 2001 to 2005, we also conducted extensive passive netting at Roosevelt Lake (see Ralph et al. 1993) aimed at capturing non-territorial flycatchers that were not readily detectable with conventional survey techniques (i.e., territorial response to tape-playback). Overall, the combination of targeted and passive netting resulted in the banding of an average of 74% (range: 68%–88%) of detected adult flycatchers in a given year. To determine gender of adult flycatchers, we used a combination of physical characteristics (presence of a cloacal protuberance for males or brood patch for females), behavioral cues, and/or genetic sexing methods (Paxton et al. 2002). Flycatchers were aged as known if the individual was first banded as either a nestling or a second-year adults (SY; based on retained rectrices (Pyle 1998), or unknown (2 or more years of age).

We tracked banded flycatchers over the 10 years primarily through resighting, supplemented by occasional recaptures. Resighting consisted of using binoculars to determine the unique color band combination on a flycatcher's legs. Resighting is a minimally intrusive method of "recapture", and the most reliable method for establishing the particular territory a flycatcher belongs to, because playback capture techniques can lure adults in from neighboring territories. To ensure the accuracy of resight data, only high-confidence resights from at least two different observers on different days were used to confirm the identity and territory of individual banded flycatchers. Computer databases were updated and queried daily to prioritize resighting efforts, allowing us to track as many as 393 uniquely color banded individuals in a given year. Field crew sizes of up to 35 personnel (USGS and AGFD combined) allowed intensive resighting of banded individuals, and resulted in high detection rates. Recaptures, especially via passive netting, provided additional detection resolution, especially for non-territorial birds.

Nest Monitoring

Nest searching and monitoring were primarily coordinated and conducted by AGFD. Nests were discovered through systematic searches of flycatcher territories and monitored fol-

lowing the Southwestern Willow Flycatcher Nest Monitoring Protocol (Rourke et al. 1999). After incubation was confirmed, each monitored nest was visited every 2–4 days until it either successfully fledged at least one young or failed. Nests were considered successful if one of the following conditions were met (see English et al. 2005): (1) one or more young were visually confirmed fledging from the nest or located near the nest; (2) adults were seen feeding at least one fledgling; (3) parents behaved as if dependent young were nearby after the nest was empty; or (4) nestlings were observed in the nest within 2 days of the estimated fledge date (12 days). From 1996 to 2000, all nests discovered at monitored breeding patches were monitored to determine reproductive success. Starting in 2001, the protocol was modified to track at least 35 banded females throughout each season at San Pedro/Gila, and 50 females at Roosevelt Lake. However, in most years there was sufficient time and resources for the majority of nests to be monitored.

To determine seasonal productivity of individuals, we used a database that linked banded individuals associated with specific territories, and those territories to the reproductive outcomes of the nesting attempts made within the territory. Individuals that were associated with the territory, based on resights, were then assigned the reproductive outcome of the nest. Only birds for which we had high confidence of their association with specific territories were used. However, even this conservative approach cannot account for possible extra-pair copulations, which could change the actual reproductive success of particular individuals (Pearson et al. 2006). Dates during which territories and nests were active were compared with the dates that an individual was detected to ensure that individuals were accounted for during each nesting attempt and throughout the breeding season. Those that could not be assigned to a territory, or that were missing for portions of the season, were excluded from the seasonal productivity analysis.

Although not all nests were monitored each year, our resighting objectives were to track banded individuals throughout the breeding season, and to locate all nests and determine breeding status of individuals. Therefore, we have high confidence that most nesting attempts by banded individuals were documented, even if we did not have information on the outcome of each. As noted above, birds with uncertain nest outcomes were excluded from the productivity analyses.

Statistical Analysis

We used analysis of variance (ANOVA) to test for differences in seasonal nest success and fecundity using the following factors: study site (Roosevelt Lake or San Pedro/Gila), year (1996–2005), sex (female or male), age (second-year to sixth-year), and habitat type (defined as native, mixed-native, mixed-exotic, or exotic vegetation). Additionally, we used regression to assess the relationship between average yearly nest predation (measured as the mean percentage of nests predated per individual per season) and precipitation (measured as the mean monthly precipitation in cm from January to May; data were from the weather station nearest to each study site).

Age based productivity was compared via ANOVA, with known-aged females as the factor (up to age sixth-year, after which sample sizes were too small to use). Measures of productivity were sex-based when specified; otherwise, general patterns of seasonal nest success and fecundity were performed using information from females only.

Lifetime productivity requires knowledge of all productivity events of an individual over its entire lifespan. Because individuals can be alive before the start of a study and after its conclusion, the only birds certain to be tracked for their entire lifetimes are those that were first banded as nestlings or first captured as second-year adults (and therefore known not to have reproduced before the study), and then were not seen for at least the last 2 years of the study (and therefore likely dead). Applying these conservative selection criteria resulted in a set of 106 birds that had a mean lifetime fecundity of 1.2 young. Because this value is lower than the seasonal fecundity during some single years, we believed it to be a falsely low estimate, probably because the sample was too small to capture the full range of individual lifetime productivity. Therefore, we adopted a slightly less stringent approach that censored (i.e., removed) individuals that were only detected in the first 2 years of the study, or only in the last 2 years. For example, individuals banded in either 1996 or 1997 and detected only in those years were excluded from the analysis, as were any individuals first banded in 2004 or 2005. Because the estimated life expectancy of flycatchers is just under 2 years (based on survivorship estimates; see chapter 2), most flycatchers live only one or 2 years as adults and therefore would have their entire lifetime productivity recorded over the course of this 10-year study. Although some individuals have lived as long as nine or more years, these are few, and their inclusion should change mean estimates of lifetime fecundity only slightly. While we cannot account for undetected permanent emigration from the study sites, the evidence suggests that such long-distance movements are fairly rare (see chapter 4), and thus should have minimal effects on the mean estimates. Nonetheless, we refer to this modified productivity estimator as Minimum Lifetime Productivity (MLP), in recognition that some amount of reproductive activity may have been missed for some long-lived individuals or emigrants.

Minimum lifetime productivity is the sum of an individual's seasonal fecundity estimates over the lifetime, as tracked over the course of this study and meeting the criteria for inclusion as described above. Individuals that were not detected for an entire breeding season or were determined to be non-territorial were included in the dataset, with zero productivity recorded for that year. However, individuals for which information was missing from one of their known breeding attempts in a season were excluded from the entire analysis. We conducted a t-test for differences in MLP by site and sex, and regressed MLP by longevity to understand the relationship between the two factors. To look at the cumulative contribution of individuals to the total number of young fledged in this

group, we ranked individuals from highest to lowest MLP, calculated their percent MLP to the total young fledged, and graphed the cumulative contribution. All statistical analysis was conducted in the software package JMP 6.0 (SAS, Inc.). Figures were plotted with SigmaPlot (SAS, Inc.).

Results

Seasonal Nest Success and Fecundity

From 1996 to 2005, the seasonal reproductive success of 543 banded females and 636 banded males was tracked at Roosevelt Lake and the San Pedro/Gila. There was a significant interaction between year and site for both seasonal nest success ($F_{9,1634} = 5.63$, $p < 0.001$) and seasonal fecundity ($F_{9,1634} = 4.85$, $p < 0.001$). Overall, seasonal nest success and fecundity was higher at San Pedro/Gila compared to Roosevelt Lake, but not in all years (table 1, fig. 2). Males had higher seasonal fecundity than females ($F_{1,1634} = 24.09$, $p < 0.001$), but there was no difference in seasonal nest success ($F_{1,1634} = 0.07$, $p = 0.79$; table 1). On average, males had higher seasonal fecundity than females at both Roosevelt Lake (0.4 higher) and the San Pedro/Gila (0.5 higher).

Seasonal nest success and fecundity are largely influenced by factors affecting the fate of individual nesting attempts, and such factors will be covered in the final report by AGFD. However, two factors that have a strong influence on female seasonal measures of productivity, largely because they influence the amount of renesting, are nest predation rates and precipitation. Nest predation was the major cause of nest failure, accounting for 61% and 71% of failures at Roosevelt and San Pedro/Gila, respectively, and the overall seasonal nest success was strongly and negatively correlated with the average proportion of nests that failed due to nest predation (Roosevelt $r^2 = 0.69$, San Pedro/Gila $r^2 = 0.60$; fig. 3). Precipitation, measured as the average monthly amount of late winter and early spring rain/snow, was also a strong nest success predictor (Roosevelt: $r^2 = 0.70$, $p = 0.027$; San Pedro/Gila: $r^2 = 0.70$, $p = 0.015$); the relationship was non-linear (quadratic; fig. 4), with the strongest relationship at low precipitation conditions (from 0.0 to 2.5 cm) but leveling off at higher precipitation levels. Average precipitation over the 10 years of this study was 2.8 cm for Roosevelt and 1.7 cm for San Pedro/Gila, which is approximately at the inflection points of the regression line. Thus, the average precipitation level at each site approximates a threshold below which nest success is strongly reduced with decreasing precipitation; above this threshold, increasing precipitation does not have a strong increasingly positive effect. Finally, we detected no difference in seasonal nest success ($F_{3,803} = 2.24$, $p = 0.08$) or seasonal fecundity ($F_{3,803} = 1.67$, $p = 0.17$) by habitat type (table 2).

Age-based Seasonal Productivity

There was a significant difference in seasonal fecundity of females, ages second-year to sixth-year ($F_{4,131} = 2.60$, $p = 0.04$), but not seasonal nest success ($F_{4,131} = 1.41$, $p = 0.23$). Differences among the age groups was driven largely by lower productivity in second-year adults, with second-year seasonal fecundity averaging 1.0 versus 1.7–1.8 for the older females, and seasonal nest success averaging 45% for second-year adults versus 54%–75% for the older females (table 3).

Minimum Lifetime Productivity

From 1996 to 2005, we tracked the yearly breeding efforts of 802 individuals to determine their minimum lifetime productivity (MLP). Mean MLP averaged 3.5 offspring (range = 0–27). While males had a slightly higher mean number of lifetime fledges (3.8) than females (3.3), this difference was not significant ($t_{764} = -1.6$, $p = 0.11$); the median for both was 3.0 young fledged per lifetime (fig. 5). In general, males had the highest number of MLP fledglings due to polygamy, but a higher proportion of males than females produced zero young, resulting in similar mean values. The number of lifetime fledges differed significantly between sites ($t_{764} = -2.6$, $p = 0.01$), being higher at the San Pedro/Gila (mean = 4.0, CI = 3.5–4.6, median = 3) than at Roosevelt Lake (mean = 3.2, CI = 2.9–3.6, median = 2).

The number of young fledged in a lifetime varied greatly among individuals (fig. 5). Over a third (37%, $n = 299$) of individuals tracked produced no offspring, but most of these individuals (76%) were detected for only one year; only 32% of individuals detected for a single year fledging at least one young. Some flycatchers that were detected for up to 5 years did not produce offspring, but all flycatchers detected for 6 or more years fledged at least one young (fig. 6). Overall, 50% of the total young fledged were attributed to just 16% of flycatchers tracked. For this dataset, the mean number of years alive was 2.5, and the mean number of years breeding was 1.8. As expected, the longer a flycatcher lived, the greater the number of lifetime fledges it produced ($r^2 = 0.53$, $F_{1,777} = 890.6$, $p < 0.001$); however, there was considerable variation around this trend. We therefore arbitrarily classified flycatchers into three groups based on minimum lifetime productivity: 10 or more young, 1–9 young, and zero young fledged (table 4). The group producing 10 or more fledges in their lifetime comprised only 8% of the monitored population, but contributed 31% of the total number of young fledged. Flycatchers in the 1–9 young per lifetime group constituted 55% of the monitored population, and contributed the remaining 69% of young fledged. The remaining 37% of individuals were never detected fledging young. Characteristics of the more successful breeders included longer lifespan, more years of attempted breeding, higher percent nest success, more polygamous pairings, and higher mean number of young fledged per year (table 4).

Table 1. Mean seasonal nest success (the percentage of successful nests per nesting attempts) and seasonal fecundity (total number of young fledged per individual per season) of Southwestern Willow Flycatchers at Roosevelt Lake and the San Pedro/Gila study sites. Sample size represents the number of banded individuals used for each estimate.

Year	Site	n	Female		n	Male	
			Average % seasonal nest success (95% CI)	Average seasonal fecundity (95%CI)		Average % seasonal nest success (95% CI)	Average seasonal fecundity (95%CI)
1996	Roosevelt Lake	10	40 (7–72)	1.0 (0.2–1.8)	14	50 (22–78)	1.3 (0.6–2.0)
	San Pedro/Gila	15	30 (7–53)	0.7 (0.2–1.3)	13	49 (24–74)	1.4 (0.7–2.1)
1997	Roosevelt Lake	18	51 (28–74)	1.7 (1.0–2.5)	24	60 (38–76)	2.2 (1.2–3.1)
	San Pedro/Gila	18	53 (31–74)	1.6 (0.9–2.3)	25	63 (45–82)	1.6 (1.1–2.1)
1998	Roosevelt Lake	18	75 (54–96)	1.9 (1.3–2.6)	28	68 (53–83)	2.7 (2.0–3.5)
	San Pedro/Gila	38	56 (41–70)	2.1 (1.5–2.7)	33	63 (50–76)	3.3 (2.4–4.2)
1999	Roosevelt Lake	36	62 (47–77)	2.1 (1.4–2.7)	43	61 (48–74)	2.6 (1.9–3.2)
	San Pedro/Gila	39	49 (36–61)	1.8 (1.3–2.3)	40	44 (33–56)	2.6 (2.0–3.2)
2000	Roosevelt Lake	39	65 (52–79)	1.9 (1.6–2.3)	60	63 (52–73)	2.4 (1.9–2.8)
	San Pedro/Gila	30	46 (31–61)	1.8 (1.2–2.3)	43	49 (37–61)	1.9 (1.3–2.4)
2001	Roosevelt Lake	70	69 (59–79)	2.2 (1.8–2.5)	66	65 (55–74)	2.7 (2.1–3.2)
	San Pedro/Gila	28	61 (46–76)	2.7 (2.0–3.4)	32	55 (40–70)	3.0 (2.2–3.8)
2002	Roosevelt Lake	31	6 (0–14)	0.1 (0.0–0.3)	47	3 (0–7)	0.1 (0.0–0.2)
	San Pedro/Gila	24	29 (10–49)	0.8 (0.3–1.4)	23	34 (15–53)	1.1 (0.5–1.7)
2003	Roosevelt Lake	90	72 (63–81)	2.0 (1.8–2.3)	77	71 (62–80)	2.6 (2.2–3.1)
	San Pedro/Gila	51	69 (58–81)	2.3 (1.9 (2.7)	30	76 (61–90)	3.2 (2.4–3.9)
2004	Roosevelt Lake	72	40 (29–51)	1.1 (0.8–1.4)	74	46 (35–56)	1.6 (1.2–2.0)
	San Pedro/Gila	55	49 (38–59)	1.9 (1.4–2.3)	41	61 (50–73)	2.8 (2.2–3.4)
2005	Roosevelt Lake	71	49 (38–60)	1.4 (1.1–1.7)	77	44 (35–54)	1.6 (1.3–1.9)
	San Pedro/Gila	52	68 (57–80)	2.3 (1.9–2.8)	39	70 (57–83)	3.3 (2.5–4.1)
Mean	Roosevelt Lake	455	56 (52–60)	1.6 (1.5–1.8)	511	53 (49–57)	2.0 (1.8–2.2)
	San Pedro/Gila	350	54 (50–59)	2.0 (1.8–2.1)	319	57 (53–61)	2.5 (2.3–2.8)

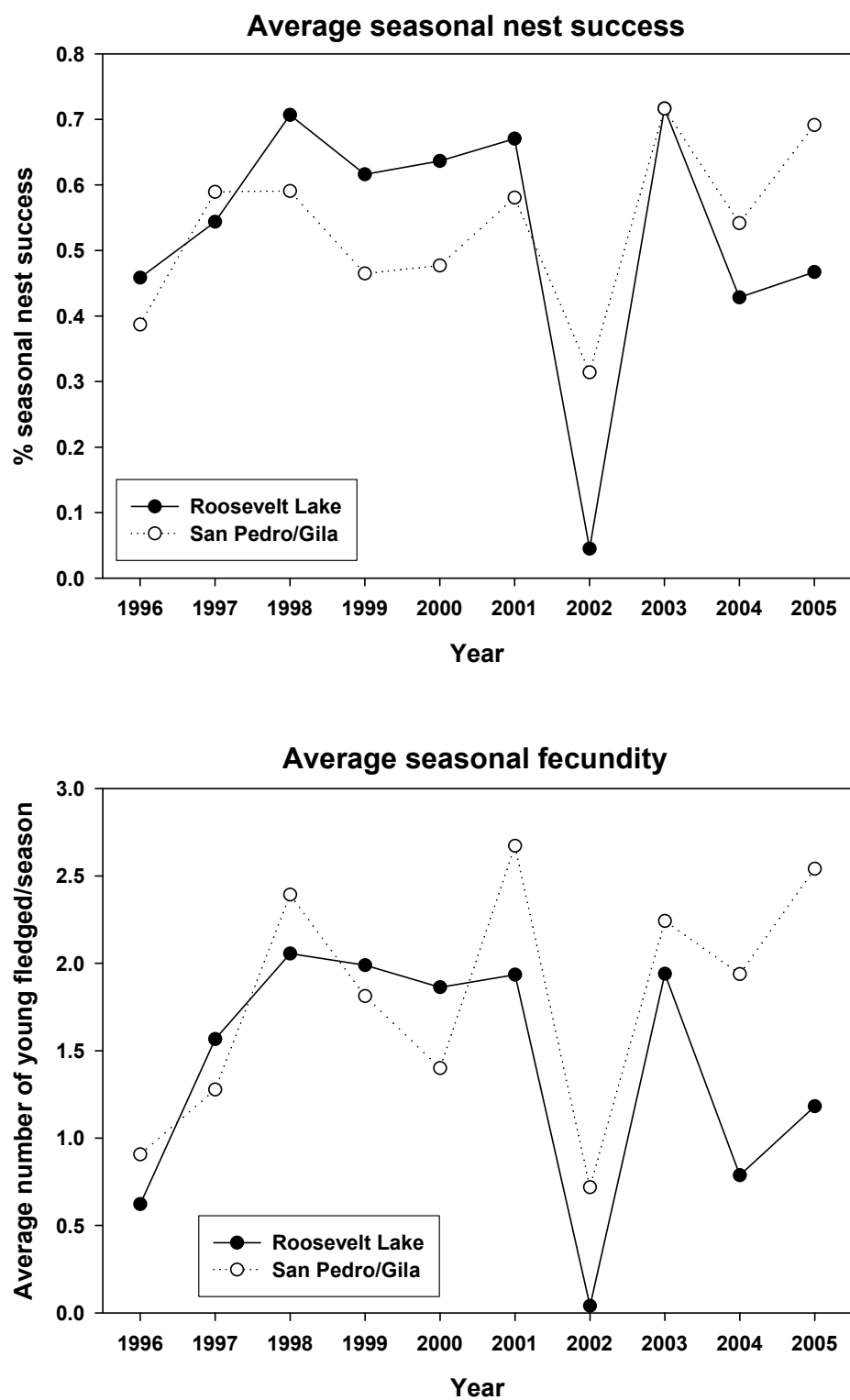


Figure 2. Average seasonal nest success and fecundity of Southwestern Willow Flycatcher females at the Roosevelt Lake and San Pedro/Gila study sites, 1996–2005.

Table 2. Average seasonal nest success and fecundity of Southwestern Willow Flycatcher females by habitat type (sites and years combined). Habitat types are native broad leaf, exotic tamarisk, and mixtures of the two vegetation types. Large overlap of 95% confidence intervals suggests no statistical difference in reproductive success by habitat type.

Habitat	n	Mean seasonal nest success (%) (95% CI)	Mean number of young fledged (95% CI)
Native	92	54 (45–64)	1.8 (1.4–2.1)
Mixed Native	170	47 (40–54)	1.5 (1.3–1.8)
Mixed Exotic	221	58 (52–63)	1.9 (1.7–2.1)
Exotic	313	58 (53–63)	1.8 (1.6–2.0)

Table 3. Average seasonal nest success and fecundity of Southwestern Willow Flycatcher females as a function of their age. Differences by age were most apparent in comparisons of second-year adults with all older adults.

Age	n	Seasonal nest success (%)		Seasonal fecundity	
		Mean	95% C.I.	Mean	95% C.I.
Second-year adult	61	45	33–57	1.0	0.7–1.3
Third-year adult	32	65	48–82	1.8	1.3–2.4
Fourth-year adult	19	61	38–83	1.8	1.0–2.7
Fifth-year adult	14	54	27–80	1.7	0.9–2.5
Sixth-year adult	6	75	31–100	1.8	0.8–2.9

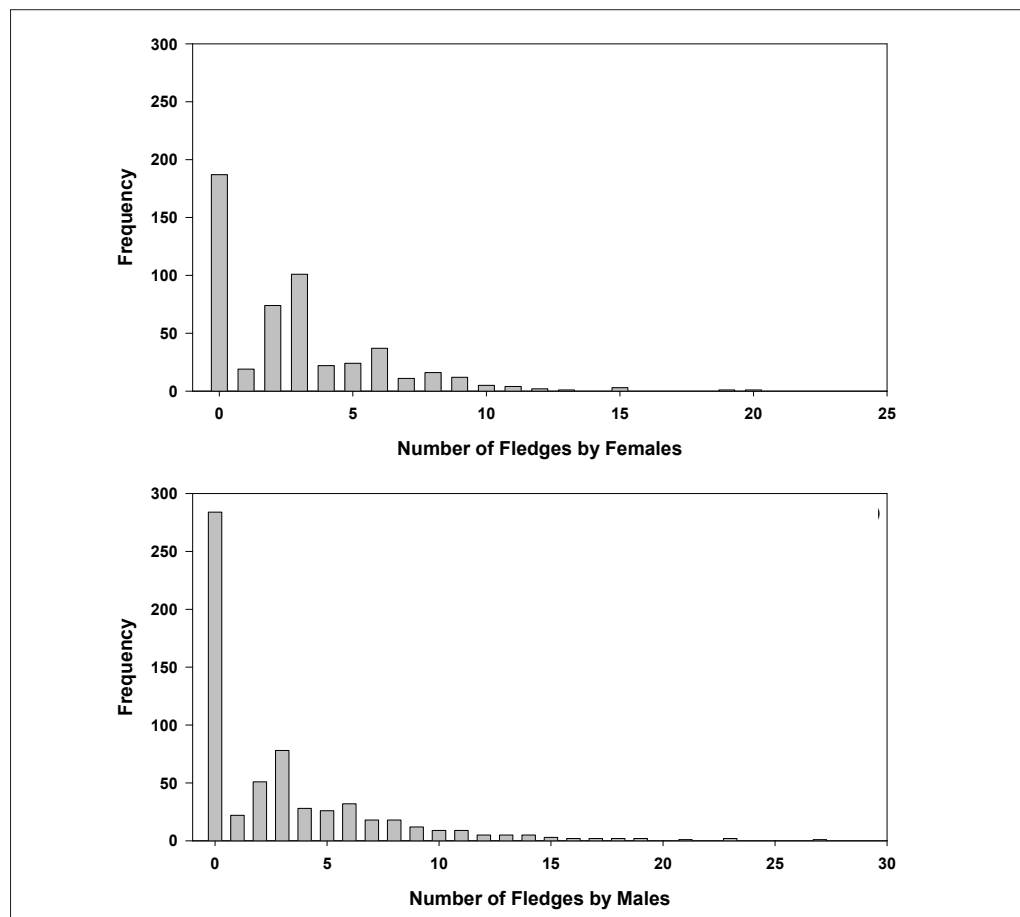


Figure 5. Frequency of the number of fledges produced (Minimum Lifetime Productivity; MLP) over the lifetime of Southwestern Willow Flycatcher females (top; mean MLP = 3.29) and males (bottom; mean MLP = 3.77). Data are for Roosevelt Lake and the San Pedro/Gila, combined.

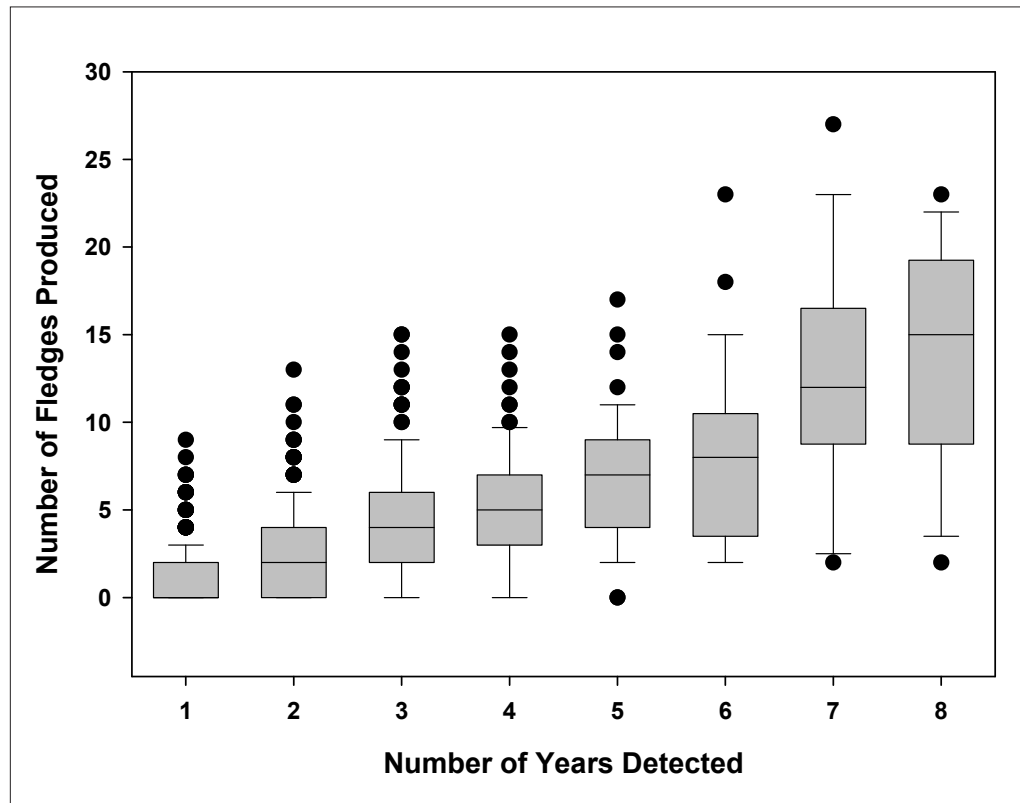


Figure 6. Number of Southwestern Willow Flycatcher fledges produced as a function of the number of years detected, 1996–2005. Mean years detected was 2.46, and the mean number of fledges produced was 3.49. Upper and lower bounds of box plot represents the 25th and 75th percentile, the line in the box represents the median, upper and lower whiskers show the 90th and 10th percentile, respectively. Black dots represent data points outside the 10th and 90th percentile. Data are for Roosevelt Lake and the San Pedro/Gila, combined.

Table 4. Minimum lifetime productivity groups by number of lifetime fledglings produced (0 young, 1–9 young, and 10 or more young) and associated attributes. Both males and females are included. For individuals considered in this analysis only, proportion of population is the proportion of individuals belonging to each of the three groups; proportion of total fledglings is how many fledglings each group contribute to all recorded fledglings; percent male reflects the sex ratio of each group; mean adult lifespan is the average lifespan of individuals from each group; years breeding is the percentage of years alive that individuals from each group were recorded as breeding; mean lifetime nests is the average number of nests produced by individuals in each group over their lifetime; nesting success is the percentage of nests for each group that were successful; polygamous nests are the percentage of nests that resulted from a polygamous pairing; mean lifetime fledges is the average number of total lifetime fledglings recorded for individuals of each group; and, mean yearly fledglings is the average seasonal fecundity of individuals from each group.

Group of individuals	N	Proportion of population (%)	Proportion of total fledglings (%)	Percent male (%)	Mean adult lifespan (%)	Years breeding	Mean lifetime nests	Nesting success (%)	Polygamous nests (%)	Mean lifetime fledglings	Mean yearly fledglings
10 or more lifetime fledglings	62	8	31	73	5.39	91%	9.03	60	54	13.61	2.71
1 to 9 lifetime fledglings	440	55	69	46	2.75	86%	3.37	53	37	4.26	1.60
0 lifetime fledglings	300*	37	0	58	1.40	48%	0.83	0	28	0.00	0.00

*Includes seven individuals of unknown sex

Discussion

Seasonal Nest Success and Fecundity

The average seasonal fecundity of females in our study (1.6 and 2.0, Roosevelt Lake and San Pedro/Gila, respectively) was higher than reported for all southwestern breeding sites (summarized in Stoleson et al. 2000), with the exception of the San Luis Rey River, CA (2.5 per female). Seasonal fecundity estimates for Willow Flycatchers outside of the range of the southwestern subspecies include 1.41 fledglings per pair in the Midwest (Holcomb 1972), 1.4 to 1.5 in northern California (Flett and Sanders 1987), and 1.81 in Oregon (Sedgwick and Iko 1999). Although the methodology used to estimate seasonal fecundity may vary among studies, and thus direct comparison of estimates may be imperfect, the range of values from other studies suggests that the level of productivity at our two study sites is at or above the normal range found elsewhere. The higher fecundity of males is presumably due to polygamy, a finding consistent with other studies (Lubjuhn et al. 2000, Davidson and Allison 2003).

The high variance in seasonal female productivity rates at our study sites, ranging from a low of 0.1 young per female (Roosevelt Lake in 2002) to a high of 2.7 (San Pedro/Gila in 2001), suggests that many factors vary spatially and temporally to influence reproductive success. Identifying the factors associated with the variation can provide insight into threats, ecology, and natural variation in the environment, as well as provide information important for demographic modeling. Many of the factors will be explored by AGFD, but several were apparent from our analysis of seasonal reproductive success. The following are factors that we found contribute to the observed variability in flycatcher's seasonal reproductive success.

Site and year interacted, explaining significant amounts of the variation observed in seasonal productivity, and functioned as "proxies" for a suite of unknown factors. Roosevelt Lake had higher measures of seasonal productivity in some years, and San Pedro/Gila in others, although the average (10 year) seasonal productivity measures were generally greater at the San Pedro/Gila study site. Sites may differ as a result of a combination of vegetation characteristics, predator types and densities, hydrology, or historical occurrences unique to each site (i.e., how long since the last scouring flood), as well as random differences one would expect when comparing samples from two distinct locations. Yearly differences may result from fluctuations in precipitation (see below), arthropod abundance, changing vegetation structure (succession), fluctuating ground water levels, etc. Thus, site and year differences are primarily important to our interpretations because they highlight the inherently high temporal and spatial variation in the reproductive success of a species that breeds in dynamic and highly variable riparian landscapes.

Perhaps contributing to site and year differences were two strong predictors of seasonal productivity: predation and

precipitation. Predation was the primary cause of nest failure for flycatchers in our study, as is the case for most open-cup nesting Neotropical migrants as well (Martin 1992). In Arizona, where flycatcher nest predators were documented by AGFD video monitoring of nests, most predation was by hawks and snakes but other nest predators were noted as well (Tudor et al. 2004).

Rainfall in arid environments like the Sonoran Desert can have important influences on breeding success (Grant and Grant 1987). In our study, the influence of late winter and spring precipitation levels on seasonal nest success was more pronounced in dry than in wet years. At Roosevelt Lake, three of four years with nest success >60% (long-term mean was 52%) had higher than average late winter and spring rainfall. The case was similar at the San Pedro/Gila, where the years of highest nest success generally had the highest late winter and spring rainfall. However, drought conditions had a much more marked effect. At both study sites, the extreme drought year of 2002 clearly stood out as the worst year for seasonal productivity, with seasonal nest success at Roosevelt as low as 6% and seasonal fecundity as low as 0.1. The influence of rainfall on reproduction is likely the result of its effect on vegetation vigor and subsequent production of invertebrate food resources (Noy-Meir 1973, Cody 1981, Boag and Grant 1984, Grant and Grant 1987). As evidence that prey availability may be a driving factor affecting reproductive success during drought years, a concurrent study at Roosevelt Lake (Durst 2004) documented a five-fold decrease in arthropod biomass in 2002 compared to 2003, a relatively normal year with regard to precipitation. Predictions of more frequent and more intense droughts in the southwestern U.S. in the face of global climate change (IPCC 2002), if realized, may negatively influence the productivity of flycatcher populations over long periods of time.

Breeding Age

The finding that older, presumably more experienced flycatchers were more productive breeders compared to first time, young breeders is consistent with other studies (McCleery and Perrins 1989, Hatch and Westneat 2007). The difference was most pronounced when comparing young adults to older adults, with the difference between older adults being slight. Presumably older adults gain valuable experience in foraging and nest site location, as well as survival and migration skills, which contribute to increased success. While the exact reasons for these age-based differences may not be apparent, they indicate that populations with a good representation of older adults may be more productive than populations comprised entirely or mostly of younger birds. The latter situation may occur at newly colonized sites, if the colonizers are primarily young birds.

Minimum Lifetime Productivity

Over this 10-year study, adult Southwestern Willow Flycatchers had a mean MLP of 3.5 fledglings per individual, with males having a higher MLP (3.8) than females (3.3). This is slightly lower than the 3.6 fledglings per adult reported for female flycatchers in Oregon by Sedgwick and Iko (1999), the only other researchers to date who have published values for Willow Flycatchers. Comparison with other bird species is of limited use, because differences in lifespan, clutch size, nest type, and many other factors can influence lifetime productivity.

Estimates of lifetime productivity are difficult to collect because they require long-term studies of sufficient length and scope to track many individuals throughout their lives. The mean life expectancy for flycatchers is just under 2 years (see chapter 2), and the mean number of years adults were detected (once having survived as juveniles) was 2.5. Although some banded individuals in this study lived for nine or more years, they were very few, and for the majority of individuals 3–5 generations of breeders were encompassed in this study. Equally important is the ability to account for all breeding efforts made by individuals. The non-detection of breeding attempts and emigration away from the study sites could bias the estimates of lifetime productivity downward. While it is certain that we missed some reproductive efforts and some permanent emigration, we believe the number missed is low and that our mean estimates are close to the true values. First, although right and left censoring individuals reduces the likelihood of including most individuals that bred before or after the study period, some long-lived individuals certainly did, but probably in small numbers. Second, although not all nests at the study sites were monitored, efforts to track all birds were made in every year, such that confidence in knowing where individuals were in each year was high. Those individuals confirmed to a territory where we did not know their nest success were excluded. Finally, although emigration from the study site is known to occur, evidence is that it is at low levels (see chapter 4), and thus we believe not likely to significantly affect our productivity estimates.

As birds age and breed over more years, they have the opportunity to increase their lifetime productivity. The mean number of minimum lifetime fledglings produced by females (3.3) was approximately double the average seasonal fecundity (1.6–2.0, at Roosevelt Lake and the San Pedro/Gila, respectively). This suggests that the average flycatcher has two successful breeding seasons in their lifetime. There was not a single age class of flycatchers that produced the most offspring, but in general birds living to older age classes had greater lifetime productivity because they had more breeding opportunities. Longevity and reproductive success may also be interrelated if some birds consistently have higher quality territories that allow them not only to be more productive, but also to live longer (Hogstedt 1980, Smith 1981).

There was substantial variation in minimum lifetime productivity; most flycatchers did not produce any offspring, while a few produced many. This closely matches a pattern

seen in many bird species (Newton 1989). The 37% of the banded population that did not produce any fledglings were present as potentially breeding adults for only an average of 1.3 years and only attempted to breed in approximately half (48%) of the years detected. For flycatchers in the categories of fledging 1–9 young and ≥ 10 young, there was a corresponding increase in the number of years they were present as potentially breeding adults (2.5 and 5.1 years, respectively), and in the proportion of years with attempted breeding (86% and 91%, respectively). Thus, an understanding of critical elements that determine lifetime productivity requires consideration of factors affecting survivorship (Newton 1989, Espie et al. 2000).

Management and Research Considerations

Habitat Restoration and Management

We did not find a difference in seasonal reproductive success between flycatchers breeding in patches dominated by saltcedar compared with those in native-dominated patches. Therefore, within the Roosevelt Lake and San Pedro/Gila study sites, there does not appear to be a potential benefit to actively removing or controlling saltcedar to increase flycatcher productivity. In some patches, removal of the dense saltcedar midstory—if not replaced quickly by willow or other native trees of similar density and structure—could reduce the suitability of the patch by reducing the vegetation density and cover. The Southwestern Willow Flycatcher Recovery Plan (USFWS 2002) discusses these considerations, with regard to whether and how to proceed with saltcedar control within patches that are currently occupied by breeding flycatchers.

Drought and Climate Change

Lower than average precipitation reduced flycatcher seasonal productivity at both Roosevelt Lake and the San Pedro/Gila. If the predictions of some current climate change models are correct, the southwestern United States will experience increasingly more frequent and severe droughts (Frederick and Schwarz 1999). This could lead to more frequent incidents of extremely low reproductive success, such as occurred at Roosevelt Lake during the 2002 drought. Ultimately, successive years of low productivity could lead to unsustainable local populations. The difference in reproductive success between the two study sites in 2002 (with Roosevelt Lake more negatively affected) highlights the value of managing for large healthy populations at multiple sites where effects of drought and other calamities may impact sites differently. Further, it may be possible to develop management actions to reduce the negative effects of repeated or severe droughts on flycatcher breeding habitat. Possibilities at Roosevelt Lake include manipulation of water tables via management of reservoir

water levels in order to maintain a moist zone for riparian trees. For riverine landscapes such as the San Pedro River, idling of groundwater pumps adjacent to flycatcher breeding habitat in dry years, or provision of supplementary water, may slow the rate of water table decline and sustain healthy tree phenology.

References

- Anders, A.D., and M.R. Marshall. 2005. Increasing the accuracy of productivity and survival estimates in assessing landbird population status. *Conservation Biology* 19:66–74.
- Arcese, P., J.N.M. Smith, and M.I. Hatch. 1996. Nest predation by cowbirds and its consequences for passerine demography. *Proceedings of the National Academy of Sciences of the United States of America* 93:4608–4611.
- Beissinger, S.R., and D.R. McCullough. 2002. Population viability analysis. University of Chicago Press, Chicago.
- Boag, P.T., and P.R. Grant. 1984. Darwin's finches (*Geospiza*) on Isla Daphne Major, Galapagos: Breeding and feeding ecology in a climatically variable environment. *Ecological Monographs* 54:463–489.
- Brown, D.E. (ed.). 1994. Biotic Communities – Southwestern United States and Northwestern Mexico. University of Utah Press, Salt Lake City, UT.
- Causey, C.F., M.G. Pollock, S.L. Durst, P.J. Newell, E.H. Paxton, and M.K. Sogge. 2006 Survivorship and movements of Southwestern Willow Flycatchers at Roosevelt Lake, Arizona—2005. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix, AZ.
- Clobert, J. and J.D. Lebreton. 1991. Estimation of demographic parameters in bird populations. *Oxford Ornithology Series* 1:75–104.
- Clutton-Brock, T.H. 1988. Reproductive success: Studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, IL, USA.
- Cody, M.L. 1981. Habitat selection in birds: The roles of vegetation structure, competitors, and productivity. *BioScience* 31:107–113.
- Davidson, R.F., and L.J. Allison. 2003. Effects of monogamy and polygyny on reproductive success in southwestern willow flycatchers (*Empidonax traillii extimus*) in Arizona. *Studies in Avian Biology* 26:118–124.
- Donovan, T.M., P.W. Jones, E.M. Annand, and F.R. Thompson III. 1997. Variation in local-scale edge effects on cowbird distribution and nest predation. *Ecology* 78:2064–2075.
- Durst, S.L. 2004. Southwestern Willow Flycatcher potential prey base and diet in native and exotic habitats. MS thesis. Northern Arizona University, Flagstaff, AZ.
- Durst, S.L., M.K. Sogge, H. English, S.O. Williams, B.E. Kus, and S.J. Sferra. 2006. Southwestern Willow Flycatcher breeding site and territory summary—2004. U.S. Geological Survey report to Bureau of Reclamation, Phoenix, AZ.
- English, H.C., A.E. Graber, S.D. Stump, H.E. Telle, and L.A. Ellis. 2006. Southwestern Willow Flycatcher 2005 survey and nest monitoring report. Arizona Game and Fish Technical Report 248.
- Espie, R.H.M., L.W. Oliphant, P.C. James, I.G. Warkentin, and D.J. Lieske. 2000. Age-dependent breeding performance in Merlins (*Falco columbarius*). *Ecology* 81:3404–3415.
- Flett, M.A., and S.D. Sanders. 1987. Ecology of a Sierra Nevada population of Willow Flycatchers. *Western Birds* 18:37–42.
- Frederick, K.D., and G.E. Schwarz. 1999. Socioeconomic impacts of climate change on U.S. water supplies. *Journal of the American Water Resources Association* 35:1563–1584.
- Grant, P.R., and B.R. Grant. 1987. The extraordinary El Nino event of 1982–83: Effects on Darwin's finches on Isla Genovesa, Galapagos. *Oikos* 49:55–66.
- Grzybowski, J.A., and C.M. Pease. 2005. Re-nesting determines seasonal fecundity in songbirds: What do we know? What should we assume? *Auk* 122:280–291.
- Hatch, M.I., and D. Westneat. 2007. Age-related patterns of reproductive success in House Sparrows *Passer domesticus*. *Journal of Avian Biology* 38:603–611.
- Hogstedt, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territory quality. *Science* 210:1148–1150.
- Holcomb, L.C. 1972. Nest success and age-specific mortality in Traill's Flycatchers. *Auk* 89:837–841.
- Intergovernmental Panel on Climate Change. 2002. Climate change and biodiversity. [Accessed 10/01/06 at: www.ipcc.ch/pub/tpbiodiv.pdf]
- Koronkiewicz, T.J., E.H. Paxton, and M.K. Sogge. 2005. A technique to produce aluminum color bands for avian research. *Journal of Field Ornithology* 76:94–97.
- Li, S.-H., and J.L. Brown. 1999. Influence of climate on reproductive success in Mexican Jays. *Auk* 116:924–936.
- Lubjuhn, T., W. Winkel, J.T. Epplen, and J. Brun. 2000. Reproductive success of monogamous and polygynous Pied Flycatchers (*Ficedula hypoleuca*). *Behavioral Ecology and Sociobiology* 48:12–17.

- Marshall, R.M. 2000. Chapter 2: Population status on breeding grounds. Pages 3–11 *in* Status, ecology, and conservation of the Southwestern Willow Flycatcher. (D.M. Finch and S.H. Stoleson, eds.) USFS Rocky Mountain Research Station, Gen. Tech. Rep. RMRS-GTR-60. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Marshall, R.M., and S.H. Stoleson. 2000. Chapter 3: Threats. Pages 13–24 *in* Status, ecology, and conservation of the Southwestern Willow Flycatcher (D.M. Finch and S.H. Stoleson, eds.). General Technical Report RMRS-GTR-60. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Martin, T.E. 1992. Breeding season productivity: What are appropriate habitat features for management? Pages 455–473 *in* Ecology and Conservation of Neotropical Landbirds (J.M. Hagan III and D.W. Johnston eds.). Smithsonian Institution Press, Washington, D.C.
- McCabe, G.J., M.A. Palecki, and J.L. Bentancourt. 2004. Pacific and Atlantic Ocean influences on multidecadal drought frequency in the United States. *Proceedings of the National Academy of Sciences* 101:4136–4141.
- McCleery, R.H. and C.M. Perrins. 1989. Great Tit. *In* Lifetime reproduction I birds. I. Newton, ed. Academic Press, New York.
- Newton, I. 1989. Lifetime reproduction in birds. Academic Press, London UK.
- Noy-Meir, I. 1973. Desert ecosystems: Environment and producers. *Annual Review of Ecology and Systematics* 4:25–51.
- Paxton, E.H., and J.C. Owen. 2002. An aging guide for Willow Flycatcher nestlings. Colorado Plateau Field Station, Northern Arizona University.
- Paxton, E.H., M.K. Sogge, T.D. McCarthey, and P. Keim. 2002. Nestling sex ratio in the Southwestern Willow Flycatcher. *Condor* 104:877–881.
- Pearson, T., M.J. Whitfield, T.C. Theimer, and P. Keim. 2006. Polygyny and extra-pair paternity in a population of Southwestern Willow Flycatchers. *Condor* 108:571–578.
- Perrins, C.M., J.-D. Lebreton, and G.J.M. Hirons. 1991. Bird population studies: Relevance to conservation and management. Oxford University Press, Oxford, UK.
- Pollock, M.G., and E.H. Paxton. 2006. Floating mist nets: A technique for capturing birds in flooded habitat. *Journal of Field Ornithology* 77:335–338.
- Pyle, P. 1998. Eccentric first-year molt patterns in certain Tyrannid flycatchers. *Western Birds* 29:29–35.
- Ralph, C.J., G.R. Geupel, P. Pyle, T.E. Martin, and D.F. DeSante. 1993. Handbook of field methods for monitoring landbirds. USFS General Technical Report PSW-GTR-144. Albany, CA; Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. 41 pp.
- Robinson, S.K., F.R. Thompson III, T.M. Donovan, D.R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987–1990.
- Rodenhouse, N.L. and R.T. Holmes. 1992. Results of experimental and natural food reductions for breeding Black-throated Blue Warblers. *Ecology* 73:357–372.
- Rotenberry, J.T. and J.A. Wiens. 1989. Reproductive biology of shrubsteppe passerine birds: Geographical and temporal variation in clutch size, brood size, and fledging success. *Condor* 91:1–14.
- Rotenberry, J.T. and J.A. Wiens. 1991. Weather and reproductive variation in shrubsteppe sparrows: A hierarchical analysis. *Ecology* 72:1325–1335.
- Rourke, J.W., T.D. McCarthey, R.F. Davidson, and A.M. Santaniello. 1999. Southwestern Willow Flycatcher nest monitoring protocol. Nongame and Endangered Wildlife Program Technical Report 144. Arizona Game and Fish Department, Phoenix, AZ. 32pp.
- Sedgwick, J.A. 2000. Willow Flycatcher (*Empidonax traillii*). *In* The Birds of North America, No. 533 (A. Poole and F. Gill eds.). The Academy of Natural Sciences, Philadelphia, PA and the American Ornithologists' Union Washington, DC.
- Sedgwick, J.A., and W.M. Iko. 1999. Costs of Brown-Headed Cowbird parasitism to Willow Flycatchers. *Studies in Avian Biology* 18:167–181.
- Smith, J.N.M. 1981. Does high fecundity reduce survival in Song Sparrows? *Evolution* 35:1142–1148.
- Smith, R.J., and F.R. Moore. 2003. Arrival fat and reproductive performance in a long-distant passerine migrant. *Oecologia* 134:325–331.
- Sogge, M.K., J.C. Owen, E.H. Paxton, S.M. Langridge, and T.J. Koronkiewicz. 2001. A targeted mist net capture technique for the Willow Flycatcher. *Western Birds* 32:167–172.
- Stoleson, S.H., Whitfield, M.J., and M.K. Sogge. 2000. Chapter 8: Demographic characteristics and population modeling. Pages 83–93 *In* Status, ecology, and conservation of the Southwestern Willow Flycatcher (D.M. Finch and S.H. Stoleson, eds.). General Technical Report RMRS-GTR-60. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.

- Tudor, A.A., P.E.T. Dockens, D.K. Bolen, and T.D. McCarthy. 2004. Predators of the Southwestern Willow Flycatcher: Identification using video cameras. Arizona Game and Fish Department Report.
- Unitt, P. 1987. *Empidonax traillii extimus*: an endangered subspecies. *Western Birds* 18:137–162.
- U.S. Fish and Wildlife Service. 1993. Proposal to list the Southwestern Willow Flycatcher as an endangered species and to designate critical habitat. *Federal Register* 58:39495–39522 (July 23, 1993).
- U.S. Fish and Wildlife Service. 1995. Final rule determining endangered status for the Southwestern Willow Flycatcher. *Federal Register* 60:10694 (February 27, 1995).
- U.S. Fish and Wildlife Service. 2002. Southwestern Willow Flycatcher recovery plan—Final. U.S. Fish and Wildlife Service, Albuquerque, NM.
- Weidinger, K. 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. *Journal of Animal Ecology* 71:424–437.
- Woodworth, B.L. 1999. Modeling population dynamics of a songbird exposed to parasitism and predation and evaluating management options. *Conservation Biology* 13:67–76.
- Woelfenden, G.E., and J.W. Fitzpatrick. 1984. *The Florida Scrub Jay: Demography of a cooperative-breeding bird*. Princeton University Press, Princeton, NJ, USA.

Chapter 4—Movement

Introduction

One of the most important life history traits of a species, and one of the least understood, is the movement of individuals over space and time (e.g., natal dispersal, immigration and emigration of adults, migration; Winkler et al. 2005). Movement and philopatry have often been associated with the acquisition and retention of higher-quality territories, respectively (Brooke 1979), and thus are adaptive to an individual's lifetime reproductive success (Greenwood and Harvey 1982, Part and Gustafsson 1989). Movement is essential for genetic variation and inbreeding avoidance (Frankham 1995), and is the foundation of metapopulation dynamics (Hanski and Gilpin 1997). Further, patterns of movement can indicate how a bird perceives its landscape and reacts to changing conditions, as well as inform our understanding of habitat choice (Cam et al. 2004, Ward 2005, Breton et al. 2006). Yet, movement patterns for highly vagile animals such as migratory birds are difficult to document. Most bird studies are restricted to small geographic areas that are insufficient to detect medium to long-distance movements, and there is a growing consensus that movement patterns and dispersal distances are poorly documented in most studies (Greenwood and Harvey 1982, Winkler et al. 2004, 2005). As a result, this crucial aspect of a species' ecology is rarely well understood.

