CONSERVATION OF SOUTHWESTERN WILLOW FLYCATCHERS: HOME RANGE AND HABITAT USE BY AN ENDANGERED PASSERINE

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Abstract

Conservation of Southwestern Willow Flycatchers: home range and habitat use by an endangered passerine

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Conservation and management of any species requires information on habitat preferences, movement, and size of area used. Defining area and habitat needs is especially difficult for migratory birds with space and habitat requirements that vary during their annual cycle. Even on breeding grounds, where many neotropical migrants are relatively well studied, information on space and habitat use during the pre- and post-nesting periods is often lacking.

The management of Southwestern Willow Flycatchers (*Empidonax trailli extimus*), an endangered neotropical migrant that breeds in riparian areas of the Southwestern United States, is hindered by lack of home range and habitat use data to estimate space requirements for conservation areas.

I used radio-telemetry to track male Southwestern Willow Flycatchers at Roosevelt Lake in Central Arizona during the summers of 2003 and 2004. I found home range size varied significantly over the season ($P = 0.04$, $n = 23$) ranging from 0.1 - 360.5 ha using a 95% fixed Kernel contour. Home ranges were smallest during the nesting season (mean= 0.38 ± 0.27 (SD) ha) largest at post-nesting (mean = 143.23 ± 163.04 ha) and variable at pre-nesting (range:

0.18 – 65.44 ha). Small home ranges during the middle of the breeding season coincided with female arrival and nesting behavior. Site fidelity and prospecting behavior may explain some of the variability I observed during the pre-nesting season. Large post-nesting home range sizes were a direct result of long distance movements of over one kilometer with birds possibly prospecting for future territories, exploiting ephemeral food resources or staging for migration.

I found that habitat use was restricted to the riparian floodplain. Mature riparian vegetation was used more than expected from availability but flycatchers were observed using young and immature habitat as well. Also, I found little indication for preferential use of native or exotic vegetation types. My data indicate that 1) home range sizes fluctuate significantly through the season, 2) post-nesting movements may greatly increase the area that birds use, 3) there is little use of non-riparian habitats at our study site, and 4) there is little support for preferential use of exotic or native habitats within mature riparian vegetation zones.

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Dedication

To the two great teachers in my life:

Dr. Steven Herman of The Evergreen State College

And

Dr. Tad Theimer of Northern Arizona University

To Dr. Steven Herman for teaching me to view the world through a naturalist's eye. And, Dr. Tad Theimer for showing me how to integrate science and natural history.

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Conservation of Southwestern Willow Flycatchers: home range and habitat use by an endangered passerine

INTRODUCTION

Conservation and management of any species requires information on habitat preferences, movement, and size of area used (Bingham and Noon 1997, Caro 1999, Pechacek 2004). Defining area and habitat needs is especially difficult for migratory birds with space and habitat requirements that vary during their annual cycle. Even on breeding grounds, where many neotropical migrants are relatively well studied (Martin 1992, Martin and Finch 1995), information on space and habitat use during the pre- and post-nesting periods is often lacking (Vega Rivera et al. 1999, 2003b; Bayne and Hobson 2001b). Assessing and selecting territories during the pre-nesting period may impact survival and productivity in that year (Brown 1969, 1975; Sergio and Newton 2003; Formica et al. 2004) while prospecting (i.e. assessing habitat (Reed et al. 1999)) at the end of the nesting season may affect territory selection the following year (Doligez et al. 2004). In addition, the demands of post-nuptial molt, pre-migratory fattening, and fledgling care all could cause birds to shift habitat use during the post-nesting period (Vega Rivera et al. 1999, 2003b).

Until recent technological advances made telemetry possible, space use by small passerines was determined by spot-mapping, which may substantially under-estimate area used by a breeding bird (Hanski and Haila 1988) especially during pre- and post-nesting periods when birds may not be exhibiting territorial behavior and are therefore hard to detect (Ettinger and King 1980, Anders et al. 1998, Norris and Stutchbury 2002). The few studies of movement and habitat use by small passerines using telemetry documented significant changes in habitat use between nesting and post-nesting periods, possibly due to prospecting behavior, molt, or staging for migration (Vega Rivera et al. 1999, 2003b; Bayne and Hobson 2001b). Understanding space and habitat requirements for the entire breeding season is important for managing landscapes to conserve endangered species (Pechacek 2004), as populations may be limited by habitat requirements during early- and late-phases of the breeding season.

The management of Southwestern Willow Flycatchers (*Empidonax traillii extimus*), an endangered neotropical migrant that breeds in riparian areas of the Southwestern United States (Sogge and Marshall 2000), is hindered by lack of home range and habitat use data to estimate space requirements for conservation areas (Paxton et al. 2003). This subspecies was listed in 1995 with habitat loss and degradation as major reasons for its decline (USFWS 1995; Marshall and Stoleson 2000). Although large-scale habitat characteristics across the breeding range (Sogge et al. 2003, Durst et al. 2005), and nest-site characteristics (Allison et al. 2003, Stoleson and Finch 2003) have been described for Southwestern Willow Flycatchers, habitat selection and habitat use at the level of territory or home range have not. (From this point forward, the terms flycatcher and Willow Flycatcher will all be used and all refer to Southwestern Willow Flycatchers).

Although Willow Flycatchers are considered riparian obligates, a recent telemetry study in central Utah on the non-endangered subspecies, *E. t. adastus*, found Willow Flycatchers using non-riparian habitat, especially when nests were placed close to the edge of the riparian zone (Bakian and Paxton 2004, Paxton et al. 2003). Whether and to what extent *E. t. extimus* also uses non-riparian habitat may be especially important for designating habitat important for species survival.

Invasion by exotic saltcedar (*Tamarix* spp.) has changed the composition of many riparian habitats throughout the Southwest (Ohmart and Anderson 1982, Hunter et al. 1985, Hunter 1988, Knopf et al. 1988, Zavaleta 2000), and its impact on Southwestern Willow Flycatchers has been controversial. Some authors have argued that saltcedar habitats are of poor quality for flycatchers (DeLoach et al. 2000, Dudley et al. 2000), while others have found that potential prey resources do not appear to be limiting in these habitats (Cohan et al. 1978, Durst 2004). Flycatchers do nest in areas with saltcedar components (Sogge et al. 2003, Durst et al. 2005) but it is unknown whether this habitat is underutilized when within home ranges.

In this study, I used radio-telemetry to address the following questions: 1) Does home range size for male Southwestern Willow Flycatchers differ among pre-nesting, nesting, and post-nesting periods of the breeding season? 2) Does non-riparian habitat make up any portion of the home range during any of these periods? 3) Are riparian stands of varying ages or composition (exotic versus native) used more or less than expected at random across these three periods?

To minimize any potential impacts telemetry could have on nest attendance of females and due to the endangered status of the sub-species, only males were used for this study.

METHODS

Study Area

This study was conducted during the 2003 and 2004 breeding seasons (May- August) along the Salt River and Tonto Creek inflows of Roosevelt Lake, Gila County, Arizona, approximately 90 km northeast of Phoenix. Mature riparian vegetation was patchily distributed at both sites, with some areas dominated by exotic saltcedar (*Tamarix ramosissima)* and others by native Goodding's willow (*Salix gooddingii*), although, most areas were a mix of these two species. Mature patches were often separated by open areas or areas dominated by young, developing riparian vegetation. Surrounding habitat was Sonoran Desert Uplands dominated by saguaro (*Carnegiea gigantea*), palo verde (*Cercidium microphyllum*), creosote (*Larrea tridentata*), and screwbean mesquite (*Prosopsis pubescens*).

The Southwestern Willow Flycatcher population at Roosevelt Lake has been studied for almost 10 years, including an ongoing demographic study that started in 1995. Roosevelt Lake had one of the largest populations of flycatchers in the Southwest with over 200 adults at the site during both years of this study (Durst et al. 2005; Newell et al. 2003, 2005). Over 70% of the population has been banded and genetically sexed; and site fidelity and nest success are known for most individuals (Smith et al 2004; Newell et al. 2003, 2005; Munzer et al. 2005).

Capture and Transmitter Attachment

Flycatchers were captured in mist nets passively or by luring with broadcasts of conspecific vocalizations (Sogge et al. 2001). Some birds tracked in this study had previously been sexed using sex-specific genetic markers. For all others, I classified a bird as male if it lacked a brood patch (indicative of females), had a wing chord length $\geq$ 70 mm (90% or greater likelihood of being male (USGS *unpubl. data*), and had previously been observed defending a territory on more than two occasions. Telemetered flycatchers were banded with a uniquely numbered, color-anodized Federal bird-band on one leg, and one metal color band on the other (Koronkiewicz et al. 2005).

I attached Holohil (Carp, Ontario) LB-2N or BD-2N transmitters (expected battery life 21 days; weight of 0.40-0.48 g) using a glue-on method (Johnson et al. 1992, Paxton et al. 2003) that was demonstrated to be safe and effective during a pilot study (Paxton et al. 2002). I glued a small piece of cloth to the back of all transmitters to increase absorbency and attachment surface area (Johnson et al. 1991, Schulz et al. 2001). With the addition of the cloth backing and the epoxy necessary to set the activation wires (LB-2N only), final weight of the transmitters was 0.46 g to 0.50 g (3.8% to 4.2% of the weight of the flycatchers), below the 5% maximum weight limit typically deemed safe (Neudorf and Pitcher 1997, Naef-Daenzer et al. 2001). Transmitters were attached using

Skin Bond® (made by Smith and Nephew®) approximately 1.5 cm above the uropygial gland, where I trimmed feathers to less than 3 mm to expose a skin surface for bonding. Transmitter attachment took approximately 20 minutes including banding and data collection.

I classified male flycatchers as one of the following four breeding status categories: pre-nesting, nesting, post-nesting, or floater. I defined these categories as: *Pre-nesting*- flycatchers exhibiting territorial behavior prior to the arrival of females; *Nesting* - territorial flycatchers that were either unpaired after arrival of females, or paired with a female that was nest-building, incubating, or feeding nestlings; *Post-nesting* - flycatchers that had made a breeding attempt but were no longer actively defending a territory or spending time with a female with young; *Floater*- non-territorial flycatchers (territorial behaviors such as singing or defending a fixed area were not observed during the nesting season of May and June). I determined the nesting stage (building, incubating, nestlings or fledglings) by observations of female behavior, monitoring nests, and/or utilizing data obtained from an on-going nest-monitoring project conducted by the Arizona Game and Fish Department (Munzer et al. 2005).

Radiotracking

I began radio-tracking the day after transmitter attachment to allow time for resumption of normal behavior following handling stress (Suedkamp Wells et al. 2003). I stratified points throughout the day by tracking birds during the morning, midday, and afternoon periods. I randomized the daily tracking schedule for individual birds, to avoid tracking birds in the same order each day. Each bird was tracked every day during a given period (morning, midday, or afternoon) until 4-6 points were obtained, at a minimum of one half hour intervals. I assumed that a half-hour interval was sufficient to assure independence of locations because this interval was greater than the time it would take a flycatcher to cross its home range, a commonly used standard for judging independence (White and Garrot 1990). Across all sampling days for each bird, each time period was sampled approximately equally.

All birds were tracked by homing-in on the signal using an R-1000 telemetry receiver (Communication Specialists) and a flexible hand held 3-elment yagi antenna (Biotrack Equipment). Only two to three observers tracked all the telemetered birds each year and all observers were trained in a similar fashion to minimize observer bias. Ideally, a flycatcher was located and visually observed, and the location recorded via GPS (Garmin Etrex Legend GPS Unit) after the flycatcher moved on to another location. If a flycatcher could not be sighted visually (usually because the bird remained high in thick canopy) the location was estimated using the telemetry signal strength to indicate when the bird was less than 10 m away. When birds were tracked to extremely dense patches of vegetation, the tracker triangulated from multiple positions along the patch edge until the bird's approximate location was ascertained. Occasionally, flycatchers moved such long distances in a short amount of time that the tracker could not home-in on the bird, and instead triangulated on the signal from 2-3 positions on hilltops above the floodplain. Positions were taken within 5 minutes of each other to decrease the possibility of the bird moving while triangulating. Signal strength from the receiver was used to estimate distance from triangulation point to the bird's location to help ascertain a location. In these cases, I used the Distance and Azimuth tool (v.1.4 e) in Arcview 3.3, to draw vectors and estimated the location to within 20 m of the intersection of these lines. At each location with visual confirmation I recorded: habitat type, vegetation type the bird was in, the height of the vegetation where the bird was seen, type of vocalizations made, type of foraging activities, and any interactions with other flycatchers. When I located a bird without visual confirmation I recorded habitat type and vocalizations.

Data Analysis

Home Range Analysis

I calculated fixed-kernel based probabilistic home range sizes for all flycatchers with at least 30 locations, the minimum number typically needed for unbiased estimates of home range sizes (Kenward 2001). I used the Animal Movement extension (Hooge and Eichenlaub 1997) in Arcview 3.3 to calculate a 95% probability home range, and a 50% probability home range corresponding to core area (Rivera et al. 2003b). I used least squares cross validation to determine kernel size, which produces an objective and accurate home range estimate (Seaman and Powell 1996). Because the data were not normally distributed I used a non-parametric Kruskal Wallis Test to test for differences between central tendencies of home range size among seasonal periods. I summarized the data as means ± SE unless otherwise noted, with alpha set at 0.05 for statistical tests.

Movement patterns

I used the Animal Movements extension (Hooge and Eichenlaub 1997) in Arcview 3.3, to calculate several measures of movement. I estimated the overall magnitude of movement by determining the distance between the two farthest opposite locations for each bird. To characterize the extent of daily movements, I also determined the mean distance between each successive location, color-coded movement vectors by date and time and plotted them in order to visualize temporal pattern of movement.