Every year migratory birds return to their breeding grounds and need to select suitable habitat in which to breed. For first time breeders, they must find suitable habitat and an unoccupied territory. Returning breeders must choose whether to return to their previous territory (if available), or move to a new location. Factors that influence these choices can have important and long-term impacts on the overall population numbers of their breeding site. Fidelity and immigration can sustain a site, while emigration can drain it (Pulliam 1988, Stacey and Taper 1997). Past reproductive success, predation risk, and changing landscapes can all influence the movement of birds. Thus, documenting the extent of movements and determining correlates that may elucidate the causal factors underlying choices of philopatry versus dispersal are critical to understanding population structure and dynamics.

The Southwestern Willow Flycatcher (*Empidonax traillii extimus*) is a small, migratory passerine that breeds exclusively in riparian habitats scattered throughout portions of the southwestern U.S. (Unitt 1987, Marshall 2000) and winters from central Mexico south to northern South America (Sedgwick 2000). Flycatcher numbers have declined precipitously as riparian habitats on the breeding grounds have been lost or

modified (USFWS 1993, Marshall and Stoleson 2000), and *E.t. extimus* was listed as a federally endangered species in 1995 (USFWS 1995). At the time of listing, many aspects of the flycatcher's biology were poorly understood (Marshall and Stoleson 2000, Stoleson et al. 2000). Few banding studies had been conducted and little was known about patterns of flycatcher movements.

From 1996 to 2005, we collaborated with the Arizona Game and Fish Department (AGFD) to conduct a large demographic study of Southwestern Willow Flycatchers in central Arizona at two core study sites, as well as multiple auxiliary breeding sites. In this chapter, we describe natal and breeding dispersal, and explore factors influencing movement patterns and territory fidelity. By linking movement patterns with habitat dynamics and productivity, we investigated potential causal factors that drove movement over the 10-year period. With as many as 80% of detected flycatchers banded in a given year at the two primary study sites, and information from other sites across the Southwest, this study allows us to develop a robust understanding of flycatcher movement patterns and factors that influence them.

Methods

Study Site

Our two focal study sites (fig. 1) were breeding populations at Roosevelt Lake (33°39'N, 110°58'W) and the San Pedro/Gila River confluence (hereafter San Pedro/Gila; 32°59'N, 110°46'W), where we conducted demographic research in cooperation with AGFD from 1996 to 2005 (Causey et al. 2006, English et al. 2006). We defined sites as a collection of riparian woodland patches, occupied by breeding flycatchers, which are collectively closer to one another than to other breeding patches, and are found within the same drainage (or along the same lake). Exact definitions of a site are difficult, and the definition of a site differs regionally (Durst et al. 2006). Likewise, we defined a breeding patch as a distinct patch of riparian vegetation which breeding flycatchers occupied, that is separated from other riparian vegetation by non-riparian habitat (e.g., open ground, scrub, river). We delineated breeding habitat patches by projecting territory locations for all years onto rectified aerial photographs, and used natural breaks or distribution of territories to estimate their approximate boundaries manually in ArcView 3.0 (ESRI, Inc).

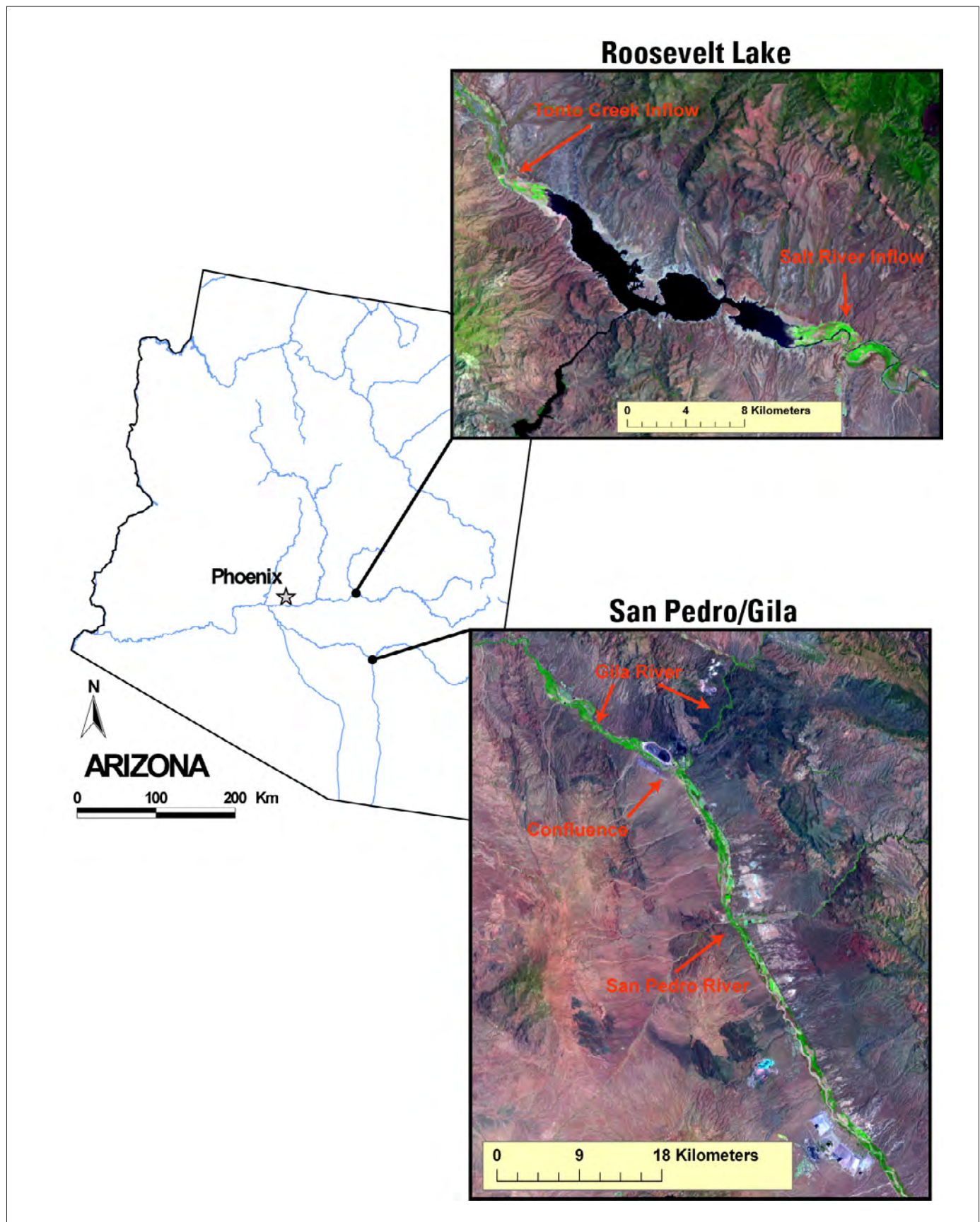


Figure 1. Location of the Roosevelt Lake and San Pedro/Gila study areas in central Arizona.

Our two study sites supported among the largest known Southwestern Willow Flycatcher breeding populations throughout the period of this study (Durst et al. 2006), with mean population sizes of 201 and 239 individuals at Roosevelt Lake and San Pedro/Gila, respectively (see chapter 5). At each site, extensive surveys were conducted at least three times in the breeding season to detect all territorial flycatchers within the immediate and surrounding areas. In addition, multiple other breeding sites in Arizona and throughout the Southwest (49–444 km away) were periodically visited, which along with cooperative efforts of other researchers allowed detection of many dispersing or moving flycatchers (fig. 2).

The breeding habitat at the Roosevelt Lake and San Pedro/Gila study sites consisted of a heterogeneous mosaic of discrete riparian forest patches of varying ages and vegetation composition, ranging from 0.2 to 43 ha in size. At both study sites, we characterized habitat at both the territory and patch level based on vegetation composition as: (1) native ($\geq 90\%$ native vegetation), (2) mixed native (50%–89% native vegetation), (3) mixed exotic (50%–89% exotic vegetation), and (4) exotic ($\geq 90\%$ exotic vegetation). Native habitat was characterized by Goodding's willow (*Salix gooddingii*) and Fremont cottonwood (*Populus fremontii*). Exotic habitat was dominated by tamarisk (saltcedar; *Tamarix spp.*). The understory vegetation consisted of a variety of grasses, forbs, and shrubs (mesquite [*Prosopis spp.*], coyote willow [*S. exigua*], tama-

risk, *Baccharis spp.*, and cocklebur [*Xanthium strumarium*]). Adjacent and surrounding non-riparian habitats were primarily composed of Sonoran Desert Uplands (Brown 1994), and in some cases agricultural lands.

Roosevelt Lake Study Site

The Roosevelt Lake study site consisted of two sub-sites each concentrated at the confluence of the reservoir and the inflows of the Salt River and Tonto Creek (approximately 30 km apart), with breeding documented as far as 12 km upstream on Tonto Creek and 9 km on the Salt River. The number of riparian patches in which breeding was documented varied over time as a result of colonization or desertion of patches, in many cases driven by fluctuating lake levels. Over the 10-year period, we documented breeding occurring in a maximum of 23 patches encompassing approximately 242 ha of riparian habitat. Long-term persistent drought conditions between 1996 and 2005 in the Southwest (McCabe et al. 2004) resulted in reservoir levels dropping to a low of 10% capacity in 2002; the exposed lakebed was colonized by riparian vegetation, which was subsequently colonized by breeding flycatchers (see chapter 6). In 2005, following high winter precipitation, Roosevelt Lake filled to near capacity, inundating much of the breeding habitat that was occupied in 2004 (see chapter 6).

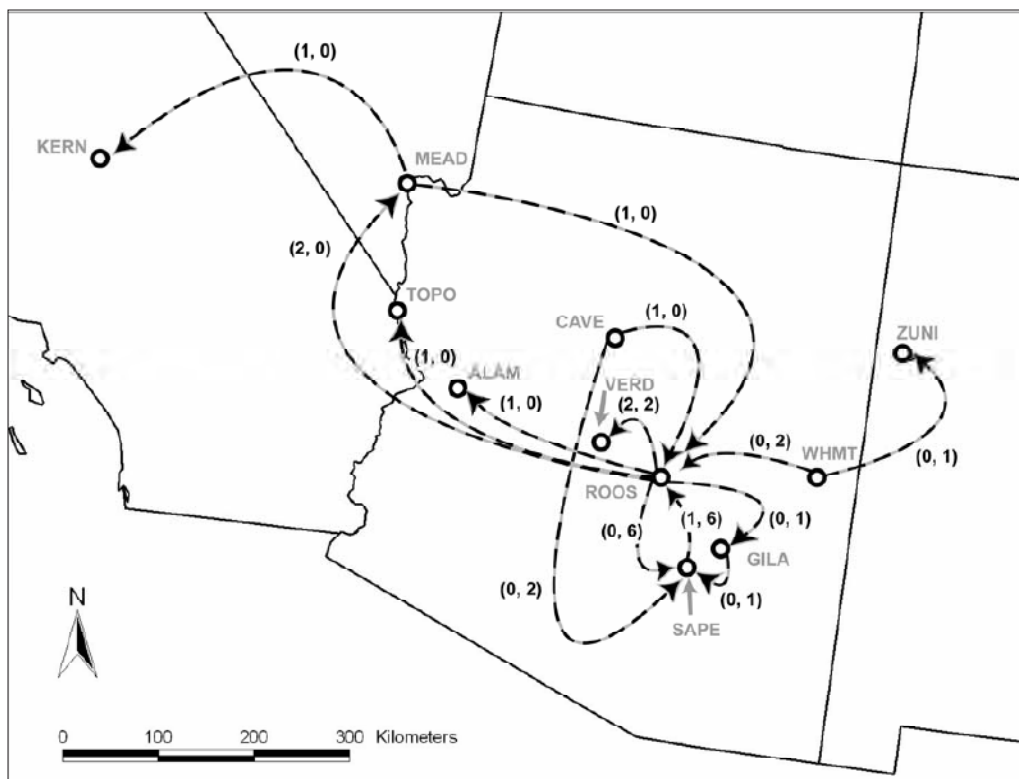


Figure 2. Thirty between-drainage dispersal events by Southwestern Willow Flycatchers (natal, breeding) were documented from 1997 to 2005. Adult movement accounted for 21 cases (ranging from 49km to 214 km), while natal dispersal accounted for 9 cases (ranging from 52km to 444 km). Sites are coded as follows: KERN=Kern River Preserve; MEAD=the Lake Mead area; TOPO=Topock Marsh; ALAM=Alamosa Lake, Browns Crossing; CAVE=Camp Verde; VERD=Horseshoe Reservoir; ROOS=Roosevelt Lake; SAPE=San Pedro/Gila River; GILA=Gila River near Safford; WHMT=White Mountains; ZUNI=Zuni Pueblo.

San Pedro/Gila Study Site

The San Pedro/Gila study site encompassed 101 km of river system, centered at the confluence of the free-flowing San Pedro River and the regulated Gila River, and extending upstream of the San Pedro to San Manuel Crossing and downstream of the Gila River to Kelvin Bridge. As with Roosevelt Lake, the number of patches changed over the 10-years, with as many as 29 habitat patches documented as supporting breeding efforts, comprising approximately 222 ha of riparian forest along this stretch.

The Roosevelt Lake and San Pedro/Gila study sites, combined with other sites, formed our study area. Other sites included Greer and Alpine in the White Mountains, AZ; Camp Verde, AZ; Gila River near Safford, AZ; Pinal Creek, AZ; Horseshoe Reservoir, AZ; Brown's Crossing near Alamo Lake, AZ; and several sites along the Colorado River including the Grand Canyon, Lake Mead, and Topock Marsh, AZ; and Mesquite and Mormon Mesa, NV (see Durst et al. 2006).

Banding and Resighting

To provide robust estimates of movement, our objective was to band as many adults and nestlings as possible over the period of this study. Nestlings and adults were banded at both Roosevelt Lake and the San Pedro/Gila from 1996 to 2005, with the exception that nestling banding at the San Pedro/Gila ceased after 2000. Each nestling was banded at 7–10 days of age (as determined via Paxton and Owen 2002) with a color-anodized, numbered federal bird band; banded nestlings detected and recaptured as adults in subsequent years were given an additional color band to produce a unique color combination to assist in resight tracking (Koronkiewicz et al. 2005). A drop of blood was taken at the time of banding for genetic gender determination (Paxton et al. 2002). Each adult captured was banded with a color-anodized, numbered federal bird band and a second color band (Koronkiewicz et al. 2005) to create a unique color combination for each individual. Adults were primarily target-netted (Sogge et al. 2001, Pollock and Paxton 2006) to allow for efficient, focused capture effort. From 2001 to 2005, we also conducted extensive passive netting operations at Roosevelt Lake (see Ralph et al. 1993) aimed at capturing non-territorial flycatchers that were not readily detectable with conventional survey techniques (i.e., tape-playback; Sogge et al. 1997). Overall, the combined netting efforts resulted in an average of 74% (range: 68%–88%) of detected flycatchers being banded in a given year at both study sites from 1996 to 2000 and at Roosevelt Lake from 2001 to 2005 (exact percentages at San Pedro/Gila are not available for this latter period). To determine gender of adult flycatchers, we used a combination of physical characteristics (presence of a cloacal protuberance for males or brood patch for females), behavioral cues, and genetic sexing methods

(Paxton et al. 2002). Adult flycatchers were aged as “known” if the individual was first banded as either a nestling or a second-year (SY: based on retained rectrices; Pyle 1998), or “unknown” (2 or more calendar years of age).

We tracked banded flycatchers over the 10 years primarily through resighting, supplemented by occasional recaptures. This process of using binoculars to determine the unique color band combination on a flycatcher's legs. Resighting is a minimally intrusive method of “recapture”, and the most reliable method for establishing the particular territory a flycatcher occupies because playback capture techniques can lure adults in from neighboring territories. To ensure high accuracy in the identification of resighted individuals, only multiple high-confidence resights from at least two different observers on different days were used to confirm the identity and territory of individual banded flycatchers. Computer databases were updated and queried daily to prioritize resighting efforts, allowing us to track as many as 393 uniquely color banded individuals in a given year. Field crew sizes of up to 35 personnel (USGS and AGFD combined) allowed for intensive detection and resighting of banded individuals, resulting in nearly all territorial flycatchers detected at the study sites being positively identified multiple times in each year. Recaptures, especially via passive netting, provided additional detection resolution, especially for non-territorial birds.

The following are definitions of the multiple types of movement behaviors we observed::

- *Between-year movement behavior*—The term used to describe the choice an adult makes upon returning to the breeding grounds: territory fidelity, patch fidelity, or movement (either between-patch or between-site).
- *Between-year movements*—Adult movement from a breeding location (or last known location) in one breeding season to a different breeding location (or first known location) in a subsequent breeding season. In most cases, movements we observed were between consecutive years, but not always (unless noted otherwise; see chapter 7). Between-year movements could be between-sites, between-patches, or within-patch. To be considered a movement within the same patch (as opposed to Territory Fidelity), birds must have moved physically at least 50 m from their previous territory (twice the average territory radius at our study sites). For non-territorial individuals, movements must have been at least 50 m from the previous detection location.
- *Breeding dispersal*—Adult movement from one breeding site to a different breeding site, between years. This term is synonymous with between-year between-site movement (above).
- *Emigration*—The detected movement of birds away from a site or patch (dependent on context) to some other location.

- *Immigration*—The detected movement of birds into a site or patch (dependent on context) from some other location.
- *Natal dispersal*—Movement from a flycatcher's natal location to the first location it was detected at as an adult. When first detected as an adult, birds could be either territorial or non-territorial (see chapter 7). The first detection may not have occurred until several years after the natal year. Once detected as an adult, all subsequent movement is defined as adult movement.
- *Patch fidelity*—Between-year, within-patch movement, with movement distance greater than 50 m. Synonymous with between-year, within-patch movement (above). This term excludes those individuals that returned to their previous year's territory, which could also be considered as a type of patch fidelity.
- *Territory fidelity*—An adult returning from the wintering grounds to its breeding territory from the previous year. We defined a return as territory fidelity if the nest location or territory center in "year t+1" was within 50 m of the nest location or territory center of an individual in "year." In this report, territory fidelity is synonymous with the term philopatry.
- *Within-season movement*—Adult movement from one location to another, detected within the same breeding season. Movement can be within the same patch, between patches, or between sites. To be considered a movement within the same patch (as opposed to Territory Fidelity), birds must have moved physically beyond neighboring territories or at least 50 m from their previous territory (twice the average territory radius at our study sites). For non-territorial individuals, movements must have been at least 50 m from the previous location. Within-season movement can be divided into the following four categories:
 1. *pre-breeders*—detected as non-territorial individuals that were then detected later in the season at another location as territory holders;
 2. *post-breeders*—flycatchers that were territory holders, but were detected in another location later in the season as non-territorial individuals;
 3. *territory switchers*—individuals that were territorial in one location, then left to become territorial in another area, with at least one territory separating the old and new location; and
 4. *non-territorial movers*—presumably floaters, that were detected at least twice at different locations, being territorial at none of these.

Statistical Analysis

Natal, Within-season, and Between-year Movement Distances

All measures of distance were calculated via straight-line distances between the two locations of interest. For example, the distance of a between-year movement is the distance from where the adult was last detected in "year t" to the first location it was detected in "year t+1". If an adult is not detected for a year (see chapter 7), distance is from the locations it was known to be at before and after the year in which it was not detected. Thus, distances given are a minimum measure of movement between two points of detection (even though birds likely did not take a direct route between the two points). To determine distance, we used ArcView 3.3 (ESRI, Inc) to obtain straight line distances (in units of 0.01 km) via the Distance Matrix extension with an Albers Equal-area projection which ensures a spatially accurate measure of distance. We evaluated statistical differences in movement distances between various factors (e.g., site, sex, age) using an ANOVA in JMP 5.0 (SAS, Inc). In addition, to evaluate the frequency of movements by distance for the two study sites, we counted the number of movements for each 5 km block, and graphed the resulting frequencies in SigmaPlot 8.0 (SPSS, Inc). For San Pedro/Gila, we fitted a quadratic regression line to the frequency of movement by distance in JMP 5.0 (SAS, Inc).

Between-year Movement Behavior

We evaluated differences in the proportion of between-year movement behavior by sex, site, and year using a chi-squared test (χ^2) in JMP 5.0 (SAS, Inc). To evaluate the frequency of between-year movement behaviors at the individual level, we used a multistate model in Program MARK (White and Burnham 1999). The multistate models provide estimates of survivorship (Φ) and detection (p) probabilities based on the between-year movement behavior, and account for the probability of transitions (Ψ), i.e., changing behaviors from one year to another. We coded an encounter history table (see chapter 2) of individual adult flycatchers, 1996–2005 (excluding Roosevelt Lake in 2005 because of the confounding effects of the inundation-caused displacement), with one of three states: (1) territory fidelity, (2) patch fidelity, and (3) movement, with both between-patch and between-site movement combined; years undetected were coded as "0". We used a multinomial logit (Mlogit) link to constrain the model to ensure that the transition probabilities among the three different behaviors all summed to 1 (see chapter 2). The survivorship estimate is the probability that an adult showing a particular behavior in "year t" survives to "year t+1", regardless of which behavior it shows in the subsequent year, and the detection probability

of a particular behavior is the probability that it is detected in “year t ” for that behavior.

Factors Influencing Territory Fidelity Versus Movement

To evaluate how different factors in one year influence between-year movement behavior in the next, we needed to consider only those individuals for which we had information in successive years. Of the initial 1,080 banded flycatcher adults at the two study sites, we detected 521 returning in at least one set of consecutive years. Of these, 276 (53%) were detected in 2 consecutive years, 122 (23%) were detected in 3 consecutive years, 53 (10%) were detected in 4 consecutive years, and 70 (14%) were detected in 5–8 consecutive years. For this analysis, we were interested in territory fidelity versus all other between-years movement behaviors. We used a logistic regression (via *proc genmod*) in SAS 9.0 (SAS, Inc.) to model factors influencing territory fidelity decisions by adult flycatchers. Based on the literature and our experience with the flycatchers, we chose *a priori* the following predictive factors to model: study site, year, unique breeding patches, number of young fledged in the previous year, territory density (the number of territories within a 200 m radius of the territory being considered), and breeding status (monogamous, polygamous, unpaired). Consideration of interactions among factors was limited to 2-way interactions to simplify interpretations. To choose between the multiple models, we used the Akaike Information Criteria (AIC) model selection approach to choose the best model(s) given the data (Burnham and Anderson 2002; see chapter 2 for a description of AIC).

Colonization and dispersal. To determine the minimum age of habitat when first colonized by breeding flycatchers, we concentrated on Roosevelt Lake where the receding lake level allowed the creation and growth of substantial riparian habitat within the period of this study. We overlaid patch boundary shapefiles over successive years of Normalized Difference Vegetation Indexes (NDVI) raster grids from LandSat TM images (1996–2005) in ArcGIS 9.0 (ESRI, Inc). The NDVI raster grids, which measure vegetation density, were masked for values below 0.33, a threshold value for riparian vegetation (see chapter 6). For a given patch, the first year that NDVI values >0.33 were detected was defined as year 1 of the riparian vegetation (i.e., the year that vegetation emerged from the ground) at that patch.

At both the Roosevelt Lake and San Pedro/Gila study sites some patches were present at the start of the study and we could not determine their ages since germination, or when they were first colonized. Therefore, we used a relative age, with the year a patch was first detected as occupied by a breeding flycatcher denoted as year one. Although relative age estimates will be less accurate for patches that already had flycatchers when first detected, changes in the number of flycatcher territories by relative age were remarkably consistent

across patches, and relative age estimates were necessary to capture a full 10–11 year window of change. We chose patches with five or more territories in at least one monitored year and were active for 4 or more years, resulting in 24 patches from Roosevelt Lake and San Pedro/Gila (Arivaipa Inflow, North, South; CB Crossing; Cooks Lake Seep; Dudleyville Crossing; GN18; GS07; Indian Hills; Kearny; Lakeshore; Mudflats; Northshore 1 and 2; Orange Peel Campground and Flats; Old Salt; San Manuel Crossing; Schoolhouse North 1 and 2; Schoolhouse South 3; Shangri-la; Tonto; and Wheatfields; see Luff et al. 2000, Causey et al. 2006). Those sites that were known to have breeding flycatchers in 1995 were included, for a maximum of 11 years considered. We excluded information from Roosevelt Lake in 2005 because of the inundation event. To make different patches supporting differing numbers of breeding territories comparable, we normalized the number of territories per patch by calculating a relative percent of territories per patch per year (dividing the number of territories in a given year by the sum of territories ever detected at the patch). These were then plotted by relative age to look at changes in the proportion of territories over time, averaged across the 24 patches.

We evaluated changes in productivity (total number of young fledged per territory) by running an ANOVA with productivity as the response (excluding 2002, an unusually low reproductive year; see chapter 3) and relative age as the predictor. To evaluate the relationship between immigration, emigration, and fidelity (territory and patch fidelity combined) and changes in the number of territories in a patch as a function of relative patch age, we correlated measures of between-year movement behaviors with changes in the number of territories. To evaluate the relative frequency of fidelity, immigration, and emigration by relative patch age (while controlling for different breeding population sizes at the different patches), we divided the number of individuals showing each of the three movement behaviors by the total number of banded birds present. We evaluated the percent change in territory numbers by dividing the number of territories in one year by the number detected in the previous year. We used a non-parametric correlation (Spearman's rho) to quantify correlations among between-year movement behaviors and changing numbers of territories as a function of relative patch age.

Statistical significance was accepted at $p < 0.05$. We graphed data with SigmaPlot 8.0 (SPSS, Inc).

Results

Natal Dispersal

Of the 498 nestlings banded from 1996 to 2004, we detected 123 in subsequent years (1997–2005); a 25% return rate with an associated apparent survivorship rate of 34% (see chapter 2). All returning nestlings but two dispersed to a non-natal patch; the two exceptions were detected 0.3 and 0.8

km away from their natal nest locations but within the same patch, a distance equivalent to some between-patch movements. Average natal dispersal distance was 20.5 km (range = 0.03–444 km; table 1). Seven natal dispersers moved to different drainages (mean distance = 214.3 km; fig. 2), while the majority ($n = 114$) returned to the same drainage, but a different patch (mean distance moved = 9.0 km;). Considering only those natal dispersers that moved between patches within the same drainage, there was no significant difference in the distance moved ($F_{1,110} = 0.20$, $p = 0.65$) between males (9.5 km \pm 1.5 SE) and females (8.5 km \pm 1.7 SE).

Adult Movement

Within-season Movement

We documented 130 individuals making within-season movements, with a mean distance of 7.5 km \pm 1.3 SE (range = 0.1 to 117; table 2). Movements occurred within a patch ($n = 37$, mean = 0.3 km \pm 0.04 SE, range = 0.1 to 1.2 km), between patches ($n = 91$, mean = 8.8 km \pm 1.2 SE, range = 0.3 to 58.2 km), and between drainages ($n = 2$, mean = 84.7 km \pm 32.3 SE, range = 52 to 117 km). Females moved farther than males ($F_{1,128} = 5.5$, $p = 0.02$); mean distance for females was 12.0 km \pm 3.5 SE (range = 0.1–117 km) versus 5.5 km \pm 1.0 SE (range = 0.1–32.2 km) for males.

We identified four categories of within-season movement (pre-breeders, post-breeders, territory switchers, and non-territorial). Territory switchers generally moved the farthest, and pre-breeders the least (table 2); however, there was much variation within groups and the difference in distances moved was marginally non-significant ($F_{3,126} = 2.53$, $p = 0.06$). Approximately half the pre-breeders were detected in the same patch, while post-breeding movements were mostly to different patches (table 2). Territory switching was the least common movement detected, accounting for only 17% of the within-season movements. Non-territorial movement, which can be thought of as two points (i.e., detections) on a continuous movement track, was documented as being conducted primarily by males and between patches.

Between-year Movement

From 1996 to 2005 we documented 712 adults making between-year movements, with distances ranging from 0.1 to 214 km (table 3). The mean distance moved by adults (9.5 km) was much less than the mean natal dispersal distance (20.5 km; $F_{1,855} = 20.4$, $p < 0.001$). Adult between-year movements included movements within a patch (range = 0.1–1.6 km), movements between patches (range = 0.2–55.4 km), and movement between drainages (range = 49–214 km; table 3). With the exception of one adult that moved into New

Table 1. Natal dispersal distances of Southwestern Willow Flycatchers in central Arizona, 1997–2005. Distances and sample sizes are grouped by: patch fidelity, those that returned to their natal patch, between-year movement, movement to a non-natal patch within the natal drainage, and between-site movement, movement to another drainage outside of the natal area.

Type of dispersal	n	Mean km (\pm SE)	Median km	Minimum km	Maximum km
Patch fidelity	2	0.6 (\pm 0.3)	0.6	0.3	0.8
Between-patch movement	114	9.0 (\pm 1.1)	2.5	0.3	40
Between-site movement	7	214 (\pm 66)	108	52	444

Table 2. Within-season movements of Southwestern Willow Flycatcher in central Arizona, 1996–2005. A within-season movement is defined as an adult detected at two locations greater than 50 m apart, within the same breeding season. Pre-breeders are non-territorial individuals encountered prior to becoming territorial in another location, territorial switchers are individuals switching from one territory to another, non-territorial adults are encountered in two different locations and non-territorial in both locations, and post-breeders are the non-territorial encounter of an individual after it has left its breeding territory of the season. The sexes of all 130 individuals were known.

Category of movement	n	% male	% within same patch	Mean km (\pm SE)	Median km	Minimum km	Maximum km
Pre-breeding	47	74	49	3.6 (\pm 1.2)	0.6	0.1	32
Territory switchers	22	50	18	13.0 (\pm 5.4)	2.2	0.1	117
Non-territorial	23	83	13	6.4 (\pm 1.9)	2.2	0.1	29
Post-breeding	38	66	18	9.8 (\pm 2.4)	2.1	0.1	58
All	130	69	28	7.5 (\pm 1.3)	1.4	0.1	117

Table 3. Southwestern Willow Flycatcher between-year movement distances documented at our two study sites, 1996–2005. Patch fidelity is movement within the previous year's patch but moving >50 m, between-patch movement represents birds returning to a different patch but within the same study site, and between-site movement represents dispersals to a different drainage.

Site	Type of movement	n	Mean km (\pm SE.)	Median km	Minimum km	Maximum km
Roosevelt Lake	Patch Fidelity	151	0.3 (\pm 0.02)	0.2	0.1	1.4
	Between-patch Movement	331	9.2 (\pm 0.6)	2.6	0.2	33.1
	Between-site Movement	8	97 (\pm 11)	86	69	144
San Pedro/Gila	Patch Fidelity	79	0.3 (\pm 0.04)	0.1	0.1	1.6
	Between-patch Movement	134	13.4 (\pm 1.0)	10.9	0.4	55.4
	Between-site Movement	9	120 (\pm 18)	98	49	214

Mexico near the Arizona border, all adult between-drainage movements we detected were among sites within the central Arizona region. There was no significant difference in the distance moved by male and female flycatchers ($F_{1,710} = 0.19$, $p = 0.66$), but San Pedro/Gila individuals moved significantly farther than Roosevelt Lake birds ($F_{1,710} = 10.2$, $p = 0.001$; fig. 3). Roosevelt Lake dispersal distances had a bimodal distribution, showing a high frequency of movement between patches within each inflow (left mode; fig. 4), and a more moderate amount of trans-lake movements (right mode; fig. 4). Movements at the San Pedro/Gila declined more linearly with distance than at Roosevelt (fig. 4). Fitting the frequency of between-patch movements along the San Pedro/Gila by distance (in 5 km increments, within-drainage only) resulted in a strong quadratic relationship ($r^2 = 0.97$, $F_{2,9} 160.4$, $p < 0.001$), suggesting the frequency of movements declined by approximately 5% for every 5 km distance from the previous year's breeding location.

Between-year Movement Behavior

The proportion of the four between-year behaviors (territory fidelity, patch fidelity, between-patch and between-drainage movements) did not differ between males and females ($\chi^2 = 1.6$, $df = 3$, $p = 0.67$), but they did vary significantly between study sites ($\chi^2 = 41.2$, $df = 3$, $p < 0.001$) and among years ($\chi^2 = 122.5$, $df = 18$, $p < 0.001$; table 4, fig. 5). San Pedro/Gila adults were more likely to return to their territories, whereas Roosevelt Lake adults were more likely to move to different patches. However, the frequencies changed over time. Most noticeable was the decline in territory fidelity at Roosevelt Lake and San Pedro/Gila in 2003, the year following a severe drought. There was also a large increase in movement at Roosevelt Lake in 2005 due to displacement of flycatchers through flooding-induced loss of most of their previous year's breeding habitat.

To understand whether individuals differed in the frequency of the between-year behaviors, we evaluated whether

certain individuals demonstrated consistent behavior (i.e., always moved or always returned to the same territory). Flycatchers with five or more consecutive movements exhibited both between-year movement and territory fidelity over those years, suggesting there were no individuals that either always moved or were always territory faithful. Results of the multistate model of the transition probabilities of between-year movement behaviors suggest that adults will frequently switch their between-year behaviors from year to year (fig. 6). Territory fidelity and between-patch movement were the most common behavior, with 57% of adults that were territory faithful in one year returning to the same territory in a subsequent year, and 46% of adults that moved in one year moving again in the subsequent year (fig. 6). Patch fidelity without returning to the same territory was the least observed behavior, with only approximately 20% of individuals doing so in a given year. Survivorship was nearly identical for all three groups, but detection probability differed: based on the multistate model, individuals that demonstrated territory and patch fidelity were highly likely to be detected, whereas those that moved had a 67% detection rate (fig. 6).

Influences and Consequences of Territory Fidelity Versus Movement

Evaluating causal factors that may influence between-year behavior (territory fidelity versus movement), we found the best AIC support for the model that included number of young fledged in the previous season, density of breeders in the previous year, patch, and an interaction of site by year (table 5). This model had 96% of the AIC weight, suggesting it was overwhelmingly the best model of those considered (table 5). The two factors that were in each of the top five models were the year by site interaction and the number of young fledged in the previous year. Site and year interaction captures a number of unmeasured and unknown environmental factors that vary by site and by year (fig. 5). The number of

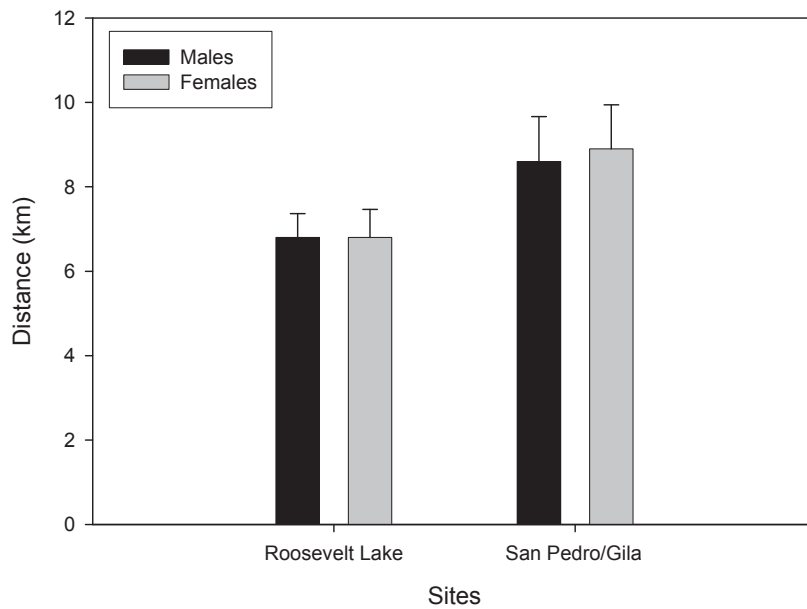


Figure 3. Average between-year movement distances of Southwestern Willow Flycatchers at the Roosevelt Lake and San Pedro/Gila study sites, 1996–2005. Movement distances were similar between sexes, but differed between sites. Error bars denote 95% confidence intervals.

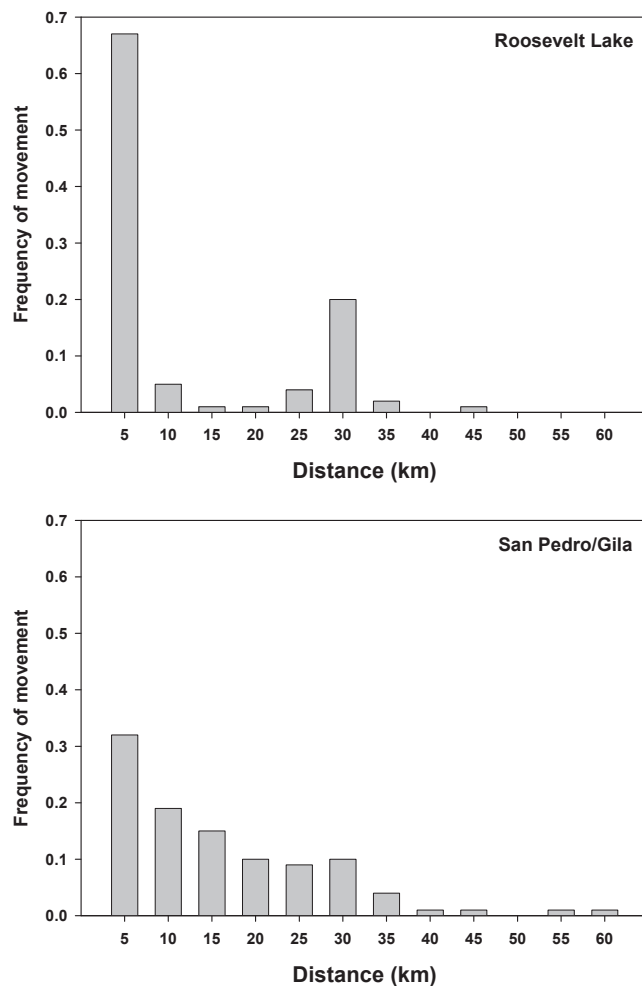


Figure 4. Within-drainage distribution of Southwestern Willow Flycatcher between-year movement distances for each of the two study sites (Roosevelt Lake and San Pedro/Gila). Movement distance patterns reflect different spatial arrangements of breeding habitat patches. Roosevelt Lake ($n=440$) consisted of breeding patches clustered on either side of the reservoir (mean distance 30 km), resulting in a bimodal distribution of distance moved, while San Pedro/Gila ($n=139$) had a relatively continuous distribution of discrete breeding habitat patches.

Table 4. The number of observed Southwestern Willow Flycatcher between-year movement behaviors by year for each of our two study sites, Roosevelt Lake (ROOS) and San Pedro/Gila (SAPE), 1997–2005. Territory fidelity is a flycatcher returning to within 50 m of its previous year's location, patch fidelity represents movement within a patch greater than 50 m, between-patch movement consists of movement to another patch within the same site, and between-site movement consists of movements to another site/drainage.

Year	Site	Territory fidelity	Patch fidelity	Between-patch movement	Between-site movement	Total individuals
1997	ROOS	4	10	5	0	19
	SAPE	4	3	9	0	16
1998	ROOS	12	11	1	0	24
	SAPE	13	7	14	2	36
1999	ROOS	9	11	7	1	28
	SAPE	23	8	14	1	46
2000	ROOS	18	16	14	1	49
	SAPE	34	8	16	0	58
2001	ROOS	42	17	27	1	87
	SAPE	31	6	10	1	48
2002	ROOS	51	17	23	0	91
	SAPE	17	5	9	1	32
2003	ROOS	34	19	59	3	115
	SAPE	9	7	11	2	29
2004	ROOS	33	27	50	0	110
	SAPE	21	16	15	1	53
2005	ROOS*	1	5	104	4	114
	SAPE	34	12	10	1	57

* Inundation of Roosevelt Lake in 2005 resulted in high movement rates due to the displacement of most flycatchers.

young fledged was a strong predictor of territory fidelity; for every young fledged, the odds of territory fidelity in the following year increased by 1.5 ($\beta = 0.3739$). Breeding density had a positive relationship with territory fidelity, with the probability of territory fidelity increasing as the density of territories increased. Effects of different patches on territory fidelity varied widely, and may be related in part to the age of the patch's vegetation (see Colonization and Dispersal section below).

Just as reproductive success influences between-season behavior (fig. 7), the choices that flycatchers make appear to affect their reproductive success in subsequent years (fig. 8, table 6). For example, those flycatchers with higher than average reproductive success in a given "year t " tended to return to the same territory again in "year $t+1$ ", and continued to do better than average (though not as well as in "year t "). Flycatchers that experienced far lower than average success in "year t " and then moved to another patch or site in "year $t+1$ " generally improved their success and fledged an average number of young. Comparatively, among those flycatchers that

showed patch fidelity, average productivity remained nearly the same (table 6).

Colonization and Dispersal

Although the direct consequences of the previous year's reproductive success had a strong influence on movement patterns, the importance of patch as a factor in the best AIC model suggests that other (unknown) influences related to patch were involved as well. Patch age may be one such consideration. During the course of this study, we observed riparian vegetation patches develop from immature stages through mature stages. Based on known-age patches at Roosevelt Lake, new riparian habitat was first colonized by breeding flycatchers when riparian vegetation was approximately 3 years old (95% C.I. = 2.5–3.5). Following colonization, the number of flycatcher territories in a patch increased for the first several years of a patch's age (based on relative age, see methods),

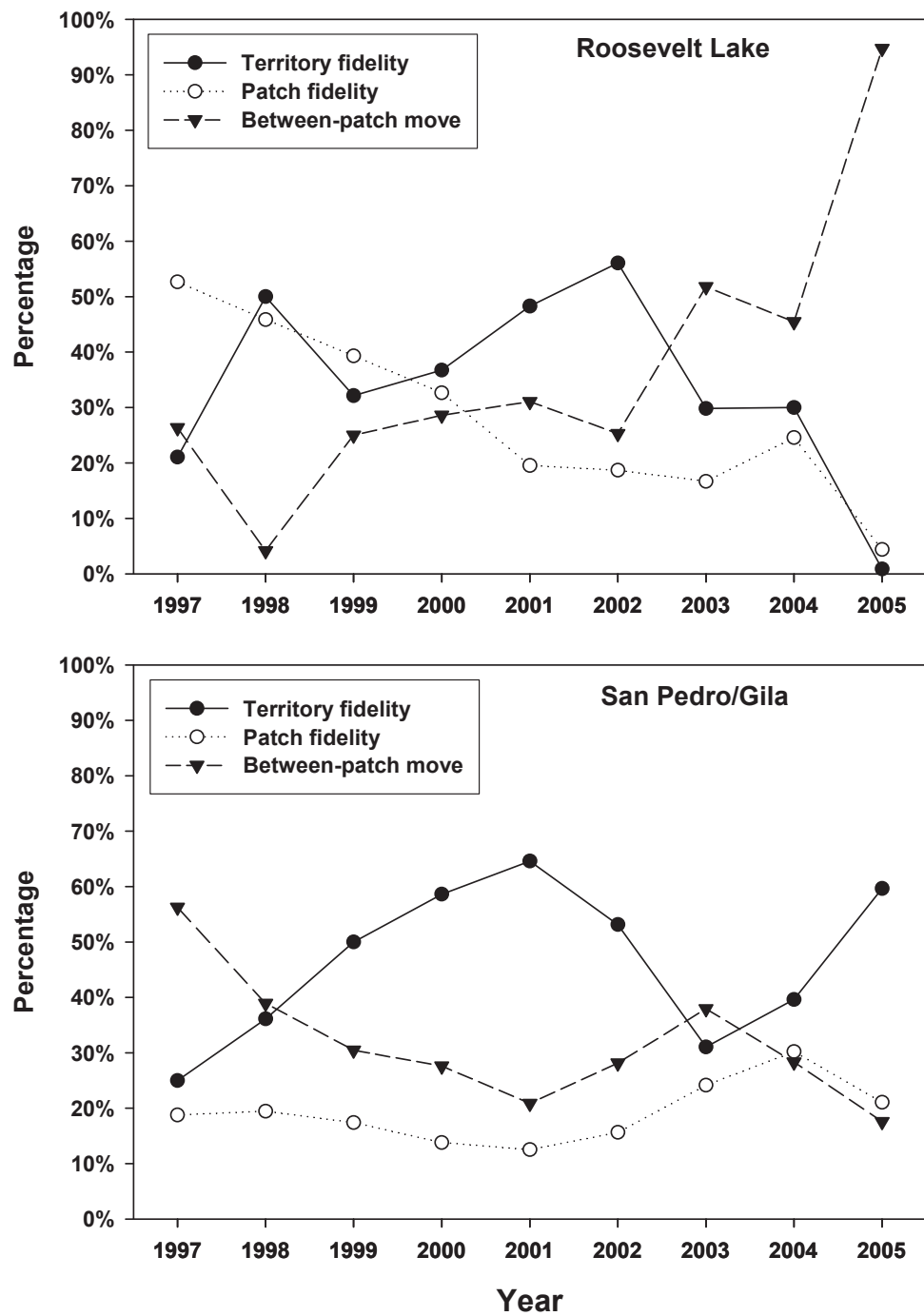


Figure 5. Frequencies of Southwestern Willow Flycatcher territory fidelity, patch fidelity, and between-year movement behaviors by study area (Roosevelt Lake and San Pedro/Gila) and by year (1997–2005). High frequency of movements at Roosevelt Lake in 2005 was in response to habitat loss and subsequent displacement due to inundation of breeding habitat. Territory fidelity is returning to the same territory; patch fidelity is returning to the same patch but >50 m from the previous territory; and between-patch movement is a shift to a different patch or drainage.

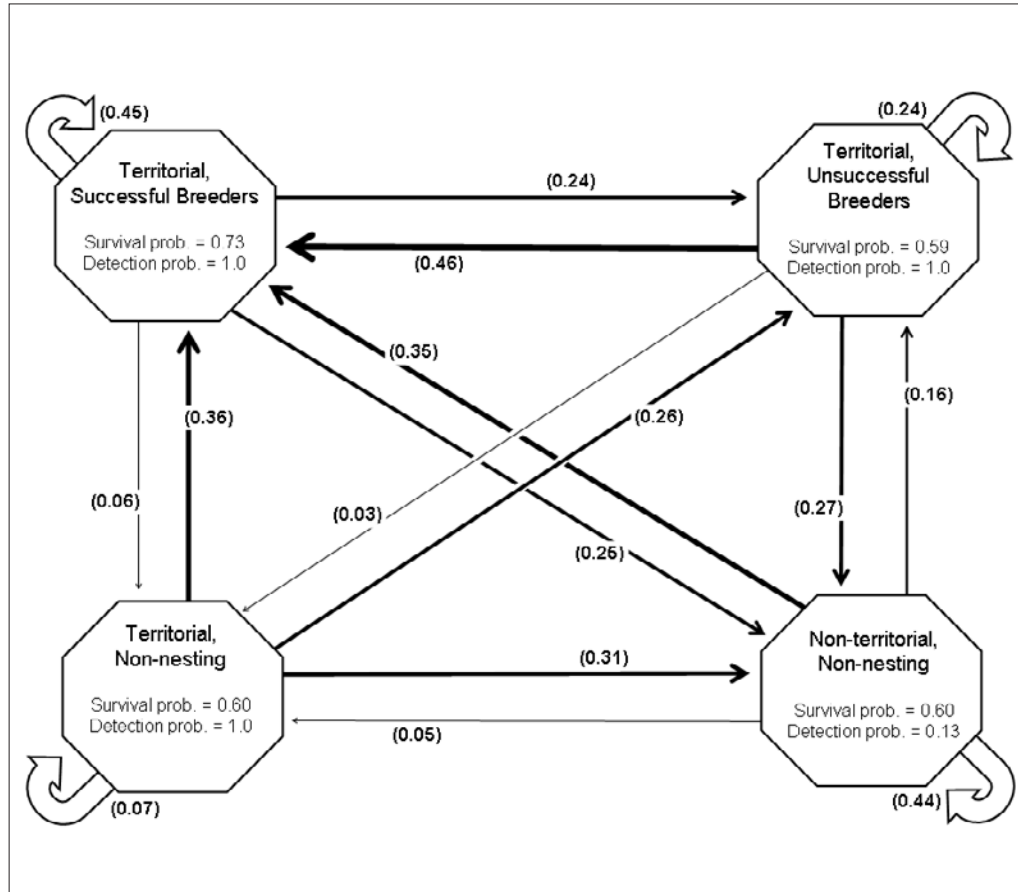


Figure 6. Graphic representation of the multistate model results indicating the average probability of an adult Southwestern Willow Fly-catcher remaining in (curved arrows) or transitioning to (straight arrows) one of the three between-year movement behaviors: territory fidelity, patch fidelity, and between-patch movement. Line width of the transitional probabilities is proportional to each probability. Territory fidelity and movement over successive years was the most frequent movement decisions, with territory fidelity favored over movement. Survivorship and detection probability for each state are indicated within the triangles. Territory fidelity is returning to the same territory; patch fidelity is returning to the same patch but >50 m from the previous territory; and movement is a shift to a different patch or drainage.

Table 5. AIC model selection results of the logistic regression models evaluating territory fidelity versus between-year movement. With each set of explanatory variables (model description) are the associated AIC value, change in AIC value (delta AIC), the relative weight the model has compared to all others considered, and the number of parameters (K). AIC ranking suggests that previous year's productivity (number of young fledged, NoFLD), territory density, individual patch characteristics, site, and year are the most parsimonious explanatory factors for territory fidelity in the Southwestern Willow Flycatcher. Only the top 5 and null (intercept only) models are shown.