Habitat Use and Availability

I used two methods to estimate habitat available to each flycatcher, one based on movements and the other using a home range estimator. For each flycatcher I calculated the arithmetic mean of all locations using spider distance analysis in the Animal Movement extension of Arcview 3.3 (Hooge and Eichenlaub 1997) and then used the distance of the farthest location as the radius of a circle centered on the centroid. Using this method, I assumed that all habitats within this circle were available to a bird at the time the bird was tracked (analogous to the methods of Menzel et al. 2001; Fig. 1). I used this method because it was based on each bird’s actual movements. Using one distance for all birds (Anders et al. 1998) may be appropriate when all birds are tracked in the same period (i.e. nesting or post-nesting), however, movement patterns may change according to the nesting cycle. The method I used controlled for variation both among seasons and among individuals. The relatively small scale at which habitat varied within home ranges precluded using other methods such as those of Marzluff et al. (2004) and the fact that many home ranges did not contain all habitat types precluded the use of methods recommended by Aebischer et al. (1993).

To investigate habitat use and selection over a more limited spatial extent, I defined habitat available to each bird as that area within its home range estimated using either minimum convex polygon (MCP) or the kernel-based 95%home range estimate (Vega Rivera et al 1999, 2003 a,b).

I used high resolution, rectified, aerial photographs to classify riparian habitat according to age as young (riparian vegetation <3 years old comprised of either saltcedar or willow), immature (riparian vegetation 3-5 years old comprised of saltcedar, willow or a mixture of the two), or mature (riparian vegetation > 5 years old). Mature patches were focal areas for the flycatchers and they comprised most of the habitat in which flycatchers bred (Allison et al. 2003). I further differentiated mature patches as native (Goodding's Willow made up >75% of the vegetation), exotic (saltcedar made up >75 % of the vegetation), and mixed (both willow and saltcedar were present but neither made up >75% of the vegetation). Upland (all non-riparian habitats above the high water mark dominated by Sonoran Desert Upland vegetation) and open areas (exposed ground that had <5% live woody vegetation ground cover) also occurred within some flycatcher home ranges (Figs. 1 and 2). Any open water that fell within the span of "available" habitat was excluded from analysis.

I calculated habitat availability for each bird as the percentage of each habitat within the extent of either the spider-based circle, MCP or kernel based home range estimates. I used a chi-squared test of heterogeneity (using the statistical software JMP 5.1) to determine whether the percent habitat used differed from the percent habitat available for each bird and then used the technique described in Neu et al. (1974) to evaluate habitat selection. I set alpha at 0.05 for these tests of heterogeneity and habitat selection.

I also tested whether percent canopy composition comprised of exotic vegetation could discriminate between bird locations and random points. I took vegetation measurements at 16 randomly selected locations of each nesting bird, and at 16 random points selected within the spider distance radius by using the extension Random Points generator v 1.3 (Jenness 2005) in Arcview 3.3. I analyzed the data using a logistic regression model in JMP 5.1.

RESULTS

Banding, Tracking and Return Rates

Banding and Tracking

I radio-telemetered 20 male flycatchers during 2003 and 15 during 2004. I obtained approximately 1300 locations from these telemetered flycatchers during 700 hours of tracking. I obtained enough locations (≥ 28) from 11 birds during 2003 and from 15 birds during 2004 to calculate home range. The mean number of locations for these birds with ≥ 28 points was 52.   Because transmitters lasted an average of 21 days and flycatchers were caught throughout the season from their arrival in spring to their departure in late summer, nesting status of each bird varied based on when it was caught (Fig. 2). During the entire study, I estimated home range size for six pre-nesting flycatchers (two in 2003 and four in 2004), 12 nesting flycatchers (seven in 2003 and five in 2004), four post-nesting flycatchers (one in 2003 and three in 2004), and one floater caught in 2003 (Appendix 1). Home range size was still increasing for some birds with < 60 locations suggesting that some of my calculated home range sizes may be underestimates.

I did not collect enough data to estimate home range size for 12 flycatchers. Of these birds, two had transmitters that failed during the first 24 hours, three had transmitters that failed during the first week after attachment and three others had transmitters that fell off before I collected enough locations for home range analysis. During 2003, three flycatchers apparently left the study area. The last of the 12 flycatchers died three days after capture. When released after transmitter attachment it fluttered to the ground and was subsequently never observed flying, although the signal indicated it was moving before death on the third day.

Return Rates

Thirteen of the 20 flycatchers radio-telemetered during 2003 (65%) returned to Roosevelt Lake in 2004, a rate comparable to that observed for all banded flycatchers at Roosevelt Lake from 2000-2004 (53-69%; Newell et al 2005). Three flycatchers from the 2003 season were re-captured and fitted with a new transmitter; home range size was estimated in both years for only one bird. All recaptured flycatchers had full re-growth of all back feathers where the 2003 transmitters had previously been attached.

Home Range and Movement Patterns

Yearly variation

Kernel based 95% home range sizes ranged from 0.1 to 360 ha ($\bar{x}$ =28.0 ± 17.4) for all Southwestern Willow Flycatchers captured during both years of the study. During 2003, home range size ranged from 0.1 to 7.6 ha ($\bar{x}$ =1.5 ± 0.7) and during 2004 from 0.2 to 360.1 ha ($\bar{x}$ =52.3 ± 31.7). The longest distance between peripheral locations of individual birds ranged from 37 to 2851 m ($\bar{x}$ =645 ± 286) and mean consecutive movements ranged from 14 to 756 m ($\bar{x}$ =124 ± 62). Home range size differed significantly among nesting seasons (Kruskall Wallis Chi-square approximation = 11.54, P=0.003) with home ranges largest during pre- and post-nesting periods and smallest during the nesting period. I did not test for differences between years, however, the home range sizes were similar between both years of the study. Detailed movement and home range maps of individual birds are given in Appendix 1 and 2.

Pre-nesting period

Although, all pre-nesting flycatchers had well-defined defended areas where they exhibited territorial behaviors such as singing and chasing other males, home ranges and movement patterns were variable. However, three (WIFL 2, WIFL 1 and WIFL 52) made movements away from their defended territory into areas where territorial behavior was not observed. The mean longest distance between sequential locations for these three flycatchers was

643 m (range= 390 – 819 m versus 20 ± 1 m for the three birds that did not move away from defended territories). WIFL 2, tracked during 2003 had a non-contiguous home range divided by the Salt River, whereas, WIFL 52, tracked during 2004, exhibited territorial behavior in one area, then moved to four other areas (up to 2 km away from the capture location) and finally settled into a new patch where territorial behavior was again exhibited (see fig. 4). A female eventually settled and nested in this latter patch (Munzer et al. 2005). WIFL 52 was not seen at Roosevelt Lake during 2003 (Newell et al. 2003) and was likely not at the site during that year. The other three pre-nesting flycatchers had contiguous home ranges and had home ranges similar in size ($\overline{x}$ = 0.27 ± 0.03 ha pre-nesting) to nesting flycatchers ($\overline{x}$ = 0.38 ± 0.08 ha nesting). Two of these pre-nesting birds were seen in the same area the year before. The mean home range size for all pre-nesting flycatchers was 9.91 ha. However, this statistic was heavily influenced by WIFL 52, a transient flycatcher that had a home range of over 50 ha. Without this bird, the mean home range size was 0.55 ha (± 0.2) with WIFL 2 still exhibiting a home range size > one ha.

Nesting period

Southwestern Willow Flycatchers had the smallest home ranges during the nesting period ($\overline{x}$ = 0.38 ± 0.08 ha). Most home ranges were contiguous, with the mean distance between points of 26 m (± 3 m) and the mean longest distance moved of 92 m (± 13 m) (Fig. 5). However, five flycatchers made short movements (under 100 m) away from their defended area. Three of these flycatchers were either un-paired or their females had left after a breeding attempt. We found the nests of the five-telemetered flycatchers; in all cases the nests were found within the 50% kernel home range.

Post-nesting period

Post-nesting Willow Flycatchers had the largest home ranges during both years ($\bar{x}$ =143.23 ± 83.52 ha) and all home ranges were non-contiguous with at least 2 use areas. Movements varied among individuals, but with some consistencies. Two flycatchers (tracked at the same site in different years) moved back and forth between their core area and the river's edge where they were seen feeding on an outbreak of Tamarisk Leafhoppers (*Opsius* spp.), a known flycatcher diet item at this site (Durst 2004). Three flycatchers made long movements away from their breeding areas and/or capture locations to areas where they stayed for extended periods (2 - 7 days). In contrast, one flycatcher moved to other breeding areas daily, sometimes moving 2 km in one day (Fig. 6). The mean of consecutive movements for post-nesting birds was 297 m, an 11-fold difference between nesting birds and a four-fold increase from the pre-nesting birds.

Floater

The one floater caught during this study had a home range of 7.57 ha, eight times larger than that of pre-nesting birds but smaller than that of most post-nesting flycatchers. This bird's wing chord was 70mm long indicating it was more than likely a male (*USGS unpubl.data*). The floater had a non-contiguous home range with three use areas all centered near other flycatcher breeding sites and with his core area overlapping another telemetered flycatcher's home range. The floater was never observed to interact with the bird occupying the territory overlapping his core area. However, he returned to Roosevelt Lake in 2004 as a breeding territorial male paired with a female (Newell et al. 2005).

Overlapping Home Ranges

Overlapping home ranges occurred during both years of the study, during both the pre-nesting and nesting stages, including overlap of 50% and 95% home ranges. Overlapping home ranges only occurred with birds sharing a territory boundary. During 2004, two pre-nesting flycatchers had adjacent territories with 19% and 29% overlap of 95% home ranges and 7% and 6% overlap in core areas. Nesting birds had overlapping home ranges during both years of the study, including two birds during 2003 and four birds during 2004. Overlap of 95% home ranges averaged 19% (± 0.44) and overlap of core areas averaged 14% (± 0.06).

Habitat Use

Habitat availability and upland habitat use

I calculated habitat availability based on three measures of the area available: spider distance, kernel, and minimum convex polygon (MCP) home range estimators. The MCP and kernel estimators encompassed similar areas, and so I only report results based on MCP method, because the kernel estimator eliminated some habitat types birds used. The areas encompassed by the spider distances were significantly greater than the areas encompassed by MCPs (Kruskall Wallis Chi-square approximation =111.6, $p < 0.0001$) and so I present results for both these definitions of availability.

Because habitat availability was determined on an individual basis, flycatchers with larger home ranges had the most ”available” habitat types, whereas flycatchers with the smallest home ranges had the fewest (Kruskall Wallis Chi-square approximation =9.27, p =0.023). As a consequence, post-nesting birds had access to seven habitat types, whereas, nesting birds had access to as few as two habitat types.

Vegetation Age and Composition

Flycatchers used mature vegetation more than expected at random during all three periods of the breeding season (Fig. 7). Although immature vegetation was used less than expected, both immature and young stands were used to some degree. Upland habitat was available to flycatchers during both years of the study, by both measures of availability. However, no flycatcher was ever observed using upland habitat even when this habitat type comprised > 40% of the habitat available to some post-nesting flycatchers.

Relative use of native, exotic, and mixed mature riparian habitats was confounded by the fact that not all birds had all three vegetation types available within the area defined by spider distance or MCP. However, three of the four pre-nesting birds, four of 13 nesting birds and all post-nesting birds had more than one available mature vegetation type available to them.

Among pre-nesting birds, one bird (WIFL 1) had all three mature habitat types available and it used native habitat more than expected from availability based on spider distance but exhibited no selection when availability was based on its MCP (Table 1). Two birds (WIFL 2 and WIFL 52) had only mixed and native mature vegetation available to them and both selected for mixed habitat when availability was based on spider distance, but exhibited no selection on the basis of MCP home range (Table 1)

Four nesting flycatchers had > one mature vegetation type available to them; six flycatchers had access to only mixed mature vegetation, and two had no access to mature vegetation. One flycatcher (WIFL 21) had access to mixed and exotic mature vegetation, and selected for exotic vegetation whereas three birds had access to native and mixed mature vegetation, and selected for mixed (Table 1).

Three of the four post-nesting flycatchers had access to mixed, native and exotic mature habitats and selected for mixed vegetation based on both measures of availability. One post-nesting flycatcher had access to only mixed and native habitat, and selected for neither (Table 1).

The percent of canopy comprised of exotic vegetation did not discriminate between flycatcher locations and randomly located points (P=0.8576, Fig. 8). The logistic regression line was nearly horizontal, suggesting that flycatchers did not select for or against presence or abundance of exotic saltcedar.

DISCUSSION

Variation in home range size through the breeding season

All Southwestern Willow Flycatchers tracked during the nesting period made short movements and had home ranges under one hectare. These results are comparable to those of other studies that have described territory size for non-endangered *E. traillii* subspecies throughout the United States: 0.3 ha for *E. t. brewsteri* (Flett and Sanders), 0.4 ha for *E. t. traillii* (Prescott 1986), 0.3-0.8 *E. t.*

traillii (Walkinshaw 1966), and 1.7 ha *E. t. adastus* (Eckhardt 1979). Only one other study used telemetry to describe home range size (Bakian and Paxton 2004), finding that home ranges of male *E. t. adastus* averaged 0.8 ha. Overall, the similarity of estimates based on telemetry and spot-mapping is surprising given that telemetry based estimates of home range size for several other species were often considerably larger than those derived from mapping song perches (Hanski and Haila 1988). My telemetry-based estimates of home range size may be underestimates due to the short, three-week lifespan of the transmitters. In contrast, spot mapping estimates are often based on observations collected during the entire nesting season.

Pre-nesting birds had highly variable home range sizes, as a result of some birds using multiple habitat patches and others occupying extremely small areas. Few studies have followed radio-telemetered birds during the pre-nesting season and therefore comparison with other studies is limited. Two other telemetry studies found differences between pre-nesting and nesting movements (Pechacek 2004, Roth et al. 2004), but neither of these studies involved migratory passerine species.