Model description	AIC	Delta AIC	AIC weight	K
site+year+density+patch+NoFLD +year*site	1053.73	0	0.961	58
site+year+NoFLD+site*year	1060.87	7.14	0.027	19
site+year+sex+NoFLD+site*year	1062.61	8.88	0.011	20
site+year+density+patch+NoFLD+site*year +patch*year	1097.65	43.92	0.000	144
site+patch+year+sex+age+BDSTAT+density +NoFLD+site*year+patch*year+density*site	1101.67	47.94	0.000	164
Null	1267.58	213.85	0.000	1

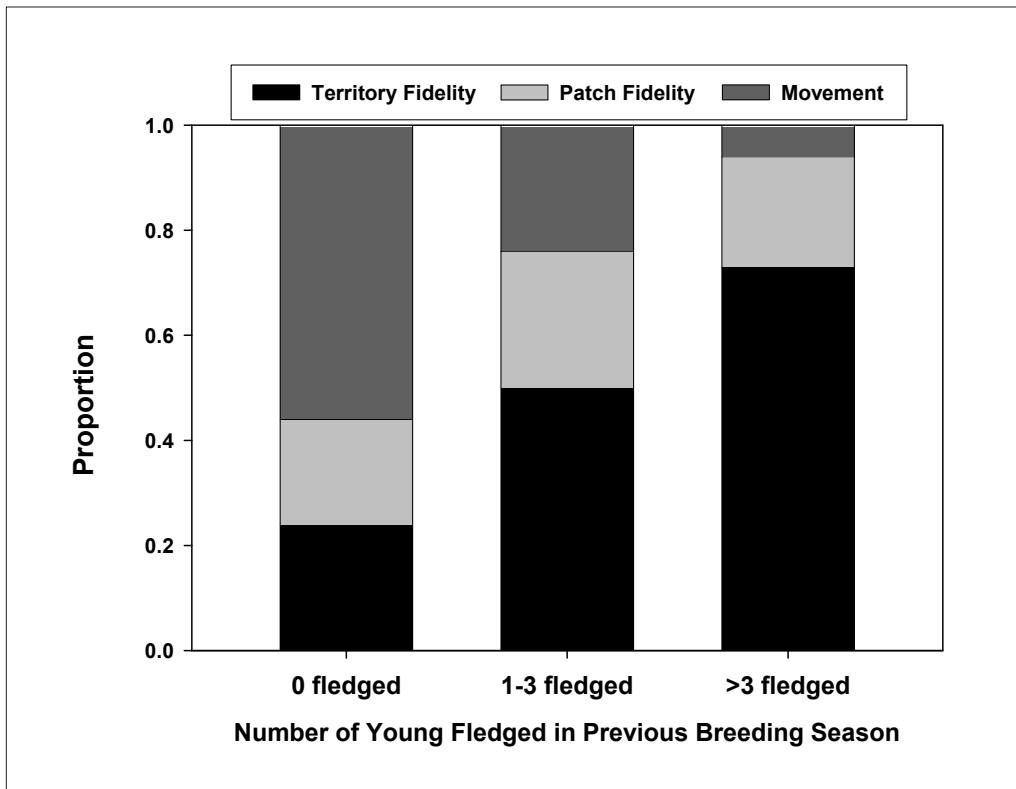


Figure 7. Southwestern Willow Flycatcher's between-year movement behavior as related to their reproductive success in the previous year. For 0, 1–3, or >3 young fledged, the proportion of adults that chose territory fidelity, patch fidelity, and between-patch movement changed. Territory fidelity is returning to the same territory; patch fidelity is returning to the same patch but >50 m from the previous territory; and movement is a shift to a different patch or drainage.

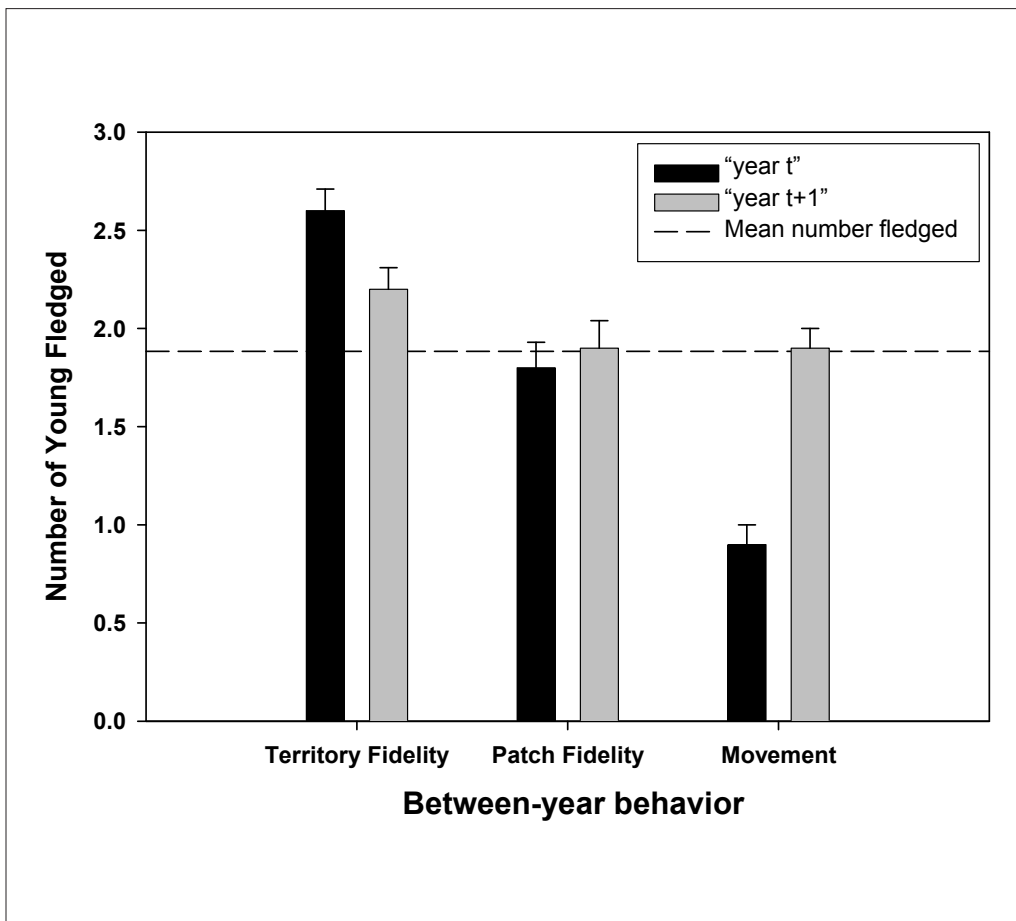


Figure 8. The relationship between Southwestern Willow Flycatchers productivity (number of young fledged per season) and movement type. Flycatchers that were territory faithful fledged more young than the overall average in the previous year, and continued to fledge more young than average in the subsequent year. Those flycatchers that moved territories within the same patch fledged slightly fewer than the average number of young and an approximately average number in the subsequent year. Flycatchers that moved between-patches tended to fledge far fewer young than average, but fledged an average number post-dispersal. Error bars are one standard error. Territory fidelity is returning to the same territory; patch fidelity is returning to the same patch but >50 m from the previous territory; and movement is a shift to a different patch or drainage.

Table 6. The relationship between movement decisions and reproductive success of Southwestern Willow Flycatchers in central Arizona. Decisions on territory fidelity versus movement in Southwestern Willow Flycatchers are influenced by productivity, and in turn influence subsequent productivity. Flycatchers that reproductively did better than average tended to remain territory faithful in the following year, and continued to do better than average. Individuals that reproductively did far worse than average tended to move, and performed much better in the following year. The % nest success is the percent of nests per territory that fledged at least one young and the # young fledged is the sum of young fledged. Territory fidelity is the between-year return to an individual's previous year's location (within 50 m), patch fidelity is an individual returning to the same patch but greater than 50 m, and movement is the return to another patch or site from the previous year.

Decision	n	Year	% nest success		# young fledged	
			Mean	95% C.I.	Mean	95% C.I.
Territory fidelity	341	t	60	56–64	2.6	2.4–2.8
		t+1	50	45–54	2.2	2.0–2.4
Patch fidelity	164	t	52	46–59	1.8	1.6–2.1
		t+1	47	42–54	1.9	1.7–2.2
Movement	237	t	29	24–34	0.9	0.7–1.1
		t+1	56	51–62	1.9	1.7–2.1
Overall	742		49	47–52	1.9	1.8–2.0

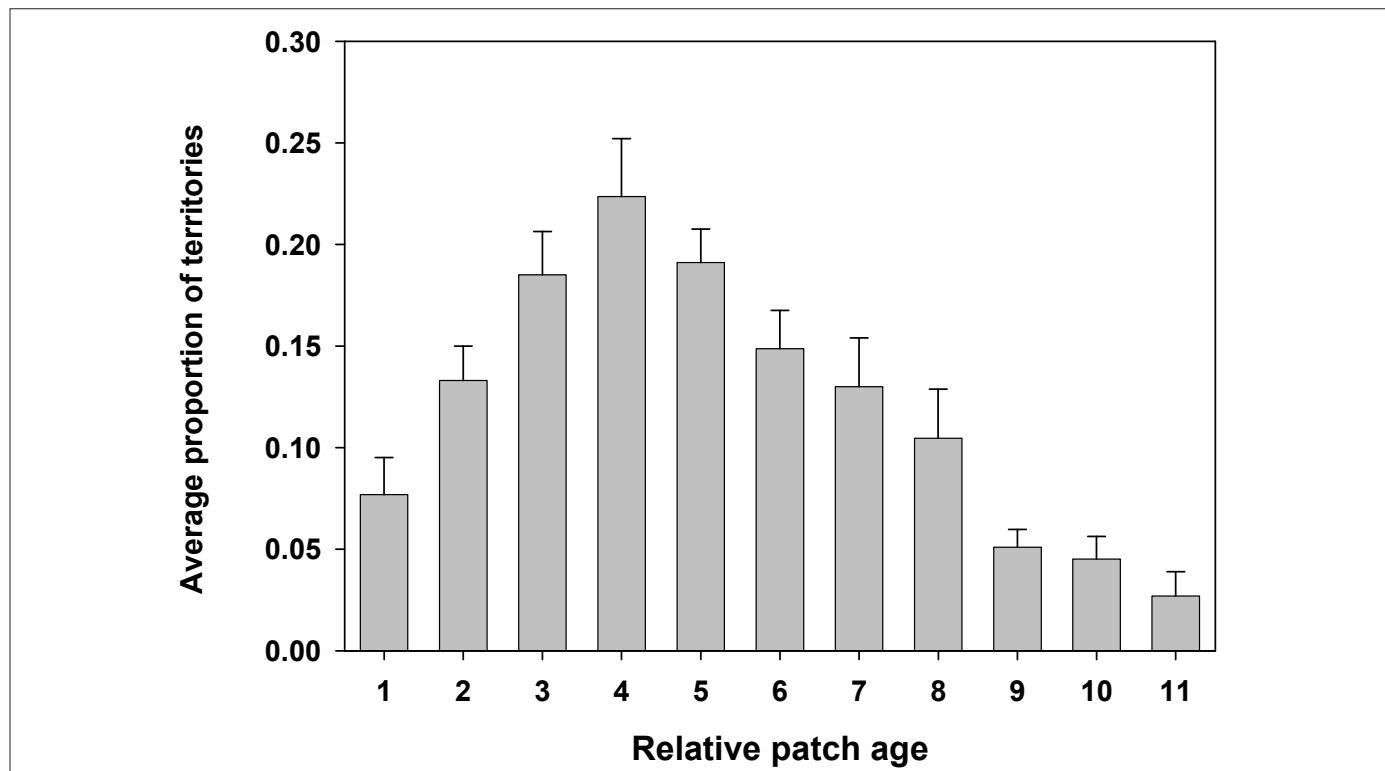


Figure 9. The relative number of Southwestern Willow Flycatcher territories in breeding patches as a function of relative age (in years). The relative age of a patch is the number of years a patch was known to be occupied, with the year discovered/colonized denoted as year one. The percent territory is the proportion, for a given year, of the sum of territories discovered throughout a patch's occupancy by flycatchers and/or the length of this study. Only patches with four or more years of occupancy and five or more territories in at least one year were included, resulting in 24 patches with a mean relative age of 7 years. Roosevelt Lake numbers from 2005 were excluded due to the confounding effects of the inundation. Error bars are one standard error. Overall, the proportion of territories increased for approximately four years and then gradually decreased with the patch's relative age.

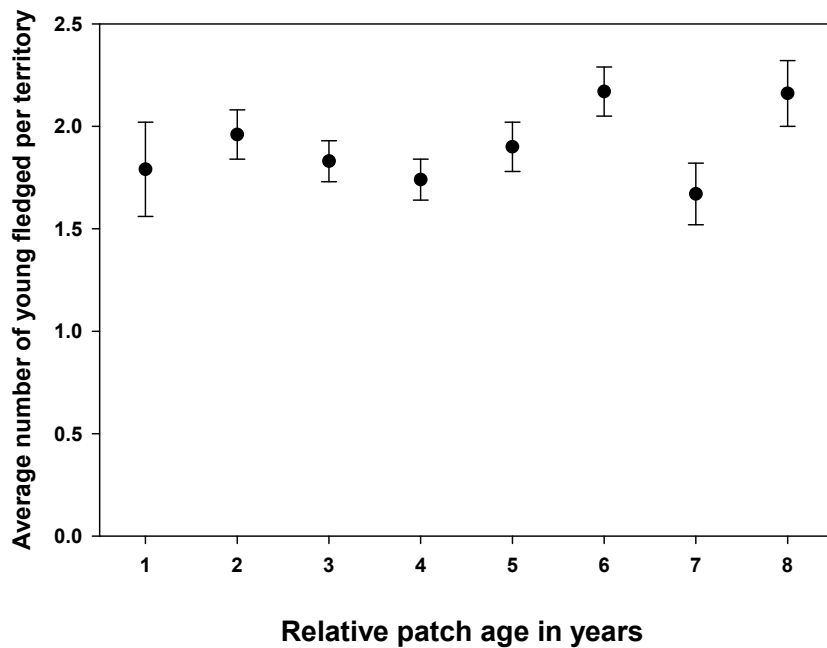


Figure 10. Average reproductive success of Southwestern Willow Flycatchers as a function of patch relative age. Reproductive success is the total number of young fledged from a territory. Reproductive success varies by relative patch age, but there is no general pattern of decline or increase by relative patch age.

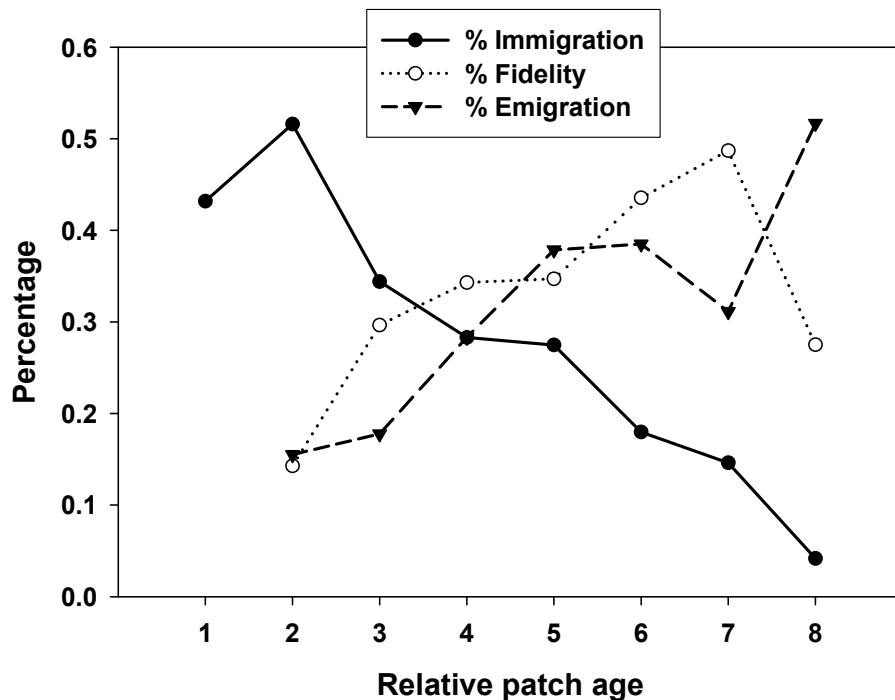


Figure 11. Southwestern Willow Flycatcher average rates of immigration, emigration, and fidelity as a function of the relative age of a patch (in years). Between-year movement behavior percentages are the number of individuals, out of the total number of banded birds present at a patch in a given year, which made immigration, emigration, or fidelity choices. The number of adults that immigrate into a patch is highest when the patch is young, then declines as the patch ages, whereas the proportion that emigrate and show fidelity increases with increasing patch age. For each patch per year, the percentage of immigration, emigration, and fidelity sum to 1.0, but the average across the 24 patches does not necessarily sum to 1. Fidelity is returning to the same patch; immigration is movement into the patch from another location; and emigration is moving out of the patch to another location.

and then decreased until, in many cases, flycatchers no longer bred there ($\chi^2 = 44.6$, $df = 10$, $p < 0.001$; fig. 9). This change in occupancy does not appear to be directly linked to productivity (fig. 10), for while there are changes in average productivity over time, the differences were marginally non-significant ($F_{7,1181} = 1.9$, $p = 0.06$) and did not match the observed patterns of occupancy (fig. 9). However, movement patterns do closely match the change in the population numbers of a patch. For the first several years of a patch's relative age, immigration into the patch was the dominant movement pattern (fig. 11), and immigration was significantly related to the changes in population size ($\rho = 0.37$, $p < 0.001$). As the patch aged, immigration decreased steadily while emigration increased and was negatively correlated to the population size ($\rho = -0.51$, $p < 0.001$). Patch fidelity also increased with the relative age of a patch ($\rho = -0.24$, $p = 0.004$; fig. 11), which may slow a patch-level population's decline, but this fidelity was by an increasingly smaller number of individuals as the patch's population size diminished.

The probability of flycatchers colonizing new breeding habitat appears to depend on distance from occupied habitat. While we documented rapid colonization of breeding habitat adjacent to occupied habitat multiple times, colonization of more distant habitat was observed less frequently. On the San Pedro River, banded flycatchers from the core breeding area were documented moving to two new areas further upstream: Catalina Wash (mean distance moved = 37 km, $n = 2$) and San Manuel Crossing (mean distance moved = 35 km, $n = 5$). Thus, some or perhaps all of the flycatchers colonizing these sites were from the San Pedro/Gila study site. Likewise, two of the closest sites near Roosevelt Lake, consisting of new breeding habitat, received Roosevelt Lake emigrants: Horseshoe Reservoir on the Verde River (mean distance = 52 km, $n = 3$) and Pinal Creek (mean distance = 16 km, $n = 4$; with an additional flycatcher from San Pedro/Gila emigrating there, a distance of 72 km). The mean distance of flycatchers moving to colonize Pinal Creek, Catalina Wash, San Manuel Crossing, and Horseshoe Reservoir was 33 km, similar to the upper end (~35 km) of within-site movement observed at Roosevelt Lake and San Pedro/Gila (fig. 7).

Discussion

Natal Dispersal

The pattern exhibited by flycatchers at our sites, where natal dispersal was more extensive than adult dispersal, is typical of most birds (Greenwood and Harvey 1982, Winkler et al. 2005). Juvenile flycatchers in our study rarely returned to their natal patch, moved farther than adults on average, and were responsible for the longest distances of movement observed. Reasons for this may include intraspecific competition for territories by older, presumably more aggressive individuals that

exclude younger adults, inbreeding avoidance, or the evolution of increased colonization potential (Payne 1991). Colonization of new habitat is an important adaptation to the dynamic nature of riparian habitat in which scouring floods and multi-successional stage vegetation leads to frequent shifts in the spatial location of breeding habitat over time (Periman and Kelly 2000; see chapter 6). It is this high natal dispersal that makes quantifying juvenile survivorship so difficult, as juveniles can easily disperse outside the boundaries of relatively small studies (Baker et al. 1995).

The longest movements recorded over the course of this study were those of dispersing juveniles (fig. 2). Three Roosevelt Lake juveniles dispersed to the Lake Mead area and Topock Marsh, AZ (maximum distance = 444 km), while one juvenile from the Lake Mead area was detected at Roosevelt Lake. In addition, one nestling banded in the Lake Mead area was detected at the Kern River Preserve, CA (M. Whitfield, personal commun.), a movement of 318 km. Over the course of this study, only juvenile flycatchers provided population "connectivity" between central and western Arizona, and between western Arizona and central California.

Only two other studies of Willow Flycatchers have detailed natal dispersal. The most similar comparison is from the Colorado River and tributaries in Arizona, California, and Nevada (Koronkiewicz et al. 2004, 2006; McLeod et al. 2005). Of 78 banded nestlings that were detected as adults, 38% moved to different study sites 20–440 km away, distances comparable to our study. In southeast Oregon, Sedgwick (2004) found no juveniles returning to one study area while as many as 67% of returning and detected juveniles returned to their natal patch at two other study areas. Natal dispersal there ranged from 40 m to 7.8 km. However, the return rate of 7.8% of all banded nestlings was much lower than what we observed (25%), and presumably many of the juveniles dispersed outside his study area (Sedgwick 2004). It is important to consider that different studies are conducted at different spatial scales, such that what is classified as site fidelity in one study may be considered between-site movement in another. Furthermore, the geographic scale and distribution of suitable habitat within the local landscape will influence dispersal patterns. For example, the presence of adjacent suitable breeding habitat should facilitate movements, whereas isolated or fragmented breeding habitat may reduce natal dispersal potential (Martin et al. 2006). Alternatively, isolated breeding patches separated by considerable distance from others could potentially increase dispersal distance (as there is nowhere else to settle in between). Given the high degree of natal dispersal we observed, and the rarity of fledglings returning to their natal patch, sites with multi-patch spatial configurations may provide optimal site characteristics for flycatchers.

Adult Movement

Within-season Movement

We detected 130 within-season movements by flycatchers from 1996 to 2005. The majority (65%) of the movements were pre- and post-breeding, both of which may be a way for flycatchers to assess the breeding potential of adjacent habitat (Vega Rivera et al. 2003). Pre-breeding movements were the most frequent within-season movement type observed in our study, probably because the movements tended to be closer to the flycatcher's eventual territories and thus adjacent to other breeding areas where we conducted the most intensive capture efforts. Nearly 75% of the detected pre-breeding movements were by males that may have been assessing habitat or neighboring territories, or determining arrival or availability of females. Telemetry work conducted at Roosevelt Lake (2003–05) indicated generally larger home ranges for males prior to arrival of females (Cardinal and Paxton 2004, 2005), even if they had already established a territory. Females may be more discerning of breeding habitat quality than are males (Sedgwick and Knopf 1992), perhaps choosing territories more quickly than males, and thus are less likely to be detected making pre-breeding movements.

Adult post-breeding movements are generally interpreted as prospecting for future breeding sites (Bayne and Hobson 2001), or as movement into a habitat that may not be suitable for breeding but is preferable or used for pre-migration staging (Vega Rivera et al. 2003). Most post-breeding movements we documented were via recaptures in other breeding locations, and thus the birds were in similar habitats for breeding and post-breeding. Radio tracking of post-breeding individuals at Roosevelt Lake documented long-distance movements within the study area, but all were confined to riparian habitat (Cardinal and Paxton 2004, 2005; Cardinal et al. 2006). Telemetered individuals moved to other breeding patches, visited areas with local insect outbreaks, and sometimes moved to relatively younger patches of riparian vegetation not yet occupied by breeding flycatchers. Given the changing nature of riparian vegetation, this prospecting behavior may allow flycatchers to gauge the suitability of future habitat, especially young developing habitat, and could be an important component of between-year movement choices.

Territory switching within a single breeding season was observed infrequently among flycatchers at our study sites. Flycatchers arrive on their breeding grounds late relative to many other migrant species (Sedgwick 2000), with approximately 3 months to breed, and rarely nest more than twice in a season (see chapter 3). It may take longer to re-nest following territory switching than it does to re-nest within the same territory (Shields 1984), so it may be advantageous for flycatchers that are attempting a second nesting opportunity to do so within the same territory. An additional difficulty in switching territories within-season is finding another territory with an available mate (Jackson et al. 1989), and it may be that only a

fraction of individuals searching for a second territory are successful in finding an unoccupied territory.

Between-year Movement Behaviors

On average, 41% of adult flycatchers moved between-years to another patch. Most movements were confined to nearby patches within the same drainage, but occasionally were to different drainages. Distance moved was in part dependent upon distribution of available breeding habitat (Paradis et al. 2002). Along the San Pedro, flycatcher dispersal frequency declined 5% for every 5 km of distance, with most individuals moving less than 40 km. However, at Roosevelt Lake where two geographically distinct riparian areas were separated by 30 km of lake, the distribution of movement distances was bimodal (corresponding to nearby patches and cross-lake patches), with a higher frequency of movements in the 30 km range than observed at San Pedro/Gila. Mean breeding dispersal distance (41 km) seen during intensive flycatcher studies on the Lower Colorado River (Koronkiewicz et al. 2004, 2006; McLeod et al. 2005) was less than our between-drainages means (97 and 120 km at Roosevelt Lake and San Pedro/Gila, respectively), but greater than the mean between-patch distances at San Pedro/Gila (13 km) and Roosevelt Lake (9 km). The differences in dispersal distance among different study areas and regions reflects the varying spatial arrangement of breeding habitat, illustrating how flycatcher dispersal tendencies are influenced by the geographic distribution of habitat at the reach, drainage, and landscape scales. The relatively linear decline in the frequency of movements with increasing distance seen at San Pedro/Gila may be similar to what was historically the normal pattern of flycatcher dispersal along southwestern riverine systems, when riparian woodlands were more evenly distributed along rivers (Graf 2006).

Flycatchers travel thousands of kilometers each year for migration, and have the potential to disperse great distance across the landscape. However, only 1% of the movements we detected were to other drainages. The 1% estimate should be viewed as a minimum, as some unknown number of dispersal events will inevitably go undetected; however, the limited number of breeding sites available to flycatchers and the multiple resight efforts at many sites over many years strongly suggest that long-distance, regional-level dispersal occurs at low levels. Nonetheless, this infrequent between-drainage movement appears adequate to sustain genetic connectivity (Busch et al. 2000), and may be important for the periodic colonization of unoccupied drainages. However, such infrequent between-drainage movements detected are probably not sufficient to sustain declining populations in distant drainages through a rescue effect, such as in breeding sites that are reproductive “sinks.” Given that occupied breeding patches can experience fluctuating flycatcher populations and may be abandoned over time (see below), long-term sustainability of drainage-level populations may require a number of suitable breeding habitat patches, preferably of different

successional stages, within the same drainage (USFWS 2002). Based on dispersal distances seen at our study sites, locations with breeding habitat that are within 30–40 km of each other will have higher meta-population connectivity, and there is a higher probability of colonization of new habitats that are within this distance. Being neotropical migrants, flycatchers clearly have high dispersal capacity, even greater than the 444 km (natal) and 214 km (adult) distances that we documented. Nonetheless, as distance increases the frequency of movement decreases, and the probability of a site being colonized is probably related to its proximity to other breeding populations.

For flycatchers, the previous year's reproductive success strongly influenced the observed behavior in the subsequent year. The higher a flycatcher's productivity in one year, the more likely it was to return to the same territory the following year. Those individuals that had higher than normal reproductive success and showed territory fidelity continued to reproduce above average, while those that did poorly and moved tended to do better than in the previous year. This is a common pattern in birds (Greenwood and Harvey 1982), and is believed to be an adaptive assessment of habitat quality and the probability of future breeding outcomes (Hoover 2003). In a study of Willow Flycatchers in Oregon, Sedgwick (2004) found similar patterns of increasing territory fidelity with increasing productivity. While we found this pattern for both males and females, Sedgwick (2004) found it only for females. He argued that males may be less likely to move, regardless of reproductive success, because it is more adaptive to return to and defend a familiar territory, as long as the habitat persists and females will settle into the territory. However, the dynamic nature of riparian systems in the Southwest may have selected for increased vagility in both male and female Southwestern Willow Flycatchers, as well as the evolution of reproductive cues associated with habitat (e.g., vegetation structure, arthropod abundance).

Colonization of Breeding Habitat

At both Roosevelt Lake and the San Pedro/Gila study sites, Southwestern Willow Flycatchers colonized breeding habitat that developed over the course of the study, suggesting they will quickly colonize new habitat when it becomes suitable for breeding (at least if it is adjacent to occupied habitat). As the level of Roosevelt Lake dropped and riparian vegetation grew on the exposed lakebed, the average age of the vegetation when first colonized was 3 years (range = 2–4 years). Riparian vegetation can grow very quickly, and in just a few years can form dense stands several meters high. Thus, rapid colonization of new breeding habitat was possible because of the rapid growth rate of riparian vegetation and the flycatcher's ability to find and quickly colonize young habitat. Based on observations of within-season movements and telemetry data (Cardinal and Paxton 2004, 2005; Cardinal et al. 2006), flycatchers will move from their general breeding patch to visit younger non-breeding vegetation (both while territorial, and pre and post-breeding), possibly to prospect for future

breeding habitat and to forage for food. It was not uncommon to hear flycatchers singing from younger vegetation a year before breeding was documented within the patch (E. Paxton, personal observation). Given the dynamic nature of riparian systems and the apparent preference flycatchers have for early successional stage habitat (see chapter 6), flycatchers may have evolved the capacity to assess the future breeding potential of vegetation in its early stages of development.

Not all colonization involved young breeding habitat; flycatchers moved into older habitat patches as well, and these older patches may serve as refugia (an area that has escaped ecological changes occurring elsewhere and so provides a suitable habitat for a species). Scouring floods can destroy large swaths of riparian forest, and fluctuating reservoir levels not only create habitat as they recede, but destroy habitat as they rise. These scouring/flooding events are most likely to impact the younger habitats that colonize the flood-prone zones of rivers and the drawdown zones of reservoirs, so these younger habitats will be lost more frequently than older habitats outside of these zones. We have seen examples of this phenomenon over the course of our study. When our research started in 1996, Roosevelt Lake was at full capacity and flycatchers were found only in mature habitat adjacent to the high water level. As the lake began to slowly recede over the following years, new riparian vegetation developed and the expanding flycatcher population at Roosevelt Lake generally moved into the newer, younger habitat (see chapter 6). By 2004, flycatchers had abandoned the historical patches in which they bred exclusively from 1994 to 1998. In 2005, high winter and spring runoff caused the lake to reach near capacity, destroying much of the newer habitat. In response, flycatchers moved back into patches they had earlier vacated or had never occupied during our study. A similar pattern may have occurred at San Pedro/Gila, where scouring floods in 1993 removed much of the vegetation adjacent to the rivers (see chapter 6). Flycatchers in 1996 were found in mature vegetation on higher ground away from the active channels on both the Gila and San Pedro Rivers. By 2005, much of the San Pedro/Gila population had moved to younger habitat that developed within the primary flow zone. Thus, mature unoccupied habitats near younger occupied breeding patches may occasionally play an important role as refugia. In doing so, they may help dampen local population fluctuations that might otherwise occur if rapid loss of breeding habitat forced flycatchers to disperse widely in search of new breeding locations.

Within a patch, flycatcher population sizes changed over time. The general pattern was for a rapid increase in the numbers of territorial flycatchers, followed by a gradual decline until, in some cases, abandonment of the patch as breeding habitat. Average productivity did not change as patches aged, and since very few natal dispersers return to their natal patch, changes in patch level population size over time appears to be driven primarily by between-year movement behavior and flycatcher lifespan. Behaviors such as immigration, emigration, and patch fidelity were significantly correlated with changes in patch population size, with immigration and emigration the

most strongly correlated. For the first several years of a patch being occupied, immigration was at its highest levels, and later declined to near zero. As immigration declined, emigration increased. Patch fidelity also increased with the age of the patch, which may have slowed the decline of a patch's population size. Because mean flycatcher life expectancy is approximately 2 years (see chapter 2), patch fidelity of surviving adults can only sustain a breeding population temporarily. Thus, immigration (both adult and natal) into a breeding patch is essential for its establishment and early persistence, while emigration can hasten the decline (Stacey and Taper 1997, Ward 2005). This suggests that sites with multiple-patch metapopulation structures may be the most stable populations over time, albeit spatially dynamic.

If individuals make a choice between movement and fidelity each year in response to habitat conditions (e.g., prey abundance, predation risks, past breeding experience in a patch, vegetation characteristics), then the observed patterns of choices can shed light on what constitutes preferred habitat. Given that productivity was not related (or only weakly related) to the age of a patch, and assuming that predation risk and prey base are closely tied to productivity, vegetation characteristics may drive changes in population size. Flycatchers in the Southwest were historically widespread in young, early-successional riparian habitat (Unitt 1987, Sedgwick 2000), and presumably have evolved a search image for the vegetation structure associated with young habitat. Thus, flycatchers may form spatially dynamic metapopulations that follow patches at different successional stages over time. Both Roosevelt Lake and San Pedro/Gila provided flycatchers with a choice of many potential breeding habitat patches of varying ages, and much of the flycatcher population growth occurred in the younger vegetation patches by the end of the study. However, many flycatcher breeding locations in the Southwest are more isolated, with apparently little nearby alternative breeding habitat. Based on our observations of flycatchers moving to and breeding in older habitats, some mature habitats are suitable for (though perhaps not preferred by) flycatchers, at least for a short period. Why flycatchers would abandon older vegetation patches when productivity appears to be constant is unknown, and deserves more research attention.

Management and Research Considerations

Managing Meta-populations Rather than Individual Breeding Patches

Historically, riparian vegetation along stretches of rivers was a rich mosaic of different aged patches for flycatchers to colonize, occupy, and eventually abandon. All riparian habitat patches are ephemeral, persisting only for the period of time

between their establishment and the next major flow and scouring event. The flycatcher appears to be well adapted to this dynamic system, and its current proclivity for movement and dispersal—especially to young habitat—is probably a result of that adaptation.

Even in today's less dynamic riparian landscapes (Graf 2006), habitat patches are subject to loss from high flows, rising reservoirs, fire, and other causes, and flycatchers will sometimes abandon some older breeding sites that still exist. Therefore, it is not safe to assume that breeding flycatchers can be sustained in an area simply by protecting the sites in which they currently breed (USFWS 2002). Rather, management for the flycatcher will be most effective if it is based on the concept of maintaining a mosaic of sites of varying age and vegetation structure. If one or a few sites are lost or decline in suitability, there could be other patches to which flycatchers would move. Based on our study, most movements occur within drainages. Therefore, this suggests that individual drainages are an appropriate scale at which to manage a mosaic of riparian patches as potential breeding patches. Movements between major drainages are infrequent, so patches in different drainages are not as likely to facilitate meta-populations dynamics. On the other hand, one meta-population can seed another, in a different drainage, and this is important for a regional framework. However, this low frequency of between-drainage movements is partially influenced by distance, and areas where drainages are close together may experience higher frequencies of movement.

The Southwestern Willow Flycatcher Recovery Plan (USFWS 2002) recognized that the flycatcher persists as a complex of meta-populations, and included recovery goals for specific geographic areas termed Recovery Units and Management Units. The units were based on USGS Hydrologic Unit Codes, derived from varying scales of landscape drainages. Flycatcher populations within individual units were believed to be more closely linked than populations in differing units. Translating our findings to the Recovery Plan's terminology, we found relatively frequent movements within the Management Unit scale, occasional movement at the Recovery Unit scale, and only infrequent dispersal from one Recovery Unit to another. Thus, results from our study of flycatcher movement behavior support the Recovery Plan's spatially explicit approach to recovering the Southwestern Willow Flycatcher.

Spatial Placement of New and Restored Habitats

The frequency of flycatcher dispersal generally decreases as the distance between patches increases. Flycatchers will readily colonize new habitat patches that are adjacent to current breeding sites, as rapidly as 3 years after vegetation establishment at Roosevelt Lake. More remote sites can also be colonized, but the frequency of flycatcher dispersal to more distant sites is lower. Therefore, the mere creation of suitable flycatcher habitat is no guarantee that the project will be suc-

cessful in attracting and supporting breeding flycatchers, at least in a 3 to 5-year timeframe.

Flycatcher habitat restoration and creation projects are likely to be most effective, in terms of rapid colonization by flycatchers, if they are located near existing breeding sites (within 30 to 40 km). Strategically placing riparian improvement projects near existing flycatcher breeding areas can also serve to strengthen the local meta-population. Considerations for riparian restoration projects are included in the Southwestern Willow Flycatcher Recovery Plan (USFWS 2002). It may be possible to establish new habitat in certain locations to serve as future stepping-stones for expanding the flycatcher population into other areas; to be effective, such sites should not be too remote from known breeding areas. Although an exact distance that would constitute "too remote" is difficult to determine, the mean adult between-site dispersal distances of 97 and 120 km (Roosevelt Lake and San Pedro/Gila, respectively) could serve as an upper limit to the distance of planned projects from existing breeding sites.

Developing Techniques to Increase Reproductive Success

Flycatchers tended to move away from a patch if breeding success was poor. In large, multi-patch breeding areas, this may result simply in flycatchers moving from one local patch to another, with no net effect on the overall breeding population size (though overall lower productivity would depress the population as a whole). However, in small, isolated breeding sites, low productivity may hasten the departure of flycatchers, and the eventual extirpation of the site. Management actions that help improve reproductive success could theoretically slow or stop the loss of flycatchers from an area, at least until new habitat could be developed. Potential techniques to improve flycatcher breeding success have not been investigated, with the exception of cowbird trapping regimes which yield variable benefits (Rothstein et al. 2003). Additional research could be directed toward developing effective ways to increase local reproductive success of breeders, especially at small sites. Increasing surface flows, raising ground water levels, and preventing overgrazing is likely to improve habitat as well as reproductive success (USFWS 2002).

References

- Baker, M., N. Nur, and G.R. Geupel. 1995. Correcting biased estimates of dispersal and survival due to limited study area: theory and an application using Wrentits. *Condor* 97:663–674.
- Bayne, E.M., and K.A. Hobson. 2001. Effects of habitat fragmentation on pairing success of Ovenbirds: Importance of male age and floater behavior. *Auk* 113:636–646.
- Breton, A.R., A.W. Diamond, and S.W. Kress. 2006. Encounter, survival, and movement probabilities from an Atlantic Puffin (*Fratercula arctica*) metapopulation. *Ecological Monographs* 76:133–149.
- Brooke, M. 1979. Differences in the quality of territories held by Wheateaters (*Oenanthe oenanthe*). *Journal of Animal Ecology* 48:21–32.
- Brown, D.E. (ed.). 1994. Biotic Communities – Southwestern United States and Northwestern Mexico. University of Utah Press, Salt Lake City, UT.
- Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference 2nd ed. Springer-Verlag, New York, NY.
- Busch, J.D., M.P. Miller, E.H. Paxton, M.K. Sogge, and P. Keim. 2000. Genetic variation in the endangered Southwestern Willow Flycatcher. *Auk* 117:586–595.
- Cam, E.J., D. Oro, R. Pradel, and J. Jimenez. 2004. Assessment of hypotheses about dispersal in a long-lived seabird using multi-state capture-recapture models. *Journal of Animal Ecology* 73:723–736.
- Cardinal, S.N., and E.H. Paxton. 2004. Home range, movement, and habitat use of the Southwestern Willow Flycatcher, Roosevelt Lake—2003. U.S. Geological Survey Report to the Bureau of Reclamation, Phoenix, AZ.
- Cardinal, S.N., and E.H. Paxton. 2005. Home range, movement, and habitat use of the Southwestern Willow Flycatcher, Roosevelt Lake—2004. U.S. Geological Survey Report to the Bureau of Reclamation, Phoenix, AZ.
- Cardinal, S.N., E.H. Paxton, and S.L. Durst. 2006. Home range, movement, and habitat use of the Southwestern Willow Flycatcher, Roosevelt Lake—2005. U.S. Geological Survey Report to the Bureau of Reclamation, Phoenix, AZ.
- Causey, C.F., M.G. Pollock, S.L. Durst, P.J. Newell, E.H. Paxton, and M.K. Sogge. 2006. Survivorship and movements of Southwestern Willow Flycatchers at Roosevelt Lake, Arizona—2005. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix, AZ.
- Durst, S.L., M.K. Sogge, H. English, S.O. Williams, B.E. Kus, and S.J. Sferra. 2006. Southwestern Willow Flycatcher breeding site and territory summary—2005. U.S. Geological Survey report to Bureau of Reclamation, Phoenix, AZ.
- English, H.C., A.E. Graber, S.D. Stump, H.E. Telle, and L.A. Ellis. 2006. Southwestern Willow Flycatcher 2005 survey and nest monitoring report. Arizona Game and Fish Technical Report 248.
- Frankham, R. 1995. Conservation genetics. *Annual Review of Genetics* 29:305–327.

- Graf, W.L. 2006. Downstream hydrologic and geomorphic effects of large dams on American rivers. *Geomorphology* 79:336–260.
- Greenwood, P.J., and P.H. Harvey. 1982. The natal and breeding dispersal of birds. *Annual review of Ecology and Systematics* 13:1–21.
- Hanski, I.A., and M.E. Gilpin. 1997. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, CA.
- Hoover, J.P. 2003. Decision rules for site fidelity in a migratory bird, the Prothonotary Warbler. *Ecology* 84:416–430.
- Jackson, W.M., S. Rohwer, and V. Nolan. 1989. Within-season breeding dispersal in Prairie Warblers and other passerines. *Condor* 91:233–241.
- Koronkiewicz, T.J., M.A. McLeod, B.T. Brown, and S.W. Carothers. 2004. Southwestern Willow Flycatcher surveys, demography, and ecology along the lower Colorado River and tributaries, 2003. Annual report submitted to Bureau of Reclamation, Boulder City, NV by SWCA Environmental Consultants, Flagstaff, AZ.
- Koronkiewicz, T.J., M.A. McLeod, B.T. Brown, and S.W. Carothers. 2006. Southwestern Willow Flycatcher surveys, demography, and ecology along the lower Colorado River and tributaries, 2005. Annual report submitted to Bureau of Reclamation, Boulder City, NV by SWCA Environmental Consultants, Flagstaff, AZ.
- Koronkiewicz, T.J., E.H. Paxton, and M.K. Sogge. 2005. A technique to produce aluminum color bands for avian research. *Journal of Field Ornithology* 76:94–97.
- Luff, J.A., E.H. Paxton, K.E. Kenwood, and M.K. Sogge. 2000. Survivorship and movements of Southwestern Willow Flycatchers in Arizona—2000. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix.
- Marshall, R.M. 2000. Chapter 2: Population status on breeding grounds. Pages 3–11 in *Status, ecology, and conservation of the Southwestern Willow Flycatcher*. (D.M. Finch and S.H. Stoleson, eds.) USFS Rocky Mountain Research Station, Gen. Tech. Rep. RMRS-GTR-60. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Marshall, R.M., and S.H. Stoleson. 2000. Chapter 3: Threats. Pages 13–24 in *Status, ecology, and conservation of the Southwestern Willow Flycatcher*. (D.M. Finch and S.H. Stoleson, eds.) General Technical Report RMRS-GTR-60. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Martin, J., J.D. Nichols, W.M. Kitchens, and J.E. Hines. 2006. Multiscale patterns of movement in fragmented landscapes and consequences of demography of the Snail Kite in Florida. *Journal of Animal Ecology* 75:527–539.
- McCabe, G.J., M.A. Palecki, and J.L. Bentancourt. 2004. Pacific and Atlantic Ocean influences on multidecadal drought frequency in the United States. *Proceedings of the National Academy of Sciences* 101:4136–4141.
- McLeod, M.A., T.J. Koronkiewicz, B.T. Brown, and S.W. Carothers. 2005. Southwestern Willow Flycatcher surveys, demography, and ecology along the lower Colorado River and tributaries, 2004. Annual report submitted to Bureau of Reclamation, Boulder City, NV, by SWCA Environmental Consultants, Flagstaff, AZ.
- Paradis, E., S.R. Baillie, and W.J. Sutherland. 2002. Modeling large-scale dispersal distances. *Ecological Modeling* 151:279–292.
- Part, T., and L. Gustafsson. 1989. Breeding dispersal in the Collared Flycatcher (*Ficedula albicollis*): possible causes and consequences. *Journal of Animal Ecology* 58:305–320.
- Paxton, E.H., and J.C. Owen. 2002. An aging guide for Willow Flycatcher nestlings. Colorado Plateau Field Station, Northern Arizona University.
- Paxton, E.H., M.K. Sogge, T.D. McCarthy, and P. Keim. 2002. Nestling sex ratio in the Southwestern Willow Flycatcher. *Condor* 104:877–881.
- Payne, R.B. 1991. Natal dispersal and population structure in a migratory songbird, the Indigo Bunting. *Evolution* 45:49–62.
- Periman, R.D., and J.F. Kelly. 2000. Chapter 4: The dynamic environmental history of southwest Willow Flycatcher habitat: A survey of changing riparian conditions through time. Pages 25–42. In *Status, ecology, and conservation of the Southwestern Willow Flycatcher*. (D.M. Finch and S.H. Stoleson, eds.) General Technical Report RMRS-GTR-60. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Pollock, M.G., and E.H. Paxton. 2006. Floating mist nets: A technique for capturing birds in flooded habitat. *Journal of Field Ornithology* 77:335–338.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- Pyle, P. 1998. Eccentric first-year molt patterns in certain Tyrannid flycatchers. *Western Birds* 29:29–35.

- Ralph, C.J., G.R. Geupel, P. Pyle, T.E. Martin and D.F. DeSante. 1993. Handbook of field methods for monitoring landbirds. USFS General Technical Report PSW-GTR-144. Albany, CA; Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture.
- Rothstein, S.I., B.E. Kus, M.J. Whitfield, and S.J. Sferra. 2003. Recommendations for cowbird management in recovery efforts for the Southwestern Willow Flycatcher. *Studies in Avian Biology* 26:157–167.
- Sedgwick, J.A. 2000. Willow Flycatcher (*Empidonax traillii*). In *The Birds of North America*, No. 533 (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, PA and the American Ornithologists' Union Washington, DC.
- Sedgwick, J.A. 2004. Site fidelity, territory fidelity, and natal philopatry in Willow Flycatchers (*Empidonax traillii*). *Auk* 121:1103–1121.
- Sedgwick, J.A., and F.L. Knopf. 1992. Describing Willow Flycatcher habitats: scale perspectives and gender differences. *Condor* 94:720–733.
- Shields, W.M. 1984. Factors affecting nest and site fidelity in Adirondack Barn Swallows (*Hirundo rustica*). *Auk* 101:780–789.
- Sogge, M.K., R.M. Marshall, T.J. Tibbitts, and S.J. Sferra. 1997. A Southwestern Willow Flycatcher Natural History Summary and Survey Protocol. National Park Service Technical Report NPS/NAUCPRS/NRTR-97/12.
- Sogge, M.K., J.C. Owen, E.H. Paxton, S.M. Langridge, and T.J. Koronkiewicz. 2001. A targeted mist net capture technique for the willow flycatcher. *Western Birds* 32:167–172.
- Stacey, P.B., and M.L. Taper. 1997. Migration within metapopulations: the impact upon local population dynamics. In: (I.A. Hanski and M.E. Gilpin., eds.) *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, CA.
- Stoleson, S.H., Whitfield, M.J., and M.K. Sogge. 2000. Chapter 8: Demographic characteristics and population modeling. Pages 83–93 In *Status, ecology, and conservation of the Southwestern Willow Flycatcher* (D.M. Finch and S.H. Stoleson, eds.). General Technical Report RMRS-GTR-60. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Unitt, P. 1987. *Empidonax traillii eximius*: an endangered subspecies. *Western Birds* 18:137–162.
- U.S. Fish and Wildlife Service. 1993. Proposal to list the Southwestern Willow Flycatcher as an endangered species and to designate critical habitat. Federal Register 58:39495–39522.
- U.S. Fish and Wildlife Service. 1995. Final rule determining endangered status for the Southwestern Willow Flycatcher. Federal Register 60:10694.
- U.S. Fish and Wildlife Service. 2002. Southwestern Willow Flycatcher final recovery plan. Albuquerque, New Mexico.
- Vega Rivera, J.H., W.J. McShea, and J.H. Rappole. 2003. Comparison of breeding and postbreeding movements and habitat requirements for the Scarlet Tanager (*Piranga olivacea*) in Virginia. *Auk* 120: 632–644.
- Ward, M.P. 2005. The role of immigration in the decline of an isolated migratory bird population. *Conservation Biology* 19:1528–1536.
- White, G.C., and K.P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46 (Supplement):s120–s139.
- Winkler, D.W., P.H. Wrege, P.E. Allen, T.L. Kast, P. Senesac, M.F. Wasson, P.E. Llambias, V. Ferretti, and P.J. Sullivan. 2004. Breeding dispersal and philopatry in the Tree Swallow. *Condor* 106:768–776.
- Winkler, D.W., P.H. Wrege, P.E. Allen, T.L. Kast, P. Senesac, M.F. Wasson, and P.J. Sullivan. 2005. The natal dispersal of Tree Swallows in a continuous mainland environment. *Journal of animal ecology* 74:1080–1090.

Chapter 5—Demographic Modeling

Introduction

Demography is the study of populations and the processes that influence their trajectories. Four primary processes, or vital rates drive demographic patterns: productivity, survivorship, immigration, and emigration. Whether a population is increasing, declining, or stable results directly from the synergism of these demographic vital rates, which collectively contribute to a population's growth potential (Beissinger and Westphal 1998). Thus, the long-term sustainability of a population is typically measured by this population growth potential. The basic vital rates of survivorship, productivity, and immigration and emigration can all be modified by environmental factors, landscape characteristics, age, sex, etc. (Beissinger et al. 2006). For species of conservation concern, it is crucial to understand which of the multiple possible factors influence that population's growth potential (Holmes et al. 1996, Stoleson et al. 2000, Schrott et al. 2005).

While it is possible to look at individual vital rates to see if they are high (e.g., productivity) or low (e.g., mortality) compared to other populations or similar species, it is necessary to consider all the vital rates together in order to understand population processes and trajectories. Demographic modeling is a process to accomplish this by combining the vital rates to understand and predict a population's potential trajectory. Reasons to construct demographic models include simplifying the relationships among the vital rates for better understanding, evaluating the impact that management actions might have on a species, and estimating future trajectories (i.e., Population Viability Analysis). The most common are deterministic models (Beissinger et al. 2006) that use fixed values for the vital rates and combine them in a predictable way. For example, a deterministic model may take a simple form such as "births + immigration – deaths – emigrations." Another example would include matrix age structured models (Caswell 2001), which incorporate information on how vital rates may change at different age classes. Deterministic models are widely employed to understand population dynamics (Pulliam 1988), demography of wildlife species (Beissinger et al. 2006), and assess the health of sensitive species (Blakesley et al. 2001).

The endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*) is a small, migratory passerine that breeds exclusively in riparian habitats scattered throughout portions of the southwestern U.S. (Unitt 1987, Marshall 2000) and winters from central Mexico south to northern South America (Sedgwick 2000). Flycatcher numbers have declined precipitously as riparian habitats on the breeding grounds have

been lost or modified (USFWS 1993, Marshall and Stoleson 2000), and *E.t. extimus* was listed as a federally endangered species in 1995 (USFWS 1995). At the time of listing, many aspects of the flycatcher's biology were poorly understood (Marshall and Stoleson 2000, Stoleson et al. 2000). In particular, little was known about the vital rates of most flycatcher populations, and early efforts to model the demographics of the flycatcher were hindered by a lack of robust vital rate estimates (Stoleson et al. 2000). Thus a major purpose for this study was to gather long-term data suitable for demographic modeling.

From 1996 to 2005, we collaborated with the Arizona Game and Fish Department (AGFD) to conduct a large demographic study of Southwestern Willow Flycatchers in central Arizona at two core study sites, as well as multiple auxiliary breeding sites. One of our main objectives was to gather the demographic information necessary to evaluate population growth at the two study sites. Vital rates collected included survivorship, movement, and productivity, as well as information on census numbers. These vital rates, developed and described in earlier chapters of this report, are the essential building blocks of the demographic modeling presented in this chapter.

Methods

Study Sites

Our two study sites (fig. 1) were breeding populations at Roosevelt Lake (33°39'N, 110°58'W) and the San Pedro/Gila River confluence (hereafter San Pedro/Gila; 32°59'N, 110°46'W), where we conducted demographic research in cooperation with AGFD from 1996 to 2005 (Causey et al. 2006, English et al. 2006). We defined sites as a collection of riparian woodland patches, occupied by breeding flycatchers, which are found within the same river drainage and geographically isolated from other such breeding sites. Exact definitions of a site are difficult, and the definition of a site differs regionally (Durst et al. 2006). Based on movement data collected over the past 10 years, each site has a high degree of movement-based connectivity within drainages suggesting a distinct breeding population.

Our two study sites supported two of the largest known Southwestern Willow Flycatcher breeding populations throughout the period of this study (Durst et al. 2006), with mean population sizes of 201 and 239 individuals at Roosevelt Lake and San Pedro/Gila, respectively. At each site, extensive survey efforts were conducted at least three times in the

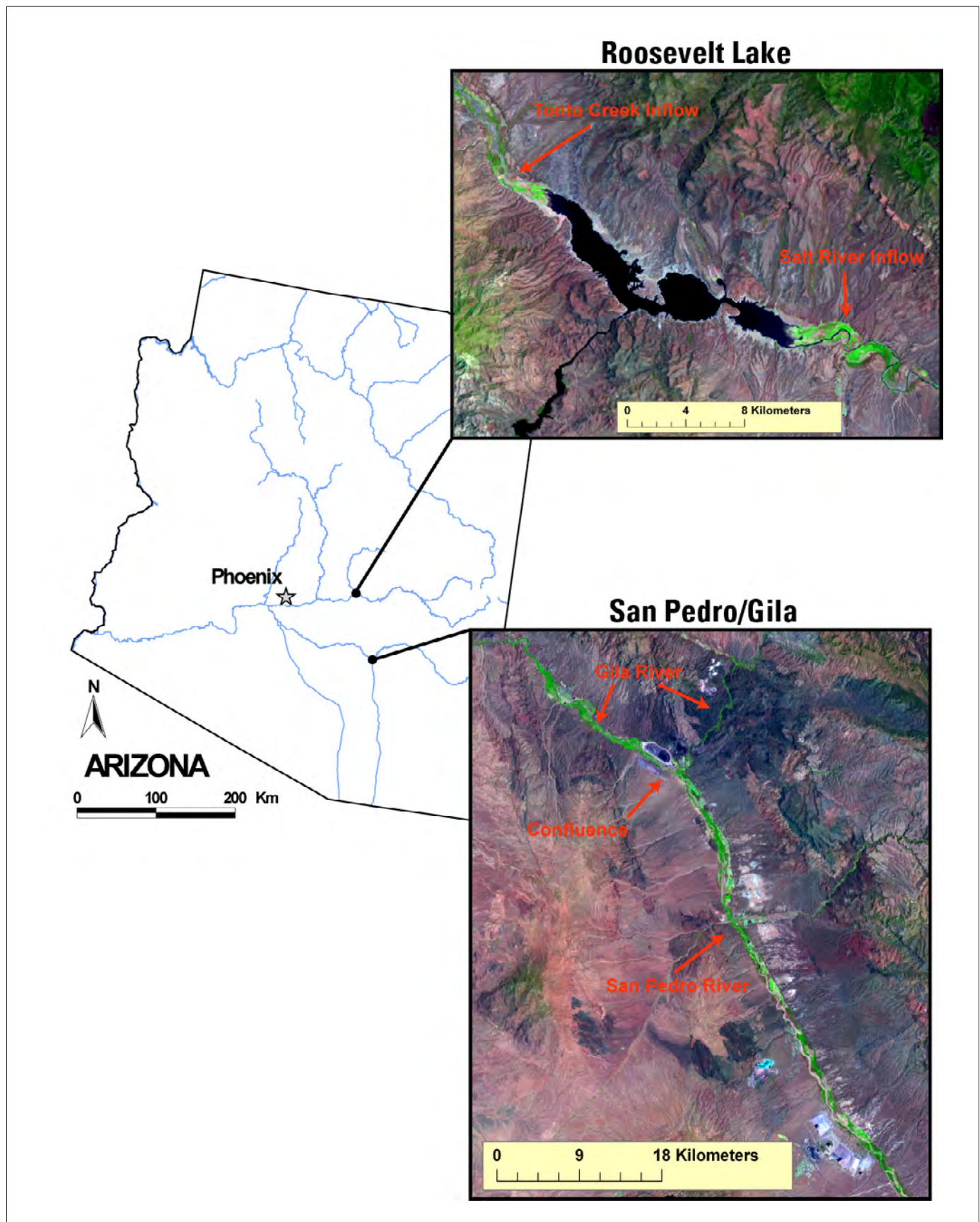


Figure 1. Location of the Roosevelt Lake and San Pedro/Gila study areas in central Arizona.

breeding season to detect all territorial flycatchers within the immediate and surrounding areas. In addition, multiple other breeding sites in Arizona and throughout the Southwest (49–444 km away) were periodically visited, which along with cooperative efforts of other researchers conducting similar studies allowed detection of dispersing flycatchers (see chapter 4).

The breeding habitat at the Roosevelt Lake and San Pedro/Gila study sites consisted of a heterogeneous mosaic of discrete riparian forest patches of varying ages and vegetation composition, ranging from 0.2 to 43 ha in size. Native habitat was characterized by Goodding's willow (*Salix gooddingii*) and Fremont cottonwood (*Populus fremontii*). Exotic habitat was dominated by tamarisk (saltcedar; *Tamarix* spp.). The understory vegetation consisted of a variety of grasses, forbs, and shrubs (mesquite [*Prosopis* spp.], coyote willow [*S. exigua*], tamarisk, *Baccharis* spp., and cocklebur [*Xanthium strumarium*]). Adjacent and surrounding non-riparian habitats were primarily composed of Sonoran Desert Uplands (Brown 1994), and in some cases agricultural lands.

Roosevelt Lake Study Site

The Roosevelt Lake study site consisted of two river drainages, the Salt River and Tonto Creek, each converging at the confluence of a reservoir. Breeding was documented as far as 12 km upstream on Tonto Creek and 5 km on the Salt River. The number of riparian patches in which breeding occurred varied over time as a result of colonization or desertion of patches, largely driven by fluctuating lake levels. Over the 10-year period, we documented breeding in a maximum of 23 patches encompassing approximately 242 ha of riparian habitat. Long-term persistent drought conditions between 1996 and 2005 (McCabe et al. 2004) resulted in reservoir levels dropping to a low of 10% capacity in 2002. The exposed lakebed was colonized by riparian vegetation, which was subsequently colonized by breeding flycatchers (see chapter 5). In 2005, following unusually high winter precipitation, Roosevelt Lake filled to near capacity, inundating much of the riparian breeding habitat occupied in 2004 (see chapter 5).

San Pedro/Gila Study Site

The San Pedro/Gila study site encompassed 101 km of river, centered at the confluence of the free-flowing San Pedro River and the regulated Gila River, and extending upstream on the San Pedro to San Manuel Crossing and downstream on the Gila River to Kelvin Bridge. As with Roosevelt Lake, the amount of riparian vegetation along the San Pedro/Gila changed over the 10-year study, with as many as 29 habitat patches supporting breeding flycatchers, comprising approximately 222 ha of riparian forest.

Vital Rates

Robust estimates of vital rates are necessary for the development of useful models and estimates of a population's demographic growth potential. The vital rate estimates that we used in our models are detailed in other chapters of this report (i.e., chapter 2, Survivorship; chapter 3, Productivity; chapter 4, Movement), and are briefly outlined here.

Census Numbers

Formal tape-playback surveys (Sogge et al. 1997) were conducted by AGFD three times each breeding season (English et al. 2006), and were supplemented extensively by near-continuous searches of potential breeding habitat throughout the season by both AGFD and USGS. All areas of accessible, suitable habitat were searched within a large area, ensuring high confidence in census numbers and territory locations for each study site. By uniquely color-banding individuals and subsequently tracking them through resights and recaptures, we estimated population size in several ways, including the total number of territories, total number of breeding individuals, and the total number of individuals present at a given site in a given year (including non-territorial individuals; see chapter 7). The census numbers presented in this report are based on survey and resight information combined, and may vary slightly from past annual reports by AGFD and USGS.

Survivorship

Survivorship estimates were based on the return rates of 1080 banded adults and 498 banded juveniles, using maximum likelihood estimates with program MARK (White and Burnham 1999), and AIC for model selection (Burnham and Anderson 2002; see chapter 2). For adults, the most parsimonious factor to explain variation in survivorship probabilities was the effect of year, with no differences in sex and site, and marginal differences among different aged adults. For juveniles, date fledged was the most important factor, with little support for the effects of yearly variation; we did not test for differences between study sites and sex among juveniles as very few juveniles were banded at San Pedro/Gila (see chapter 2).

Accurate estimates of survivorship probabilities are difficult to obtain. Survivorship probabilities often suffer the consequences arising from the practicalities of field studies, including small sample sizes, small proportions of the population banded, low detection rates, and unknown levels of permanent emigration. However, our survivorship estimates are robust because large numbers of flycatchers were banded annually, a majority of detected flycatchers at both sites were banded in any given year, and our annual detection rate was high (78% detection probability on average; see chapter 2). While banding and resighting efforts were reduced at San

Pedro/Gila from 2001–05, there was no apparent effect on survivorship estimates (see chapter 2). Although we detected adult and juvenile dispersal from our study sites (see chapter 4), emigration rates were relatively low and had minimal effects on our survivorship estimates, with most movements occurring within a study site.

Productivity

Measuring the productivity of banded birds allowed us to estimate seasonal and lifetime productivity (see chapter 3). Once territories were found, efforts were made to identify mating status (monogamous, polygamous, or unpaired) and locate nests. Nests were monitored regularly by AGFD (Rourke et al. 1999) to determine the number of young fledged. Individuals were monitored throughout each breeding season and across years to determine seasonal fecundity (the total number of young fledged per individual per season) and an estimate of minimum lifetime productivity (the sum of an individual's seasonal fecundity over their lifetime; see chapter 3). Productivity varied significantly by year, study site, and age (second-year adults versus older adults).

Immigration and Emigration

Immigration and emigration, defined as juvenile and adult dispersal into or out of the study sites, respectively, were estimated by tracking the movement of banded individuals between our two study sites and at other breeding locations (see chapter 4). Over the 10-year study period, 98% of adult and 94% of juvenile movements we detected were within each of the two study sites, suggesting that between-site movements are rare and primarily by juvenile flycatchers. There was certainly some unknown number of individuals that dispersed out of the study sites undetected, and immigration of unbanded individuals is impossible to distinguish from local recruitment. However, modeling of movements within our study sites suggested there is a sharp decrease in the frequency of movements at increasing distances; movements over 30–40 km were infrequent. Because most between-site movements would require movements of more than 30–40 km, and usually much farther, and the evidence suggests that immigration/emigration was infrequent, we do not believe that immigration/emigration play a strong role in the population dynamics at the study site level. However, within the model (below), permanent emigration is accounted for as an undifferentiated portion of the survivorship estimates, because these estimates include both birds that die and birds that permanently leave the study area. Therefore, we also needed to provide the model an estimate of immigration as well. To do so, we used the average rate of between-site movement for both adults and juveniles.

Demographic Models

We utilized a deterministic model to explore the relationships among the vital rates, and estimated the population growth potential of the two study sites. The deterministic model we used is typically referred to as the “BIDE” model (Birth + Immigration - Death - Emigration). The model produces a value, λ , which describes the discrete (yearly) per capita rate of growth of a population given the vital rates entered into the model. Values of λ at 1.0 suggest a stable population, values above 1.0 suggest an increasing population, and values below 1.0 indicate a declining population. Several forms of the model exist, and we used the form (Pulliam 1988):

$$\lambda = \text{adult survivorship} + (\text{juvenile survivorship} \times (\text{seasonal fecundity}/2)) + \text{immigration}$$

As noted above, emigration is accounted for in the survivorship estimates, and so does not appear as a separate vital rate in this model equation. Seasonal fecundity is divided by two to generate the number of daughters produced per female (assuming a fledgling sex ratio of 50:50); this is a common demographic modeling approach that helps avoid issues of polygamy and extra-pair paternity. All graphs were created with SigmaPlot 8.0 (SPSS, Inc).

Results

Observed population trends

From 1996 to 2005, populations at both the Roosevelt Lake and San Pedro/Gila study sites increased in size overall and between most years (table 1, fig. 2). Year-to-year measures of change in the number of territories, the number of territorial adults, and the numbers of all detected adults (territorial and non-territorial combined) increased, with an overall 10-year average yearly increase of approximately 25% (table 1). However, the early years of the study period had greater year-to-year changes than did the latter half, which may indicate a study-bias due to improved survey techniques and the addition of new breeding locations in later years (particularly at the San Pedro/Gila study site). Therefore, excluding the first several years may provide a more accurate estimate of average observed population growth. Doing so results in estimates of population change of 1.18 for an 8-year period (1998–2005) and 1.08 for a 5-year period (2001–05). While all estimates of average population change indicate growth, there were some years when population measures decreased compared to the previous year (table 1). At Roosevelt Lake there was a

Table 1. Census numbers of Southwestern Willow Flycatchers at the Roosevelt Lake and San Pedro/Gila study sites, Arizona, 1995–2005. For each site and year are the census results for the number of territories detected and the change from the previous year (N_{t+1}/N_t), the number of territorial adults detected and change from the previous year (N_{t+1}/N_t), and the total number of adults detected (territorial and non-territorial combined) and change from the previous year (N_{t+1}/N_t). Overall, these three change estimates were remarkable similar to each other and between the two study sites.

Year	# Territories		Territorial individuals		All detected individuals	
	n	change	n	change	n	change
Roosevelt Lake						
1995	17	-	34	-	34	-
1996	35	2.06	62	1.82	64	1.88
1997	41	1.17	74	1.19	85	1.33
1998	50	1.22	93	1.26	99	1.16
1999	78	1.56	149	1.60	160	1.62
2000	111	1.42	212	1.42	233	1.46
2001	141	1.27	257	1.21	288	1.24
2002	142	1.01	177	0.69	296	1.03
2003	139	0.98	254	1.44	288	0.97
2004	215	1.55	326	1.28	413	1.43
2005	170	0.79	290	0.89	344	0.83
10-year mean	-	1.26	-	1.24	-	1.26
8-year mean	-	1.19	-	1.19	-	1.19
5-year mean	-	1.09	-	1.06	-	1.08
San Pedro/Gila						
1995	20	-	40	-	40	-
1996	35	1.75	70	1.75	73	1.83
1997	60	1.71	113	1.61	124	1.70
1998	87	1.45	167	1.48	176	1.42
1999	118	1.36	229	1.37	245	1.39
2000	125	1.06	230	1.00	247	1.01
2001	110	0.88	214	0.93	216	0.87
2002	158	1.44	271	1.27	278	1.29
2003	167	1.06	267	0.99	289	1.04
2004	166	0.99	311	1.16	321	1.11
2005	182	1.10	344	1.11	348	1.08
10-year mean	-	1.25	-	1.24	-	1.24
8-year mean	-	1.15	-	1.15	-	1.14
5-year mean	-	1.08	-	1.08	-	1.07

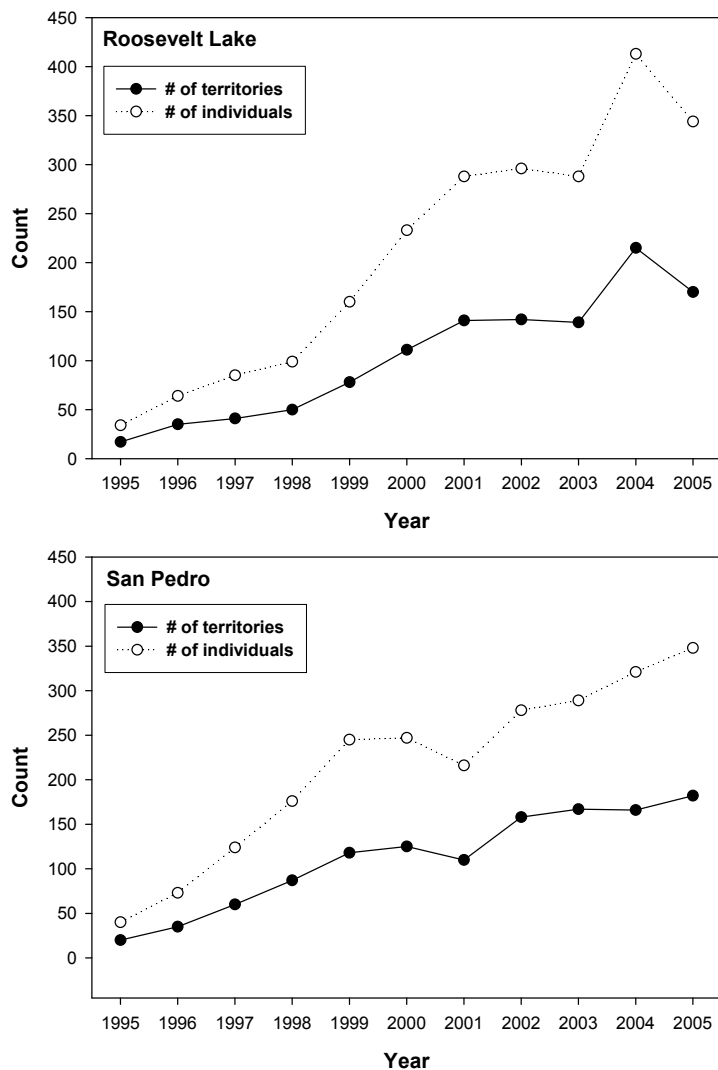


Figure 2. Observed changes in the number of territories and total number of Southwestern Willow Flycatchers detected at the Roosevelt Lake and San Pedro/Gila study sites, 1995 to 2005. Average yearly observed change was 1.25, 1.17, and 1.08 for 10-year (1996–2005), 8-year (1998–2005), and 5-year (2001–05), respectively.

slight decline in 2003, following the 2002 drought year. There was also a sharper decline in 2005, when much of the 2004 breeding habitat was inundated by rising reservoir levels at Roosevelt Lake. At the San Pedro/Gila, there was a decline in the number of territorial individuals in 2001; however, there was no decline after the 2002 drought.

Flycatcher Vital Rates

Flycatcher vital rates varied among years and between the two study sites. Measures of both survivorship (table 2) and seasonal fecundity (table 3) indicate a large degree of variability from year to year. Adult survivorship averaged 64% (range = 53%–73%), while juvenile survivorship averaged 34% (range = 13%–57%; table 2, see chapter 2). Survivorship did not vary among sites for adults, and analysis of juvenile survivorship is for Roosevelt Lake only (see chapter 2). Productiv-

ity also varied significantly among years, and between the two study sites (table 3; see chapter 3). Average seasonal fecundity was 1.6 for Roosevelt Lake females and 2.0 for San Pedro/Gila females. Productivity was highest in the wettest years (1998, 2001, 2003, [additionally 2005 for San Pedro/Gila]), and lowest in the driest years (1996, 2002; table 3).

Rates of immigration and emigration based on movements of banded birds to and from each study site were low and ranged from 0%–2% in any given year (see chapter 4), and there was no evidence of unbalanced dispersal/movement, with immigration and emigration approximately equal. Though known emigration was infrequent, juveniles were more likely to disperse away from the study sites (6% of all detected juvenile movements) than were adults (2% of adult detected movements). To counteract the inclusion of emigration in the survivorship estimates, we used the average dispersal numbers of adults and juveniles to derive an average

Table 2. Maximum likelihood survivorship probabilities (percent) of adult and juvenile Southwestern Willow Flycatchers at the Roosevelt Lake and San Pedro/Gila study sites, Arizona, 1996–2005. Values given are the sample size (n), percent survivorship, and 95% confidence interval (C.I.). Values for juveniles were calculated only for Roosevelt Lake; rates for adults are combined for both sites, because we found no statistical difference between sites (see chapter 2).

Year	Juvenile			Adult		
	n	Percent	95% C.I.	n	Percent	95% C.I.
1996–97	4	38	4–89	87	53	41–65
1997–98	21	13	3–43	120	53	45–62
1998–99	24	21	8–42	137	63	54–71
1999–2000	62	26	14–44	197	56	50–63
2000–01	71	31	20–45	241	66	59–72
2001–02	107	41	28–54	264	73	66–80
2002–03	2	57	7–96	282	67	61–73
2003–04	121	41	27–56	301	68	61–74
2004–05	86	32	19–50	393	57	51–63
10–year average	498	34	27–40	1080	64	62–66

Table 3. Average seasonal fecundity of female Southwestern Willow Flycatchers at the Roosevelt Lake and San Pedro/Gila study sites, Arizona, 1996–2005. Seasonal fecundity is the total number of young fledged per female in a breeding season (see chapter 3).

Year	Roosevelt Lake			San Pedro/Gila		
	n	fecundity	95% C.I.	n	fecundity	95% C.I.
1996	24	1.0	0.2–1.8	28	0.7	0.2–1.3
1997	42	1.7	1.0–2.5	43	1.6	0.9–2.3
1998	46	1.9	1.3–2.6	71	2.1	1.5–2.7
1999	79	2.1	1.4–2.7	79	1.8	1.3–2.3
2000	99	1.9	1.6–2.3	73	1.8	1.2–2.3
2001	136	2.2	1.8–2.5	60	2.7	2.0–3.4
2002	78	0.1	0.0–0.3	47	0.8	0.3–1.4
2003	167	2.0	1.8–2.3	81	2.3	1.9–2.7
2004	146	1.1	0.8–1.4	96	1.9	1.4–2.3
2005	148	1.4	1.1–1.7	91	2.3	1.9–2.8
Study period average		1.6	1.5–1.8		2.0	1.8–2.1

observed immigration rate of 3% which was incorporated into the demographic model.

Deterministic Projections of Population Growth

Using mean survivorship (adult = 0.64, juvenile = 0.34), study-period seasonal fecundity values (Roosevelt Lake = 1.6; San Pedro/Gila = 2.0; tables 2 and 3), and an average immigration rate (0.03), the estimated lambda value is 0.94 for Roosevelt Lake and 1.01 for the San Pedro/Gila. This suggests that Roosevelt Lake has a population growth potential that should lead to a decline of 6% per year given the mean vital rates, while San Pedro/Gila is estimated to have the potential to increase slightly by 1% each year, on average. Yearly estimates of lambda at Roosevelt Lake ranged from 0.67 to 1.21, with a

geometric mean of 0.87. At the San Pedro/Gila, lambda ranged from 0.63 to 1.31, with a geometric mean of 0.91 (table 4).

Our modeled population growth potential (lambda) was lower than the actual observed population growth at the study sites. Because the true means of the vital rates are unknown, and therefore could be higher or lower than our estimates, we evaluated how this uncertainty affected lambda estimates. Given that the discrepancy between calculated lambda and the observed population change suggests that the vital rates are underestimates, we only evaluated the upper ends of possible values. To do so, we repeated the modeling after increasing the mean values of all the parameters by one standard error (SE) and two standard errors. This resulted in higher lambda estimates of 1.06 and 1.19 for Roosevelt Lake and 1.14 and 1.28 for San Pedro/Gila (one and two SE increases, respectively).

Table 4. Yearly vital rates and estimated lambda values for Southwestern Willow Flycatchers at the Roosevelt Lake and San Pedro/Gila study sites, Arizona, 1996–2005. Survivorship values are the same for both sites, but seasonal fecundity is site specific.

Year	Survivorship (%)		Seasonal	
	Adult	Juvenile	fecundity	Lambda
Roosevelt Lake				
1996–97	53	38	1	0.75
1997–98	53	13	1.7	0.67
1998–99	63	21	1.9	0.86
1999–2000	56	26	2.1	0.86
2000–01	66	31	1.9	0.98
2001–02	73	41	2.2	1.21
2002–03	67	57	0.1	0.73
2003–04	68	41	2	1.12
2004–05	57	32	1.1	0.78
10-year average	64	34	1.6	0.94
San Pedro/Gila				
1996–97	53	38	0.7	0.69
1997–98	53	13	1.6	0.66
1998–99	63	21	2.1	0.88
1999–2000	56	26	1.8	0.82
2000–01	66	31	1.8	0.97
2001–02	73	41	2.7	1.31
2002–03	67	57	0.8	0.93
2003–04	68	41	2.3	1.18
2004–05	57	32	1.9	0.90
10-year average	64	34	2.0	1.01

The lambda values resulting from the two SE increases are derived from values of the vital rates that were approaching the 95% upper confidence level of their respective mean, and therefore are statistically plausible values for the true mean of the vital rates. These increases in the vital rates brought the population growth potential closer to the observed population changes (fig. 3). This analysis assumes that these higher vital rates are realistically achievable by birds at our sites, an assumption supported by the fact that measured vital rates in some years had values that exceeded two SEs of the mean vital rates (table 4).

Estimates of lambda will vary as each of the vital rates changes, and it is instructive to explore what a specific vital rate would need to be to achieve a target lambda value. For example, at the mean adult survivorship rate of 64% and mean juvenile survivorship of 34%, the seasonal fecundity necessary for a lambda of 1.25, 1.18, and 1.08 (observed

population growth at different temporal scales) would be 3.4, 3.0, and 2.4, respectively (fig. 4). However, at a higher juvenile survivorship rate (45%), the female fecundity necessary for the same lambda of 1.25, 1.18, and 1.08 would be 2.6, 2.3, and 1.8, respectively (fig. 4). Thus, higher juvenile survivorship (or adult survivorship) lowers the seasonal fecundity values needed to sustain a population. Conversely, higher seasonal fecundity values would mean that a population can be sustained with lower survivorship.

Discussion

The difference between our demographic model estimates and the observed population growth at the two study sites

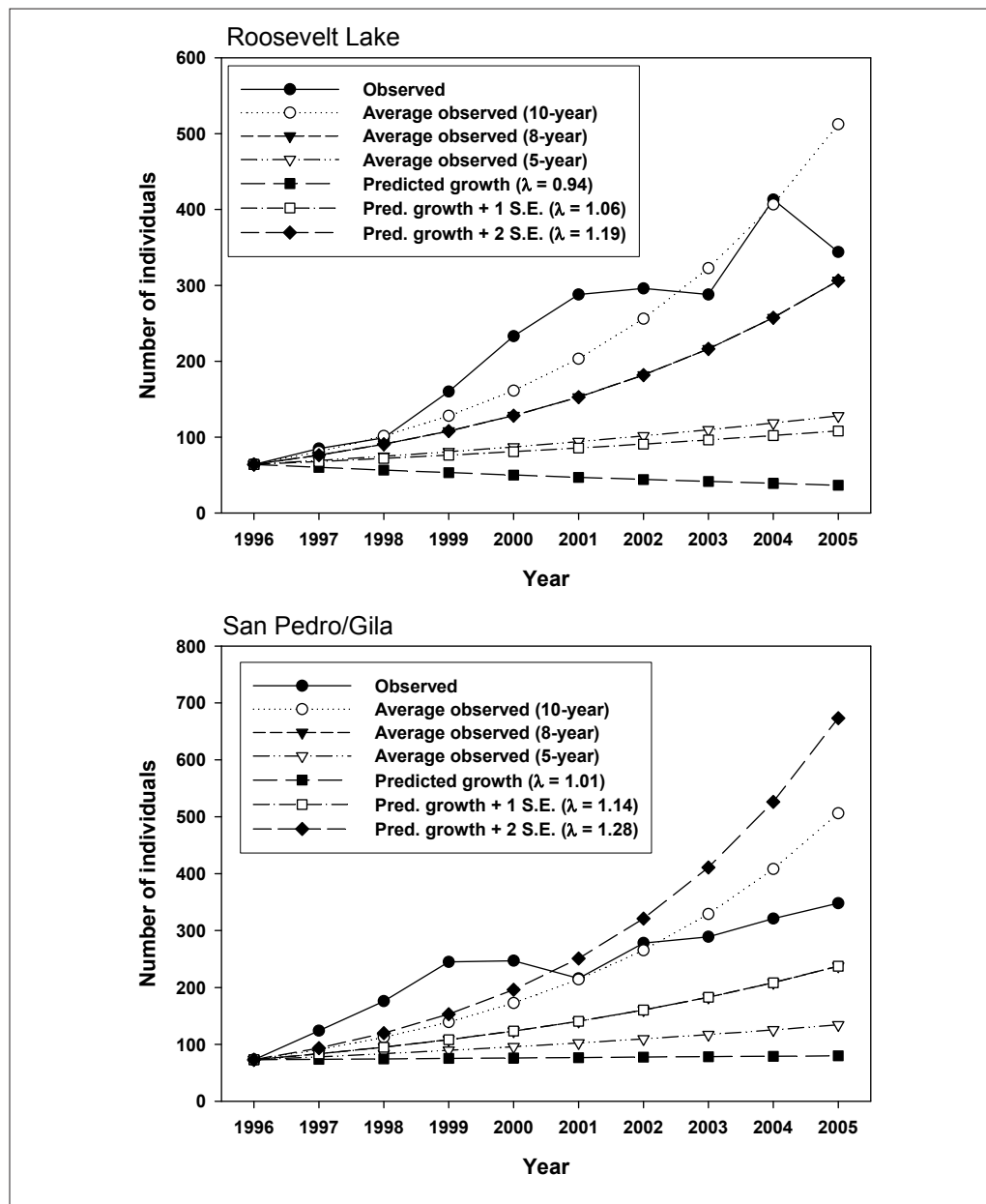


Figure 3. Projections of population growth at the Roosevelt Lake and San Pedro/Gila study sites, 1996–2005. Projections include actual observed census numbers (closed circle), population change expected at average observed change for 10-year average (1996–2005; open circle), 8-year average (1998–2005; closed triangle), and 5-year average (2001–05; open triangle), predicted growth at observed lambda (closed square), predicted population growth with vital rates increased by 1 (open square) and 2 (closed diamond) S.E. of the mean values. Population census size in 1996 was used to start the projections at Roosevelt Lake ($n=64$) and San Pedro/Gila ($n=73$).

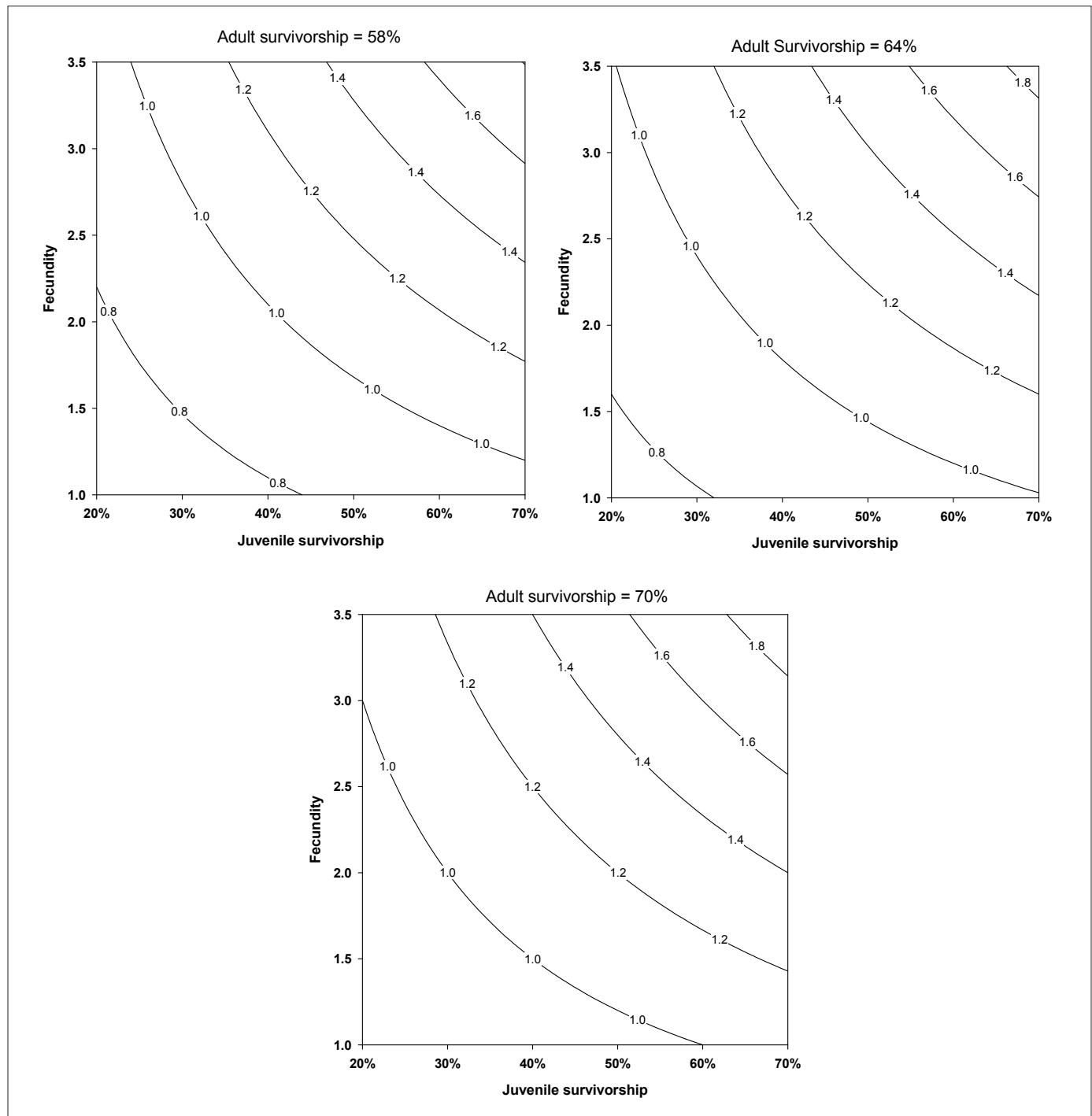


Figure 4. Isobar graphs showing the relationship of adult and juvenile survivorship and seasonal fecundity on estimates of lambda. Each panel represents a separate adult survivorship value, with the x-axis containing a range of possible juvenile survivorship estimates, and the y-axis containing a range of possible seasonal fecundity values. Isobars represent the lambda values expected (in 0.2 increments) given a particular combination of vital rates. For example, at the average adult survivorship of 64%, a seasonal fecundity of 3.5 and juvenile survivorship of 20% would result in a lambda of approximately 1.0, whereas the same fecundity but a juvenile survivorship of 70% would result in a lambda of approximately 1.9.

suggests the models we used are underestimating each population's growth potential, with the magnitude of the discrepancy dependent on the time frame over which we consider the observed population change. The observed lambda, based on annual population censuses for both study sites, averaged 1.25 for 1996–2005 and 1.08 for 2001–05. However, the calculated lambdas were lower: 0.94 for Roosevelt Lake and 1.01 for the San Pedro/Gila study sites. A difference between estimated lambda and observed population trends is not uncommon (Beissinger and Westphal 1998, Akcakaya et al. 2003), although most studies do not have a good sense of their actual population growth trajectory. In cases where estimates of lambda suggested a decline when the population under study was believed to be stable or growing (Akcakaya et al. 2003, Blakesley et al. 2001, Budnik et al. 2000, Jones et al. 2004, Keyser et al. 2004), it is often assumed that one or more of the vital rates were poorly measured (Akcakaya et al. 2003). The discrepancy between observed population growth and estimated lambda in our study could arise from one or more factors: the census numbers were inaccurate, one or more of our vital rates are inaccurate, or the models used to describe potential population growth are inappropriate. We explore these possibilities below.

Census Numbers

One of the major objectives of this 10-year study was to produce highly accurate counts of all territories within the defined study sites. Standardized surveys supplemented by intensive area searches gave us high confidence that our census estimates were robust, at least for the number of territories and territorial individuals within the areas searched. Additionally, all areas of suitable habitat that could be reached and were contiguous or adjacent to the study area were surveyed.

Although census efforts were extensive, several factors could influence the accuracy of the population estimates. Land ownership is one such factor. Within the Roosevelt Lake study area, most sites were on public lands and accessible to surveyors; portions of private land on Tonto Creek constituted a very small portion of the breeding habitat. However, much of the land on the San Pedro/Gila is privately owned, and permission to access lands increased over time such that more sites were surveyed and new areas were contributing to the census numbers (although permission to access some lands were lost over time as well). Delays between habitat development and surveys at a particular site could be another factor. Over much of the study period, the amount of breeding habitat at Roosevelt Lake increased substantially, and it is possible that some young habitat supported breeding flycatchers for a year or two before we discovered them. A final consideration is that rates of population increase (based on surveys) were highest in the early years of the study. While there may be biological reasons for this, it may also be due in part to refinement and improvement of survey techniques and skills over time, including a greater emphasis on surveying potential breeding habitat

at Roosevelt Lake, and the access to more private lands on the San Pedro/Gila study site.

Overall, despite some degree of uncertainty over which time frame of census numbers to consider, we believe the census numbers are a good approximation of the actual population size at the two study sites. Therefore, the true rate of increase probably lies between our highest (1996–2005) and lowest (2001–05) estimates, such that our observed population growth rate can be used to retrospectively assess the strength of the demographic models' ability to describe population growth potential at the sites during the period surveyed. Thus, the discrepancy between the estimate growth potential and the observed population size change is 12%–31% average yearly change at Roosevelt Lake, and 9%–24% at San Pedro/Gila.

Adult Survivorship

Adult survivorship is the vital rate typically believed to have the greatest impact on the population growth models (based on matrix elasticity tests; Stoleson et al. 2000). We believe our adult survivorship estimates are robust because (1) they are based on the long-term tracking of over 1,000 individuals, (2) we used maximum likelihood methods to estimate survivorship, and (3) we had high detection rates for adults, suggesting most individuals were detected if alive (see chapter 2). Additionally, we assessed the potential confounding effects of permanent emigration on survivorship estimates, by looking at how survivorship estimates changed with increasing spatial scale, and concluding that we were accurately tracking most adults (see chapter 2). Survivorship did not differ between sites, suggesting that the different levels of banding and resighting between the study sites in the last half of the study did not influence survivorship estimates; further, evidence suggested that most mortality occurred away from the breeding grounds. Adult survivorship did vary yearly, by as much as 20% (range = 53%–73%), and thus a 10-year mean value does not necessarily reflect the year-to-year variation. However, most yearly values were within 10% or less of the overall mean.

Juvenile Survivorship

Juvenile survivorship rates are also generally believed to have a great influence on population growth models. As with adults, our juvenile survivorship estimates benefited from the long-term tracking of many individuals, and the use of maximum likelihood estimation. However, although we banded nearly 500 nestlings over the course of this study, and employed extensive efforts to detect those that survived and returned, our detection rate for second-year (SY) adults was lower than that of adults (51%; see chapter 2). Many nestlings that were banded were not detected again until after their second year, and 41% of those that were detected as SY were not territorial (see chapter 2). Thus, detection of second-year adults was difficult. Additionally, our juvenile survivorship

estimates are based on Roosevelt Lake, and the San Pedro/Gila may have higher (or lower) survivorship estimates. Finally, the longest movements we detected, especially to other drainages, were by juveniles, reinforcing the idea that a greater proportion of juveniles could be leaving the site than we detected doing so.

However, while there are several possible reasons why our juvenile survivorship estimates may not be as robust as those for adults, it is not necessarily a major contributor to the discrepancy between the estimated growth potential and the observed population size changes. For example, when juveniles survive and return to the study sites but are not detected, they do not contribute to either the population census or the observed population growth. Once they become territorial and attempt to breed, they have a high probability of being detected and therefore are accounted for in both the estimated lambda and the census numbers. Non-detected permanent emigration of juveniles is incorporated into the survivorship estimates, but immigration of young adults into the study sites is difficult to detect. However, our juvenile survivorship probabilities are equal to or higher than other comparable passerine studies (see chapter 2), so there is no evidence to suggest we are substantially underestimating survivorship. Finally, our juvenile survivorship rates would have to increase by approximately 22%–30% to produce the observed lambda of 1.08–1.25; while juvenile survivorship probability may reach this level some years, our data suggest that in most years it does not.

Fecundity

Given the large number of nests monitored each year, and the intensive efforts to track individuals throughout the season, our estimates of seasonal fecundity at the two study sites are also believed to be robust. The only apparent source of bias in our estimates is that banded females are more likely to be older adults, which would bias the estimate of seasonal fecundity toward higher, rather than lower values. The isobar graphs (fig. 4) suggest that seasonal fecundity would have to be approximately 2.4–3.4 young fledged per season, 0.4 to 1.8 more young fledged than average, to obtain a lambda of 1.08–1.25 (assuming average adult and juvenile survivorship rates). While some years approached this higher rate, others were much lower. Similarly, the average minimum lifetime productivity (see chapter 3) was 3.3 offspring per individual (1.7 daughters per female). Based on our average juvenile survivorship (34%), this level of lifetime productivity would mean that one adult produces on average only 0.56 “replacement” flycatchers in its lifetime—a rate that is unsustainable. Nonetheless, the seasonal fecundity rates recorded in this study were at or above most estimates from other Willow Flycatcher populations, suggesting the rates are not outside the norm.

The models we used assumed an equal sex ratio of young produced. Earlier studies documented that while the overall sex ratio of young from four Arizona study sites was 1:1

male to female, it varied from site to site (Paxton et al. 2002). Evaluating the sex ratio from 1996 to 2000, Roosevelt Lake was biased toward females while San Pedro/Gila was biased toward males. While modeling a female bias at the Roosevelt Lake study site would increase the lambda estimates, the male bias at the San Pedro/Gila would reduce the estimated lambda. More work is needed to explore the full implications of nestling sex ratios on the growth potential at both of these study sites.

Immigration and Emigration

Immigration and emigration can potentially have profound effects on population growth. Most studies have no information on rates of immigration and emigration, assume the rates to be equal (canceling each other out in terms of population growth), and therefore do not consider immigration and emigration in their demographic models. Pulliam (1988) pointed out that in habitats with different quality and productivity levels, this assumption may not be accurate. For example, populations with high productivity can have estimates of population growth potential far exceeding what is observed (source populations), while others that are stable have lambda estimates that could not sustain the populations (sinks). Pulliam (1988) suggested that the source populations may be sustaining the sink populations, and cautioned that immigration and emigration can be important to understanding the population dynamics.

Therefore, one explanation for the discrepancy between the census numbers and estimated growth potential at the Roosevelt Lake and San Pedro/Gila study sites is that they are population sinks being supported by an influx of individuals emigrating from other breeding sites. There is certainly some level of undetected immigration into the study sites, but it is unfortunately impossible to distinguish between immigration and the local recruitment of unbanded individuals. Further, the maximum-likelihood survivorship estimates incorporate permanent emigration into their estimates (though not distinguishable from mortality), so in running our model we attempted to provide some estimate of immigration as well. The correction that we made (3% per capita immigration) is based on the observed rate of between-site movement of banded birds, and may be an underestimate.

Overall, though, with the location and size of many breeding populations of the Southwestern Willow Flycatcher known (Durst et al. 2006), we think it unlikely that growth of the Roosevelt Lake and the San Pedro/Gila sites, two of the largest populations known, was primarily due to immigration from other breeding populations. For this to be the case, substantial numbers of individuals would need to have moved into the two study sites from elsewhere in most years to account for the discrepancies in population change. Although we believe that our estimated low rates of immigration and emigration reflect the typical situation, it is possible that other sites occasionally contribute an unusual number of emigrating individu-

als that could bolster the population size of our study areas. However, although immigration is one plausible explanation for why the model results differed from observed growth, and may have helped to increase the population growth at the study sites, we feel it is unlikely to have been the primary driver of the observed population change.

Clearly, the discrepancies between the observed population growth and the estimated lambda are difficult to explain. Stoleson et al. (2000) made one of the first attempts to model the demographic growth potential of the Southwestern Willow Flycatcher. Using available data from a variety of sources and sites, they estimated population-wide lambdas under conservative, intermediate, and optimistic vital rate scenarios and arrived at values of 0.46, 0.78, and 1.11, respectively. This large range reflects considerable variability in the data available to them, and they concluded their study with a call for more research to generate better vital rates. Vital rates from our two study sites are at the upper end of the range presented by Stoleson et al. (2000), primarily reflecting better estimates of survivorship, and thus both Stoleson et al. (2000) and our work indicated population growth potential substantially lower than the documented rate of population change at our two study sites. A demographic study of the Kern River Preserve population in California (Noon and Farnsworth 2000) found similar results. Overall lambda estimates of 0.89 were estimated, even though the population was not correspondingly declining. These modeling attempts suggest that different types of demographic models will need to be employed for flycatchers to provide a better fit with their actual demographic dynamics. For example, if in fact movement is largely contributing to the growth of these populations, then a meta-population spatial approach could be used to model where the birds are moving from and patterns of movement across the landscape. However, it may be that new classes of models will need to be developed that can better mimic flycatcher population dynamics, and future efforts in this area may yield useful results.

At this point, the most parsimonious explanation for the discrepancy between actual and model-predicted population growth may be a consistent underestimation of all vital rates. For example, if we increased our fecundity, juvenile survival, and adult survival by 10% (assuming they were underestimated by that amount), the model-generated lambda would approach 1.2 without requiring any one of the vital rates to change dramatically (e.g. 38% to 42% juvenile survival, 64% to 70% adult survival, and 2.0 to 2.2 fecundity). Additionally, a higher rate of immigration than estimated would close the gap between the observed and estimated growth rates, especially if the 5-year (2001–05) estimates of observed population change (8% annual growth) were used.

Considering both year-to-year estimates of population growth potential and the actual observed population change, breeding flycatcher populations at our study sites appear to have a lambda somewhere near 1.0. This suggests that in good years they will exceed 1.0, and in bad years they may fall short of that threshold. If Roosevelt Lake and San Pedro/Gila

are dependent on emigrants from other sites, then their fate is tied with breeding populations at a regional level. However, periods of drought resulted in lower productivity (see chapter 3), and estimates of lambda for those years dipped to their lowest levels. Climate models projecting changes in climate due to global warming generally agree that droughts in the southwestern U.S. will become more frequent and more severe in the coming centuries (Seager et al. 2007). Additionally, population growth in the Southwest has been increasing such that water demands are generally rising, and stressors on riparian habitat may increase in the future. Thus, long-term predictions of population viability must be taken cautiously given the many uncertainties regarding future events.

Management and Research Considerations

Population Dynamics

The lambda estimates for our two study sites were just above and a little lower than 1.0, and well below the observed census-based population growth. This suggests that either the two study sites are population sinks, sustained and growing via emigrants from other sites, or that the model (or the vital rate estimates it is based on) are poorly reflecting the population dynamics of the study sites. More research may help clarify which of these two scenarios is the true cause of this discrepancy. Regardless, the observed population growth was real, suggesting that these two populations can sustain themselves given adequate breeding habitat, and no significant change in the vital rates of the population and/or in the rate of emigrants from other sites.

Population Monitoring

While vital rate values and the lambda values generated via demographic modeling can inform us about the health of a population during the period that we studied it, projecting these models far into the future can be misleading. The farther forward that population growth is projected, the lower the accuracy and greater the uncertainty in the projections. For instance, vital rates may change over time, the amount of suitable breeding habitat could vary, and future changes in climate and human land practices all could affect future flycatcher population trends in unpredictable ways. Relying solely on modeling estimates to direct future management would be problematic at best, especially with regard to population trends over the long term. Therefore, at least periodic population monitoring is needed if managers seek to track the progress of populations or to verify whether vital rates have remained stable.