A migratory passerine returning to its breeding site must make important decisions about territory selection, which will eventually affect survivorship and productivity (Brown 1969, 1975; Sergio and Newton 2003; Formica et al. 2004). Larger home ranges during the pre-nesting period are consistent with exploratory behavior undertaken to assess habitat quality (e.g. prospecting) (Reed et al. 1999, Doligez et al. 2002, 2004; Pärt and Doligez 2003). In Wild Turkeys, females that prospected over the largest area or greatest diversity of habitat types had greater reproductive success (Badyaev et al. 1996). While I could not directly address this hypothesis because of small sample sizes and lack of data on reproduction, half of the pre-nesting flycatchers I tracked assessed multiple habitat patches. Two flycatchers moved to patches occupied by other flycatchers before females occupied their defended area. One flycatcher (WIFL52) caught at the beginning of the season, traveled through four habitat patches occupied by other flycatchers, moving over 700 m before settling in one area. Early season assessment of large areas could contribute to higher reproductive output by facilitating discovery and occupancy of the highest quality territories.

Variation in pre-nesting prospecting could be explained by differences among birds in previous experience at a site. Birds returning to a familiar site may engage in less prospecting because habitat assessment may have occurred during previous years. One of the flycatchers with a very large home range in the pre-nesting season (WIFL 52) had not been recorded at Roosevelt Lake the year before I tracked it and may have been unfamiliar with the area. In contrast, a flycatcher with one of the smallest pre-nesting home ranges (WIFL 51) had bred during the previous five years in the same area at Roosevelt Lake (Newell et al. 2005).

Post-nesting birds all made long-distance movements away from their nesting area, a finding consistent with other studies of migrant passerines (Cherry 1985, Rappole and Ballard 1987, Vega Rivera et al. 1999, 2003b). Two birds left their nesting areas and moved to another site, remaining there until I lost their telemetry signal five days to two weeks later. The other two birds moved more frequently and returned to their breeding patch several times. Variation in post-nesting behavior has been described by Vega Rivera et al. (2003b) for Scarlet Tanagers (*Piranga olivacea*), ranging from establishment of new home ranges by some birds to movement back to their breeding territories by others. Bayne and Hobson (2001b) hypothesized that some post-breeding movements of radio-marked Ovenbirds (*Seiurus aurocapillus*) may have involved prospecting, which may have been the case for flycatchers as well. Flycatcher habitat is dynamic, with often dramatic annual changes in river levels and riparian plant growth. Flycatchers may need to prospect by exploring different habitats to detect changes affecting the location of high quality territories. Switzer's site fidelity model (1993) argues that animals occupying spatially and temporally variable habitat may not exhibit site fidelity, which is consistent with animals prospecting more frequently in dynamic systems to assess changes to habitat.

The one floater tracked during this study showed a preference for habitat in which other flycatchers were breeding. Although this bird did not exhibit territorial behavior anytime while monitored, he was found almost always near breeding flycatchers.

The presence of floaters may suggest saturation of breeding habitat (Smith 1978, Winker 1998). The floater was captured during 2003, a year after record-setting drought (NOAA 2003) resulted in near complete reproductive failure of the population during 2002 (Newell et al. 2003, Smith et al. 2004). Given the reduction in population size that followed, saturation of suitable breeding habitat may not be the best explanation for his behavior. Instead, this bird may have been exhibiting an alternative breeding strategy by searching for either extra-pair fertilizations (a phenomenon documented in Willow Flycatchers (Pearson 2002, *USGS unpubl. Data*), prospecting for a future territory, or unsuccessfully monitoring the area for a vacancy (Bayne and Hobson 2001a, Tobler and Smith 2004).

Exploitation of ephemeral food resources

Although some flycatchers may have moved long distances during this study to assess habitat, others moved long distances to exploit an abundant food resource (Krebs 1971). During the post-nesting period, two birds were observed foraging outside their breeding areas in habitat with temporarily high densities of aquatic insects and/or tamarisk leafhoppers (*Opsius* sp). One area had ephemeral insect flushes exploited by flycatchers during both years of the study, although involving different birds each year. Exploiting abundant food resources may be especially important during the post-nesting season when birds are staging for migration, and may explain why marked birds of other species are found outside of breeding territories (Cherry 1987, Rappole and Ballard 1987) and exhibit long movements away from breeding areas (Bayne and Hobson 2001b, Vega Rivera et al. 2003b).

Habitat use and selection

The male Southwestern Willow Flycatchers tracked during this study at Roosevelt Lake made no use of upland vegetation. This result differs from observations of *E. t. adastus* in central Utah, where > 60% of all tagged birds used upland vegetation during both years of the study (Bakian and Paxton 2004, *Bakian unpublished data*). This difference may be attributable to the wide floodplain around Roosevelt Lake, which resulted in little upland vegetation within 50 m of flycatcher breeding areas, in contrast to the central Utah study area, where a narrow canyon resulted in ample upland vegetation within 10 m of some flycatcher nests (Bakian and Paxton 2004). Upland vegetation also differed between the Utah and Arizona study areas. In Utah, vegetation consisting of mixed shrub (*Artemesia sp.*, *Ribes sp.*, *Chrysothamnus sp.*) and forest (*Picea sp.*, *Abies sp. Pseudotsuga sp.* and *Populus sp.*) may have been more attractive to flycatchers than the Sonoran Desert uplands surrounding Roosevelt Lake.

Male Southwestern Willow Flycatchers used riparian stands of all ages during all three periods of the breeding season at Roosevelt Lake, but used mature riparian vegetation most frequently, consistent with previous work that documented most breeding birds in mature habitat (Allison et al. 2003). However, all birds made some use of immature and young vegetation, which often surrounded the mature patches at Roosevelt Lake. In fact, two flycatchers used immature habitat almost exclusively during the 2004 nesting period. Because riparian vegetation grows rapidly, immature habitat may quickly increase in quality as it develops the dense canopy and thick understory that flycatchers apparently prefer. Roosevelt Lake's water levels have fluctuated markedly (from 9% capacity in 2002 to 30% capacity in 2004; SRP 2005) during the past 8 years, exposing and inundating areas of the lakebed, with an overall net increase in riparian habitat. Flycatchers have responded to this change by moving from older patches to younger patches over time (Newell et al. 2003, 2005).

Non-native saltcedar has become an important component of the riparian vegetation around Roosevelt Lake; flycatchers in this study did not strongly avoid habitats with saltcedar components. This is consistent with other recent studies that suggest saltcedar-dominated habitat is suitable for flycatchers in some areas (Durst 2004, Owen et al. *in press*, Sogge et al. *in press*). Six of the birds I studied during the nesting period were in areas dominated by a mixture of exotic and native vegetation, so much so that these were the only habitat available based on MCP and Spider distance estimates. Although some birds used native vegetation more than expected based on availability, one bird used exotic more. Habitat selection occurs at multiple spatial scales (Johnson 1980, Hutto 1985, Aebischer et al. 1993), and whether birds in this study may have selected habitat at broader scales by settling preferentially in areas dominated by one vegetation type or another was beyond the scope of this study.