Demographic Modeling

Given the discrepancies between the observed changes in population size at our two study sites versus what was predicted via demographic models, we believe that further work is warranted to develop new models to better describe flycatcher population dynamics. Documenting the vital rates of a population of interest is an important step for informed management, but to fully understand whether those vital rates are sufficient to sustain a population requires consideration of the synergistic contribution that all vital rates have to overall population health. The models we employed are used widely in most other comparable studies, yet may not be able to fully capture the dynamic nature of flycatcher population demography. While current models can act as a starting point, new modeling directions may be necessary before demographic models can be used with confidence in the future for managing the Southwestern Willow Flycatcher. The long-term and multiscale demographic data collected during our study could be serve as the foundation for testing new model approaches.

Limiting Factors for Flycatcher Populations

Ultimately, a key question to ask with regard to the eventual recovery of the flycatcher in the Southwest is whether they are habitat limited or demographically limited. If limited by suitable breeding habitat, then the key to recovery is promoting an increase in the amount of riparian habitat across the flycatcher's range. Based on the observed population growth during this study, flycatchers (at least at our two study sites) would have the potential to expand into new habitats if it were suitable and available. However, this growth may be sustain by immigration, a situation that may not occur in other, more isolated populations. Thus, any increase in the occupation of suitable breeding habitat may be slow or fast and may vary by region or among different populations. There may be areas with suitable breeding habitat that are unoccupied because there are not enough flycatchers to occupy all available habitat, creating a lag time between creation of the suitable habitat and full occupancy. Therefore, flycatchers may be limited by both breeding habitat and demographics, and effective future management will likely need to address both potential limiting factors.

References

- Akcakaya, H.R., J.L. Atwood, D. Breininger, C.T. Collins, and B. Duncan. 2003. Metapopulation dynamics of the California Least Tern. *Journal of Wildlife Management* 67:829–842.
- Beissinger, S.R., J.R. Walters, D.G. Catanzaro, K.G. Smith, J.B. Dunning, S.M. Haig, B.R. Noon, and B.M. Stith. 2006. Modeling approaches in avian conservation and the role of field biologists. *Ornithological Monographs* 59:1–56.
- Beissinger, S.R., and M.I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62:821–841.
- Blakesley, J.A., B.R. Noon, and D.W.H. Shaw. 2001. Demography of the California Spotted Owl in northeastern California. *Condor* 103:667–677.
- Brown, D. E. (Ed.). 1994. *Biotic Communities – Southwestern United States and Northwestern Mexico*. University of Utah Press, Salt Lake City, UT.
- Budnik, J.M., M.R. Ryans, and F.R. Thompson. 2000. Demography of Bell's Vireo in Missouri grassland-shrub habitats. *Auk* 117:925–935.
- Burnham, K.P. and D.R. Anderson. 2002. *Model selection and multimodel inference*. Springer-Verlag Publishers, New York.
- Caswell, H. 2001. *Matrix population Models: Construction, Analysis, and Interpretation*. 2nd ed. Sinauer Associates, Sunderland, Massachusetts.
- Causey, C.F., M.G. Pollock, S.L. Durst, P.J. Newell, E.H. Paxton, and M.K. Sogge. 2006. *Survivorship and movements of Southwestern Willow Flycatchers at Roosevelt Lake, Arizona—2005*. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix, AZ.
- Durst, S.L., M.K. Sogge, H. English, S.O. Williams, B.E. Kus, and S.J. Sferra. 2006. *Southwestern Willow Flycatcher breeding site and territory summary—2005*. U.S. Geological Survey report to Bureau of Reclamation, Phoenix, AZ.
- English, H.C., A.E. Graber, S.D. Stump, H.E. Telle, and L.A. Ellis. 2006. *Southwestern Willow Flycatcher 2005 survey and nest monitoring report*. Arizona Game and Fish Technical Report 248.
- Holmes, R.T., P.P. Marra, and T.W. Sherry. 1996. Habitat-specific demography of breeding Black-throated Blue Warblers (*Dendroica caerulescens*): Implications for population dynamics. *Journal of Animal Ecology* 65:183–195.
- Jones, J., J.J. Barg, T.S. Sillett, M.L. Veit, and R.J. Robertson. 2004. Minimum estimates of survival and population growth for Cerulean Warblers (*Dendroica cerulea*) breeding in Ontario, Canada. *Auk* 121:15–22.
- Keyser, A.J., M.T. Keyser, and D.E.L. Promislow. 2004. Life-history variation and demography in Western Bluebirds (*Sialia mexicana*) in Oregon. *Auk* 121:118–133.

- Marshall, R.M. 2000. Chapter 2: Population status on breeding grounds. Pages 3–11 *in* Status, ecology, and conservation of the Southwestern Willow Flycatcher. (D.M. Finch and S.H. Stoleson, eds.) USFS Rocky Mountain Research Station, Gen. Tech. Rep. RMRS-GTR-60. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Marshall, R.M., and S.H. Stoleson. 2000. Chapter 3: Threats. Pages 13–24 *in* Status, ecology, and conservation of the Southwestern Willow Flycatcher (D.M. Finch and S.H. Stoleson, eds.). General Technical Report RMRS-GTR-60. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- McCabe, G.J., M.A. Palecki, and J.L. Bentancourt. 2004. Pacific and Atlantic Ocean influences on multidecadal drought frequency in the United States. *Proceedings of the National Academy of Sciences* 101:4136–4141.
- Noon, B.R., and M. Farnsworth. 2000. Demographic analysis of the Southwestern Willow Flycatcher: Kern River population. Report to the Bureau of Reclamation.
- Paxton, E.H., M.K. Sogge, T.D. McCarthy, and P. Keim. 2002. Nestling sex ratio in the Southwestern Willow Flycatcher. *Condor* 104:877–881.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- Rourke, J.W., T.D. McCarthy, R.F. Davidson, and A.M. Santaniello. 1999. Southwestern Willow Flycatcher nest monitoring protocol. Nongame and Endangered Wildlife Program Technical Report 144. Arizona Game and Fish Department, Phoenix, AZ. 32pp.
- Schrott, G.R., K.A. With, and A.W. King. 2005. Demographic limitations of the ability of habitat restoration to rescue declining populations. *Conservation Biology* 19:1181–1193.
- Seager, R., M. Ting, I. Held, Y. Kushnir, J. Lu, G. Vecchi, H. Huang, N. Harnik, A. Leetma, N. Lau, C. Li, J. Velez, and N. Naik. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science Express*, 5 April 2007.
- Sedgwick, J.A. 2000. Willow Flycatcher (*Empidonax traillii*). *In* The Birds of North America, No 533 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.
- Sogge, M.K., R.M. Marshall, T.J. Tibbitts, and S.J. Sferra. 1997. A Southwestern Willow Flycatcher Natural History Summary and Survey Protocol. National Park Service Technical Report NPS/NAUCPRS/NRTR-97/12.
- Stoleson, S.H., M.J. Whitfield, and M.K. Sogge. 2000. Demographic Characteristics and Population Modeling. Pages 83–93 *in* Status, Ecology, and Conservation of the Southwestern Willow Flycatcher. Finch, D.M. and S.H. Stoleson (eds). USDA Forest Service Rocky Mountain Research Station General Technical Report RMRS-GTR-60.
- Unitt, P. 1987. *Empidonax traillii eximius*: An endangered subspecies. *Western Birds* 18:137–162.
- U.S. Fish and Wildlife Service. 1993. Proposal to list the Southwestern Willow Flycatcher as an endangered species and to designate critical habitat. *Federal Register* 58:39495–39522.
- U.S. Fish and Wildlife Service. 1995. Final rule determining endangered status for the Southwestern Willow Flycatcher. *Federal Register* 60:10694.
- White, G.C., and K.P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:s120–s139.

Chapter 6—Spatial Modeling

Introduction

Habitat is essential for the presence, persistence, and long term viability of any wildlife species and thus understanding the relationship between wildlife populations and habitat characteristics is crucial for the long term management of species and communities (Morrison et al. 1998). Habitats for avian species provide basic resources including food, shelter, and protection from predators. Habitat for breeding must provide additional resources including nest structure support, extra food resources for raising young, and protection from nest predators. Thus, species need to be well adapted to their habitat, and understanding their habitat needs is important for management and conservation.

However, habitat relationships are complex, involving many factors, and as such quantifying habitat relationships is difficult (Cody 1985). Additionally, habitat may vary in its level of quality (Pulliam 1988), and linking habitat quality to lifetime fitness of species is the ultimate goal of wildlife-habitat relationship research (Wiens 1989). An important first step to understanding these relationships is to be able to predict the occurrence and estimate the amount of available breeding habitat for a species in a given area. This can be done at multiple scales, from the nest site to the full geographic range of a species, but as the geographic scale increases, the difficulty in accurately identifying potential suitable habitat increases (Cody 1985). One approach to quantifying habitat use over a large area is by developing Geographic Information Systems (GIS) based models. GIS modeling allows the characterization of habitat and the ability to predict suitable breeding habitat over a large area. In addition to issues of scale, temporal change in habitat adds an additional level of complexity to the problem. In habitats that are dynamic over short time scales, models can be improved by incorporating variables or factors that reflect temporal change (Reino 2005). Although using these approaches requires detailed information about the presence/absence or abundance of a species, it can ultimately provide an important tool that can be applied over a large geographic area.

The Southwestern Willow Flycatcher (*Empidonax traillii extimus*) is a small, migratory passerine that breeds exclusively in riparian habitats scattered throughout portions of the southwestern U.S. (Unitt 1987, Marshall 2000), and winters from central Mexico south to northern South America (Sedgwick 2000). Flycatcher numbers have declined precipitously as riparian habitats on the breeding grounds have been lost or modified (USFWS 1993, Marshall and Stoleson 2000), and *E.*

t. extimus was listed as a federally endangered species in 1995 (USFWS 1995). Because of the perceived link of declining numbers and loss of breeding habitat, substantial research has been directed toward determining flycatcher habitat requirements, especially at the landscape level. Yet there is still much that is unknown about why flycatchers occur in some areas but not others, and an exact understanding of the habitat requirements of the flycatcher is still elusive. Additionally, the riparian habitats upon which the flycatcher depends are spatially and temporally dynamic. Because of this, flycatcher breeding sites are constantly shifting across the landscape, making determination of suitable breeding habitat and protection of such habitat all the more difficult.

In 1999 the Arizona Game and Fish Department (AGFD) developed a GIS-based model (i.e., spatially explicit) of flycatcher breeding habitat in south-central Arizona (Hatten and Paradzick 2003). It was a generalist model designed to predict both riverine and reservoir habitats, and has been used in a statewide mapping effort (Dockens et al. 2004), and along the Rio Grande in New Mexico (Hatten and Sogge 2007). The AGFD model has been successful at identifying riparian areas where flycatcher nests are most likely to be located, but it is not as specific as desired for some management applications. That is, the AGFD model is good at finding patches of riparian vegetation that contain flycatcher nests, but it is less good at eliminating areas where nests do not occur.

We used the AGFD model as our starting point in this modeling exercise, expanding upon it in several important ways. First, we increased the number of spatial variables examined to determine if the AGFD model could perform better. Second, we included data from all territories, not just those with nest locations, to obtain a broader representation of occupied habitat, rather than basing the model only on habitat in which actual nesting occurred. Third, because riverine and reservoir/lake systems differ in the amounts and types of riparian habitat, we modeled them separately to increase model accuracy within each specific system. Fourth, because riparian habitat is dynamic and experiences repeated cycles of habitat creation and destruction, we incorporated temporal variables into some of our models that characterized habitat stability and variability. Lastly, we evaluated the relationships between spatial attributes and demographic characteristics (e.g., productivity, mating status) in order to explore whether spatial characteristics that help predict suitable habitat could also distinguish between different levels of habitat quality (e.g., nests in higher quality habitat have higher productivity).

Methods

Study Site

Our two study sites were breeding populations at Roosevelt Lake (33°39'N, 110°58'W) and the San Pedro/Gila River confluence (hereafter San Pedro/Gila; 32°59'N, 110°46'W) from 1996 to 2005 (fig. 1), where we conducted demographic research in cooperation with AGFD (Causey et al. 2006, English et al. 2006). These two sites supported among the largest known Southwestern Willow Flycatcher breeding populations throughout the period of this study (Durst et al. 2006), with mean population sizes of 201 and 239 individuals at Roosevelt Lake and the San Pedro/Gila, respectively. At each site, extensive survey efforts were conducted throughout the breeding season to detect all territorial flycatchers within the immediate and surrounding areas.

The breeding habitat at Roosevelt Lake and the San Pedro/Gila consisted of a heterogeneous mosaic of discrete riparian forest patches of varying ages and vegetation composition, ranging from 0.2 to 43 ha in size. At both study sites, vegetation patches were composed of native, exotic, or a mixture of native and exotic tree species. Native habitat was characterized by Goodding's willow (*Salix gooddingii*) and Fremont cottonwood (*Populus fremontii*). Exotic habitat was dominated by tamarisk (saltcedar; *Tamarix spp.*). The understory vegetation consisted of a variety of grasses, forbs, shrubs (mesquite [*Prosopis spp.*], coyote willow [*S. exigua*], tamarisk, *Baccharis spp.*, and cocklebur [*Xanthium strumarium*]). Adjacent and surrounding non-riparian habitats were primarily composed of Sonoran Desert Uplands (Brown 1994), and in some cases agricultural lands.

Although vegetation and general habitat structure was the same for both study sites, each site was distinct in geomorphology, extent of water regulation, and history.

Roosevelt Lake Study Site

Roosevelt Lake is a large reservoir fed by the Salt River and Tonto Creek. It is a major source of water for the city of Phoenix, and is allowed to fluctuate freely depending on precipitation and water demand. Breeding locations were found within the reservoir bed, at the confluence of the reservoir and the inflows of the Salt River and Tonto Creek, extending as far as 12 km upstream. Although lake levels have fluctuated annually, the overall trend for the reservoir from 1995 to 2004 was a decline due to long term drought conditions (fig. 2). Because of lowering reservoir levels, the lakebed was exposed and colonized by riparian vegetation. This new habitat was subsequently occupied by breeding flycatchers, such that in 2004 most breeding flycatchers were in lakebed habitat with the lowest territory being well below the maximum reservoir level. In 2005, following unusually high winter precipitation, Roosevelt Lake filled to near capacity, inundating much of the breeding habitat occupied in 2004. Breeding was documented

in up to 23 patches comprising 242 ha of riparian habitat, although the number of patches and amount of habitat changed over the course of the study.

San Pedro/Gila Study Site

The San Pedro/Gila study site consisted of 101 km of riverine habitat, centered at the confluence of the free-flowing San Pedro River and regulated Gila River. The number of habitat patches varied over the years, but we documented breeding in as many as 29 distinct habitat patches comprising approximately 222 ha of riparian forest. The San Pedro/Gila study site also changed over the period of this study, though for different reasons than the Roosevelt Lake reservoir. In particular, high water flows (such as measured along the Gila River downstream from the San Pedro confluence; fig. 3) create scouring floods that can remove large tracts of riparian vegetation. As the riverine riparian vegetation recovered, it created multiple vegetation patches of differing successional stages. Additionally, some flycatcher breeding patches, especially along the San Pedro River, receive substantial water input from agriculture runoff.

Surveys and Monitoring

Southwestern Willow Flycatcher breeding surveys were conducted from 1995 to 2005 along Tonto Creek and the Salt River at Roosevelt Lake, and along the Gila and San Pedro Rivers (fig. 4), following a standardized presence/absence survey protocol (Sogge et al. 1997). Potential flycatcher breeding habitat was surveyed by AGFD using tape playback at least three times a season; in addition, sites were searched for flycatchers multiple times between the standard survey periods. Due to intensive survey efforts each year, little potential breeding habitat was left unsurveyed and we believe no breeding patches went undetected within the defined study area (fig. 4). Once a flycatcher was detected, intensive searches were conducted to document breeding status (monogamy, polygamy, or unpaired), locate nests, and monitor productivity. For each territory detected a specific spatial location was recorded in Universal Transverse Mercator (UTM) coordinates. The exact spatial location was based on one of the following criteria: (1) the location of the first nest; (2) the next subsequent nest location; or (3) the center of the male's defended territory when nest was located or for unpaired males.

Nests were monitored following the Southwestern Willow Flycatcher Nest Protocol (Rourke et al. 1999). After incubation was confirmed, monitored nests were visited every 2–4 days until the nest fledged young (presumed) or failed due to predation, parasitism, desertion, abandonment, weather, infertility, or other causes. Most re-nests followed a failed nesting attempt; however, double brooding, a re-nest following a successful nesting attempt, was encountered occasion-

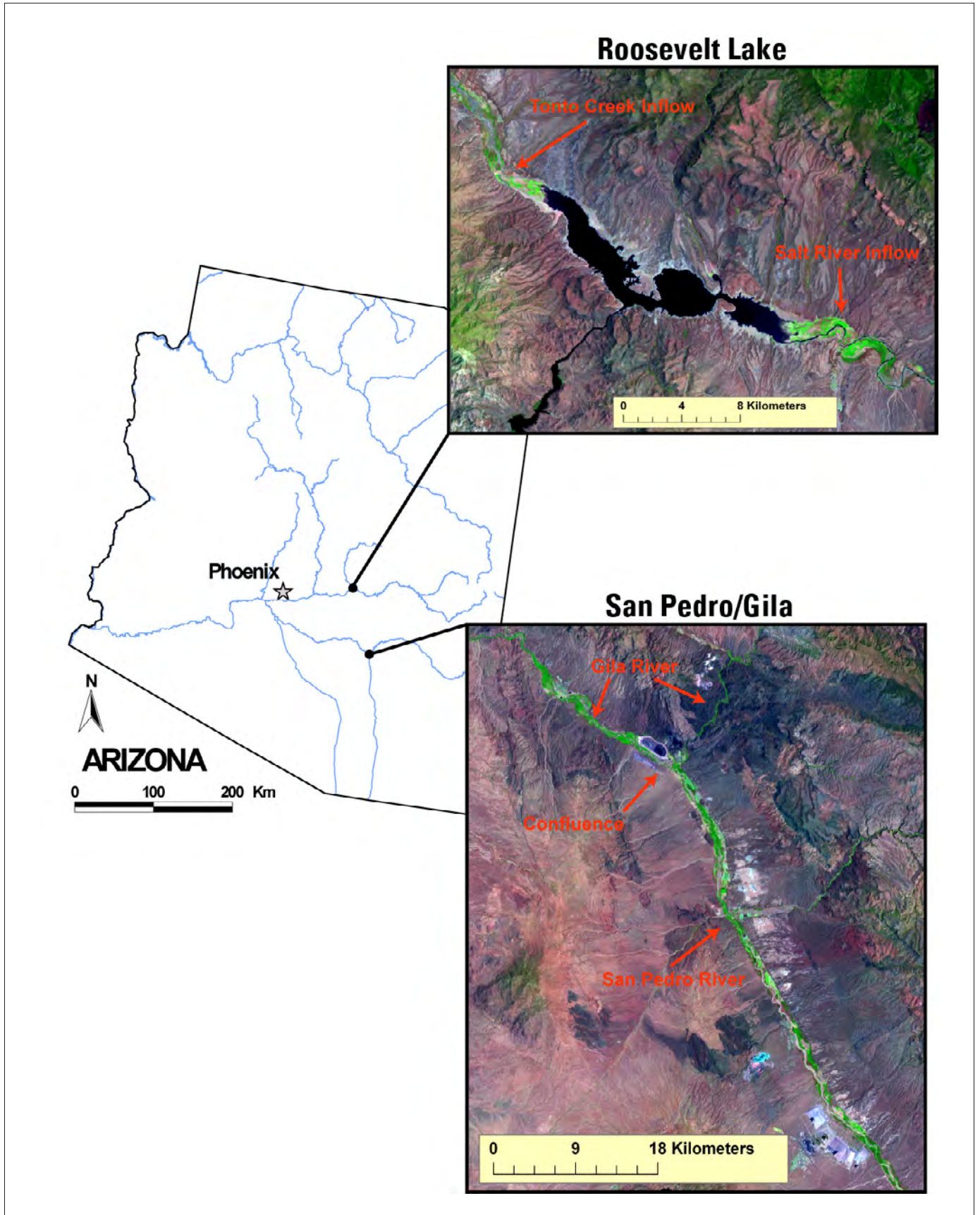


Figure 1. Location of the Roosevelt Lake and San Pedro/Gila study areas in central Arizona.

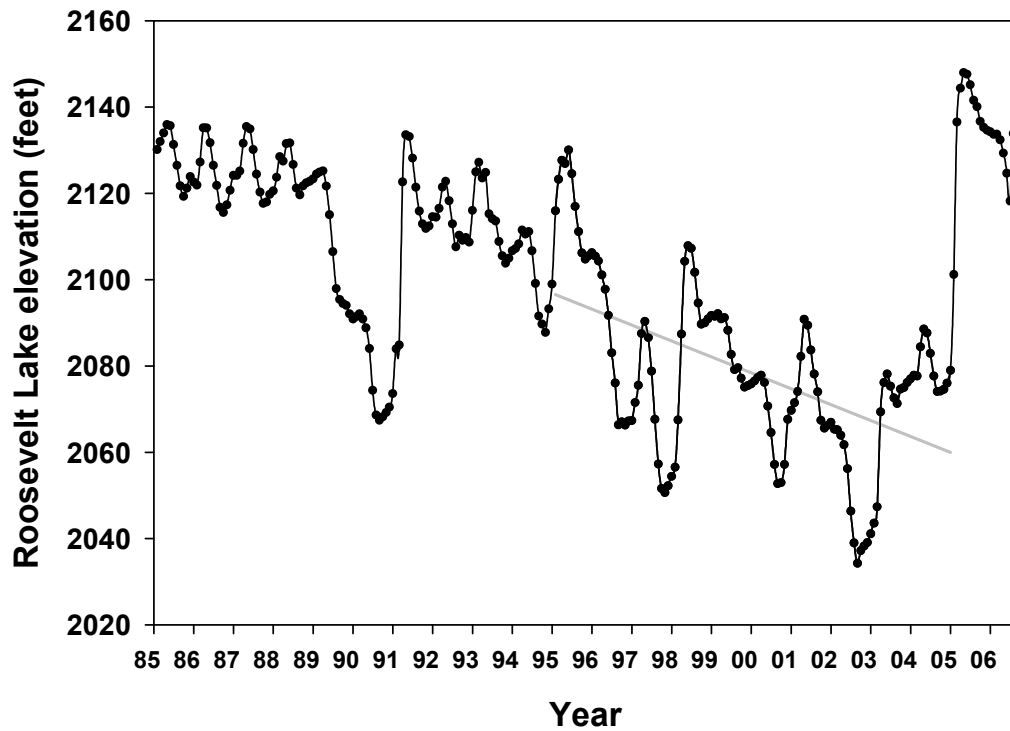


Figure 2. Lake level fluctuations at Roosevelt Lake reservoir from 1985 to 2005, with 1995–2004 regression line of general trend toward lower lake levels. Each solid circle is a mean monthly value of lake level elevation.

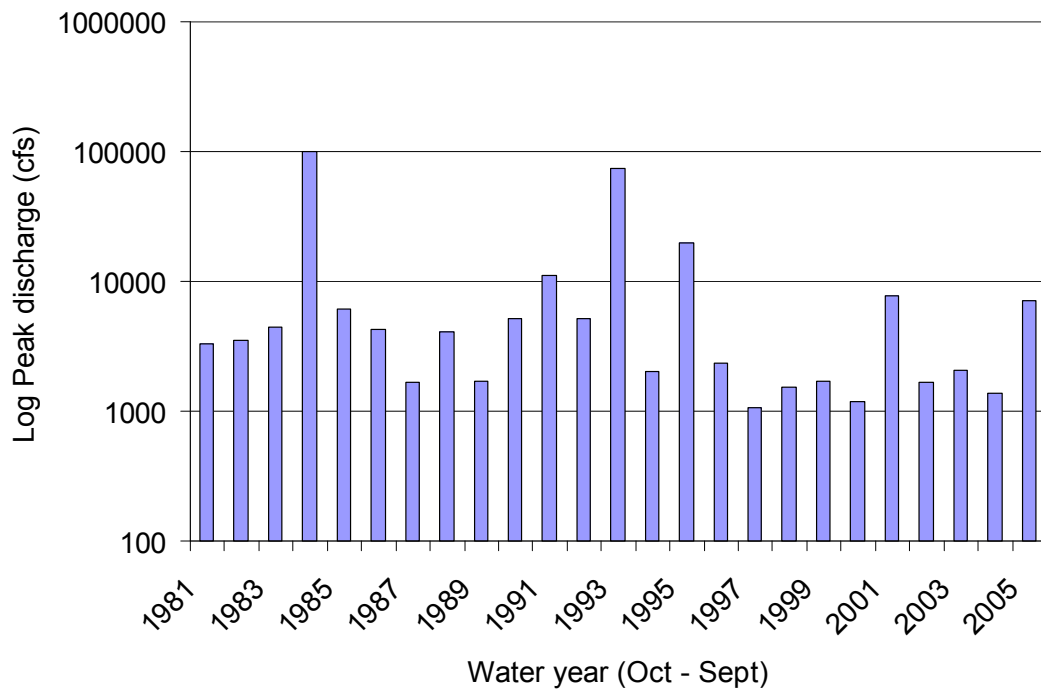


Figure 3. Peak discharge (cfs) at the Kelvin gage, Gila River, between 1981 and 2005. Gage station was located downstream of the San Pedro/Gila River confluence, and corresponds to flows from both the regulated Gila River and unregulated San Pedro River.

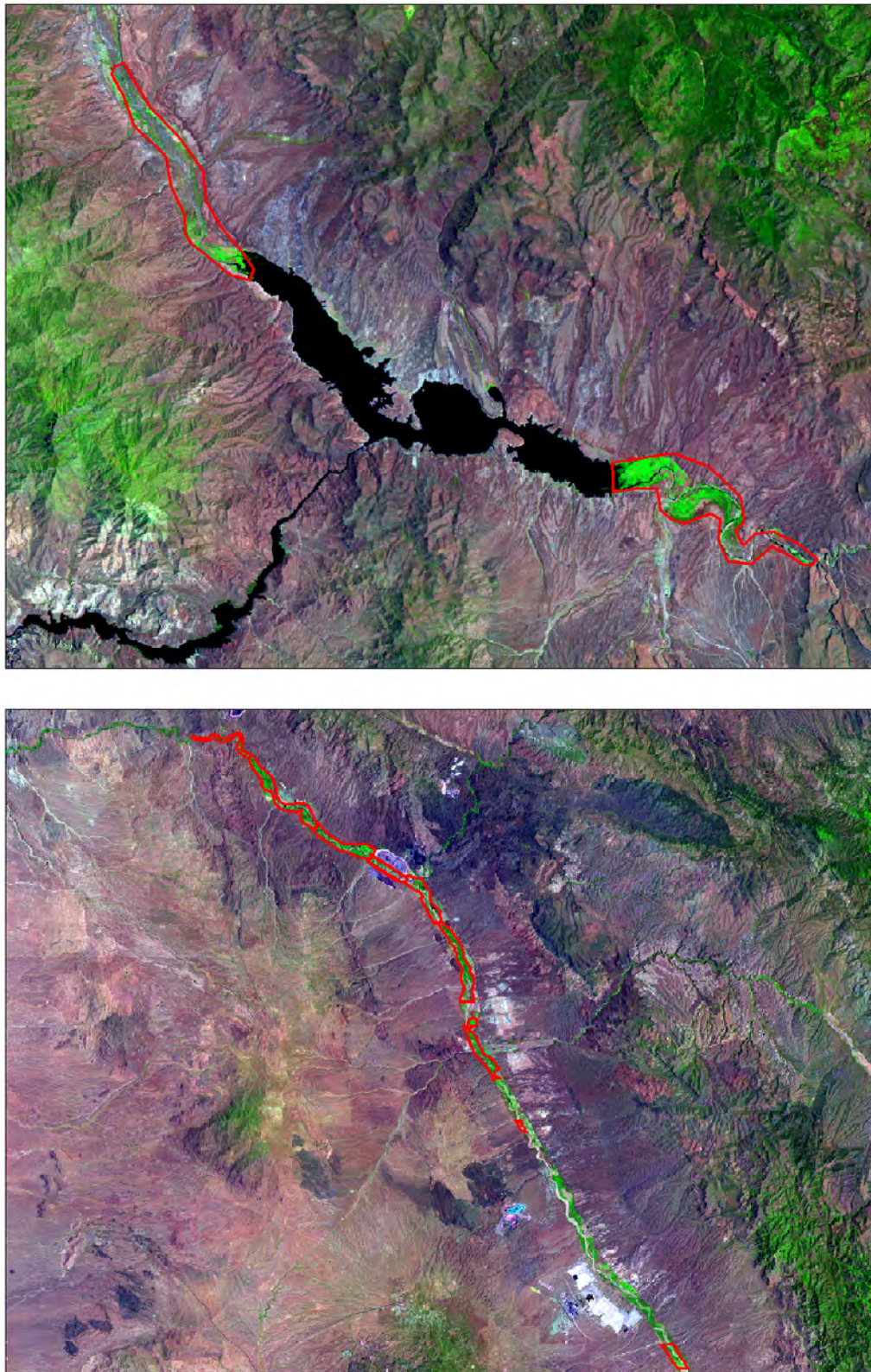


Figure 4. Areas in which Southwestern Willow Flycatcher surveys were conducted and habitat modeled (area contained within the red lines) at the Roosevelt Lake (top) and San Pedro/Gila (bottom) study sites.

ally. A nest was considered successful if it fledged at least one flycatcher nestling.

Spatially Explicit Modeling

Spatial Variables

We developed a set of GIS predictor variables with fine resolution and broad scope to characterize vegetation and floodplain features at multiple scales (table 1). Vegetation and floodplain features were characterized in discrete 30x30 m (0.09 ha) cells obtained from Landsat Thematic Mapper (TM) imagery and a USGS Digital Elevation Model (DEM), respectively. We focused upon predictor variables extractable from TM or DEM data because they could be created for any part of the project area, and throughout the state. We examined vegetation density, amount of edge habitat, and proximity of territories to patch boundaries because these are thought to be important to flycatchers (Sogge et al. 1997, Sogge and Marshall 2000), and width of floodplain because it can influence riparian plant community establishment and persistence (Szaro 1990, Stromberg 1993). We did not examine vegetation species or successional stage, two variables which may influence habitat selection (Sogge et al. 1997, Sogge and Marshall 2000), because they could not be accurately extracted from TM imagery. We also explored for the first time the spatial-temporal component of habitat because it has been found to be an important factor in the development of bird habitat models (Reino 2005).

We created riparian-vegetation density grids (0.09-ha cells) for the project area with TM imagery and ERDAS Imagine software (Atlanta, GA). We selected TM images (path 36, row 37) that were acquired during cloud-free periods inside the months of June or July, 1985–2005. We created riparian-vegetation density grids in a manner similar to Hatten and Paradzick (2003): (1) we calculated the Normalized Difference Vegetation Index (NDVI), which correlates with relative density and biomass of green vegetation (Avery and Berlin 1992), considering only an area within 1.6 km of perennial/intermittent waters, and (2) we distinguished riparian vegetation from non-riparian (Sonoran Upland) vegetation by selecting NDVI values >0.126 . We created two additional riparian-vegetation density grid spatial layers that were found to be important (Hatten and Paradzick 2003) by selecting NDVI values >0.336 (ND_TOP3) and NDVI >0.413 (ND_BEST; table 1).

We used ArcInfo GRID focal functions (ESRI 1992) to explore different spatial scales by characterizing vegetation and floodplain features within 0.3 to 72 ha circular neighborhoods, then stored results from each operation in a separate grid. We calculated the proportion of neighborhood covered in dense vegetation (NDVI >0.413) with a FOCALSUM function, with the percentage relative to the neighborhood size. We characterized floodplain size (ha) with SLOPE and FOCALSUM functions from the DEM because the floodplain was

incised and flatter (slope <2.5 degrees) than its surroundings. We identified the distance between riparian and non-riparian features of the riparian-vegetation density grid with the EUCLIDISTANCE function. We characterized heterogeneity in vegetation density with a FOCALSTD function by calculating the standard deviation among 12 NDVI classes.

In addition to the spatial variables that were created from a single year of vegetation data, we created a class of temporal variables that characterized the variability, stability and changes in predicted flycatcher breeding habitat over a range of years. We accomplished this by running the recalibrated spatial models (LakeModel_1 or RiverModel_1) in successive years, populating them with TM imagery data specific to each year modeled (i.e., vegetation characteristics), and then subtracting the five probability classes (e.g., 0%–20%, 21%–40%, etc.) that each model produced (with probability classes derived from the logistic modeling, see below). This technique resulted in an interval-scaled change detection variable grid that contained values from -5 through 5. If a change variable's class value was negative, the quality of predicted habitat declined over the time interval modeled. If the change variable's class value was positive, the quality in predicted habitat increased. We also characterized the density and stability in predicted breeding habitat by calculating the mean and standard deviation (*SD*), respectively, over 5-, 10-, and 15-year time intervals. Characterizing the vegetation temporally required that we overlay the model probability grids that were output for each year and calculating the descriptive statistics with GIS GRID functions (ESRI 1992).

Response Variables

We used the presence or absence of flycatcher territories to relate the spatial variables with the occurrence of flycatcher territories. To develop a dataset for characterizing and modeling flycatcher breeding habitat, we employed a case-control sampling design (Keating and Cherry 2004) at Roosevelt Lake in 2004 ($n = 215$) and San Pedro/Gila in 2000 ($n = 125$). Because the two study sites have different histories, we used a different survey year for the two study sites, with the year selected offering the best survey coverage and capturing a period of high flycatcher numbers within both young and old vegetation. We complimented the location of territories (presence) by creating an equal number of nonuse (absence) locations that were randomly generated in areas that had been searched and found to be void of flycatcher territories during the breeding season of the year modeled. We used one half of the territory and nonuse locations for model construction and the remaining half to challenge (i.e., validate) the models. To create the most specific models possible, we excluded non-riparian and marginal riparian vegetation from our modeling by only sampling and modeling riparian areas where NDVI cell values exceeded 0.126 (Hatten and Paradzick 2003). Retrospective sampling provided a practical way to examine our

Table 1. We created 39 predictor variables to characterize vegetation or floodplain features at Southwestern Willow Flycatcher territories and random nonuse locations in south-central Arizona (Roosevelt Lake and San Pedro/Gila). Use sites contained a flycatcher breeding territory (0.09 ha) and nonuse sites (0.09 ha) did not. We extracted vegetation variables from Landsat Thematic Mapper imagery (30-m resolution; 0.09 ha), and floodplain characteristics from digital elevation models. We also created change (temporal) grids for modeling by running lake and riverine models in two different years and then subtracting the probability classes output by the model. Variables with a prefix of ND were derived from NDVI; variables with a prefix of MOD are probability classes that were derived from the refit Model₉₉ (lake or riverine); and variables with a prefix of CH are change detection variables that were derived from running the refit Model₉₉ (lake or riverine) at 2 or more time intervals. Distances are from the 30 m grid that a territory was found in to the nearest point of the feature of interest. (^a 1 = Roosevelt Lake study site; 2 = San Pedro/Gila study site)

Variable	Study site ^a	Description
CH_1Y	1,2	Change (magnitude and direction) in probability class (1-yr interval)
CH_1YR	2	Absolute change in probability class (1-yr interval)
CH_2Y	1,2	Change (magnitude and direction) in probability class (2-yr interval)
CH_2YR	2	Absolute change in probability class (2-yr interval)
CH_3Y	1,2	Change (magnitude and direction) in probability class (3-yr interval)
CH_3YR	2	Absolute change in probability class (3-yr interval)
CH_4Y	1,2	Change (magnitude and direction) in probability class (4-yr interval)
CH_4YR	2	Absolute change in probability class (4-yr interval)
CH_5Y	1,2	Change (magnitude and direction) in probability class (5-yr interval)
CH_5YR	2	Absolute change in probability class (5-yr interval)
CREEKDIST2K	2	Distance to perennial/intermittent stream in 2000
distndbest	1,2	Distance from interior of patch to patch edge (NDVI > 0.41)
Disttop3	1,2	Distance from interior of patch to patch edge (NDVI > 0.33)
Ed120	2	Edge density in 120-m radius
Ed180	1,2	Edge density in 180-m radius
Ed240	2	Edge density in 240-m radius
Ed300	2	Edge density in 300-m radius
Ed360	2	Edge density in 360-m radius
FLOOD10	1,2	Amount of floodplain in 41-ha circle (from 10-m DEM)
FLOOD30	1,2	Amount of floodplain in 41-ha circle (from 30-m DEM)
LAKEDIST	1	Distance from lake surface
MOD_CV5Y	1,2	Variability (CV) in probability classes (5-yr interval)
MOD_CV10YR	2	Variability (CV) in probability classes (10-yr interval)
MOD_CV15Y	2	Variability (CV) in probability classes (15-yr interval)
MOD_MN5Y	1,2	Mean probability class (5-yr interval)
MOD_MN10Y	2	Mean probability class (10-yr interval)
MOD_MN15Y	2	Mean probability class (15-yr interval)
MOD_SD5Y	1,2	Variability (SD) in probability classes (5-yr interval)
MOD_SD10Y	2	Variability (SD) in probability classes (10-yr interval)
MOD_SD15Y	2	Variability (SD) in probability classes (15-yr interval)
Nd_12	1,2	Interval-scaled NDVI variable (12 classes)
nd_best	1,2	Binary - densest vegetation (NDVI values > 0.41)
Nd_best4	1,2	Amount of ND_BEST in 120-m radius
nd_rap	1,2	Riparian density and biomass (NDVI value)
Nd_sd4	1,2	Variability (SD) in NDVI in 120-m radius
Nd_top3	1,2	Binary – NDVI > 0.33 inside 30-m cell
patchbest	1,2	Size of patch (NDVI values > 0.41)
Patchtop3	1,2	Size of patch (NDVI values > 0.33)
Perint_sp	1,2	Distance to perennial/intermittent stream in 1992

survey data and is well suited for animals that exhibit preferences for rare habitat types (Ramsey et al. 1994).

Comparing vegetation and floodplain characteristics around the breeding territory locations with the randomly selected nonuse locations, we examined habitat association at multiple spatial scales (Ripple et al. 1991) by characterizing vegetation and floodplain features within different-sized neighborhoods of territory and nonuse locations. We characterized neighborhood variables at multiple scales (0.3–72 ha) within concentric circles (e.g., amount of densest vegetation [ND_BEST4]; table 1). Other variables such as patch size (e.g., PATCHBEST) were characterized within irregularly shaped contiguous patches that could be any size. For clarification, we defined fine scales as 0.09–1.1 ha; the smaller value is the 30-m resolution limit of TM imagery, and the higher value corresponds to the upper end of flycatcher territory sizes (Cardinal and Paxton 2005). We selected intermediate (2.5–28 ha) and coarse scales (>41 ha) to characterize riparian forest patches and floodplains, respectively (Hatten and Paradzick 2003).

We adjusted our database to minimize the effects of temporal and spatial autocorrelation (Legendre 1993) because breeding flycatchers have high territory fidelity between years (see chapter 4) and are tightly clustered (Hatten and Paradzick 2003). To identify patterns in dispersion, we used nearest neighbor index (Boots and Getis 1988, Chou 1997). We found territories were significantly clumped at Roosevelt Lake in 2004 ($Z = -26.0$, $p < 0.001$) and San Pedro/Gila in 2000 ($Z = -20.5$, $p < 0.001$), with a mean nearest neighbor (MNN) distance of 59 m and 50 m, respectively. Thus we minimized clustering in the data by randomly removing 50% of territories, producing a MNN of 103 m for Roosevelt Lake and 156 m for San Pedro/Gila, with all territories that we removed from the model development stage later used during the model challenge (i.e., validation) stage.

Model Building and Selection

We used binary logistic regression to identify habitat associations and to develop equations useful for spatially explicit GIS habitat models, considering both univariate and multivariate models. Logistic regression is ideal for evaluating relationships between predictor variables and flycatcher occurrence because presence/absence data are binary. We evaluated more than 20 multivariate models, but for brevity's sake discuss only 11 in this report: 6 models for Roosevelt Lake (LakeModels: 3 spatial and 3 spatial-temporal) and 5 models for San Pedro/Gila (RiverModels: 3 spatial and 2 spatial-temporal models). The first model that we built for each system (LakeModel_1 and RiverModel_1) was obtained by fitting the four covariates in the AGFD model to annual-specific data at San Pedro/Gila and Roosevelt Lake. This approach resulted in recalibrated SWFL breeding habitat models for Roosevelt Lake and San Pedro/Gila (i.e., lake or riverine, respectively). All of the other models we considered contained additional or fewer variables. To reduce the chance of producing over-

fit models that result from too many predictor variables and too few events per variable (EPV), we maintained an $EPV \geq 10$ (Peduzzi et al. 1996). Thus, for each covariate in a given model, we ensured that there were at least 10 flycatcher territories. This restricted the maximum number of variables per model subset to 10 at Roosevelt Lake and 6 at San Pedro/Gila.

We used ArcInfo (GRID) to calculate and map the relative quality of breeding habitat within 0.09-ha (30x30 m) cells. We calculated the relative quality of breeding habitat (P) with the following equation: $P_i = e^{g(x)} / 1 + e^{g(x)}$, where $g(x)$ is the linear combination of parameter estimates obtained from the logistic regression (Hosmer and Lemeshow 1989; Keating and Cherry 2004). Relative habitat quality is based upon the probability of a flycatcher territory occurring within a given cell based on the logistic regression under consideration. Each model assigned cells a probability between 1% and 98%, depending on the logistic regression equation employed, which we reclassified into 1 of 5 possible probability classes: 1 = 1%–20% 2 = 21%–40%; 3 = 41%–60%; 4 = 61%–80%; and 5 = 81%–98%.

Because the models and the systems modeled are complex, we used a number of methods to judge how well the models fit the data. Each method can tell us different aspects of the model's fit, and some models may have good results with one method but poor results with another. Thus, it is important to look at multiple methods to fully understand how well the model performs. To assess the accuracy of the models in a spatially explicit manner, we assessed model fit and accuracy with a validation dataset (territories not used in model development) and a classification table (Norusis 1999) using 108 control locations at Roosevelt Lake from 2004, and 67 control locations at San Pedro/Gila from 2000. Control locations were breeding territories not used in model development and were between 1 and 5 cells (30–150 m) from the territory locations used in model development.

We used density of territories within the five probability classes as our measure of fit, reasoning that higher-probability habitat should contain more territories (Hatten and Paradzick 2003). Model accuracies depended upon a probability cutpoint that we used to extract suitable versus unsuitable breeding vegetation (i.e., cells) from the model probability value assigned to each grid. For this report, we set the probability cutpoint at 50%, with all cells $\leq 50\%$ probability considered unsuitable and cells with a probability $> 50\%$ suitable. Breeding territories that fell outside of predicted habitat were counted as an omission error (Story and Congalton 1986), whereas cells that were predicted suitable but found to be empty (contained no breeding territory) were counted as a commission error. We examined model accuracies at this 50% probability cutpoint by calculating (1) model sensitivity (1 – omission error), (2) specificity (1 – commission), and (3) overall model accuracy (sensitivity + specificity / 2).

Additional methods used to evaluate the strength of our models in explaining the presence or absence of flycatcher territories included the G statistic (Hosmer and Lemeshow 1989),

Nagelkerke's pseudo r^2 (Nagelkerke 1991), and a receiver operating characteristic (ROC) statistic. The G statistic and Nagelkerke r^2 are roughly equivalent to the F and r^2 statistics, respectively, in linear regression. ROC summarizes the tradeoffs between model sensitivity and commission error (Fawcett 2004). The closer ROC is to 1, the better the overall fit of the model at all possible cutpoints. Additionally, we checked for linearity between the logit and the continuous variables with the Box-Tidwell test (Box and Tidwell 1962). If nonlinearity was observed, we examined model fit by transforming the covariate (e.g., squared, categorical, exponential).

We examined the temporal accuracy of the models between 1995 and 2005 with linear regression (decade R^2), overlaying predicted breeding habitat (number of cells predicted as suitable habitat) and territory numbers (number of cells containing territories) specific to each year. We had to restrict the temporal regression analysis to 1995 and later because accurate flycatcher survey data did not exist prior to 1995. However, we used the predicted habitat between 1985 and 1994 to create some of the temporal variables and to examine trends in flycatcher breeding habitat. The temporal analysis required that we populate each spatial model with annual-specific vegetation characteristics derived from a unique TM scene for that year. In contrast, the floodplain variables were treated as a geomorphic constant in our models (calculated only once from a single DEM). Finally, to decide between models with similar degrees of fit, we qualitatively assessed the biological plausibility of each model. For this criterion, models with a more understandable biological mechanism were deemed preferable to models without clear biological mechanisms. After selecting the best spatial and spatial-temporal models for each area, we summarized the amount of predicted breeding habitat for each year between 1985 and 2005, generating histograms to display the variability in predicted habitat over this 20-year period.

Demographic Analysis

In addition to territory-habitat associations, we evaluated the utility of the spatial models to predict two important demographic indicators, productivity and territory status. To accomplish this, we created a georeferenced table that contained all the territory locations, per year, spatial layers, and demographic attributes. While the demographic information was collected from the entire breeding season in each year, the spatial values collected from the TM images (e.g., NDVI) were measured during the mid-June period of each year (see above). All measures of productivity were at the territory level. For all territories without missing data, we calculated the total number of young fledged (presumed; see chapter 3). Productivity estimates were made irrespective of territory holders, and zero nesting attempts (e.g., unpaired males) were recorded as zero productivity. Territory status (monogamous, polygamous, and unpaired) was recorded for those territories where

there was sufficient information. To evaluate correlations between the seasonal number of young fledged per territory and spatial information, we used Spearman's nonparametric correlation ρ . ANOVAs were used to test differences in spatial values by territory status, with mean values tested using a Shapiro-Wilks goodness-of-fit test for normality before being used. All statistical analyses were conducted in the statistical software JMP vs. 6.0 (SAS, Inc.), and all graphs were created in Sigma Plot 2000 (SAS, Inc.). Statistical significance was accepted at $p < 0.05$.

Results

Roosevelt Lake Models

Univariate Analysis

The majority (78%) of the spatial variables we evaluated were significantly associated with the presence of flycatcher territories in 2004 (table 2). Ranked by G -statistic values, some of the most informative variables were distance from lake or river, vegetation density characteristics (NDVI), and temporal characteristics (e.g., mean model probability, change detection; table 2). Most coefficients were positively associated with the presence of flycatcher territories. For example, the odds of a flycatcher territory being present in a given area with the highest NDVI values (ND_TOP3, NDVI > 0.33) was 13.8 times that of an area with NDVI ≤ 0.33 (obtained by exponentiating the coefficient). Negative relationships (i.e., a decreased probability of a territory being present) were distance from lake or creek, positive changes in a probability class within the first or second year of the change detection, and variation (CV) in NDVI within a 4.5-ha neighborhood (1999–2004).

Multivariate Models

All three spatial lake models (LakeModels 1–3, table 3) improved classification accuracy when compared with the original AGFD model at Roosevelt Lake. LakeModel_1 improved overall classification by 9.5%, LakeModel_2 by 11.1%, and LakeModel_3 by 13.2%. The improvement in overall accuracy was obtained through an increase in model specificity (i.e., 1 - commission error), which increased progressively from 42.1% (Model_99) up to 72% (LakeModel_3). Conversely, at a 50% cutpoint Model_99 had the highest model sensitivity (93.5%), indicating it performs well for identifying potential habitat, but does so at a cost of poor specificity (table 3). LakeModel_3 had the best overall fit when challenged with the validation set, but its decade R^2 was the lowest of the spatial models, suggesting that it was overfit for the year 2004. LakeModel_2 had the second highest accu-

Table 2. Univariate logistic regression results for Roosevelt Lake ($n = 215$). Variables are presented in order of descending G values. Larger G values indicate a stronger association between the predictor and response variable (presence of territories), while the sign of the coefficient (β) indicates the direction of the association. All change detection variables (grids) were created by running the lake model between two or more time intervals and describing the changes (i.e., mean, SD, etc.). If the change variable's class value was positive, the relative quality of predicted habitat increased in the time interval modeled, while a negative value indicates that the relative quality of predicted habitat declined in the time interval modeled.

Variable	β	G	p-value	Description
LAKEDIST	-0.001	59.6	<0.001	Distance from lake surface (NDVI < -0.2)
MOD_MN5Y	0.918	59.1	<0.001	Mean probability class between 1999 and 2004
ND_TOP3	2.622	53.2	<0.001	Vegetation density at site (0.09 ha) [NDVI > 0.33]
CH_BEST5Y	0.059	43.3	<0.001	Change in densest vegetation in 4.5-ha circle (1999–2004)
ND_SD5Y	0.145	38.45	<0.001	SD in vegetation density in 4.5-ha circle (1999–2004)
CH_5Y	0.477	34.85	<0.001	5-yr change in probability class 2001–2004
MOD_SD5Y	1.306	33.89	<0.001	5-yr SD in probability classes 1999–2004
ND_BEST4	0.048	33.2	<0.001	Amount (%) of densest vegetation in 4.5-ha circle
PATCHBEST	0.015	24.78	<0.001	NDVI > 0.43 (contiguous cells)
ND_MN5Y	0.053	22.24	<0.001	Mean density of vegetation in 4.5-ha circle (1999–2004)
CH_BEST4Y	0.039	21.5	<0.001	Change in densest vegetation in 4.5-ha circle (2000–2004)
CH_BEST3Y	0.063	19.1	<0.001	Change in densest vegetation in 4.5-ha circle (2001–2004)
PATCHSIZE	0.006	18.97	<0.001	Size of patch (NDVI > 0.43)
PATCHSIZEB	0.004	15.89	<0.001	Size of patch (NDVI > 0.33)
CH_1Y	-0.593	15.38	0.001	1-yr change in breeding habitat 2003–2004
DISTTOP3	0.006	13.28	<0.001	Distance from patch edge (NDVI > 0.33)
FLOOD30	0.046	12.4	0.002	Amount of floodplain in 41-ha circle (30-m DEM)
CH_4Y	0.288	11.32	0.001	4-yr change in probability classes (2000–2004)
CREEKDIST02	-0.002	7.71	0.005	Distance from 2002 creek channel (Tonto or Salt R.)
CH_3Y	0.257	7.22	0.01	3-yr change in probability classes (2001–2004)
FLOOD10	2.861	6.5	0.014	amount of floodplain or flat in 41-ha circle (10-m DEM)
CH_2Y	-0.204	3.16	0.079	2-yr change in probability classes (2002–2004)
CH_BEST2Y	0.014	0.9	0.344	Change in densest vegetation in 4.5-ha circle (2002–2004)
CH_BEST1Y	-0.015	0.88	0.354	Change in densest vegetation in 4.5-ha circle (2003–2004)
ND_SD4	64	0.7	0.38	SD in NDVI (vegetation heterogeneity) in 4.5-ha circle
ND_CV5Y	-0.05	0.04	0.849	Variation (CV) in NDVI in 4.5-ha circle (1999–2004)
MOD_CV5Y	0.001	0	0.998	Variation (CV) in probability classes 1999–2004

racy, as judged by the validation set and the highest decade R^2 ; therefore, we believe it is the best spatial lake model.

Two spatial-temporal models (LakeModels 4 and 6) made significant improvements in the Nagelkerke r^2 values compared to the spatial models, indicating improvement in their ability to predict where flycatcher territories would be in 2004 (table 3). However, while LakeModel_6 had the highest Nagelkerke r^2 , its decade r^2 was almost zero, suggesting it was overfit for the 2004 data. In contrast, LakeModel_5 had a lower Nagelkerke r^2 but its decade R^2 was the best of all models considered (table 3). Therefore, we believe LakeModel_5 is the best model for evaluating multiple years.

LakeModel_2, which provided the best spatial accuracy and Decade R^2 score of the spatial models, contained the four covariates found to be important in Model_99, plus a distance to creek variable (CREEKDIS; table 4). The WALD statistic indicates that vegetation density at the site (ND_TOP3) was the most influential covariate, followed by floodplain width (FLOOD30), distance to creek (CREEKDIS), and amount and variability in dense vegetation in a 120-m radius (ND_BEST4 and ND_SD4, respectively). LakeModel_2 also produced an excellent fit between its 5 probability classes (i.e., model probabilities divided into 20% intervals) and territory density (fig. 5), explaining 98% of the variability in territory density

Table 3. Spatial and spatial-temporal models resulting from the multivariate logistic regression analysis at Roosevelt Lake (n = 215). Model_1 was obtained by fitting a set of covariates found to be important in 1999 (Hatten and Paradzick 2003; Model_99) to 215 use/nonuse locations from Roosevelt Lake in 2004. To calculate accuracy statistics for these models, we set the probability cutpoint for all models at 50% (cells with a probability value $\leq 50\%$ were considered unsuitable for breeding, values $> 50\%$ were considered suitable). Highlighted models are the best for each category.

LakeModel ^a	r ^{2b}	Pres ^c	Ab ^d	all ^e	ROC ^f	DecadeR ^{2g}	Density ^h	Predicted ⁱ
Spatial models								
Model_99	NA	93.5	42.1	67.8	NA	0.65	0.12	845.6
LakeModel_1	0.43	88.9	54.2	71.6	0.83	0.68	0.14	671.6
LakeModel_2	0.47	80.6	72.0	76.3	0.85	0.74	0.19	462.9
LakeModel_3	0.53	84.2	72.0	78.1	0.87	0.31	0.23	403.6
Spatial-temporal models								
LakeModel_4	0.62	77.8	70.1	74.0	0.91	0.41	0.14	608.7
LakeModel_5	0.51	65.7	71.0	68.4	0.86	0.82	0.13	551.2
LakeModel_6	0.68	75.0	59.8	67.4	0.93	0.03	0.17	483.3

^aRefer to table 4 for model parameters

^bNagelkerke pseudo r² statistic

^cPercent of presence sites correctly classified (sensitivity)

^dPercent of absence sites correctly classified (specificity)

^eOverall model accuracy (sensitivity + specificity) / 2 as determined from validation dataset (n = 107)

^fReceiver operating characteristic (ROC) test (area under the curve)

^gExplained variability in the inter-annual fluctuations in # of flycatcher territories between 1995 and 2004

^hTerritory density at a 50% cutpoint

ⁱAmount of predicted breeding habitat at a 50% cutpoint

NA = stat not applicable for the original model because dataset contained lake and riverine data

with the following polynomial: territory density = $0.008(X^2) + 0.011(X) - 0.009$, where X is the model probability class. In contrast, the best fitting spatial-temporal model (LakeModel_5) produced a threshold-like relationship between the five probability classes and territory density (fig. 5), with 6.7% found within classes 1 and 2, 18.7% within class 3, and 78.4% within classes 4 and 5. LakeModel_5 was comprised of two spatial variables that quantified the density of vegetation at the site (ND_TOP3) and the variability in vegetation density within a 120-m radius (ND_SD4), plus two temporal variables that characterized the stability and variability of habitat (MOD_MN5Y and MOD_SD5Y, respectively) over a 5-year period. Both models did well in many of the measures, and while we believe LakeModel_5 is superior, it requires multiple years of TM imagery; in the absence of such temporal information, LakeModel_2 is an acceptable substitute.

San Pedro/Gila Models

Univariate Analysis

The 10 top scoring predictor variables at San Pedro/Gila (as determined by the *G* statistic) were associated with either riparian vegetation density (NDVI values), proximity to patch edges, or temporal changes in habitat quality (table 5). Five of the top ten predictor variables characterized the relative density and biomass of green riparian vegetation at the location of the territory, or the amount of densest riparian vegetation (NDVI > 0.41) within a 120-m radius (ND_BEST4; table 5). Another three of the top ten predictor variables characterized the temporal variability and stability in breeding habitat quality between 1990 and 1995, and 1990–2000 (MOD_MN5Y, MOD_MN10Y, MOD_SD5Y). The final two best predictors were measures of distance from patch edge (the distance of a territory to the outer edge at two different riparian-vegetation density thresholds [DISTTOP3 and DISTNDBEST]).

Table 4. Model parameters of multivariate logistic regression models developed and tested for Roosevelt Lake (n = 215). Accuracy and model fit statistics are displayed in table 3. LakeModel_1 was created by fitting a set of covariates that were found to be important in a previous study of flycatcher habitat (Hatten and Paradzick 2003) to use/nonuse locations and vegetation characteristics collected in 2004 at Roosevelt Lake. LakeModel_2 is the same as LakeModel_1 except that it contains a proximity variable (distance to river). LakeModels 5 and 6 are spatial-temporal models that incorporate changes in predicted habitat (change-detection grids) observed between 1999 and 2004, at different time intervals.

Variable	β	S.E.	Wald	df	Sig.	Odds	95% C.I. for Odds	
							Lower	Upper
LakeModel_1 (constant = -7.288)								
ND_TOP3	2.035	0.59	11.901	1	0.001	7.649	2.408	24.3
ND_SD4	0.547	0.144	14.516	1	0	1.729	1.304	2.291
FLOOD30	0.06	0.018	11.448	1	0.001	1.062	1.025	1.099
ND_BEST4	0.056	0.021	7.213	1	0.007	1.057	1.015	1.101
LakeModel_2 (constant = -6.046)								
ND_TOP3	2.032	0.594	11.723	1	0.001	7.631	2.384	24.424
ND_SD4	0.387	0.154	6.276	1	0.012	1.472	1.088	1.992
FLOOD30	0.057	0.018	10.583	1	0.001	1.059	1.023	1.096
ND_BEST4	0.058	0.021	7.539	1	0.006	1.060	1.017	1.104
CREEKDIS	-0.003	0.001	8.627	1	0.003	0.997	0.996	0.999
LakeModel_3 (constant = -2.348)								
ND_TOP3	2.608	0.508	26.320	1	0.000	13.575	5.012	36.768
FLOOD30	0.055	0.018	8.913	1	0.003	1.056	1.019	1.095
CREEKDIST	-3.235	0.809	16.010	1	0.000	0.039	0.008	0.192
LAKEDIST	-0.402	0.091	19.589	1	0.000	0.669	0.560	0.799
LakeModel_4 (constant = -8.769)								
ND_TOP3	2.756	0.738	13.940	1	0.000	15.739	3.704	66.884
ND_SD4	0.758	0.183	17.145	1	0.000	2.134	1.491	3.056
FLOOD30	0.073	0.021	12.529	1	0.000	1.075	1.033	1.120
ND_BEST4	0.060	0.025	5.610	1	0.018	1.062	1.010	1.116
MOD_CH3Y	0.991	0.251	15.628	1	0.000	2.693	1.648	4.401
MOD_CH2Y	-1.106	0.294	14.195	1	0.000	0.331	0.186	0.588
MOD_CH1Y	-0.634	0.213	8.829	1	0.003	0.531	0.349	0.806
LakeModel_5 (constant = -5.386)								
ND_SD4	0.235	0.097	5.906	1	0.015	1.265	1.046	1.528
ND_TOP3	1.327	0.568	5.460	1	0.019	3.769	1.238	11.472
MOD_MN5Y	0.893	0.182	24.104	1	0.000	2.443	1.710	3.489
MOD_SD5Y	1.512	0.327	21.388	1	0.000	4.534	2.389	8.605
LakeModel_6 (constant = -4.732)								
ND_TOP3	3.628	0.674	28.946	1	0.000	37.653	10.040	141.209
ND_SD4	0.339	0.153	4.882	1	0.027	1.403	1.039	1.895
FLOOD30	0.078	0.023	11.995	1	0.001	1.082	1.035	1.131
CREEKDIST	-3.277	1.070	9.374	1	0.002	0.038	0.005	0.308
LAKEDIST	-0.362	0.105	11.909	1	0.001	0.696	0.567	0.855
CH_3Y	0.766	0.260	8.658	1	0.003	2.152	1.292	3.585
CH_2Y	-0.943	0.299	9.954	1	0.002	0.390	0.217	0.700
CH_1Y	-0.749	0.245	9.322	1	0.002	0.473	0.292	0.765

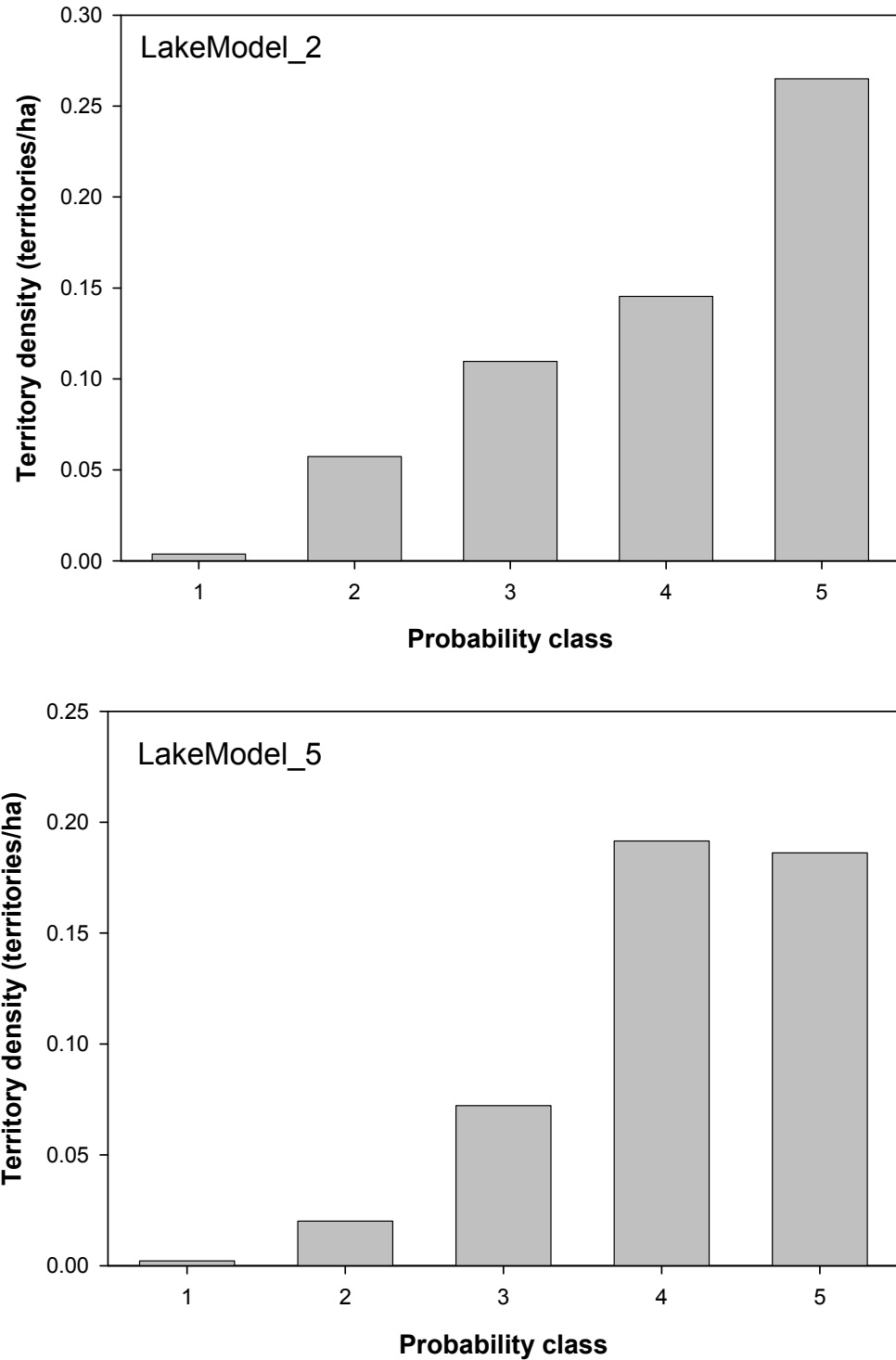


Figure 5. The density of flycatcher breeding territories ($n = 107$) increased across five model-generated probability classes at Roosevelt Lake, based on both spatial (LakeModel_2) and spatial-temporal modes (LakeModel_5). Densities were obtained by dividing the number of flycatcher breeding territories (from a validation dataset) by the area contained within each probability class. Actual flycatcher densities would have been 2x higher if we had used the full dataset instead of the validation dataset (a random subset of the total dataset).

Table 5. Univariate logistic regression results for the San Pedro/Gila study site (n = 125). The test statistic (G) is calculated as $-2(\text{change in log likelihood})$ for the constant only model versus the full model (constant and predictor variable). Variables are presented in order of descending G values. Larger G values indicate a stronger association between the predictor and response variable (presence of territories). If the change variable's class value was positive, the relative quality of predicted habitat increased in the time interval modeled, while a negative value indicated that the relative quality of predicted habitat declined in the time interval modeled.

Variable	β	G	p-value	Description
nd_rap	14.82	64.07	<0.001	Riparian density and biomass (NDVI value)
MOD_MN5Y	1.01	50.48	<0.001	Mean probability class 1995–2000
Nd_12	0.48	49.75	<0.001	Interval-scaled NDVI variable (12 classes)
nd_best	2.78	48.31	<0.001	Binary - densest veg (NDVI > 0.41)
Nd_best4	0.11	45.58	<0.001	Amount of veg (NDVI > 0.41) in 120-m radius
Nd_top3	2.92	43.68	<0.001	Binary – NDVI > 0.33
Disttop3	0.05	40.01	<0.001	Distance from patch edge (NDVI > 0.33)
distndbest	0.06	37.79	<0.001	Distance from patch edge (NDVI > 0.41)
MOD_MN10Y	0.95	37.12	<0.001	Mean probability class (1990–2000)
MOD_SD10Y	1.88	32.05	<0.001	SD in probability classes (1990–2000)
Ed120	0.014	31.54	<0.001	Edge density in 120-m radius
MOD_SD15Y	1.78	28.28	<0.001	SD in probability classes (1985–2000)
FLOOD30	0.058	27.7	<0.001	Amount of floodplain in 41-ha circle (30-m DEM)
Ed180	0.016	22.36	<0.001	Edge density in 180-m radius
FLOOD10	4.46	21.98	<0.001	Amount of floodplain in 41-ha circle (10-m DEM)
MOD_MN15Y	0.69	21.54	<0.001	Mean probability class 1955–2000
Ed300	0.021	17.08	<0.001	Edge density in 300-m radius
patchbest	0	14.68	<0.001	Size of patch (NDVI > 0.41)
Ed360	0.022	14.39	0	Edge density in 360-m radius
CH_5	0.47	13.78	0	Absolute change in probability class (5-yr interval)
MOD_SD5Y	0.83	7.66	0.006	SD in probability classes (1995–2000)
CH_2Y	0.37	6.63	0.01	Change in prob class (+/-) between 1998 and 2000
CH_5Y	0.24	6.3	0.012	Change in prob class (+/-) between 1995 and 2000
CH_4Y	0.33	4.79	0.03	Absolute change in probability class (4-yr interval)
CH_3Y	0.26	4.37	0.04	Change in prob class (+/-) between 1997 and 2000
Nd_sd4	0.31	4.08	0.04	SD in NDVI in 120-m radius
Perint_93	0.003	3.8	0.05	Distance to perennial/intermittent stream (alris layer)
Patchtop3	0	3.32	0.07	Size of patch (NDVI > 0.33)
CH_4y	0.2	3.05	0.08	Change in prob class (+/-) between 1996 and 2000
Perint_2k	-0.002	1.85	0.17	Distance to perennial/intermittent stream in 2000
CH_1Y	0.2	1.53	0.22	Change in prob class (+/-) between 1999 and 2000
MOD_CV5Y	-0.57	0.96	0.33	CV in probability classes (1955–2000)
CH_1	0.17	0.89	0.34	Absolute change in probability class (1-yr interval)
MOD_CV15Y	0.48	0.78	0.39	CV in probability classes (1985–2000)
CH_3	0.12	0.71	0.4	Absolute change in probability class (3-yr interval)
CH_2	0.09	0.31	0.57	Absolute change in probability class (2-yr interval)
MOD_CV10Y	0.27	0.21	0.65	CV in probability classes (1990–2000)
Ed240	0.003	0.001	0.98	Edge density in 240-m radius

The remaining 33 predictor variables characterized four functional groups: habitat fragmentation, floodplain size, patch size, and heterogeneity in vegetation density. The top scoring variable in each functional group, in order of occurrence, was edge density within a 120-m radius (ED120), amount of floodplain within a 360-m radius (41-ha circle; FLOOD30), patch size (NDVI > 0.413), and heterogeneity in vegetation density within a 120-m radius (4.5-ha circle; ND_SD4). Distance to the pre-flood 1993 stream channel (PERINT_93) was significant, but no significant difference was detected for distance to the 2000 channel (table 5).

Multivariate Models

The three spatial riverine models made minimal improvements in overall classification accuracy (<6%) when compared to Model_99 (table 6). The refit Model_99 (RiverModel_1) improved overall accuracy by 1%. RiverModel_2, which included a distance to creek variable (CREEKDIS), decreased overall model accuracy by 7%. In contrast, RiverModel_3, which contained only a riparian density variable (ND_RAP) and a floodplain width variable (FLOOD30), increased overall

accuracy by 5.2%, but achieved a poor decadeR², suggesting it was overfit (table 6).

The amount of predicted habitat and territory density varied by model at a 50% cutpoint (table 6). When compared to Model_99, RiverModel_1 reduced the amount of predicted habitat by 22.1%, while increasing territory density by 16.7% at a 50% cutpoint. Thus, RiverModel_1 was more specific and sensitive than Model_99. RiverModel_2 was not as sensitive or accurate as RiverModel_1, while RiverModel_3 had the greatest density of the four spatial RiverModels and the least amount of predicted habitat. Given the poor decadeR² of RiverModel_3, we believe RiverModel_1 is the best spatial model for San Pedro/Gila.

The two spatial-temporal RiverModels (10 and 14, table 6) outperformed the spatial RiverModels in most model accuracy and fit categories, with 6% and 13% improvements in Nagelkerke *r*² values and the highest overall accuracy from the validation set; this increased overall classification accuracy by 6% compared to Model_99. Both spatial-temporal RiverModels performed similarly across all categories, which is not surprising since they shared two of the same variables (ND_RAP and MOD_SD10Y). However, RiverModel_10

Table 6. Spatial and spatial-temporal models resulting from the multivariate logistic regression analysis at the San Pedro/Gila study site (n = 125). RiverModel_1 was obtained by fitting a set of covariates found to be important in 1999 (Hatten and Paradzick 2003) to 125 use/nonuse sites from the San Pedro/Gila in 2000. To calculate accuracy statistics for these models, we set the probability cutpoint for all models at 50% (cells with a probability value ≤50% were considered unsuitable for breeding, values >50% were considered suitable). Highlighted models are the best for each category.

RiverModel ^a	r ^{2b}	Pres ^c	Ab ^d	All ^e	ROC ^f	DecadeR ^{2g}	Density ^h	Predicted ⁱ
Spatial models								
Model_99	NA	98.4	59.7	79.1	NA	0.48	0.030	2035
RiverModel_1	0.61	87.3	72.6	80.0	0.90	0.5	0.035	1586
RiverModel_2	0.64	84.1	62.9	73.5	0.91	0.52	0.031	1704
RiverModel_3	0.63	88.9	77.4	83.2	0.92	0.18	0.037	1527
Spatial-temporal models								
RiverModel_10	0.68	88.9	79.0	84.0	0.93	0.42	0.038	1482
RiverModel_14	0.69	90.5	77.4	84.0	0.93	0.52	0.037	1523

^aRefer to table 7 for model parameters

^bNagelkerke pseudo *r*² statistic

^cPercent of presence sites correctly classified (sensitivity)

^dPercent of absence sites correctly classified (specificity)

^eOverall model accuracy (sensitivity + specificity) / 2 as determined from validation dataset (n = 107)

^fReceiver operating characteristic (ROC) test (area under the curve)

^gExplained variability in the inter-annual fluctuations in # of flycatcher territories between 1996 and 2005

^hTerritory density at a 50% cutpoint

ⁱAmount of predicted breeding habitat at a 50% cutpoint

NA = stats not applicable for Model_99 because dataset contained lake and riverine data

Table 7. Model parameters of multivariate logistic regression models that we developed and tested for the San Pedro/Gila study site ($n = 125$) in 2000. RiverModel_1 was created by fitting four covariates that were found to be important in a previous study of flycatcher (Hatten and Paradzick 2003) to 125 use/nonuse sites and vegetation characteristics in June 2000.

Variable	β	S.E.	Wald	df	Sig.	Odds	95% C.I. for Odds	
							Lower	Upper
RiverModel_1 (constant = -7.46)								
ND_BEST4	0.09	0.02	14.37	1	0.00	1.10	1.05	1.15
ND_SD4	0.63	0.24	6.67	1	0.01	1.87	1.16	3.02
ND_TOP3	2.24	0.65	11.70	1	0.00	9.37	2.60	33.80
FLOOD30	0.04	0.02	6.66	1	0.01	1.05	1.01	1.08
RiverModel_2 (constant = -8.66)								
FLOOD30	0.04	0.02	4.98	1	0.03	1.04	1.01	1.08
ND_BEST4	0.11	0.03	14.90	1	0.00	1.12	1.06	1.19
ND_SD4	0.74	0.26	8.29	1	0.00	2.10	1.27	3.47
ND_TOP3	2.10	0.68	9.52	1	0.00	8.13	2.15	30.75
STREAMDIS	0.00	0.00	4.38	1	0.04	1.00	1.00	1.01
RiverModel_3 (constant = -8.37)								
ND_RAPa	0.15	0.03	28.20	1	0.00	1.16	1.10	1.23
FLOOD30	0.06	0.02	11.77	1	0.00	1.06	1.03	1.10
RiverModel_10 (constant = -10.6)								
MOD_SD10Y	2.55	0.67	14.68	1	0.00	12.81	3.48	47.24
MOD_MN10Y	0.78	0.29	6.97	1	0.01	2.17	1.22	3.87
ND_RAPa	0.134	0.032	17.96	1	0.00	1.143	1.075	1.216
RiverModel_14 (constant = -8.10)								
ND_RAP	14.34	3.23	19.73	1	0.00	169162	3021	9471007
MOD_CV10Y	-5.66	2.09	7.30	1	0.01	0.003	0.001	0.21
MOD_SD10Y	4.34	1.12	14.91	1	0.00	76.96	8.49	697.70

^aCoefficient multiplied by 100 to correct for non-normality

contained a 10-yr mean (MOD_MEAN10Y) and RiverModel_14 contained a 10-yr CV (MOD_CV10Y), both of which were output by RiverModel_1. RiverModel_14 did better for the decade R^2 and we believe it is the best spatial-temporal RiverModel.

RiverModel_1, which provided the best accuracy from both a spatial and Decade R^2 perspective, contained the same four covariates as Model_99, but fit specifically to San Pedro/Gila (table 7). The WALD statistic showed that the amount of dense vegetation within a 120-m radius (ND_BEST4) was the most influential covariate, followed by vegetation density at the site (ND_TOP3), variability in dense vegetation in a 120-m radius (ND_SD4), and amount of floodplain within a 360-m radius (FLOOD30). RiverModel_1 also produced an excellent fit between its five probability classes and territory density (fig. 6), explaining 95% of the variability in nest density with the following polyno-

mial: territory density = $0.0052x^2 - 0.0176x + 0.0151$, where X is the model probability class. Both spatial-temporal RiverModels (10 and 14) obtained 23%–27% greater territory densities and 25%–27% less predicted habitat than Model_99 (at a 50% cutpoint; table 6). From a temporal accuracy assessment, though, there was little observed difference between the spatial (0.18–0.52) and spatial-temporal RiverModels (0.42–0.52). Both spatial-temporal RiverModels contained change-detection variables that spanned a 10-year time frame (MOD_CV10Y, MOD_SD10Y), plus a vegetation density variable (ND_RAP; table 7). While not dramatic, RiverModel_10 did achieve an 8.6% increase in territory density over RiverModel_1, while decreasing predicted habitat by 6.6%. Thus, the temporal dimension of breeding habitat did modestly increase the sensitivity and specificity compared to the best spatial model.

Flycatcher Habitat: 1985–2005

Amount of Predicted Habitat Over Time

The amount of predicted habitat between 1985 and 2005 changed markedly, though not necessarily progressively, at both Roosevelt Lake and San Pedro/Gila (fig. 7, table 8). At Roosevelt Lake, there was a general increase in the amount of habitat from 1985 to 2004, particularly in the 1995–2004 period (fig. 7), but the amount of habitat fluctuated along with lake levels. Most noticeable is the drop in predicted habitat in 2005, when the reservoir rose to near capacity; reduction in habitat was due to both the inundation of suitable and occupied habitat, as well as the model having difficulty predicting the semi-inundated habitat that was occupied by flycatchers in 2005. At the San Pedro/Gila, the amount of predicted habitat also fluctuated over the 20-year period (fig. 7, table 8). The least amount of habitat occurred in years of flood (1985, 1993) and severe drought year (2002). Habitat was greatest in the periods between these roughly 10-year events.

The amount of estimated habitat varied based upon which model was used and what cutpoint we selected (table 9) (fig. 8, table 8). Changes in the cutpoint for determining suitable habitat are trade-offs between specificity and sensitivity, as increasing specificity decreases sensitivity, and vice versa (table 9); thus the best cutpoint varies by model, and which cutpoint is best should be evaluated with specific management objectives in mind. Additionally, the model used can change the amount of predicted habitat. Generally, the spatial-tempo-

ral model at Roosevelt Lake predicted more habitat, but the proportion of additional habitat predicted varied by year. At the San Pedro/Gila study site, the spatial-only model tended to predict more habitat, but not in all years (fig. 8).

Factors Influencing Changing Amounts of Habitat

At Roosevelt Lake, the strongest factor influencing the amount of predicted habitat was the lake elevation. Roosevelt Lake's water level hovered between 2,120 to 2,140 ft elevation from 1985 to 1989, then fluctuated greatly between 1989 and 2006 (2,035–2,150 ft; fig. 2). In spite of the fluctuations, there was a general downward pattern in water surface elevations between 1992 and 2003, before rising again in 2005. The amount of predicted habitat at Roosevelt Lake inversely mirrored the water level, with the least predicted habitat in the highest water years of 1985 and 2005, and an irregular increase in the predicted habitat between 1991 and 2004. From 1985 to 2005, the correlation between water level and predicted habitat was strong (-0.86 , $p = 0.004$), indicating that low reservoir levels provide more habitat for flycatchers than high reservoir levels. While rainfall may contribute to overall amounts of predicted habitat, the relationship between rainfall and amount of predicted habitat was confounded by the strong relationship of the lake level; years with heavy precipitation saw increasing lake levels and reduction in the amount of predicted habitat.

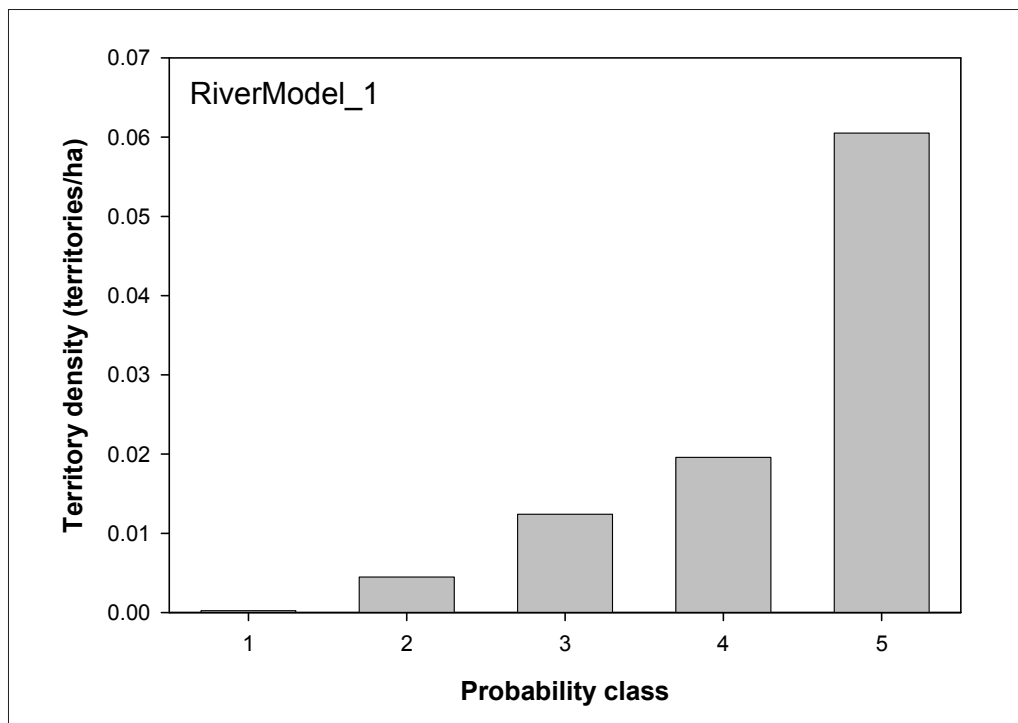


Figure 6. The density of flycatcher territories ($n = 62$) found within five probability classes at San Pedro/Gila, produced from spatial model RiverModel_1. Densities were obtained by dividing the number of flycatcher breeding territories (from a validation dataset) by the area contained within each probability class. Actual flycatcher densities would have been 2x higher if we had used the full dataset instead of the validation dataset (a random subset of the total dataset).

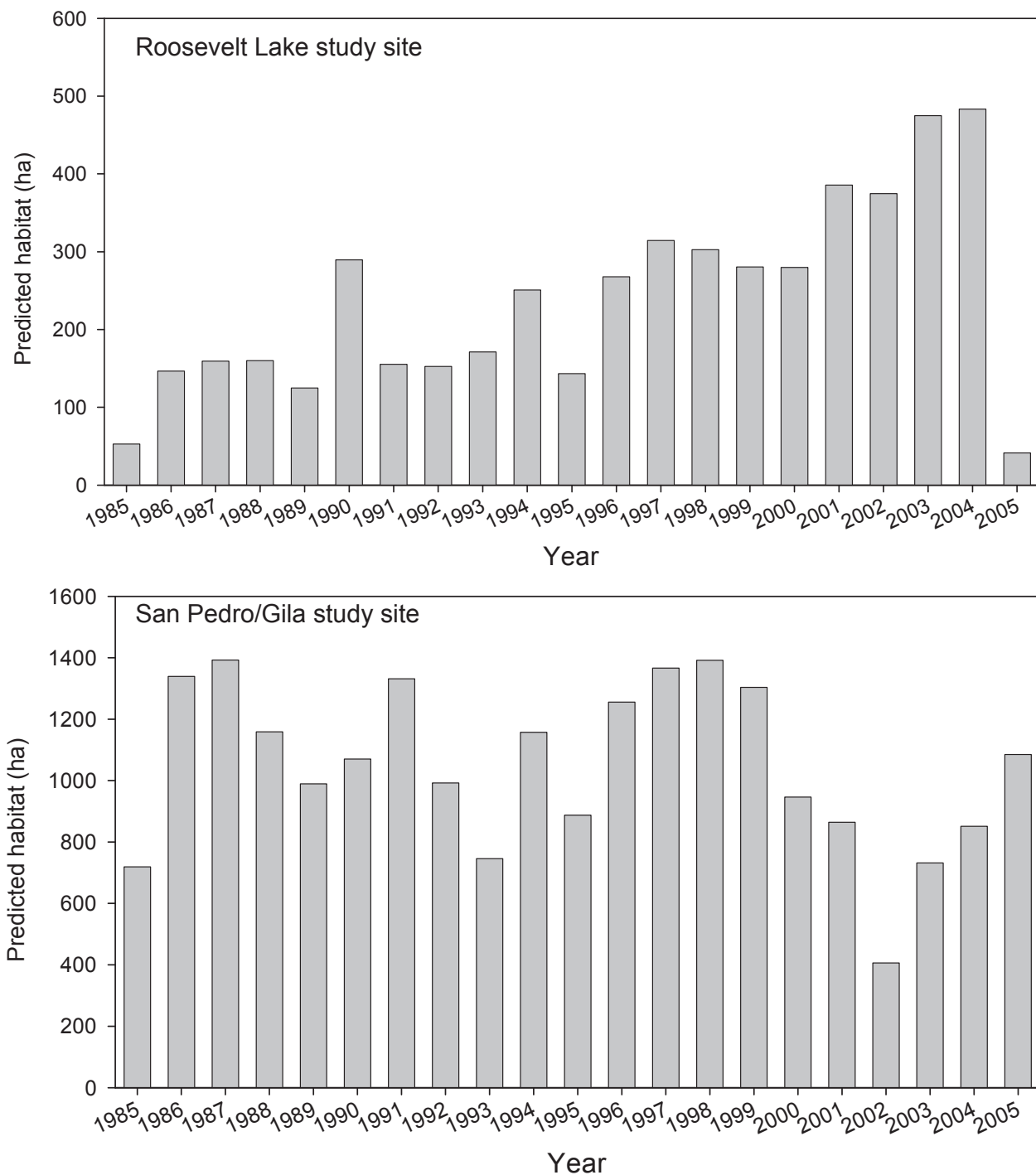


Figure 7. Amount of predicted habitat, 1985–2005, at the Roosevelt Lake (top) and San Pedro/Gila (bottom) study sites. Roosevelt Lake predicted habitat was from LakeModel_2, using a 50% cutpoint, while San Pedro/Gila predicted habitat was from RiverModel_1, using a 50% cutpoint. See table 9 for the exact amount of hectares per model per year.

Table 8. Amount of predicted habitat (in ha) at the Roosevelt Lake and San Pedro/Gila study sites using the best spatial and spatial-temporal models from each site. Spatial models were run from 1985 to 2005, while the spatial-temporal models (which include information from earlier years) were run from 1995 to 2005. For all models, we used a 50% cutpoint to determine the amount of predicted habitat.

Year	Roosevelt Lake study site		San Pedro/Gila study site	
	LakeModel_2	LakeModel_5	RiverModel_1	RiverModel_14
1985	53	NA	719	NA
1986	146	NA	1339	NA
1987	159	NA	1393	NA
1988	160	NA	1158	NA
1989	125	NA	989	NA
1990	290	NA	1070	NA
1991	155	NA	1331	NA
1992	152	NA	992	NA
1993	171	NA	746	NA
1994	251	NA	1157	NA
1995	143	213	887	797
1996	268	294	1255	1082
1997	314	347	1366	1217
1998	303	376	1392	1240
1999	280	393	1303	1187
2000	280	376	946	910
2001	386	448	864	845
2002	375	458	406	685
2003	475	553	732	819
2004	483	556	851	864
2005	41	55	1085	1021

At the San Pedro/Gila, we found a strong quadratic relationship ($r^2 = 0.51$) between winter rains (October – March) and mean density of riparian vegetation ($\text{NDVI} > 0.41$) (fig. 9; $\text{Mean NDVI} = 0.01(\text{RAIN}) - 0.001(\text{RAIN}^2) + 0.458$). Additionally, there was a weaker but significant quadratic relationship between fall/winter rains and predicted flycatcher habitat at San Pedro/Gila ($r^2 = 0.37$, $p\text{-value} = 0.017$; $\text{predicted habitat} = 1007.04 + 262.8(\text{RAIN}) - 17.999(\text{RAIN}^2)$). The years with the lowest mean NDVI values corresponded to years with the heaviest fall/winter rains (1985, 1993, 1995) or extreme droughts (2002). Given the importance of vegetation density in our models, it is not surprisingly that the amount of predicted habitat was lowest during the drought year in 2002. Perhaps correspondingly, the years with the greatest amount of predicted habitat (1987 and 1998) followed major flood events by 4 to 5 years.

Over a 20-year interval at San Pedro/Gila, patch numbers were lowest in 1985 and highest in 1994. An examination of the satellite imagery revealed that the scouring flood of 1982 appeared to have removed huge swaths of the riparian vegetation, greatly reducing the number of patches; thus, 1985 had

relatively few patches. As the riparian vegetation increased from 1985 to 1992, there was a corresponding increase in the number of patches. In 1993 another large flood fragmented the riparian corridor again. However, unlike the 1982 flood that was much larger, the 1993 flood apparently fractured but did not remove much of the riparian habitat, leading to an increased number of patches. From 1994 until 2005 there appeared to have been a slow revegetation process during which the number of distinct patches decreased due to consolidation, resulting in fewer but larger patches.

Relationship of the Amount of Habitat and Flycatcher Numbers

At Roosevelt Lake, there was a strong positive relationship between the increase in predicted habitat and the increasing number of territories (1995–2004), with a correlation of 0.90 ($p < 0.001$) using the amount of predicted habitat (50% cutpoint) for LakeModel_5 (fig. 8). Fitting a regression line to the relationship suggests (if the relationship were causal) that

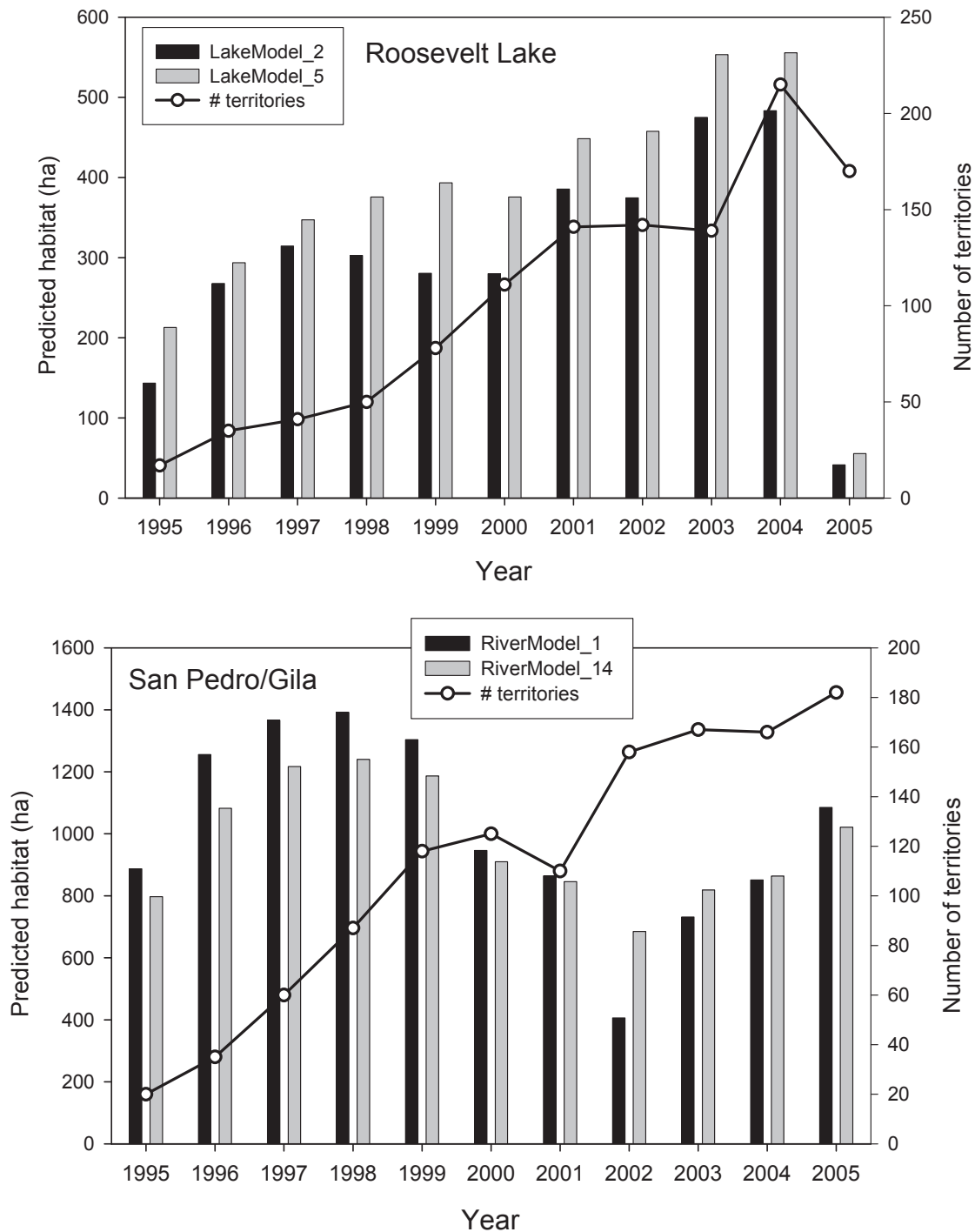


Figure 8. The amount of predicted habitat and number of flycatcher territories at the Roosevelt Lake (top) and San Pedro/Gila (bottom) study sites, 1995–2005. For each site, the best spatial (LakeModel_2 and RiverModel_1) and spatial-temporal (LakeModel_5 and RiverModel_14) models were used at a 50% cutpoint to predict the amount of habitat (Roosevelt Lake and San Pedro/Gila, respectively). The number of detected flycatcher territories were overlayed to show relationship with the amount of changing habitat and changes in the number of territories. See table 9 for exact amounts of predicted habitat.

Table 9. Accuracy results for the best models at the Roosevelt Lake and San Pedro/Gila study sites were obtained by overlaying predicted breeding habitat and the non-modeled validation use/nonuse locations. If a cutpoint was 50%, all cells with a probability $\leq 50\%$ were coded unsuitable, and cells with a probability $> 50\%$ were coded suitable. Habitat is the amount of vegetation considered suitable for flycatcher breeding at a given cutpoint. The density of territories (territories / ha) was determined by dividing the number of territories by the area considered suitable at each cutpoint. Presence (Pres) refers to the percent of territories correctly classified (model sensitivity), absence (Abs) refers to the percent of nonuse sites correctly classified (model specificity), and the overall accuracy (All) refers to the combined accuracy: (sensitivity + specificity) / 2.

	50% cutpoint			60% cutpoint			70% cutpoint			80% cutpoint		
	Pres	Abs	All	Pres	Abs	All	Pres	Abs	All	Pres	Abs	All
Roosevelt Lake												
Model_ 99	93.5	42.1	67.8	93.5	49.5	71.5	91.7	51.4	71.55	83.3	58.9	71.1
Habitat (ha)	845.6			762.1			680.9			549.2		
Nests	101			101			99			90		
Density	0.12			0.13			0.15			0.16		
LakeModel_2	80.6	72	76.3	75	77.6	76.3	64.8	82.2	73.5	52.8	86.9	69.85
Habitat (ha)	462.9			385.1			312.8			234.2		
Nests	87			81			70			57		
Density	0.19			0.21			0.22			0.24		
LakeModel_5	65.7	71	68.35	61.1	76.6	68.85	49.1	40.6	44.85	43.5	87.8	65.65
Habitat (ha)	551.2			465.0			386.3			311.2		
Nests	71			66			53			47		
Density	0.13			0.14			0.14			0.15		
San Pedro/Gila												
Model_ 99	98.4	59.7	79.1	90.5	64.5	77.5	80.9	79.0	80.0	76.2	82.2	79.2
Habitat (ha)	2035			1684			1327			910		
Nests	61			57			51			48		
Density	0.03			0.03			0.04			0.05		
RiverModel_1	87.3	72.6	80.0	82.5	80.6	81.5	73.0	85.5	79.2	62.9	87.1	75.0
Habitat (ha)	1586			1309			1002			644		
Nests	55			52			46			39		
Density	0.03			0.04			0.05			0.06		
RiverModel_14	90.5	77.4	84.0	84.1	79.0	81.6	81	85.5	83.2	69.8	93.5	81.6
Habitat (ha)	1523			1234			938			634		
Nests	57			53			51			44		
Density	.04			.04			.05			.07		

one flycatcher territory is supported for every 2 ha of predicted habitat. However, the pattern at San Pedro/Gila was markedly different. The correlation between the number of flycatcher territories at San Pedro/Gila and the amount of predicted habitat from RiverModel_14 (at a 50% cutpoint) was negative and weak (-0.33 , $p = 0.31$). For example, the amount of predicted habitat declined at the San Pedro/Gila from 2000 to 2004, yet the number of flycatcher territories continued to increase (fig. 8).

Demographic Relationships to Spatial Characteristics

In general, the spatial variables that provided the strongest relationships in predicting territories had much weaker relationships with productivity variables (table 10). Although there were a number of correlations that were statistically significant, the relationships were generally weak, with all correlation coefficients under 0.2. NDVI values did not differ based on flycatcher territory status (unpaired, monogamous breeding, or polygamous; $F_{2,1826} = 0.05$, $p = 0.96$) nor did NDVI neighborhood values ($F_{2,1853} = 0.85$, $p = 0.43$). However, model probability did differ between territory status categories ($F_{2,1825} = 3.76$, $p = 0.02$), with unpaired territories having a lower mean model probability (0.61) versus monogamous (0.66) and polygamous (0.66) territories; this pattern was similar between sites. However, as with the models that

predicted territory occurrence, the Roosevelt Lake and San Pedro/Gila study sites had different relationships between the spatial information and several of the demographic variables (table 10). For example, the neighborhood average of NDVI values (ND_BEST4) had a stronger relationship to total young fledged at San Pedro/Gila ($\rho = 0.1859$) than at Roosevelt Lake ($\rho = 0.1047$), while the NDVI value at the specific territory (ND_RAP) provided a stronger relationship at Roosevelt Lake ($\rho = 0.1713$) than the San Pedro/Gila ($\rho = 0.0901$).

Discussion

The starting point for increasing our understanding of the relationships between flycatcher breeding site selection and spatial characteristics was to build upon the GIS-based habitat model developed in 1999 by AGFD (Hatten and Paradzick 2003). The AGFD model (Model_99) is a generalized habitat model, designed to predict flycatcher habitat in both reservoir and riverine systems. Model_99 has been used to predict flycatcher breeding habitat in riverine and reservoir systems statewide (Dockens et al. 2004), assess changes in breeding habitat at Roosevelt Lake between 1985 and 2001 (Paradzick and Hatten 2004), and assist in the definition of critical habitat (USFWS 2005). However, fitting spatial models separately to each specific system (i.e., lake vs river) led to improved models for both systems because each have different under-

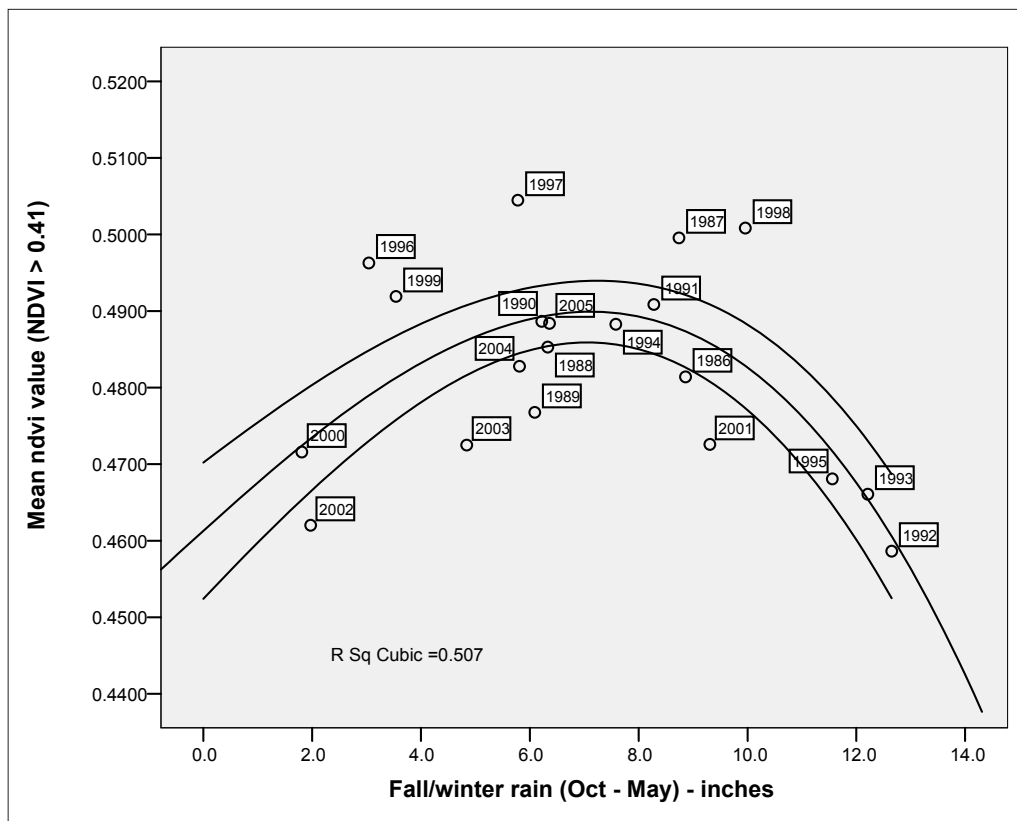


Figure 9. The quadratic relationship between fall/winter rains and mean riparian vegetation density (considering NDVI values of 0.41 or greater) at the San Pedro/Gila study site. Those years with the lowest mean NDVI values corresponded to years with the heaviest Fall/Winter rains (1992, 1993, 1995), presumably due to floods, or extreme drought (2002), presumably due to water-stressed vegetation, with years of intermediate rainfall having the highest NDVI values.