Although other researchers have described major changes in habitat selection between nesting and post-nesting periods (Rappole and Ballard 1987;Vega Rivera 1999, 2003b), flycatchers at Roosevelt Lake did not shift to different habitat types at the end of the breeding season. Post-nesting birds were most frequently found in habitat patches used during the nesting period. The only shift in habitat use was increased use of immature habitats; a shift that could indicate heightened prospecting in areas that would be in later stages of development during the coming year. Just as likely, however, birds stopped in these areas while moving between breeding patches.

Management Implications

Nesting period home ranges substantially under-represented the total area used by male Southwestern Willow Flycatchers during the breeding season because pre- and post-nesting home ranges were much larger than during the nesting period. In contrast to some other neotropical migrants, flycatchers during this study did not substantially change use or selection of habitats during different periods, suggesting that habitats used during the nesting period met the demands for pre- and post-nesting periods. Although flycatchers in this study primarily used mature riparian vegetation, they also used younger habitat, suggesting that a mix of development stages should be maintained. Within mature stands, birds did not avoid areas with substantial non-native saltcedar, suggesting that extensive removal of saltcedar may not be necessary for maintaining suitable flycatcher habitat. Although flycatchers did not use upland habitats during this study, uplands may be important components of home ranges in other drainages with smaller floodplains or different upland plant communities.

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Tables and Figures

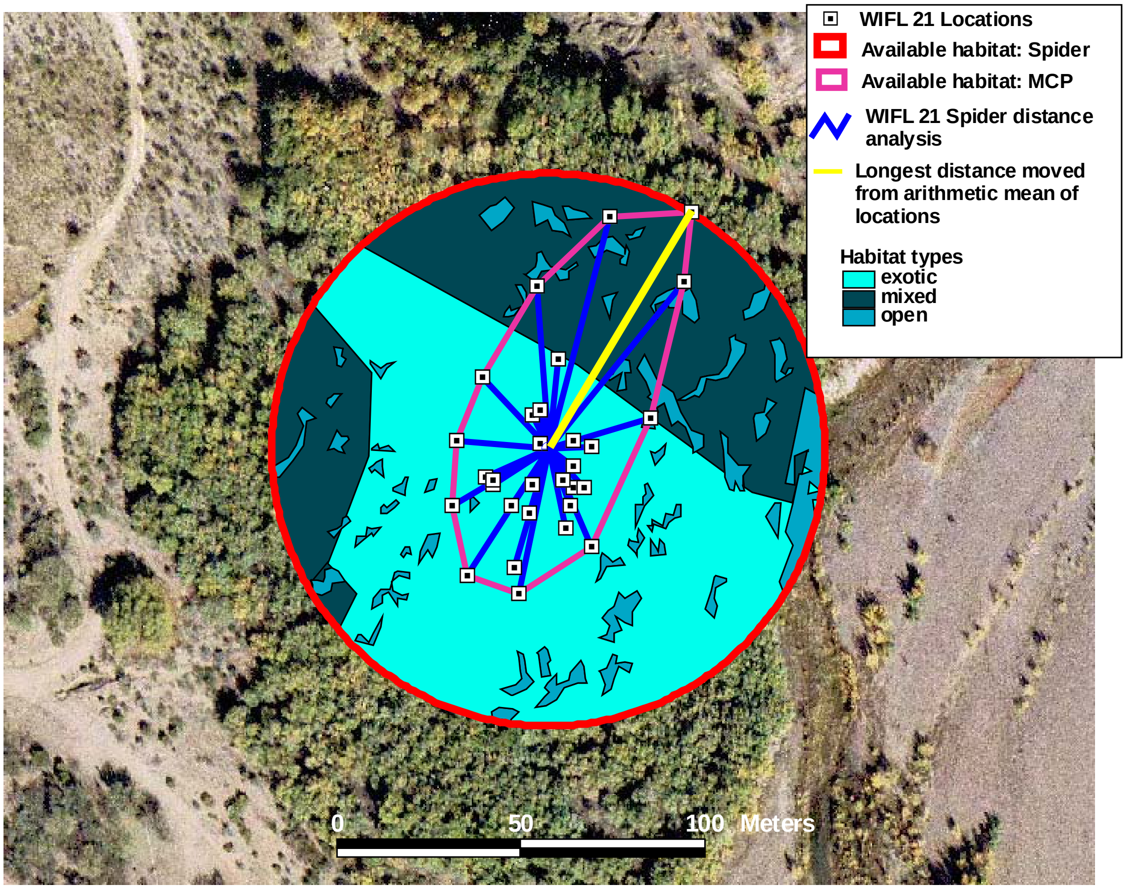

Figure 1. Habitat availability for a nesting flycatcher. Telemetry defined locations are shown by the boxes with dark circles. The spider distance analysis is shown with blue lines and the yellow line indicates the longest distance moved from the arithmetic mean of all locations. The area considered available based on spider distance is the area within the red circle and the minimum convex polygon is shown in pink. Habitat types are indicated by dark blue for mixed habitat, light blue for exotic and medium blue for open areas.

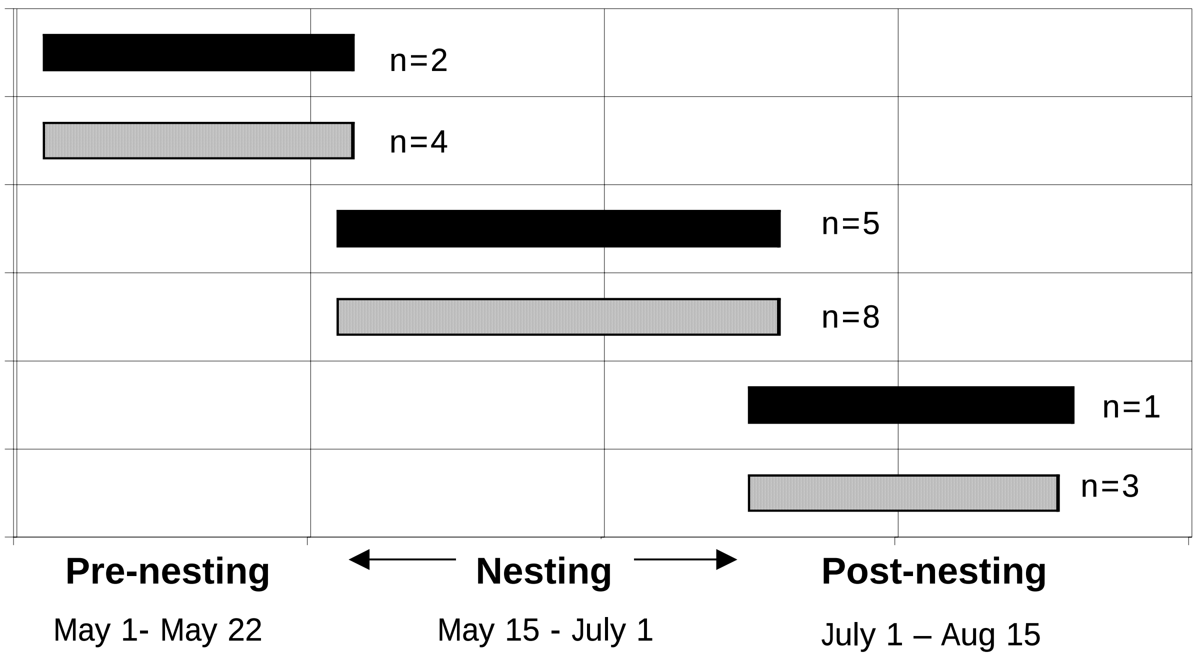

Figure 2. Breeding periods and dates birds were monitored for all male flycatchers with > 28 locations. 2003 flycatchers are shown in black, 2004 birds are dotted boxes. The X-axis represents nesting stage and the approximate dates of each breeding stage.