Table 10. Spearman's correlation (ρ) results of productivity (number of young fledged) and spatial characteristics for the Roosevelt Lake and San Pedro/Gila study sites (Bold = $p < 0.05$)

Variable	Roosevelt Lake		San Pedro/Gila	
	n	ρ	n	ρ
Distance from creek (CREEKDIST2K)	762	0.0212	894	-0.0095
Model probability value	746	0.0725	885	0.0695
Distance from patch edge (DISTTOP3)	762	0.1076	894	0.0936
Neighborhood NDVI value (ND_BEST4)	762	0.1047	894	0.1859
Neighborhood NDVI standard deviation (ND_SD4)	762	0.003	894	-0.0423
NDVI value (ND_RAP)	738	0.1713	894	0.0901
Patch size (PATCHTOP3)	623	0.0884	729	0.1537

lying drivers that influence habitat establishment, development, and persistence. Overall, the efforts presented here greatly improved our ability to predict flycatcher habitat, increased our insight into flycatcher habitat needs and the dynamics of their habitat, and led to the development of more powerful tools.

Spatial Models

Reservoir and riverine systems are fundamentally different in many characteristics, and our data supported our prediction that developing separate spatially-explicit models for these two types of riparian habitat could result in significantly better model fit. Modeling specifically at Roosevelt Lake produced the greatest improvements observed over the Model_99. In particular, the distance to river increased model specificity, as it decreased the probability of including habitat patches that were farther from the rivers, which earlier models could not exclude. The importance of distance to water (both river and lake) may be related to the age of habitat, with younger habitat developing closer to water due to fluctuations in lake levels leaving bare ground suitable for vegetation establishment and development. Based on movement patterns, it appears flycatchers prefer younger habitat when it is available (see chapter 4). Floodplain width was also important because it relates to several key parameters that affect vegetation development and growth, including sediment/substrate availability and water table depth. Another distinction between the lake models versus Model_99 was the increased importance of NDVI values at the territory location versus in a surrounding area (neighborhood). This may reflect the fact that patches tend to be much larger at Roosevelt Lake compared to the San Pedro/Gila, and therefore the vegetation may be more uniform around each territory than at the San Pedro/Gila where there are smaller patches with more adjacent edge.

The river-specific models for the San Pedro/Gila were much closer to the generalized Model_99, which suggests that Model_99 was more closely fitted for a riverine system than a

reservoir system. Therefore, improvements in fit were negligible for the spatial only considerations. Unlike Roosevelt Lake, distance to water had little influence on the performance of the models. This may be due to a number of reasons that are possibly related and not mutually exclusive. For example, a high water table (which promotes riparian vegetation density and vigor) may occur away from the active channel due to uneven topography within the floodplain and subsurface water flow. Occupied patches that were away from the river may also have been supported by water from adjacent agriculture or wastewater. It may also be that a patch has better long-term persistence probability if it is not within the major scour zone of the active channel. Additionally, heterogeneity in NDVI (SD or CV) was an important factor in the river models, perhaps relating to stability versus dynamics of riparian habitat along the river, flooding, degree of edge, development of new/young habitat at periphery of older vegetation, etc.

Spatial-temporal Models

The greatest increase in accuracy came from applying a temporal component to both the Roosevelt Lake and San Pedro/Gila models. The importance of the temporal component within the model demonstrates that flycatcher habitat is a dynamic rather than static environment, and including this in models predicting suitable riparian habitat is important. The dynamic nature of riparian habitat has ramifications for flycatcher movement patterns and metapopulation dynamics. Although there is evidence that flycatchers will visit young habitat in the year or two preceding occupation, it is likely that flycatchers determine suitability in the year that they settle into a territory. Therefore, the temporal aspects of the model may be a surrogate for features that the spatial-only model has not directly measured but that flycatchers use to determine age and stability. For example, vegetation structure and density can be partially inferred from NDVI, but multiple years of high NDVI values in the same place may reflect a more static, homogeneous, or older vegetation structure that is not favored

by flycatchers. More study is needed to understand these links between the temporal modeling of habitat and what a flycatcher perceives in the breeding season.

For Roosevelt Lake, the best spatial-temporal model included a 5-year mean of NDVI values, which may help the model identify (as low probability) the very young vegetation that has a high NDVI value but has not reached an age to provide the structural density and complexity required by nesting flycatchers. Many of the temporal models fitted to Roosevelt Lake had unexpected or contrary relationships, and we believe that the stochastic nature of the reservoir fluctuations confounded modeling efforts. For example, from 1995 to 2005, the reservoir water level generally declined, but it did increase in some years—most dramatically in 2005. Thus, while the general trend was for more habitat to emerge on the exposed lakebed, there were several times during this period when habitat was destroyed. Nonetheless, fluctuating reservoirs can provide suitable habitats for flycatchers, and in some ways mimic the cycle of habitat creation and destruction that historically occurred in large river systems. Thus, although we might consider a reservoir system to be more stable than a riverine one, fluctuating lake levels may in fact create many of the dynamic disturbance events and responses that riverine habitats typically experience on less regulated rivers.

At the San Pedro/Gila, temporal consideration was also important, with the best temporal scale being 10 years. This temporal period may correspond with the roughly 10-year cycles of flood and drought that had such a marked effect on the amount of predicted habitat. Thus, approximately every 10 years in this 20-year period we saw a decrease in predicted flycatcher habitat, followed generally by an increase in predicted habitat peaking at 5 years post-event, then declining until another event restarted the cycle. One important consideration is that the year in which the model is built (2000 for the case of the San Pedro/Gila) will influence the exact statistical relationships of the model. Building the same model in other years may change some of those relationships. One approach for future efforts would be to build models in multiple years and average the resulting models for an even more temporally robust model.

Reservoir Versus Riverine Systems

Both differences and similarities in the model structures for the two systems can help elucidate habitat characteristics correlated with flycatcher presence. Overriding all other considerations is the importance of NDVI-based variables, both for the lake and river system breeding habitats, which underscores the importance of dense, vigorous riparian vegetation as a major selection criteria for breeding flycatchers. Additionally, heterogeneity in NDVI is important, reflecting factors such as canopy roughness, patchiness, habitat mosaic, openings, and different vegetation types. This suggests that beyond dense riparian vegetation, flycatchers chose habitat that is heterogeneous in structure. This use of heterogeneous struc-

ture may be related to foraging behavior and diet, by providing open spaces to hawk insects as well as increased arthropod biomass and diversity associated with higher environmental heterogeneity.

One of the primary differences between our reservoir and river models was that distance to water was important at Roosevelt Lake but not at the San Pedro/Gila. At Roosevelt Lake, flycatchers quickly established territories in developing habitat that was closer to the receding lake, and used refuge habitat near rising water levels during inundation years; these two characteristics may explain the strong relationship between territories and distance to water. At San Pedro/Gila, some models showed that habitat farther from the river was more likely to be occupied, perhaps due to scouring flood impacts, water table influences, or importance of agriculture runoff at some breeding locations. Scouring floods in 1985 and 1993 may have destroyed much of the habitat directly adjacent to the river, forcing flycatchers into riparian woodlands farther from the river.

Another difference between the two systems was that patch size was more important for the San Pedro/Gila models than the Roosevelt Lake models. Patch sizes at Roosevelt Lake were typically larger, which may reduce the importance of patch size as a predictive factor there compared to the more fragmented San Pedro/Gila study site. Probably related, the scale of NDVI differed between the two systems, with the lake models favoring a local scale (ND_RAP) of NDVI compared to Model_99 (120m radius scale), whereas the river model also favored the neighborhood estimate. The stronger effect of a neighborhood NDVI value at the San Pedro/Gila may reflect the typically smaller habitat patches.

Predicted Habitat

Predicting an exact amount of suitable habitat for breeding flycatchers is difficult, and the amount of predicted habitat can vary for two important model-based reasons. First, all of the spatial and spatial-temporal models produce suitability probabilities per spatial cell between 0% and 100%. While flycatchers are far more likely to be found in high probability areas, some are found in low probability areas. However, to predict the amount of habitat a cutpoint, or probability threshold, needs to be chosen at which “suitable” (i.e., high model probability) habitat is dichotomously distinguished from “unsuitable” (i.e., low model probability) habitat. For all models, lower cutpoint will lead to greater amounts of predicted habitat and higher model sensitivity, but lower model specificity. Inversely, as the cutpoint is increased, the model’s specificity increases, but the amount of predicted habitat and the sensitivity decrease. This is an issue inherent with all models of this kind, and there is no perfect cutpoint. Overall, the spatial models built for this study were better in both sensitivity and specificity than the more generalized model (Model_99). The new models predict less high-probability habitat compared to Model_99, while improving classification accuracy. The large

improvement provided by LakeModel_2 shows that the first modeling effort (Model_99) did not evaluate a crucial variable for understanding a reservoir system compared to a river system—distance from water.

Another source of variation in the amount of predicted habitat is the choice of which model is used. At Roosevelt Lake, the amount of habitat predicted per year differs among the top spatial (LakeModel_2) and spatial-temporal model (LakeModel_5) at a 50% cutpoint. This is also true for the San Pedro/Gila study site for RiverModel_1 and RiverModel_14. In general, the models for each system show similar trends, varying only in the exact amount of habitat. Thus, it is important to keep in mind that determining the amount of predicted habitat is a much more challenging prospect than the already difficult task of identifying breeding habitat. Nonetheless, the differences between the estimates of habitat are relatively small, suggesting that the models are converging on a true, but undeterminable amount of suitable breeding habitat.

The amount of predicted habitat changed over time, as highlighted by the better performance of the spatial-temporal models. At Roosevelt Lake, the maximum amount of predicted habitat was in 2004, while the least amount of habitat was in the following year (2005) when the lake rose to inundate most historical breeding habitat (fig. 7). The amount of predicted habitat also fluctuated at the San Pedro/Gila study site, being greatest in 1987 and 1998, and lowest amount during the severe drought in 2002, with nearly a 1,000-ha difference between the year with the most habitat and that with the least.

The changes in the amount of predicted habitat at our two study sites are ultimately linked to water and time. At Roosevelt Lake, the fluctuating reservoir levels had an overwhelming effect on the amount of habitat, as very little of the total habitat was above the reservoir's maximum level between 1995 and 2005. At the San Pedro/Gila, rainfall and its influence on river flows had a dominant effect. In general, too little rainfall (such as in 2002) or too much (e.g., scouring floods) decreased the amount of predicted habitat at the San Pedro/Gila site, with the highest levels of predicted habitat occurring in the middle-range of rainfall for this period.

Linking Flycatcher Numbers to the Amount of Habitat

At Roosevelt Lake, the changes in the number of breeding flycatchers appeared to be related to the amount of predicted habitat. As the amount of predicted suitable habitat increased, the breeding population at Roosevelt Lake increased. The availability of this new habitat, coupled with successful productivity of flycatchers, may have led to the observed parallel expansion of habitat and the flycatcher population at Roosevelt Lake. However, at the San Pedro/Gila there was no apparent relationship between the amount of predicted habitat and the increasing population size. For example, the amount of predicted habitat declined at the San Pedro/Gila from 2000 to 2004, yet the number of flycatcher

territories continued to increase. It may be that flycatcher populations along the San Pedro, which has 2–3 times more predicted habitat than Roosevelt Lake for a similar population of flycatchers, may not have been limited by breeding habitat over the course of our analysis (1995–2005); there may never have been enough flycatchers to occupy all suitable habitat. Instead, San Pedro numbers may have been more influenced by other factors such as survivorship, predation, productivity, or dispersal outside the drainage. Because the two study sites show different relationships between predicted habitat and the number of territories, linking the amount of habitat needed to support each territory remains elusive.

Demographic Relationships with Spatial Characteristics

The spatial models were constructed to predict the occurrence of flycatcher territories, and the way in which they were developed did not take into account factors such as habitat quality (e.g., higher productivity, higher survivorship). Although habitat identified as having a higher probability of supporting a flycatcher territory is inferred to be higher quality habitat than locations with lower probabilities, density by itself does not necessarily equate to quality (van Horne 1983). At both sites, there may be occupied habitat of both high and low quality in terms of how habitat influences or mediates productivity, survivorship, and ultimately lifetime fitness. Thus, a direct link between probability of occurrence and habitat quality cannot be assumed.

Based on our expanded modeling, the relationship between productivity and measures of spatial habitat quality (as defined by our models) was weak, suggesting that factors not measured by the spatial variables are also influencing productivity, given a flycatcher territory location. Two such possible factors are predator density and arthropod biomass. Thus, we believe that there may be value in having future spatial modeling efforts investigate whether incorporating other measures of habitat quality, such as arthropod biomass and densities of nest predators, can improve spatial models of habitat quality.

Management and Research Considerations

Considering Temporal Changes

Both the strong support for the spatial-temporal models, and the changes in predicted habitat over a 20-year period at both Roosevelt Lake and San Pedro/Gila, demonstrate the dynamic nature of riparian habitat and the importance of considering temporal changes in management and modeling efforts. For example, safeguarding existing flycatcher breeding sites might provide sufficient protection in the short-term, but over a long period habitat at protected sites may be destroyed,

degraded, or simply mature beyond optimal age and structure that the flycatchers will use. Thus, habitat management plans that focus at the level of a drainage or region, as recommended by the Southwestern Willow Flycatcher recovery plan (USFWS 2002), are more likely to succeed than those that target only specific, finite breeding locations.

Identifying, Quantifying, and Evaluating Habitat

As with earlier work by AGFD (Dockens et al. 2004), these GIS models can be used to identify potential flycatcher habitat across large regions for the purpose of prioritizing future survey locations and potential restoration or mitigation properties. At a more local level, land managers can use the models to identify the probability that flycatchers may be breeding on their land, although this approach is not a substitute for on-the-ground surveys where suitable habitat exists. Managers may be able to use the models to plan riparian restoration strategies; e.g., to choose areas that are already near the desired structure (based on probability class) and therefore more likely to reach target NDVI values more quickly. These models can be applied at a range of scales, from regions and drainages to a specific patch of riparian habitat. The GIS models could also be an effective tool for applying Adaptive Management principles to restoration efforts, by tracking and evaluating different restoration treatments over time, and adjusting on-the-ground activities or future restoration plans based on the response of riparian habitat.

Future Research Needs

We believe that an important next step in understanding the model performance and its relationship to habitat variables is to quantify how key physical factors drive the NDVI values within the riparian systems. Doing so would require a multidisciplinary and multiscale modeling effort that examines factors such as climate patterns, groundwater levels, river flows, and geomorphology. If this can be successfully accomplished, a Decision Tool could be developed by which managers could test various “what if” scenarios to determine river or reservoir operations, or future climate scenarios, would influence amount, distribution, and suitability of flycatcher habitat (as modeled via NDVI). Another important extension of modeling would be to testing how these models, developed from riparian areas in the Sonoran Desert Uplands, perform when applied to riparian habitats in other areas (see Hatten and Sogge 2007). Additionally, newer satellite imagery with greater resolution may provide better detection of flycatcher habitat, and future modeling efforts should explore these next-generation satellite images. Finally, this research underscores the importance of understanding and incorporating the drivers for temporal change riparian habitat in riverine and reservoir systems, and how these may differ from drainage to drainage.

References

- Avery, T.E., and G.L. Berlin. 1992. *Fundamentals of remote sensing and aerialphoto interpretation*. Fifth Edition. Macmillan, New York, New York.
- Boots, B.N., and A. Getis. 1988. *Point pattern analysis*. Sage, Beverly Hills, California, USA.
- Box, G., and P. Tidwell. 1962. Transformation of the Independent Variables, *Technometrics* 4 (1962): 531–550.
- Brown, D.E. (ed.). 1994. Tropical-subtropical desertlands. Pages 180–221 in *Biotic communities: Southwestern United States and northwestern Mexico*. University of Utah Press, Salt Lake City, Utah.
- Cardinal, S.N., and E.H. Paxton. 2005. Home range, movement, and habitat use of the Southwestern Willow Flycatcher, Roosevelt Lake—2004. U.S. Geological Survey Report to the Bureau of Reclamation, Phoenix, AZ.
- Causey, C.F., M.G. Pollock, S.L. Durst, P.J. Newell, E.H. Paxton, and M.K. Sogge. 2006. Survivorship and movements of Southwestern Willow Flycatchers at Roosevelt Lake, Arizona—2005. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix, AZ.
- Chou, Y. 1997. *Exploring spatial analysis in Geographic Information Systems*. OnWord Press. Santa Fe, New Mexico.
- Cody, M.L. (ed.). 1985. *Habitat selection in birds*. Academic Press, San Diego, California.
- Dockens, P.E.T., C.E. Paradzick, and J.R. Hatten. 2004. Application of a Southwestern Willow Flycatcher GIS-based habitat model: an estimate of breeding habitat in Arizona, 2001. Pages 28–59 in P. E. T. Dockens and C. E. Paradzick, eds. *Mapping and monitoring Southwestern Willow Flycatcher breeding habitat in Arizona a remote sensing approach*. Nongame and Endangered Wildlife Technical Report 223. Arizona Game and Fish Department, Phoenix, Arizona.
- Durst, S.L., M.K. Sogge, H. English, S.O. Williams, B.E. Kus, and S.J. Sferra. 2006. Southwestern Willow Flycatcher breeding site and territory summary—2004. U.S. Geological Survey report to Bureau of Reclamation, Phoenix, AZ.
- English, H.C., A.E. Graber, S.D. Stump, H.E. Telle, and L.A. Ellis. 2006. Southwestern Willow Flycatcher 2005 survey and nest monitoring report. Arizona Game and Fish Technical Report 248.
- Environmental Systems Research Institute (ESRI). 1992. *Cell-based modeling with Grid*. ESRI, Redlands, CA.

- Fawcett, T. 2004. ROC Graphs: Notes and Practical Considerations for Researchers. Technical report, Palo Alto, USA: HP Laboratories http://home.comcast.net/~tom.fawcett/public_html/papers/ROC101.pdf
- Hatten, J.R., and C.E. Paradzick. 2003. A multiscaled model of southwestern willow flycatcher breeding habitat. *Journal of Wildlife Management* 67: 774–788.
- Hatten, J.R., and M.K. Sogge. 2007. Using a remote sensing/GIS model to predict southwestern willow flycatcher breeding habitat along the Rio Grande River, New Mexico. U.S. Geological Survey Open File Report 2007-1207.
- Hosmer, D.W., and S. Lemeshow. 1989. *Applied Logistic Regression*. First Edition. John Wiley and Sons, New York, New York, USA.
- Keating, K.A., and S. Cherry. 2004. Use and interpretation of logistic regression in habitat-selection studies. *Journal of Wildlife Management* 68: 774–789.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659–1673.
- Marshall, R.M. 2000. Chapter 2: Population status on breeding grounds. Pages 3–12 *In* Status, ecology, and conservation of the Southwestern Willow Flycatcher. (D.M. Finch and S.H. Stoleson, eds.) USFS Rocky Mountain Research Station, Gen. Tech. Rep. RMRS-GTR-60.
- Marshall, R.M., and S.H. Stoleson. 2000. Chapter 3: Threats. Pages 13–24 *In* Status, ecology, and conservation of the Southwestern Willow Flycatcher (D.M. Finch and S.H. Stoleson, eds.). General Technical Report RMRS-GTR-60. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Morrison, M.L., B.G. Marcot, and R.W. Mannan. 1998. *Wildlife-habitat relationships: concepts and applications*. 2nd ed. University of Wisconsin Press, Madison, Wisconsin.
- Nagelkerke, N.J.D. 1991. A note on general definition of the coefficient of determination. *Biometrika* 78:691–692.
- Norusis, M.J. 1999. *SPSS regression models 10.0*. SPSS, Chicago, Illinois, USA.
- Paradzick, C.E., and J.R. Hatten. 2004. Southwestern Willow Flycatcher habitat change detection analysis: Roosevelt Lake, 1985–2001. Pages 60–82 *in* P. E. T. Dockens and C. E. Paradzick, eds. Mapping and monitoring Southwestern Willow Flycatcher breeding habitat in Arizona a remote sensing approach. Nongame and Endangered Wildlife Technical Report 223. Arizona Game and Fish Department, Phoenix, Arizona.
- Peduzzi, P., J. Concato, E. Kemper, T.R. Holford, and A.R. Feinstein. 1996. A simulation study of the number of events per variable in logistic regression analysis. *Journal of Clinical Epidemiology* 49:1373–1379.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- Ramsey, F.L., M. McCracken, J.A. Crawford, M.S. Drut, and W. J. Ripple. 1994. Habitat association studies of the Northern Spotted Owl, Sage Grouse, and Flammulated Owl. Pages 189–209 *in* N. Lange, L. Ryan, L. Billard, D. Brillinger, L. Conquest, and J. Greenhouse, eds. *Case studies in biometry*. Wiley, New York, New York, USA.
- Reino, L. 2005. Variation partitioning for range expansion of an introduced species: the common waxbill *Estrilda astrild* in Portugal. *Journal of Ornithology* 146:4–377.
- Ripple, W. J., D.H. Johnson, K.T. Hershey, and E.C. Meslow. 1991. Old-growth and mature forests near spotted owl nests in Western Oregon. *Journal of Wildlife Management* 55:316–318.
- Rourke, J.W., T.D. McCarthy, R.F. Davidson, and A.M. Santaniello. 1999. Southwestern Willow Flycatcher nest monitoring protocol. Nongame and Endangered Wildlife Program Technical Report 144. Arizona Game and Fish Department, Phoenix, AZ. 32pp.
- Sedgwick, J.A. 2000. Willow Flycatcher (*Empidonax traillii*). *In* The Birds of North America, No. 533 (A. Poole and F. Gill eds.). The Academy of Natural Sciences, Philadelphia, PA and the American Ornithologists' Union Washington, DC.
- Sogge, M.K., and R.M. Marshall. 2000. A survey of current breeding habitats. Pages 43–56 *in* D. M. Finch, and S. H. Stoleson, eds. Status, ecology, and conservation of the Southwestern Willow Flycatcher. U.S. Forest Service General Technical Report RMRS-60.
- Sogge, M.K., S.J. Sferra, and T.J. Tibbitts. 1997. A Southwestern Willow Flycatcher natural history summary and survey protocol. National Park Service Cooperative Studies Unit, U.S. Geological Service Colorado Plateau Research Station, Northern Arizona University. NRTR-97112.
- Stromberg, J.C. 1993. Riparian mesquite forests: a review of their ecology, threats, and recovery potential. *Journal of the Arizona-Nevada Academy of Science* 27:111–124.
- Story, M., and R.G. Congalton. 1986. Accuracy assessment: a user's perspective. *Photogrammetric Engineering and Remote Sensing* 52: 397–399.
- Szaro, R. C. 1990. Southwestern riparian plant communities: site characteristics, tree species distributions, and size-class structures. *Forest Ecology and Management* 33/34:315–334.

- Unitt, P. 1987. *Empidonax traillii extimus*: an endangered subspecies. *Western Birds* 18:137–162.
- U.S. Fish and Wildlife Service. 1993. Proposal to list the Southwestern Willow Flycatcher as an endangered species and to designate critical habitat. *Federal Register* 58:39495–39522 (July 23, 1993).
- U.S. Fish and Wildlife Service. 1995. Final rule determining endangered status for the Southwestern Willow Flycatcher. *Federal Register* 60:10694 (February 27, 1995).
- U.S. Fish and Wildlife Service. 2005. Designation of critical habitat for the Southwestern Willow Flycatcher (*Empidonax traillii extimus*); Final rule. *Federal Register* 70:60886 (October 19, 2005).
- Van Horne, B. 1983. Density as a Misleading Indicator of Habitat Quality. *Journal of Wildlife Management* 47:893–901.
- Wiens, J.A. 1989. *The ecology of bird communities*. Cambridge University Press, New York, New York.

Chapter 7—Non-territorial Floaters

Introduction

Among bird species there are a wide variety of social systems, ranging from flocking groups to solitary individuals. These social systems can have major effects on the distribution of groups and individuals on the landscape and within a given habitat. A very common social system among birds and other vertebrate groups is territoriality (Maher and Lott 2000), wherein an individual (or group) defends and excludes others from a particular geographic area or other resource. Territoriality is generally considered to provide the dominant, territory-holding individual with benefits such as better survival and reproductive potential. However, defending a territory involves higher energy output due to advertising and aggression, and carries increased risk of injury (from interactions with other individuals) or predation (because advertising individuals are more easily detected). Therefore, individuals defend territories only when the benefits outweigh the costs, a concept that Brown (1969) termed “economic defendability.”

Territoriality among birds has been widely recognized for over a century, primarily because the territorial songs and displays of birds are generally conspicuous and often pleasing to human observers. As bird banding became a more widely used research tool in the early to mid-1900s, researchers became aware that not all individuals in a given area succeeded in establishing territories, though it was generally assumed that they would if the opportunity arose. In one of the first detailed syntheses of territorial behavior, Nice (1941) described how birds that fail to obtain territories form a “reserve supply” of individuals that will serve as replacements in the case of death of local territory holders. Her work stimulated additional attention to the phenomenon of territoriality, and a decade later Stewart and Aldrich (1951) published the first experiment to determine how quickly and to what degree territory holders would be replaced when removed (via shooting) during the breeding season. Over the course of roughly 4 weeks, 425 adult birds (302 males) of more than 24 species were removed from an area that initially supported 148 territorial males. They reported a steady influx of new birds, with replacements occurring very quickly, typically the next morning. Based on these results, Stewart and Aldrich (1951) wrote that “... a large, surplus, “floating” population of unmated males must have been present...” This appears to be the origin of the term “floater”, which has since come to be used to describe a non-territorial individual of a typically territorial species.

Territorial behavior is therefore a mechanism by which local populations may be regulated, in terms of abundance

and distribution, in part by forcing some individuals into a non-territorial lifestyle as a floater. This phenomenon of floating appears to be widespread and has now been documented among diverse bird taxa including songbirds, raptors, waterfowl, and shorebirds (Zack and Stutchbury 1992, Newton 1998). Based on Newton’s synthesis of removal experiments and other studies, the percentage of non-territorial non-breeders in a population can be highly variable (range = 6%–52%), and even within a single study population, the relative percentage of non-territorial birds varies seasonally and annually (Newton 1998). Floaters probably occur within most territorial bird species, but because they live a relatively secretive life among the breeding individuals, they are much more difficult to detect and therefore comparatively understudied.

Given the presence of floaters and territorial breeders within a species, what factors determine whether an individual is territorial or non-territorial at a given point in its life? Much research has shown that food supply strongly affects territorial behavior (Zach and Stutchbury 1992, Maher and Lott 2000); territory holders generally have more assured access to food resources due to familiarity with the location of resources or increased feeding rates. However, extreme food abundance or shortage can lead to a lower ratio of benefits to costs, such that individuals will abandon territory behavior. For example, resources may be so dispersed that the energetic costs of defending a large area outweigh the benefits; conversely, if resources are so abundant that they are not potentially limiting, there may be relatively little benefit gained from the energy required to exclude others (van Riper 1984). Another important factor is the amount of suitable breeding habitat in relation to the local abundance of the species. If there is too little habitat to support the entire population in an area, some individuals that are “potential settlers” will be excluded from being territory holders (Stewart and Aldrich 1951, Zach and Stutchbury 1992, Snetsinger et al. 2005). This scenario could occur with a stable population that experiences a loss of habitat, or as a result of a rising bird population in an area of stable habitat. The age and sex of an individual also seem to play a role; in most species male floaters outnumber females (presumably due to male-biased sex ratios), and younger birds are floaters more often than older birds (Zack and Stutchbury 1992, Newton 1998).

The Willow Flycatcher (*Empidonax traillii*) is a small migratory passerine that is considered to be aggressively territorial on the breeding grounds (Sedgwick 2000) and at wintering sites (Koronkiewicz et al. 2006). This strong territorial behavior and response to intruding conspecifics forms

the basis for targeted survey protocols (Sogge et al. 1997) and capture techniques (Sogge et al. 2001). However, there has been surprisingly little published evidence of the existence of floater Willow Flycatchers. Stafford (1986) observed a supernumerary bird (i.e., a non-parent) feeding flycatcher fledglings of a pair he was studying in the Sierra Nevada mountains of California, and speculated that it may have been a floater. Sogge et al. (1997) described three non-territorial Southwestern Willow Flycatchers (*Empidonax traillii eximius*) that were present among a very small population of flycatchers (range of 2–11 territories per year) along the Colorado River in the Grand Canyon. At the Kern River in California, small numbers of floater Southwestern Willow Flycatchers were frequently present among the breeding population (M. Whitfield, personal commun.), and Pearson et al. (2006) determined through genetic studies that some of these non-territorial males fathered young in the nests of territorial males. On the wintering grounds, Koronkiewicz et al. (2006) documented floaters of both sexes at sites supporting male and female winter territory holders. Still, the overall prevalence of floating among Willow Flycatchers has remained unclear, possibly because of the intense efforts needed to detect and characterize floaters. Furthermore, the mechanisms that may influence whether a bird chooses territoriality or floating have not been previously studied for Willow Flycatchers.

From 1996 to 2005, the U.S. Geological Survey (USGS) collaborated with the Arizona Game and Fish Department (AGFD) to conduct a large-scale demographic study of Southwestern Willow Flycatchers at two large breeding sites in central Arizona. At one of our study sites, Roosevelt Lake, we attempted to determine the degree to which floaters were present and the factors that might affect whether a bird was territorial or non-territorial. We also investigated the possible consequences of being a floater, in terms of their lifetime contribution to the breeding population. These questions were of interest because floaters, if present in large numbers, could represent a substantial but generally “undercounted” part of the flycatcher population—both locally and rangewide. Furthermore, because of the possible link between food, habitat, territorial behavior, and local population growth, the prevalence of floaters might provide evidence of ecological factors that are currently affecting the distribution and demography of this flycatcher population.

Methods

Study Site

To evaluate the issue of floaters, we focused on a population of birds at Roosevelt Lake (33°39'N, 110°58'W), where field work from 2001 to 2005 (see below) provided the extensive passive netting and resighting efforts needed to determine if non-territorial birds were present. This site supported one of the largest known Southwestern Willow Flycatcher breeding

populations during our study period (Durst et al. 2006), with a mean population size of over 200 individuals per year from 1996 to 2005. Extensive surveys were conducted at least three times in each breeding season to detect all territorial flycatchers within the immediate and surrounding areas.

The breeding habitat at Roosevelt Lake consisted of a heterogeneous mosaic of discrete riparian forest patches of varying ages and vegetation composition, ranging from 0.2 to 43 ha in size. Native habitat patches were characterized by Goodding's willow (*Salix gooddingii*) and Fremont cottonwood (*Populus fremontii*). Exotic habitat was dominated by tamarisk (saltcedar; *Tamarix* spp.). The understory vegetation consisted of a variety of grasses, forbs, and shrubs (mesquite [*Prosopis* spp.], coyote willow [*S. exigua*], tamarisk, seep willow [*Baccharis* spp.], and cocklebur [*Xanthium strumarium*]). Adjacent and surrounding non-riparian habitats were primarily composed of Sonoran Desert Uplands (Brown 1994).

The Roosevelt Lake site consisted of two sub-sites located at the inflows of the Salt River and Tonto Creek. The number of riparian patches in which breeding occurred varied over time as a result of colonization or desertion of patches, in many cases driven by fluctuating lake levels. A long-term drought in the Southwest between 1996 and 2004 resulted in reservoir levels dropping to a low of 10% capacity in 2002; that year was classified as an extreme drought (McCabe et al. 2004). In 2005, following unusually high winter precipitation and associated runoff, Roosevelt Lake filled to near capacity, inundating much of the breeding habitat that was occupied in 2004 (see chapter 6).

Banding and Resighting

Our objective was to band as many adults and nestlings as possible in order to detect and track individual birds over the period of this study. We banded nestlings from 1996 to 2004 at 7–10 days of age (as determined via Paxton and Owen 2002) with a color-anodized federal bird band; banded nestlings recaptured as adults in subsequent years were given an additional color band to produce a unique color combination (Koronkiewicz et al. 2005). Each adult captured through 2005 was banded with a color-anodized Federal band and a second color band (Koronkiewicz et al. 2005) to create a unique color combination for each individual. Territorial adults were primarily target-netted (Sogge et al. 2001, Pollock and Paxton 2006) to allow for efficient, focused capture effort. A drop of blood was taken from adults and nestlings at the time of banding for genetic gender determination (Paxton et al. 2002).

From 1996 to 2000, we had occasional captures and resightings of birds that we could not assign to a territory, leading us to suspect the presence of floaters. Therefore, from 2001 to 2005 we added extensive passive netting operations (see Ralph et al. 1993) in areas with occupied flycatcher territories, aimed at capturing non-territorial birds that might be present but unlikely to be detected with conventional survey techniques (i.e., tape-playback; Sogge et al. 1997). Overall,

the combination of target and passive netting resulted in an average of 74% (range: 68%–88%) of all detected flycatchers being banded in a given year. To determine gender of adult flycatchers, we used a combination of physical characteristics (presence of a cloacal protuberance for males or brood patch for females), behavioral cues, and/or genetic sexing methods (Paxton et al. 2002). Adult flycatchers were aged as “known” if the bird was first banded as either a nestling or a second-year adults (SY: based on retained rectrices; Pyle 1998); otherwise, they were considered as after-hatch year (AHY), which was an unknown-age category for purposes of our analyses.

We tracked banded territorial flycatchers primarily through resighting, supplemented by occasional recaptures via passive netting. Resighting consisted of using binoculars to determine the unique color band combination on a flycatcher’s legs. To ensure high accuracy in the identification of individuals, only high-confidence resights from at least two different observers on different days were used to confirm the identity and territory of individual banded flycatchers. Computer databases were updated and queried daily to prioritize resighting efforts, allowing us to track hundreds of uniquely color banded individuals in a given year. Large field crew sizes (USGS and AGFD combined) allowed for intensive detection and resighting of banded individuals, resulting in nearly all territorial flycatchers at the study sites being positively identified multiple times in each year. Recaptures, especially via passive netting, provided additional detection resolution, especially for non-territorial birds.

Differentiating Territorial and Non-territorial Birds

In general terms, we define a floater as a bird that is present at a site but does not establish a breeding territory throughout the course of a given breeding season. Determining that a bird was a floater is challenging because it is based on “negative proof” (i.e., evidence that a bird was not territorial). It is easy to eliminate as floaters those birds that are clearly territorial (e.g., repeatedly detected as singing, paired, or nesting). However, there is a possibility of misclassifying a bird that was territorial but was simply not observed being so, which could lead to overestimating the number of floaters. Given this, we felt it was appropriate to use a systematic and conservative approach to determine which birds we considered floaters. Within this chapter, we use the terms non-territorial and floater interchangeably.

Our first step in determining which birds were non-territorial was to create a large database of all flycatchers and every detection of them from 2001 to 2005 (termed the “Encounter History”). We conducted a series of step-wise selections to extract a subset of our initial 3,748 Encounter History records, to separate non-territorial birds from territorial and “unknown” birds. Note that our criteria for non-territorial status were based on year-by-year behavior, so that a bird was considered a floater if it was non-territorial in any

single year, but only for the year that the behavior was exhibited. Some birds in some years did not have enough detection information to classify as either territorial or non-territorial, and were excluded from the analysis.

Territorial birds included all birds confirmed to an active territory (typically through repeated detection of singing or aggressive behavior), paired with a territorial bird, or documented as nesting. We eliminated from the potential floater database all individuals that were documented exhibiting territorial behavior in a given breeding season.

Non-territorial birds are individuals that were seen (via color band resights) or recaptured one or more times in a given year, but were never observed engaging in territorial behaviors such as singing, territory defense, nesting, or feeding young. Birds classified as non-territorial were considered to be such for an entire breeding season. Many birds classified as non-territorial were detected via passive netting only one time and never seen again in that year; however, there were some instances of non-territorial birds being detected up to five times in a season. In some cases, such multiple detections spanned as long as one month. In these cases of multiple detections, the cumulative evidence indicated that those individuals were not territorial.

To determine if any additional individuals should be excluded from the group of birds initially placed within the non-territorial group, we considered physiological evidence, flycatcher migration ecology, and patch-specific survey and capture effort. For example, based on breeding physiology, female flycatchers only exhibit a brood patch if they have initiated a nesting attempt. Therefore, we excluded from the non-territorial group 43 records of females that were not positively linked to a territory or nest during a season but that had a brood patch (possibly from nesting very early in the season). We also excluded four individuals that were detected in only a single encounter prior to 01 June or after 15 July, and might therefore have been migrants (Sogge et al. 1997, Sedgwick 2000) rather than non-territorial. Finally, because flycatchers at the Bermuda Flat habitat patch were first discovered so late in the 2004 breeding season (07 June), our resight and capture efforts there may have been inadequate to confidently confirm all territorial and breeding activity of flycatchers within the patch. Thus, a high proportion of birds here could have been incorrectly classified as non-territorial. For this reason, we excluded all birds detected at Bermuda Flats from the floater database.

Data Analysis

The final dataset included records for 134 floater events (133 separate individuals, with one bird non-territorial in 2 separate years). We summarized basic information such as number of floaters per year by age class (for known age individuals) and sex, and percentage of floaters in the total population. We used χ^2 contingency tables to compare the population age structure each year of non-territorial and terri-

torial birds, and a Mann-Whitney U test to test for differences in the lifetime productivity (number of fledges per individual) of birds that were always territorial and those with at least one floater event.

In order to determine if floating was related to breeding success in years prior to or following a floater event, we compared the number of records, number of nests and successful nests, the percent nest success, the number and percent of polygamous nests, the number young fledged, and the number fledged per nest between non-territorial and territorial birds. We also used regression analysis to determine if the proportion of non-territorial birds in a given year was related to the overall population productivity during that year, or in the preceding year.

Results

Prevalence and Characteristics

We documented 134 individual non-territorial events (i.e., a flycatcher being non-territorial for a season) between 2001 and 2005. The number of floaters varied widely per year (range = 7–68; table 1). In all years except 2002, there were relatively few floaters ($n < 25$); however, the number was more than double that in 2002 ($n = 68$). The relative percentage of floaters in the overall population was usually less than 10%, but rose to 25% in 2002.

Among the 133 individuals that were classified as non-territorial, all but one floated for only a single year. Of the 124 known-sex floater events, 105 (85%) were by males and 19 (15%) by females (table 1). A disproportionately large percentage of floater events for both sexes occurred in the drought

year of 2002; 79% of female events and 46% of males events. Among known-age floaters (table 2), 88% were age second-year adults (SY; the year following fledging). This held true for both sexes, with 75% of females and 91% of males being age SY. Overall, 30 (23%) floaters were returning nestlings.

As a group, floaters were generally younger than the territorial birds. Considering only known-age birds, there was a significantly greater proportion of older (ASY; after-second-year) territorial birds compared to non-territorial birds in 2001, 2002, and 2004. There were no known age non-territorial birds in 2003, and only 8 in 2005 (evenly split between the two age classes).

Relationships with Productivity

For flycatchers that attempted breeding before and after their non-territorial year, individual nest success and productivity did not differ substantially before and after a floating year (table 3). There was only a slight increase post-floating in the percent nesting success and percent of polygynous nests. There was no difference in the mean number of young fledged per nest, and the mean number of fledges per individual was not significantly different.

There were significant relationships between some productivity measures and the percent of non-territorial birds in the population. The percentage of floaters in a year was negatively correlated with both the average number of fledglings per female ($r^2 = 0.84$, $p = 0.03$) and the total number of young fledged at Roosevelt ($r^2 = 0.80$, $p = 0.04$) in that year. However, the percent of floaters in the population was not significantly correlated with average fledglings per nest nor total fledges in the previous year ($r^2 = 0.36$, $p = 0.20$ for both). The mean lifetime productivity of birds that had a non-territorial breeding season was lower than for birds that were territo-

Table 1. The number of non-territorial, territorial nesting, and total Southwestern Willow Flycatchers detected each year at Roosevelt Lake, 2001 through 2005. Roughly half of all non-territorial events occurred in 2002.

Year	Non-territorial ¹			Territorial birds	Total Population ²	Percent non-territorial ³
	Male	Female	Total			
2001	17	2	19	164	245	8
2002	48	15	68	93	273	25
2003	7	0	7	172	229	3
2004	21	1	24	163	379	6
2005	12	1	16	164	291	6

¹ Includes 133 individuals, one of which was non-territorial in 2 years

² Estimates are from USGS annual reports for Roosevelt Lake. Total population differs from the sum of total non-territorial and territorial birds due to the presence of a class of unknown birds (excluded from our analyses).

³ Based on the percent of the total population.

Table 2. Age and sex of Southwestern Willow Flycatchers during floater events, based on known-age and known-sex individuals at Roosevelt Lake 2001–05. Most floaters were young (SY) and male.

Sex	Second-year (SY)	Third-year (TY)	Fourth-year (4Y)	Fifth-year (5Y)	Total known age
Female	10	3	0	0	13
Male	50	4	0	1	55
Sexes Combined	60	7	0	1	68

Table 3. Productivity of non-territorial Southwestern Willow Flycatchers for which there were nesting attempts in the years preceding (Pre) and following (Post) a non-territorial year, at Roosevelt Lake 2001–04 (2005 is excluded because the study ended in that year and no post-year data were collected).

Year and status	n	Number of nests	Percent nest success	Percent polygynous	Number fledged per nest	Mean fledges per individual (SE)
Pre	14	14	57	29	1.4	1.4 (0.4)
Post	55	62	60	32	1.4	1.5 (0.2)

rial in every year detected (table 4); significantly so for males ($U = -5.2$, $p < 0.001$) and for both sexes combined ($U = -4.9$, $p < 0.01$), but not for females ($U = -0.05$, $p = 0.60$).

Discussion

In their summaries of territorial behavior literature, Newton (1998) and Maher and Lott (2000) noted that individuals will generally defend and monopolize any resources that they can, but defense can become increasingly impractical due to the influence of the environmental factors. The optimal behavior for any individual may be to accept the social status (territorial or non-territorial) with the greatest net benefit at that time. As a result, individuals may switch between floating and territoriality at different stages of life or under varying environmental conditions, such that adoption of the “inferior” non-territorial lifestyle may be a “conditional strategy” (Kamil and van Riper 1982, Zack and Stutchbury 1992, Newton 1998). Floaters do not necessarily completely forfeit all opportunity for reproductive success (Barber and Robertson 1999, Pearson et al. 2006), as non-territorial males can potentially engage in extra-pair copulations (i.e., mate with a female of a territory holder). Floater females could lay eggs in the nest of a territorial pair, as has been shown in Herring Gulls (*Larus argentatus*; Shugart et al. 1987); however, this behavior is unrecorded in Willow Flycatchers. Still, territoriality appears in general to be the preferred state for most bird species and confers better survival and reproductive potential (Zack and Stutchbury 1992, Maher and Lott 2000).

During the first 5 years of our Roosevelt Lake work (1996–2000), periodic captures and sightings of “unknown”

flycatchers led us to believe that there were floater birds among the territorial breeders. Our efforts from 2001 to 2005 confirmed that floaters were present each year, and in some years comprised a substantial part of the population. This is not surprising given that floating is now a widely known behavior among a large number of bird and other vertebrate species that are generally considered as territorial (Zack and Stutchbury 1992, Newton 1998, Maher and Lott 2000). Moreover, Stafford (1986), Sogge et al. (1997), Pearson et al. (2006) described observations that suggested the presence of non-territorial Willow Flycatchers. However, floating has not yet been well documented among North American Tyrannids or *Empidonax* flycatchers. We searched the on-line Birds of North America accounts (<http://bna.birds.cornell.edu/BNA/>; search terms “floater”, “non-territorial”, and “nonterritorial”), and found that breeding season floaters have been reported only among Black Phoebe (*Sayornis nigricans*; Wolf 1997), Eastern Phoebe (*Sayornis phoebe*; Weeks 1994), and Olive-sided Flycatchers (*Contopus cooperi*; Altman and Sallabanks 2000). Thus, our study provides the most complete assessment to date of non-territorial behavior in Willow Flycatchers of any subspecies, or in other *Empidonax* flycatchers.

The presence of floaters in a population of an endangered species like the Southwestern Willow Flycatcher—during each year we investigated—suggests that there are more individuals present than the local habitat can support in terms of breeding. Snetsinger et al. (2005) described a similar presence of floaters among the critically endangered Puaiohi (*Myadestes palmeri*), and proposed that the population level was at the carrying capacity of its current habitat. Thus, even though available breeding habitat at Roosevelt Lake was generally increasing from 2001 to 2004, the local flycatcher population

was productive enough that available habitat did not keep pace with the increasing number of flycatchers.

Floater Characteristics and Prevalence

More than 80% of the known-sex floater events that we detected (105 of 124) involved male flycatchers, which is a pattern consistent with most other studies (Newton 1998, Maher and Lott 2000). Although less common than males, non-territorial females were also present each year at Roosevelt Lake. The predominance of younger (SY) birds as floaters (86% of known-age birds) is also consistent with the general pattern seen in most other studies (Newton 1998, Maher and Lott 2000).

The prevalence of floating at Roosevelt Lake was highly variable by year. There appeared to be a relatively low “background” level (3%–8%) in most years, and a large increase in 2002 (25%; discussed below). The variability we observed falls within that described for an array of bird studies summarized by Newton (1998), who also noted that even among a single study population, the relative percentage of non-territorial birds varies both annually and seasonally.

In our study, fewer than half of non-territorial flycatchers returned and established territories in later years. This is as expected, given that the overall return rate for adult flycatchers in our population was 55% (see chapter 2). Thus, the proportion of non-territorial birds that return each year is similar to that for the overall population.

The Costs of Non-territoriality

In a species such as the Willow Flycatcher, which has a short average lifespan (see chapter 2) and only moderate nesting success per year (see chapter 3), we would expect individuals to be territorial whenever possible. In addition, an individual that floats more than one year may be foregoing the majority of potential breeding opportunities during its lifetime. Thus, we expected that Southwestern Willow Flycatchers at Roosevelt Lake would generally not be non-territorial for multiple years. This was indeed the case, in that all but one (>99%) of the floaters in our study did so for only a single year.

Also because of their short average life span, we would expect that Southwestern Willow Flycatchers that spend a season as non-territorial will have lower lifetime productivity than flycatchers that breed every year. Engaging in a non-territorial year had a definite cost in productivity among male flycatchers at Roosevelt Lake, with an greater than 50% decrease in the number of fledged young over their lifetime (females and males, respectively). Female floaters also had lower mean lifetime productivity than territorial females, but the difference was not statistically significant. We believe that the lack of statistical significance in females is a function of the small sample size of non-territorial individuals ($n = 19$), and that

females who float do incur a substantial lifetime reproductive cost.

If non-territorial behavior increased later breeding success, floating might be a suitable “strategy” to use for habitat prospecting (Zack and Stutchbury 1992). However, Southwestern Willow Flycatchers at Roosevelt Lake experienced much the same annual nest success and breeding productivity in the year before and after floating, so there was no annual productivity benefit to having been non-territorial in the previous year.

It is important to note that non-territorial male Southwestern Willow Flycatchers still retain some chance of productivity during their floater year, as they can potentially infiltrate a territorial area and engage in extra-pair copulations with receptive females. Our estimates of lifetime reproductive success indicate that floaters would on average need to sire two successful young via extra-pair copulations to match the success of territorial males (table 4). In the only study that quantified extra-pair paternity by non-territorial Southwestern Willow Flycatchers, Pearson et al. (2006) documented that four nonterritorial males at the Kern River in California sired six offspring, for an average of 1.5 young per male. Thus, the cost of floating in terms of reduced lifetime reproductive success may not be as great as suggested by estimates based solely on nests when birds were known to be territorial.

Why Be a Floater?

The factors that influence floating and territorial behavior among birds in general are not completely understood, and interpreting their relative roles is complicated by the fact that they may interact in complex ways and vary from year to year. Furthermore, this suite of factors may affect different sexes and age groups differently. Still, there is a general understanding of the major benefits and costs of territoriality and floating.

Habitat availability and quality are key factors in territorial behavior of most birds. Given the potential costs of territorial behavior, especially for males, a shortage of high-quality breeding habitat could lead males to adopt a floater role (Zack and Stutchbury 1992, Maher and Lott 2000). For example, if there is insufficient suitable breeding habitat to support all potential territorial males, younger and less experienced males may be unsuccessful at supplanting another bird or may choose to be non-territorial rather than attempt to displace an already established male. However, floaters appear frequently to be relegated to lower-quality habitats (Newton 1998, Githiru et al. 2006), which may have physiological condition and survival costs, adding to the negative consequences of not establishing and holding a territory in good quality habitat. We do not suspect that there was an overall shortage of suitable breeding habitat at Roosevelt Lake; indeed, suitable habitat (as we perceived it) generally increased from 1996 to 2005 (see chapter 6). However, the extreme drought in 2002 decreased the vigor and vegetative cover of the riparian habitat patches at Roosevelt Lake, which may have substantially reduced the amount of suitable breeding habitat for the pool of potentially

Table 4. The number of fledglings produced per lifespan of Southwestern Willow Flycatchers classified as non-territorial in at least one year, and those that were territorial in every year detected. The difference in lifetime productivity between floaters and territorial birds was statistically significant for males ($U = -5.2$, $p < 0.001$) and for both sexes combined ($U = -4.9$, $p < 0.01$), but not for females ($U = -0.05$, $p = 0.60$). Overall sample size includes 14 unknown sex birds.

	Overall		Males		Females	
	Mean \pm SE	95% CI	Mean \pm SE	95% CI	Mean \pm SE	95% CI
Always Territorial	2.84 \pm 0.18 n = 406	2.48–3.20	3.49 \pm 0.34 n = 171	2.83–4.16	2.40 \pm 0.20 n = 231	2.01–2.79
At least one non-territorial year	1.46 \pm 0.26 n = 133	0.95–1.97	1.49 \pm 0.31 n = 104	0.87–2.11	2.05 \pm 0.58 n = 19	0.83–3.27

territorial males, and thereby brought about the very high level of floating we observed in that year.

Male birds may also float rather than breed during a given year in order to assess various areas within a site, to guide selection of a future territory location (Zack and Stutchbury 1992, Newton 1998). At Roosevelt Lake, Cardinal (2005) and Cardinal et al. (2006) documented pre- and post-breeding movements by male Southwestern Willow Flycatchers that are consistent with this “prospecting” concept. However, because the individuals in these studies bred in the same year as these potential prospecting movements, they would not be classified as floaters. Still, the purpose and value of the movements may be analogous, though the relative value of prospecting for an entire breeding season (and foregoing reproduction) is uncertain compared to the lost productivity potential.

It is more challenging to determine how female Willow Flycatchers would benefit from floating. Male flycatchers will frequently have multiple females in their territory and contribute relatively little to the care of nestlings (Davidson and Allison 2003; see chapter 3). Therefore, assuming no exclusion behavior from females already present (none has yet been reported), any female interested in breeding could hypothetically settle to nest within an existing territory and would not need to adopt a floater role. However, it is possible that floating may serve a similar habitat “assessment” function for females and males, allowing them to later choose among the different potential settlement areas. The generally young age of both male and female floaters at Roosevelt Lake is consistent with this scenario, but does not exclude other causes of non-territorial behavior.

Food availability is another major driver of territoriality (Maher and Lott 2000), and one which may affect both sexes similarly. Birds will generally defend food resources when they are abundant and defensible (Newton 1998). Although our data on productivity, survivorship, and population increases at Roosevelt Lake (see chapters 2, 3, and 5) suggest that food supply was not generally limiting in most years, we believe that the decreased food availability played a major role in the very high level of floating in 2002. In that breeding

season, many birds failed to establish territories, pair, or initiate nests; nest success and productivity were very low among those pairs that did try to nest (Smith et al. 2003). Durst (2004) found that 2002 was a year of very low invertebrate abundance and biomass at Roosevelt Lake compared to 2003. Thus, the relative lack of food resources in the 2002 season may have (1) reduced the relative benefits of expending energy to defend a territory, (2) prevented birds from being in suitable physiological condition to initiate breeding, or (3) forced birds to range widely to acquire sufficient food for basic survival. All of these factors could potentially lead many birds to become floaters.

The dramatically reduced food base in 2002 (Durst 2004) may have had a particularly telling influence on female floating. Body condition of females directly affects whether they attempt to breed; if energy reserves, physiological conditions, or food resources are not above the threshold needed to support breeding activities, the bird may not attempt to pair or nest (Sturkie 1986, Vezina and Williams 2003). The large number and comparatively high ratio of female floaters in 2002 suggests that their physiological/energetic condition may have been too poor to induce breeding in that year. Thus, the 2002 drought and its attendant lowered prey availability probably account for the majority of the female floaters events over the course of our entire study, as most were detected in 2002 only. Note that this lack of food resources may have influenced floating and territoriality in males as well, given that male Southwestern Willow Flycatchers may be more energetically and physiologically stressed than females during the breeding season (Owen et al. 2005).

An imbalanced sex ratio in which there are fewer females could also lead to floating by males (Marra and Holmes 1997), because defending a territory (even if in good habitat) will not necessarily result in procuring a mate. However, Sedwick (2000) reported an approximate 50:50 adult sex ratio in a study of Willow Flycatchers in Oregon, and Paxton et al. (2002) showed a female-biased sex ratio among Southwestern Willow Flycatchers at Roosevelt Lake from 1996 to 2000. So there is no evidence to suggest that a male sex bias is a major factor in floating at Roosevelt Lake or other breeding sites.

Overall, our data indicate that non-territorial behavior is triggered by local habitat conditions during a given breeding season, rather than by factors in the preceding year such as habitat quality or an individual's reproductive success. The reasons for this conclusion are several. First, most non-territorial birds were floaters during their first potential breeding season, so there was no opportunity for previous breeding experience to be a factor. Second, among the group of older non-territorial birds that has previously bred, there was no significant difference in productivity pre- or post-floating; so floating did not appear to be triggered by poor reproductive success of that individual. Third, the proportion of non-territorial flycatchers was lower in years with high population productivity (mean number of fledges per individual, and total fledges in the population). If habitat quality (especially food availability) is a major factor in determining Southwestern Willow Flycatcher productivity, as is often assumed for many bird species (Newton 1998), then floating at Roosevelt Lake was lowest in the years of highest habitat quality. The very high level of floating during the extreme drought year (2002) was a dramatic example of this relationship, but the overall pattern held true over the 2001–05 period.

Flycatchers Not Detected for an Entire Breeding Season

In defining our dataset of non-territorial birds, we excluded 97 individuals that were observed repeatedly at Roosevelt Lake over multiple years (2001–04), but were not detected in one or more years in which they were known to be alive because of subsequent detections. For purposes of this discussion we refer to them as “non-detected” birds. As was the case for non-territorial birds, the number of non-detected records varied per year (range = 8–39 individuals), as did the proportion within the total population (range = 3%–14%); both were greatest during the 2002 drought. However, unlike floaters, over half of non-detected birds (53 of 97) were female, and more non-detected individuals (54% of known age birds) were older than SY. Also, there was a higher percentage of returning nestlings among non-detected birds (34%) compared to non-territorial birds (23%).

We do not know what these individuals were doing in the year that they were not detected. The most straightforward possibility is that they may simply have been at Roosevelt Lake but not detected. However, because of the generally high detectability of territorial flycatchers and the extensive field effort at the site, we do not think it likely that many of the non-detected birds were territorial. It is more likely that non-detected birds would be in the non-territorial group: present but unobserved because of their inconspicuous behavior. If this is the case, then the actual number of non-territorial flycatchers at Roosevelt Lake would total 231, and range from 16 to 107 per year (almost double our current non-territorial estimate). However, the different age and sex characteristics of these non-detected birds compared to those we considered floaters

suggest that they may have been exhibiting a fundamentally different behavior. For example, the non-detected birds may also have been present as undetected floaters or breeders at some other breeding site (especially at sites without intense monitoring), then returned to Roosevelt Lake in subsequent years. Although we have seen a few one-way movements of Southwestern Willow Flycatchers among distant breeding sites (see chapter 4), we do not know the probability of a bird from Roosevelt Lake moving to another site for a season and then returning.

Other possibilities that might explain the missing year for non-detected birds are more intriguing, but their likelihood is unknown. For example, non-detected birds may have been traveling throughout the breeding season among widely dispersed riparian areas. If this type of behavior occurs, it would represent a previously undescribed “super floating” behavior by individuals that are prospecting for potential breeding habitats on a broad, landscape level. Another possibility is that some portion of the non-detected flycatchers may have stayed on the wintering grounds or undergone only a partial northward migration. This would be an example of “partial migration” (Dingle and Drake 2007). For partial migrant species, migration is dependent upon environmental conditions and individual behavior, such that not all individuals migrate in all years (Ramenofsky and Wingfield 2007). Relatively few bird species have shown evidence of partial migration (Nilsson et al. 2006), and the Willow Flycatcher and other North American *Empidonax* are considered to be completely migratory species (e.g., see Sedgwick 2000). However, given that “classic” examples of migration may be the exception rather than the rule (Dingle and Drake 2007), and that we know relatively little about the wintering and migration ecology of the Willow Flycatcher (USFWS 2002), the possibility of “atypical” migratory behavior in Southwestern Willow Flycatchers may warrant investigation.

Additional Research Opportunities

Although we have made substantial progress in documenting and understanding non-territorial flycatchers at Roosevelt Lake, there is still much we do not know. The degree of floating is variable over time, and possibly among sites. Coupled with changing environmental conditions over space and time, it is particularly challenging to document the underlying factors that drive territoriality versus floating behavior in a given year. From a practical standpoint, non-territorial birds are difficult to detect and therefore hard to study and document. As a result, research geared toward better understanding floaters is likely to be effort intensive and costly, at least within large sites.

Our study was conducted at one of the largest known Southwestern Willow Flycatcher breeding sites, and we do not know to what degree our results are representative of what may be occurring at smaller sites. Similarly, we do not know if high-quality sites have larger floater Willow Flycatcher

populations than low quality sites, as was shown for some other species (Zack and Stutchbury 1992, Githiru et al. 2006). In terms of individual behavior, the term “floater” conjures images of random, wandering movements among the general population. However, Smith (1978) described well-defined home ranges and other social organization among floater Rufous-collared Sparrows (*Zonotrichia capensis*); we do not know to what degree there is such social structure among non-territorial Southwestern Willow Flycatchers.

However, even with extended research, we may not be able to move far beyond describing the general patterns shown by most territorial birds. Individuals will generally be territorial when possible, but variations in available habitat, food resources, sex ratios, and other environmental parameters will interact in complex ways to produce the relative levels of territoriality and floating at any given time and place.

Management Considerations

Given the data from this study, combined with observations made at other sites (Stafford 1986, Sogge et al. 1997, Pearson et al. 2006), we suspect that floaters are present among many Southwestern Willow Flycatcher populations, especially the larger ones or those that are expanding rapidly beyond the availability of suitable habitat at a given breeding site. However, given the challenge of detecting non-territorial birds, it will be difficult to accurately determine the proportion of non-territorial birds in any particular site without extensive, targeted efforts to do so.

Because floaters are not readily detected by standard survey techniques, more flycatchers may be present at a site than would be indicated by simply counting territories, especially in years with extreme environmental conditions. However, although floater populations may be variable among sites and years, our data suggest that in most years a population estimate that fails to include floaters would still be within 5%–10% of an estimate that did. This may be a reasonable level of accuracy when estimating the number of flycatchers at most sites.

Although in most years floaters comprise a relatively small proportion of Southwestern Willow Flycatchers at any one site, floaters in these areas could play several important demographic roles. First, because floaters likely indicate that habitat is saturated with territorial birds, floaters that remain in an area through the breeding season could act as rapid local replacements for any breeding birds that suffer mortality due to predation, and thereby maintain a stable breeding population. Second, floaters could help buffer between-year fluctuations. This may have occurred in 2003, when the population reduction following the previous year’s drought was not as great as expected based on the very low breeding productivity in 2002. Third, excess birds, those we would define as either floaters or non-detected birds, could act as longer distance dispersers that colonize unoccupied habitat or more distant occupied habitat, thereby playing an important role in regional

metapopulation dynamics. Fourth, floaters and non-detected birds may help maintain genetic structure of populations, by contributing to local gene pools by siring extra-pair offspring or by maintaining gene flow when they move across larger regional areas.

The presence of non-territorial birds each year at Roosevelt Lake, even in the presence of generally expanding riparian habitat, suggested that this population was expanding faster than new suitable breeding habitat. In other sites where the number of territorial Southwestern Willow Flycatchers remains relatively unchanged over time but reproductive success suggests the population should be expanding, the amount of suitable habitat could be limiting. Such sites could be candidate areas for potentially increasing the number of flycatchers by evaluating the local availability of breeding habitat and augmenting it where it appears to be a limiting factor.

References

- Altman, B., and R. Sallabanks. 2000. Olive-sided Flycatcher (*Contopus cooperi*). In *The Birds of North America*, No. 502 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, Pennsylvania.
- Barber, C.A., and R.J. Robertson. 1999. Floater males engage in extrapair copulations with resident female Tree Swallows. *Auk* 116:264–269.
- Brown, D.E. (ed.). 1994. *Biotic Communities: Southwestern United States and Northwestern Mexico*. University of Utah Press, Salt Lake City, Utah.
- Brown, J.L. 1969. Territorial behavior and population regulation in birds. *Wilson Bull.* 81: 293–329.
- Cardinal, S. 2005. Conservation of Southwestern Willow Flycatchers: home range and habitat use by an endangered passerine. MS thesis. Northern Arizona University, Flagstaff, Arizona.
- Cardinal, S.N., E.H. Paxton, and S.L. Durst. 2006. Home range, movement, and habitat use of the Southwestern Willow Flycatcher, Roosevelt Lake, AZ—2005. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix, Arizona.
- Davidson, R.F., and L.J. Allison. 2003. Effects of monogamy and polygyny on reproductive success in Southwestern Willow Flycatchers (*Empidonax traillii eximius*) in Arizona. *Studies in Avian Biology* 26:125–130.
- Dingle, H., and V.A. Drake. 2007. What is migration? *Bioscience* 57:113–121.
- Durst, S.L. 2004. Southwestern Willow Flycatcher potential prey base and diet in native and exotic habitats. MS thesis. Northern Arizona University, Flagstaff, AZ.

- Durst, S.L., M.K. Sogge, H. English, S.O. Williams, B.E. Kus and S.J. Sferra. 2006. Southwestern Willow Flycatcher breeding site and territory summary—2005. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix, Arizona.
- Githiru, M., L. Lens, L.A. Bennun, and C. Perrins. 2006. Experimental evidence of 'floaters' in two isolated populations of an Afrotropical forest bird. *Ostrich* 77:28–35.
- Kamil, A.C., and C. van Riper III. 1982. Within territory division of foraging space by male and female Amakihi (*Loxops virens*). *Condor* 84:117–119.
- Koronkiewicz, T.J., E.H. Paxton, and M.K. Sogge. 2005. A technique for aluminum color-bands for avian research. *Journal of Field Ornithology* 76:94–97.
- Koronkiewicz, T.J., M.K. Sogge, C. van Riper III, and E.H. Paxton. 2006. Territoriality, site fidelity, and survivorship of Willow Flycatchers wintering in Costa Rica. *Condor* 108:558–570.
- Maher, C.R., and D.F. Lott. 2000. A review of ecological determinants of territoriality within vertebrate species. *American Midland Naturalist* 143:1–29.
- Marra, P.P., and R.T. Holmes. 1997. Avian removal experiments: do they test for habitat saturation or female availability? *Ecology* 78:947–952.
- McCabe, G.J., M.A. Palecki, and J.L. Bentancourt. 2004. Pacific and Atlantic Ocean influences on multidecadal drought frequency in the United States. *Proceedings of the National Academy of Sciences* 101:4136–4141.
- Newton, I. 1998. Population limitation in birds. Academic Press, New York, New York.
- Nice, M.M. 1941. The role of territory in bird life. *Transactions of the Linnean Society*, New York, New York.
- Nilsson, A.L.K., T. Alserstam, and J. Nilsson. 2006. Do partial migrants differ in their responses to weather? *Auk* 123:537–547.
- Owen, J.C., M.K. Sogge, and M.D. Kern. 2005. Habitat and gender differences in the physiological condition of breeding Southwestern Willow Flycatchers. *Auk* 122:1261–1270.
- Paxton, E.H., and J.C. Owen. 2002. An aging guide for Willow Flycatcher nestlings. U.S. Geological Survey Colorado Plateau Field Station, Flagstaff, Arizona.
- Paxton, E.H., M.K. Sogge, T.D. McCarthy, and P. Keim. 2002. Nestling sex ratio in the Southwestern Willow Flycatcher. *Condor* 104:877–881.
- Pearson, T., M.J. Whitfield, T.C. Theimer, and P. Kiem. 2006. Polygyny and extra-pair paternity in a population of Southwestern Willow Flycatchers. *Condor* 108:571–578.
- Pollock, M.G., and E.H. Paxton. 2006. Floating mist nets: a technique for capturing birds in flooded habitat. *Journal of Field Ornithology* 77:335–338.
- Pyle, P. 1998. Eccentric first-year molt patterns in certain Tyrannid flycatchers. *Western Birds* 29:29–35.
- Ralph, C.J., G.R. Geupel, P. Pyle, T.E. Martin, and D.F. DeSante. 1993. Handbook of field methods for monitoring landbirds. USFS General Technical Report PSW-GTR-144. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. Albany, California.
- Ramenofsky, M., and J.C. Wingfield. 2007. Regulation of migration. *Bioscience* 57:135–143.
- Sedgwick, J.A. 2000. Willow Flycatcher (*Empidonax traillii*). In *The Birds of North America*, No 533 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, Pennsylvania.
- Shugart, G.W., M.A. Fitch, and G.A. Fox. 1987. Female floaters and nonbreeding secondary females in Herring Gulls. *Condor* 89:902–906.
- Smith, A.B., A.A. Woodward, P.E.T. Dockens, J.S. Martin, and T. D. McCarthy. 2003. Southwestern Willow Flycatcher 2002 survey and nest monitoring report. Nongame and Endangered Wildlife Program, Technical Report # 210. Arizona Game and Fish Department, Phoenix, Arizona.
- Smith, S.M. 1978. The 'underworld' in a territorial sparrow: adaptive strategy for floaters. *American Naturalist* 112:571–582.
- Snetsinger, T.J., C.M. Herrmann, D.E. Holmes, C.D. Hayward, and S.G. Fancy. 2005. Breeding ecology of the Puaiohi (*Myadestes palmeri*). *Wilson Bulletin* 117:72–84.
- Sogge, M.K., R.M. Marshall, T.J. Tibbitts, and S.J. Sferra. 1997. A Southwestern Willow Flycatcher Natural History Summary and Survey Protocol. National Park Service Technical Report NPS/NAUCPRS/NRTR-97/12.
- Sogge, M.K., J.C. Owen, E.H. Paxton, S.M. Langridge and T.J. Koronkiewicz. 2001. A targeted mist net capture technique for the Willow Flycatcher. *Western Birds* 32:167–172.
- Sogge, M.K., T.J. Tibbitts, and J.R. Pettersen. 1997. Status and breeding ecology of the Southwestern Willow Flycatcher in the Grand Canyon. *Western Birds* 28:142–157.
- Stafford, M.D. 1986. Supernumerary adults feeding Willow Flycatcher fledglings. *Wilson Bulletin* 98:311–312.
- Stewart, R.E., and J.W. Aldrich. 1951. Removal and repopulation of breeding birds in a Spruce-Fir forest community. *Auk* 68:471–482.
- Sturkie, P.D. 1986. *Avian Physiology*, 4th ed. Springer-Verlag, New York.

- U.S. Fish and Wildlife Service. 2002. southwestern Willow Flycatcher final recovery plan. Albuquerque, New Mexico.
- van Riper, C., III. 1984. The influence of nectar resources on nesting success and movement patterns of the Hawaii Amakihi (*Hemignathus virens*). *Auk* 101:38–46.
- Vezina, R., and T.D. Williams. 2003. Plasticity in body composition in breeding birds: What drives the metabolic costs of egg production? *Physiological and Biochemical Zoology* 76:716–730.
- Weeks, H.P., Jr. 1994. Eastern Phoebe (*Sayornis phoebe*). In *The Birds of North America*, No. 94 (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C.
- Wolf, B.O. 1997. Black Phoebe (*Sayornis nigricans*). In *The Birds of North America*, No. 268 (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C.
- Zack, S., and B.J. Stutchbury. 1992. Delayed breeding in avian social systems: the role of territory quality and “floater” tactics. *Behaviour* 123:194–219.

Chapter 8—Conclusions

This study, which culminated in this report, was conceived and initiated over a decade ago, shortly after the Southwestern Willow Flycatcher was listed as endangered (USFWS 1995). Prior to its listing, the flycatcher had received relatively little research attention. At the time of listing there had been no long-term or large-scale ecological studies of the flycatcher within Arizona, and only one such study of this subspecies elsewhere—a long-term research project at the Kern River Preserve in California (Whitfield and Strong 1995). Thus, most facets of Southwestern Willow Flycatcher survivorship, productivity, movements, habitat use, and other aspects of breeding ecology were largely unknown; completely so for the populations at Roosevelt Lake and the San Pedro/Gila study sites.

Our research was designed to provide flycatcher information that was needed for management and recovery (USFWS 1996). Specifically, through surveys, nest monitoring, and intensive tracking of banded birds, this study was to generate information deemed to be important to managers, as described by Arizona Partners in Flight (Marshall 1995, Sferra et al. 1995) and the Roosevelt Lake Biological Opinion (USFWS 1996):

- Quantify (at multiple scales) habitat characteristics, in terms of patch area and shape, proximity to water, stand age, landscape matrix, and topography
- Develop and implement quantitative habitat descriptions of riparian patches, territories, and nest sites occupied by flycatchers
- Quantify site fidelity, natal dispersal, and adult dispersal within and among years
- Determine age structure of populations
- Estimate rates of survivorship for different age classes and among different populations
- Determine the effects of age on nesting success, and yearling and adult survival
- Characterize nesting success
- Determine the relation between nesting success and movements within and between years
- Determine the relationship between nesting success and habitat

- Determine the presence, size, and age of floaters in relation to population size and quality of habitat
- Compare nesting success in exotic and native plant communities

This joint study by the U.S. Geological Survey (USGS) and the Arizona Game and Fish Department (AGFD) has provided large amounts of new data that directly address the research needs outlined above, and others as well. It is the most extensive research project conducted to date on the endangered Southwestern Willow Flycatcher in length of time, geographic scale, and complexity. Our goal was to gather data and glean insights that would be directly applicable to the conservation and management of the flycatcher, even beyond Roosevelt Lake and San Pedro/Gila study sites. Furthermore, we hoped to stimulate researchers to conduct similar studies elsewhere for comparative purposes, and to build upon our work to develop “next level” hypotheses and research projects. Our interim results, released as a series of USGS annual reports (e.g., Causey et al. 2005), have already been extensively used in recovery planning (USFWS 2002) and critical habitat designation (USFWS 2005), and have helped guide management activities such as habitat conservation plans and habitat assessments.

The purpose of this Conclusion chapter is to integrate and synthesize the major results from the earlier chapters of this report, and present a summary of their implications with regard to the following issues:

- The role of reservoirs in the conservation of the flycatcher
- Flycatcher response to reservoir rise at Roosevelt Lake
- The importance of scale in management
- The dynamic nature of this species and its habitats
- Patterns of habitat use
- Implications for riparian restoration
- Implications for flycatcher monitoring
- Drought effects
- Future research directions

Role of Reservoirs

The development and operation of reservoirs were listed as contributing factors in the historical decline of Southwestern Willow Flycatchers (USFWS 1995), and reservoirs are often perceived as a continuing threat to the recovery of the species (Graf et al. 2002). While there is little direct documentation of the impacts of reservoirs on flycatchers, there are many places where reservoirs have inundated historically occupied habitat, as well as potential habitat, and dams have modified the downstream hydrology of many river systems such that suitable flycatcher habitat can no longer be supported (USFWS 2002, Graff 2006). However reservoirs can play a positive role by providing breeding habitat at the periphery of the reservoir that can help offset the lack of breeding habitat downstream. At Roosevelt Lake, the drawdown of the reservoir exposed extensive lakebed sediment that rapidly developed into apparently high-quality breeding habitat that subsequently supported a rapid increase in the population size of breeding flycatchers at that site.

Elsewhere, other reservoirs have played similar roles in creating habitat for Southwestern Willow Flycatcher populations. In California, the broad floodplain at the inflow of the Kern River to Lake Isabella has supported breeding flycatchers for over 30 years (Whitfield and Strong 1995). In Arizona, reservoir drawdown zones have supported breeding flycatchers at Lake Mead (Colorado River), Alamo Lake (Bill Williams River), and Horseshoe Reservoir (Verde River; Graber et al. 2007). In New Mexico, lower reservoir levels at Elephant Butte Reservoir (Rio Grande) allowed the development of new riparian habitat in which the local flycatcher population expanded from fewer than 10 territories in 1995 to over 175 by 2006 (Moore and Ahlers 2006).

To some degree, the cycle of riparian development and loss within a reservoir drawdown zone may be an analog for the natural pattern of riparian habitat dynamics in the Southwest. Along unregulated rivers, riparian vegetation within the hydrologically active channel is periodically scoured by high flows, and then establishes and regenerates over the next several years until the next scouring flood event. This often creates, at a drainage scale, riparian habitat patches of different age, structure, and composition; among these will be the younger habitats that are favored by Southwestern Willow Flycatchers. This mirrors what occurred at Roosevelt Lake during the course of our study and at Elephant Butte Reservoir during approximately the same period (Moore and Ahlers 2006). However, it is important to note that reservoir geomorphology and the timing and nature of water operations will largely determine the degree to which the lakebed is exposed and new suitable riparian habitat develops, and ultimately how long the habitat will persist. Therefore, some reservoirs and operating criteria can be conducive to developing suitable flycatcher habitat, while others may not provide the right conditions. Still, the potential exists to manage reservoirs in ways that would create, enhance and maintain flycatcher habitat,

which could be an important tool for maintaining populations in the face of future environmental challenges such as drought (see below). More study is needed to identify the features that promote riparian habitat creation, and which reservoirs have the potential for such benefits.

Response to Reservoir Rise

This project was initiated as a result of a Biological Opinion associated with the increased water levels made possible by the modification of Roosevelt Dam (USFWS 1996). At the outset of this project, we expected that within the first few years Roosevelt Lake would rise and inundate the habitat that was used by breeding Southwestern Willow Flycatchers. Therefore, one of our primary goals was to determine how flycatchers would respond to this inundation; would they stay within flooded habitat at Roosevelt, move into adjacent riparian habitat above the high water level, or perhaps disperse to more distant breeding sites on the San Pedro River or elsewhere? Due to the long-term drought that began in 1996, lake levels did not rise to the new conservation pool level until the final year of our study in 2005. In the interim, riparian vegetation developed in the exposed lakebed and was colonized by breeding flycatchers. The Arizona Game and Fish Department has prepared a separate report that details the variety of flycatcher responses to the rise in lake levels (Ellis et al., 2008). Here we summarize a few general observations related to the major components of our study.

Most of the habitat in which flycatchers bred from 1996 to 2004 was completely or partially inundated in 2005. The amount of remaining suitable breeding habitat (as we perceived it) in 2005 was substantially less than in the previous year, leading us to believe that only a small fraction of the 2004 population would return. Instead, there were 170 territories in 2005, 79% of the number in 2004. However, many of the 2005 territories were found in riparian patches that flycatchers had either not bred in during the 10-years of the study, or had not bred in for many years. This suggests that these “novel” habitat patches, which were not initially utilized by a large and growing breeding population within the immediate area for multiple years, were either (1) rejuvenated by the high winter precipitation, (2) acted as refuge habitat by displaced flycatchers that would normally not use it, or (3) a combination of both. Irrespective of the reason, the novel patches provided important habitat for breeding flycatchers in 2005.

Therefore, the inundation at Roosevelt Lake did not trigger the large emigration/dispersal event that we had expected. Rather, most flycatchers returned to the site and attempted to breed in the riparian patches that remained. Thus, even in the face of a large scale and dramatic habitat perturbation, most movement remained local, to nearby patches that remained relatively undisturbed farther upstream. This underscores the flycatcher’s high fidelity to previous breeding areas and

highlights the importance of refuge habitat to which flycatchers can move following loss of a breeding site. Based on the movements we observed, refuge habitat will be most effective if it is available in close proximity (within 30–40 km) to existing breeding sites.

Scale of Management

We observed a consistently high degree of between-year, within-drainage movement by the Southwestern Willow Flycatchers at both Roosevelt Lake and the San Pedro/Gila study sites. Movements were common, resulting in high connectivity, between breeding patches that were less than 30–40 km apart. This has changed our concept of the spatial scale at which to define a flycatcher breeding site. In the early years of the study, each individual breeding patch was considered a separate site. However, the high degree of connectivity between the breeding patches led us to conclude that, from a flycatcher's perspective, breeding patches in close proximity to one another were all one functional site. As distance increased, movement decreased, and there was a low frequency of movement between drainages. Thus, there was a clear threshold at which frequent movement and connectivity among patches within 30–40 km could be readily distinguished from infrequent movement between areas that were farther apart. Thus, we believed that the most appropriate scale to delineate a site was the drainage level, recognizing that metapopulation connectivity (though infrequent movements) occurred at the region level. Therefore, management of flycatcher breeding sites will be most effective if done at a drainage scale, rather than focusing only on individual breeding patches, and emphasizing the management of patches of riparian vegetation with high connectivity (USFWS 2002).

Dynamic Species and Dynamic Habitat

Because the Southwestern Willow Flycatcher is a riparian obligate, it is subject to highly variable environmental conditions over space and time. Accordingly, we found high variability in most life history traits; between years, among breeding sites and patches, and at different spatial and temporal scales. This has been shown to be true in other aspects of flycatcher ecology, such as diet (Drost et al. 2003) and prey base (Durst 2004). Because data from any single year or site cannot necessarily be extrapolated to others, there are risks to basing management decisions on short-term data, or in using data from sites that may be ecologically very different. Management actions need to recognize this inherent variability to be effective.

In the Southwest, most riparian habitats are also dynamic and undergo repeated cycles of establishment, growth, and destruction. Under favorable conditions, riparian vegetation can grow or recover quickly, and become suitable Southwest-

ern Willow Flycatcher breeding habitat in a relatively short time (USFWS 2002). For example, at Roosevelt Lake, flycatchers began breeding in some patches in which the vegetation was only 3 years old. On the other hand, our data suggest that occupancy of the habitat can start to decline within 5 years of colonization, and many patches became unoccupied within 10-years or less. However, these older habitats may continue to support flycatchers if hydrological conditions change (e.g., non-scouring floods may reinvigorate older riparian vegetation), if adjacent habitat is suddenly lost and the older habitat becomes refuge habitat, or if alternative habitat is not available. Therefore, although potential breeding habitat can develop relatively quickly, the suitability of a given patch may be ephemeral. Accordingly, the Southwestern Willow Flycatcher recovery plan (USFWS 2002) emphasizes the need to maintain a mosaic of patch ages and structure within a given drainage, and notes the importance of managing for the processes that will create and maintain riparian habitat dynamics.

In general terms, the dynamics of riparian habitat creation and loss cycles were similar at Roosevelt Lake and the San Pedro/Gila. In both cases, existing older habitat was periodically lost, and new habitat became established and grew rapidly. However, our spatial modeling showed that each system responded differently with regard to hydrology, climate, temporal scale, and spatial scale (especially patch size). These differences suggest that riparian habitat in reservoir and riverine systems may operate at different temporal scales that are not necessarily linked, leading to potentially very different population dynamics, even when those systems are relatively close geographically and support similar habitat matrices. Through time, the number of flycatchers breeding in a particular patch will change. Thus, focusing on achieving target population and habitat goals at the drainage or regional level, as recommended by the recovery plan (USFWS 2002), will be the most successful long-term management strategy.

Habitat Use

Southwestern Willow Flycatchers typically breed in dense riparian habitat along streams or other wetlands (USFWS 2002). However, flycatchers showed a substantial degree of flexibility, using a range of different patch sizes and plant species composition. Although this is currently widely known and accepted (USFWS 2005), it was not well understood when this study began.

At both Roosevelt Lake and the San Pedro/Gila, flycatchers bred in patches that ranged from monotypic willow to monotypic saltcedar. This supports the view that Southwestern Willow Flycatchers respond more to habitat structure, microclimate, and patch-level characteristics than they do to plant species composition (USFWS 2002). This idea is further supported by the strong performance of our spatial habitat models that were good predictors of occupied habitat despite the fact that they did not include any plant species composition

variables. Because flycatchers occupied both native and exotic habitats, we were able to determine whether flycatchers breeding in saltcedar experienced lower productivity or survivorship than those in willow or mixed willow/saltcedar patches. Our analyses showed that flycatchers did not suffer any detectable negative consequences from breeding in saltcedar. This is consistent with the findings of Owen et al. (2005) and Sogge et al. (2006, *in press*). However, throughout the Southwest there are many saltcedar-dominated and native-dominated habitats in which flycatchers do not breed (USFWS 2002, Sogge et al. *in press*). Therefore, the use of any riparian patch—native or exotic—as breeding habitat will be site specific and will depend on the spatial, structural, and ecological characteristics of that particular patch and the potential for flycatchers to colonize and maintain populations within it.

Based on patterns of flycatcher movement among riparian patches, breeding habitat may be most suitable or attractive when it is relatively young (at least 3 years of age, but less than 10–15 years). However, flycatchers will continue to occupy older habitat especially when patches of younger vegetation are lost or unavailable; thus, older patches and atypical habitat (e.g., narrow stringers of vegetation) may periodically serve as “refugia” for a local population until new patches develop. This illustrates the importance of creating and maintaining a mosaic of riparian habitat patches within a drainage (USFWS 2002), so that at least some of the patches will be suitable for breeding flycatchers at any given time, and flycatchers will have alternative patches to move to if some are lost to inundation, scouring, fire, drought, or other disturbance.

Restoration Implications

There are many challenges inherent in riparian restoration in the Southwest (USFWS 2002), especially with regard to providing the geomorphological and hydrological conditions necessary for riparian establishment and persistence. However, under the proper conditions, riparian vegetation can develop rapidly, and Southwestern Willow Flycatchers can subsequently respond by quickly colonizing sites once the habitat characteristics are suitable. We observed young habitat at Roosevelt Lake being occupied within 3 years after development, and similar settlement patterns have been documented at Elephant Butte Reservoir in New Mexico (Moore and Ahlers 2006). Therefore, in some areas it is possible for managers to rapidly create or restore substantial amounts of riparian habitat, and for flycatcher populations to quickly react to and benefit from the new habitat.

The location of riparian restoration projects will affect the likelihood and speed at which Southwestern Willow Flycatchers find and colonize a site (USFWS 2002). Restoration projects near existing breeding sites will likely increase the

probability of colonization; based on our movement data, distances up to 30–40 km appears best. However, more distant sites may still be colonized, especially if they are located within the same drainage as current sites.

The spatial habitat models that we developed can serve as useful tools in riparian restoration efforts. For example, the models can be used to identify riparian patches that are close to desired conditions, thus requiring less active management to reach restoration goals. Alternatively, the model can be used to find “lower probability” patches where restoration may greatly increase the habitat value. Another potential use is in tracking restoration progress over time by monitoring the amount of habitat in the different model probability categories. Progress toward management goals could be measured periodically, and restoration activities modified accordingly. Finally, the model may allow managers to decide when a restoration site has developed sufficiently to warrant the beginning of flycatcher occupancy surveys.

Monitoring Implications

It is clear from both Roosevelt Lake and the San Pedro/Gila study sites that local Southwestern Willow Flycatcher populations can change in size quickly. This is true for both population growth and decline in a particular breeding patch or area. Therefore, it cannot be assumed that local or regional flycatcher populations will remain static over time, or even over the course of a few years. Demographic models are useful in simulating future population trajectories, but it does not appear that our model projections have closely matched observed trends. Therefore, periodic surveys and monitoring are important for accurately tracking the status and trends of flycatcher breeding sites and populations. Based on our data, monitoring efforts that follow the standard survey protocol (Sogge et al. 1997) will likely fail to detect non-territorial floaters; however, there are relatively few floaters in most years, so population counts will not be greatly affected.

Flycatcher breeding habitat can develop or be lost over a period of only a few years, especially where there has been a change in human activities (grazing, fire, water management) or natural drivers such as climate (e.g., droughts, scouring floods). Therefore, the persistence of a currently occupied patch is not assured over the long term. Similarly, an area currently without suitable breeding habitat may develop suitable habitat in the future. In much the same way that periodic flycatcher surveys are necessary to track status of the birds, periodic riparian habitat surveys will be important in tracking habitat trends in a given area. The spatial habitat models that we developed could serve as a foundation for habitat monitoring efforts, by quantifying riparian habitat changes and drawing attention to where these have occurred.

Drought Impacts

The Southwest experienced a long-term drought over the course of this study. In the year of most severe drought (2002), there was strong evidence that it affected virtually all aspects of Southwestern Willow Flycatcher ecology, especially at Roosevelt Lake. Nest success and productivity were all greatly reduced, and the degree of non-territorial behavior (and thus lost productivity) was dramatically higher. Although the Roosevelt and San Pedro/Gila flycatcher populations persisted through the drought, and eventually increased to above pre-drought levels, it is clear that the 2002 drought was a major disturbance event for the flycatchers.

This raises an important question as to whether the flycatcher population at Roosevelt Lake could sustain itself over multiple years of extreme drought. The near total collapse of reproductive success in a single drought year like 2002, coupled with the short average lifespan of Southwestern Willow Flycatchers, strongly suggests that several successive years of extreme drought could cause a major population crash and possible extirpation of flycatchers, the speed of which would depend on the starting population size. This is an important consideration with respect to forecasting the long-term persistence of flycatchers at our study sites, and possibly elsewhere. For example, most climate change models predict increased drought frequency and severity in the Southwest (Seager et al. 2007). Therefore, long-term management of Southwestern Willow Flycatchers will be more effective if it considers how flycatcher habitat and breeding populations may respond to changes in southwestern climate, and whether there are management actions that can ameliorate any negative effects. Reservoirs could potentially serve a unique role in adapting to changing hydrologic regimes through operations that favor riparian habitat development and persistence in drawdown zones or along regulated rivers downstream; however, such uses will need to be reconciled with the ongoing demand for water by cities and agriculture.

Future Research Needs and Directions

As noted above and in chapter 1, we have learned a great deal from this study of Southwestern Willow Flycatchers and their habitats. Still, there are a number of topics that warrant additional research attention, because they have direct implications for the conservation and management of the flycatcher.

- Are small populations different? Our study involved some of the largest known breeding populations; smaller and more isolated populations may function differently. However, few smaller sites have been studied in detail. This is an important issue because many Southwestern Willow Flycatcher breeding sites are comprised of fewer than 10 territories and geographically isolated from other known breeding sites (Durst et al. 2006). We do not know levels of productivity,
- movement, and survivorship of these small populations, or whether they act primarily as population sinks or sources (Kus et al. 2003). Directing additional research toward small populations rangewide can help us answer these key questions.
- Improved demographic modeling and forecasting. Despite the intense field efforts and extensive modeling that we conducted, our demographic models did not perform well in describing changes that occurred during our study. However, it is useful to understand the synergistic relationship among vital rates (e.g., survivorship, productivity), and using this to develop an accurate model of flycatcher populations would allow for evaluations of management actions, impacts of climate change, etc.. Therefore, we encourage the continued refinement and testing of the demographic models, using the Roosevelt Lake and San Pedro/Gila datasets as a foundation. We also believe that new models may be needed to more adequately take into account the dynamic nature of flycatcher populations and habitat, and the metapopulation dynamics of the subspecies.
- Spatial models as decision tools for managers. At present, the spatial habitat models that we developed can be used to look at current and past characteristics of Southwestern Willow Flycatcher habitat, which is useful in a variety of ways. However, the model cannot be extended into the future, nor used to test “what if” alternatives based on different future conditions (e.g., reservoir operations, flow regimes, changing climate, etc.). To do so would require a multidisciplinary modeling effort to quantitatively link NDVI values, upon which our model is based, and the factors that influence riparian habitat vigor (soils, geology, groundwater, hydrology, etc). We believe that developing an integrative model is an important next step, and would set the stage for forecasting capability. This would allow managers to evaluate how different scenarios affect riparian habitat, and to choose alternatives with the greatest probability of achieving their goals. These models can be applied to management of Southwestern Willow Flycatchers, as well as the wide array of wildlife dependent upon riparian systems, especially in the southwestern United States.
- Role and impact of diseases. One important aspect of flycatcher ecology that has received almost no attention is disease. There is virtually no information available on the prevalence and nature of disease in any of the Willow Flycatcher subspecies (Marshall and Stoleson 2000, Sedgwick 2000). Yet disease, especially new and highly pathogenic introduced forms, can have devastating effects on native bird populations, especially for endangered species. West Nile Virus (WNV) has recently become established in the Southwest and

is now widespread in Arizona, having been found in mosquito, bird, or human populations in almost every county (Arizona Department of Health Services). In the early 2000s, we collected mosquito samples and avian blood samples at Roosevelt Lake to determine if WNV was present. We found no evidence of the virus in mosquitoes, but confirmed it was present in at least two bird species (but not the Southwestern Willow Flycatcher; USGS unpublished data). Given that Tyrannid flycatchers, the bird family to which Willow Flycatchers belong, evolved in the New World, and that WNV is of Old World origin, flycatchers may be very susceptible to this disease. The same could be true of Highly Pathogenic Avian Influenza (HPAI), which has not yet been found in North America but which has the potential for eventual establishment through natural or human-assistance dispersal. We believe that future Southwestern Willow Flycatcher management and conservation would benefit from proactive research on the types and prevalence of diseases among flycatchers.

- Migration ecology. The overwhelming majority of research on the Southwestern Willow Flycatcher has been conducted on the breeding grounds (Sogge 2000, Stoleson et al. 2000). While this is a critically important period in the flycatcher's life history, as a Neotropical migrant it spends more than two-thirds of its annual cycle outside of the breeding grounds. Although flycatcher surveys and research have increased on the wintering grounds (Koronkiewicz 2002, Lynn et al. 2003, Schuetz et al. 2007), there is a dearth of information about the migration period (though see Yong and Finch 1997). This relative lack of data is problematic, given that migration habitat and behavior are key determinants of whether birds arrive on the breeding grounds in suitable condition to nest. Furthermore, most Willow Flycatcher mortality appears to occur during migration (see chapter 2). Therefore, we believe that effective long-term conservation of the Southwestern Willow Flycatcher requires additional research on migration, including stopover habitat selection and use, foraging ecology, and physiology.

References

- Causey, C.F., M.G. Pollock, S.L. Durst, P.J. Newell, E.H. Paxton, and M.K. Sogge. 2005. Survivorship and movements of Southwestern Willow Flycatchers at Roosevelt Lake, Arizona—2005. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix, AZ. 59 pp.
- Drost, C.A., E.H. Paxton, M.K. Sogge, and M.J. Whitfield. 2003. Food habits of the Southwestern Willow Flycatcher during the nesting season. *Studies in Avian Biology* 26:96–103.
- Durst, S.L. 2004. Southwestern Willow Flycatcher potential prey base and diet in native and exotic habitats. M.S. Thesis. Northern Arizona University, Flagstaff, Arizona.
- Durst, S.L., M.K. Sogge, H.C. English, S. O. Williams III, B. E. Kus, and S. J. Sferra. 2006. Southwestern Willow Flycatcher breeding site and territory summary—2005. U.S. Geological Survey, Southwest Biological Science Center report to Bureau of Reclamation, Flagstaff, Arizona. Arizona Game and Fish Department Nongame and Endangered Wildlife Technical Report 249.
- Ellis, L.A., D.M. Weddle, S.D. Stump, H.C. English, and A.E. Graber. 2008. Southwestern Willow Flycatcher final survey and monitoring report. Arizona Game and Fish Department, Research Technical Guidance Bulletin #10, Phoenix, Arizona, USA.
- Graber, A.E., D. Weddle, H.C. English, S.D. Stump, H.E. Telle, and L.A. Ellis. 2007. Southwestern Willow Flycatcher 2006 Survey and Nest Monitoring Report.
- Graf, W.L. 2006. Downstream hydrologic and geomorphic effects of large dams on American rivers. *Geomorphology* 79:336–360.
- Graf, W.L., J. Stromberg, and B. Valentine. 2002. Rivers, dams, and Willow Flycatchers: A summary of their science and policy connections. *Geomorphology* 47:169–188.
- Koronkiewicz, T.J. 2002. Intraspecific territoriality and site fidelity of wintering Willow Flycatchers (*Empidonax traillii*) in Costa Rica. MS thesis. Northern Arizona University. Flagstaff, Arizona.
- Kus, B.E., P.P. Beck, and J.M. Wells. 2003. Southwestern Willow Flycatcher populations in California: distribution, abundance, and potential for conservation. *Studies in Avian Biology* 26:12–21.
- Lynn, J.C., T.J. Koronkiewicz, M.J. Whitfield, and M.K. Sogge. 2003. Willow Flycatcher winter habitat in El Salvador, Costa Rica, and Panama: characteristics and threats. *Studies in Avian Biology* 26:41–51.
- Marshall, R.M. 1995. Research and data needs for the endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*). Arizona Partners in Flight, U.S. Fish and Wildlife Service (<http://sbsc.wr.usgs.gov/cprs/research/projects/swwf/wiflneed.asp>).

- Marshall, R.M., and S.H. Stoleson. 2000. Threats. *In* Status, ecology, and conservation of the Southwestern Willow Flycatcher. (D.M. Finch and S.H. Stoleson, eds.) USFS Rocky Mountain Research Station, Gen. Tech. Rep. RMRS-GTR-60.
- Moore, D., and D. Ahlers. 2006. 2006 Southwestern Willow Flycatcher study results: selected sites along the Rio Grande from Velarde to Elephant Butte Reservoir, New Mexico. Report by the Bureau of Reclamation, Denver, Colorado.
- Owen, J.C., M.K. Sogge, and M.D. Kern. 2005. Habitat and gender differences in the physiological condition of breeding Southwestern Willow Flycatchers. *Auk* 122:1261–1270.
- Schuetz, J.G., M.J. Whitfield, and V.A. Steen. 2007. Winter Distribution of the Willow Flycatcher (*Empidonax traillii*) in Guatemala and Mexico. Report by the Southern Sierra Research Station, Weldon, California.
- Seager, R., M. Ting, I. Held, Y. Kushnir, J. Lu, G. Vecchi, H. Huang, N. Harnik, A. Leetma, N. Lau, C. Li, J. Velez, and N. Naik. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science Express*, 5 April 2007.
- Sedgwick, J.A. 2000. Willow Flycatcher (*Empidonax traillii*). *In* The Birds of North America, No. 533 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, Pennsylvania.
- Sferra, S.J., R. Meyer, and E. Corman. 1995. Arizona Partners in Flight 1994 Southwestern Willow Flycatcher survey. Nongame and Endangered Wildlife Program Technical Report 69. Arizona Game and Fish Dept., Phoenix, AZ.
- Sogge, M.K. 2000. Breeding season ecology. Pages 57–70 *in* Status, Ecology, and Conservation of the Southwestern Willow Flycatcher. Finch, D.M. and S.H. Stoleson (eds). USDA Forest Service Rocky Mountain Research Station General Technical Report RMRS-GTR-60. 131 pp.
- Sogge, M.K., R.M. Marshall, T.J. Tibbitts, and S.J. Sferra. 1997. A Southwestern Willow Flycatcher Natural History Summary and Survey Protocol. National Park Service Technical Report NPS/NAUCPRS/NRTR-97/12. 37 pp.
- Sogge, M.K., E.H. Paxton, and A.A. Tudor. 2006. Saltcedar and Southwestern Willow Flycatchers: lessons from long-term studies in central Arizona. Pages 238–241 *in* C. Aguirre-Bravo, P. J. Pellicane, D. P. Burns, and S. Draggan, eds. Monitoring Science and Technology Symposium: Unifying Knowledge for Sustainability in the Western Hemisphere. 2004 September 20–24; Denver, Colorado. Proceedings RMRS-P-42CD. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.
- Sogge, M.K., S.J. Sferra, and E.H. Paxton. *In press*. Saltcedar as habitat for birds: implications for riparian restoration in the Southwest. *Restoration Ecology*.
- Stoleson, S.H., J. Agyagos, D.M. Finch, T. McCarthey, J. Uyehara, and M.J. Whitfield. 2000. Research Needs. Pages 119–128 *in* Status, Ecology, and Conservation of the Southwestern Willow Flycatcher. Finch, D.M. and S.H. Stoleson (eds). USDA Forest Service Rocky Mountain Research Station General Technical Report RMRS-GTR-60. 131 pp
- U.S. Fish and Wildlife Service. 1995. Final rule determining endangered status for the Southwestern Willow Flycatcher. *Federal Register* 60:10694–10715 (February 27, 1995).
- U.S. Fish and Wildlife Service. 1996. Biological opinion on the operation of the modified Roosevelt Dam. Arizona Ecological Services Office, Phoenix, Arizona.
- U.S. Fish and Wildlife Service. 2002. Southwestern Willow Flycatcher (*Empidonax traillii eximius*) final recovery plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico.
- U.S. Fish and Wildlife Service. 2005. Designation of critical habitat for the Southwestern Willow Flycatcher (*Empidonax traillii eximius*), Final Rule. *Federal Register* 70:60886–61009 (October 19, 2005).
- Whitfield, M.J., and C.M. Strong. 1995. A Brown-headed Cowbird control program and monitoring for the Southwestern Willow Flycatcher, South Fork Kern River, California. California Department of Fish and Game, Bird and Mammal Conservation Program Report 95-4, Sacramento, California. 17 pp.
- Young, W., and D.M. Finch. 1997. Migration of the Willow Flycatcher along the middle Rio Grande. *Wilson Bulletin* 109:253–268.