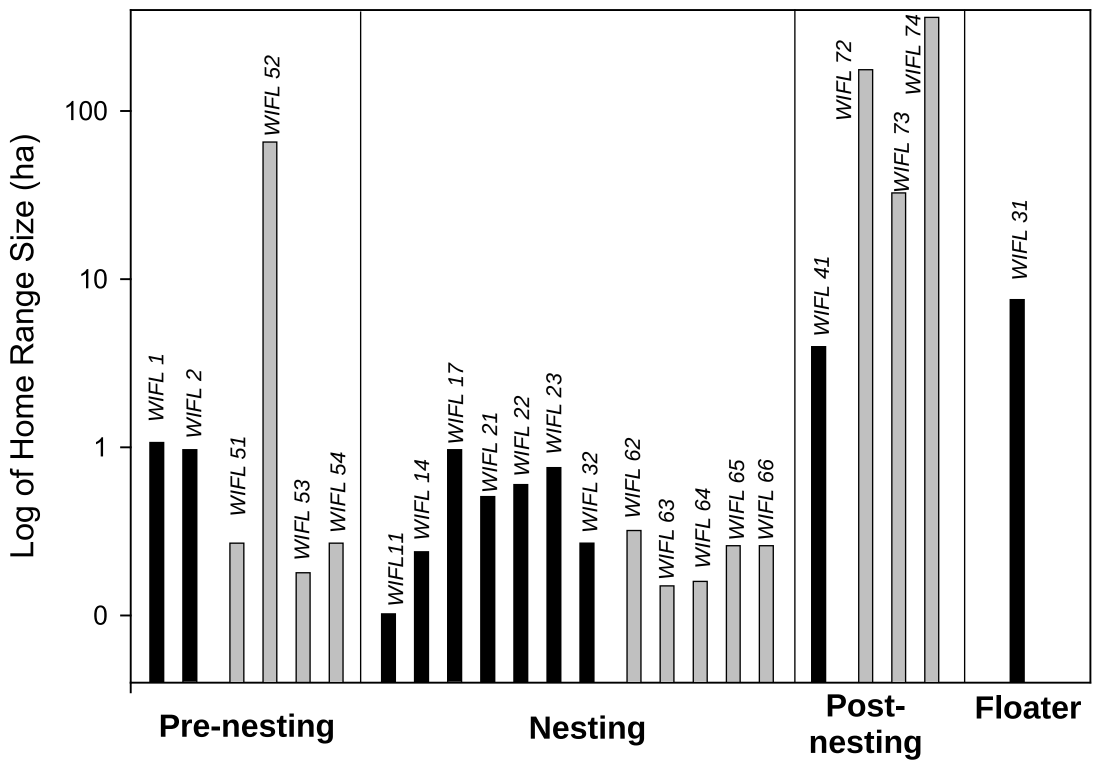

Figure 3. Log home range size (hectares) for all flycatchers with >28 locations based on nesting stage. 2003 birds = black bars, 2004 = gray bars.

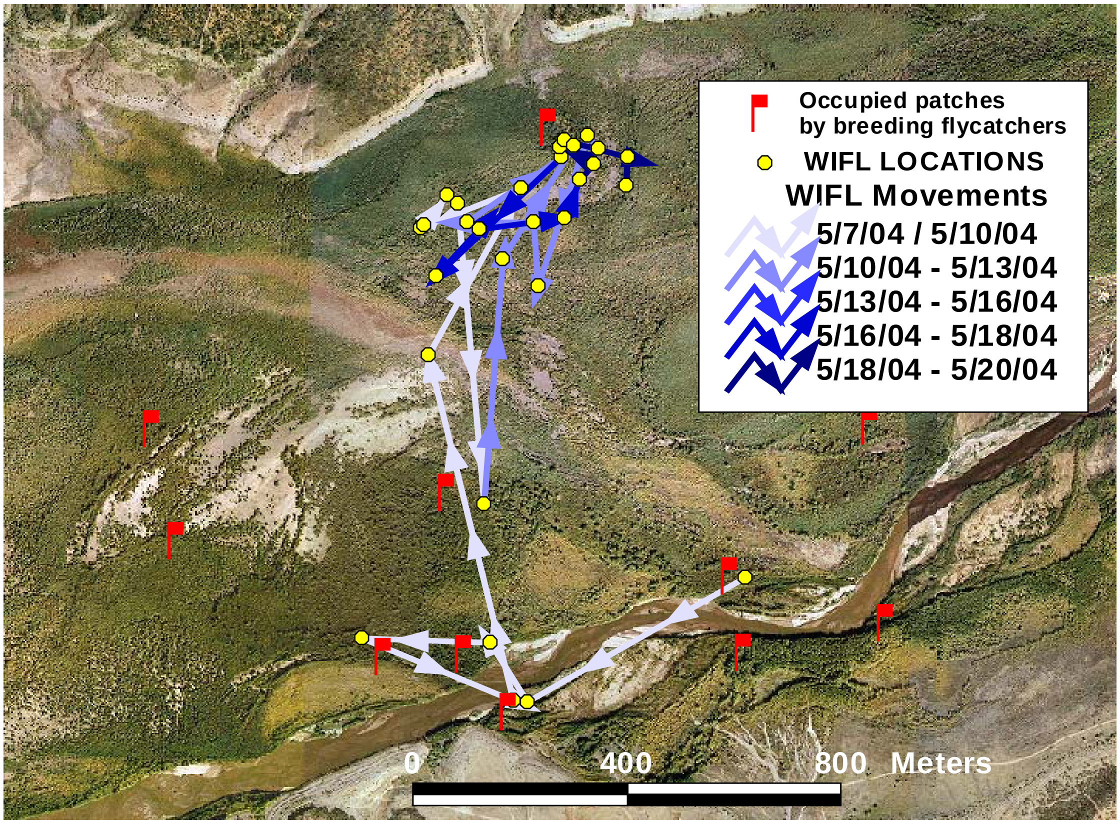

Figure 4. Movement patterns for WIFL 52, a pre-nesting flycatcher. Yellow dots indicate a location for WIFL 52. Red flags indicate occupied habitat by breeding flycatchers in 2004. Graduated blue arrows indicate the bird's movement during the time it was tracked.

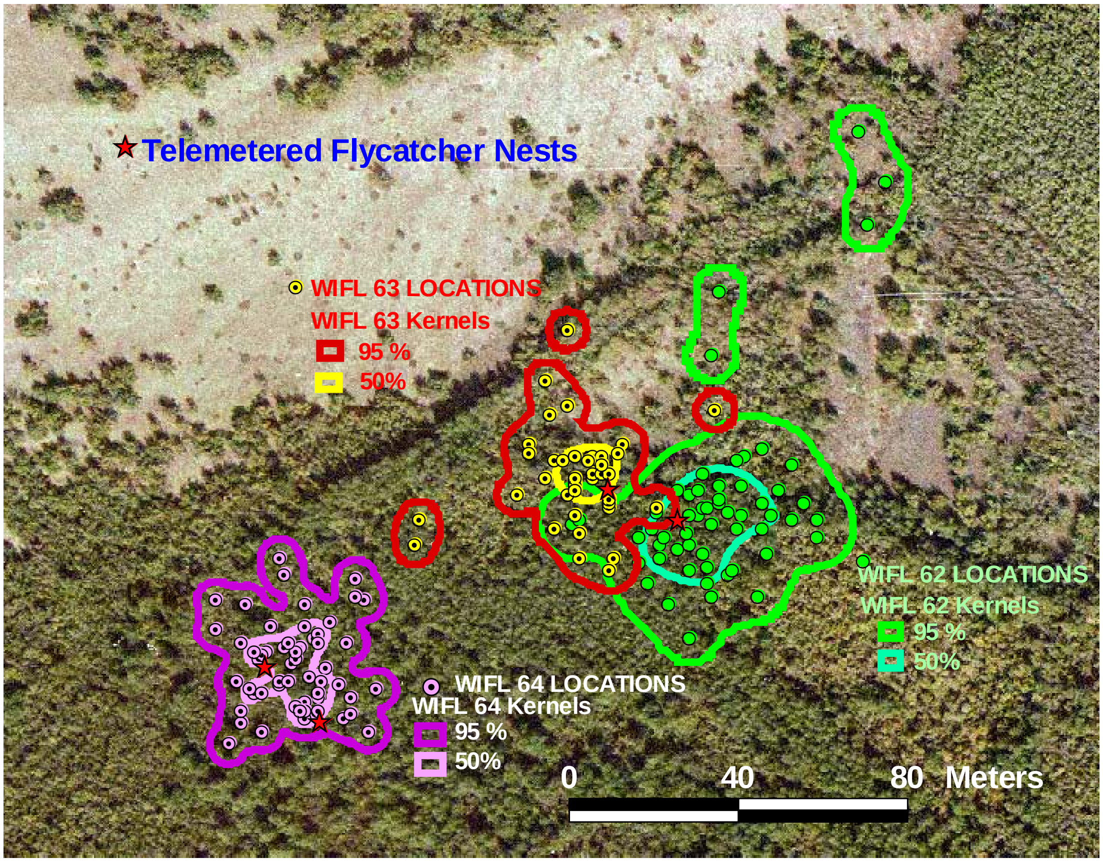

Figure 5. Home ranges (95% kernel contours) and core areas (50% kernel contours) for three male flycatchers tracked simultaneously during the nesting period of 2004. WIFL 64 locations and home range are indicated in green, WIFL 63 in red and yellow and WIFL 64 in purple.

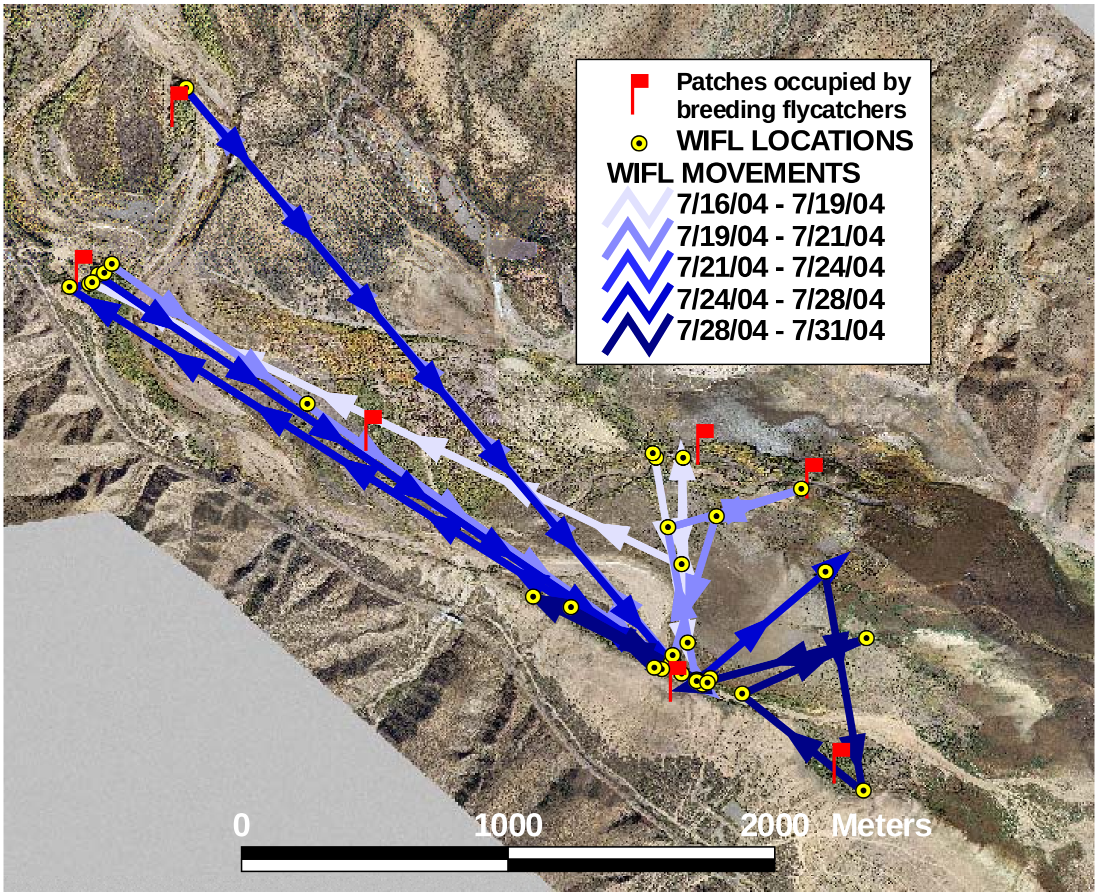

Figure 6. Movement patterns for WIFL 74, a male flycatcher followed during the post-nesting period. Yellow dots are telemetry locations and red flags indicate areas where other flycatchers bred in 2004. Blue arrows indicate movement for WIFL 74 graduated by time.

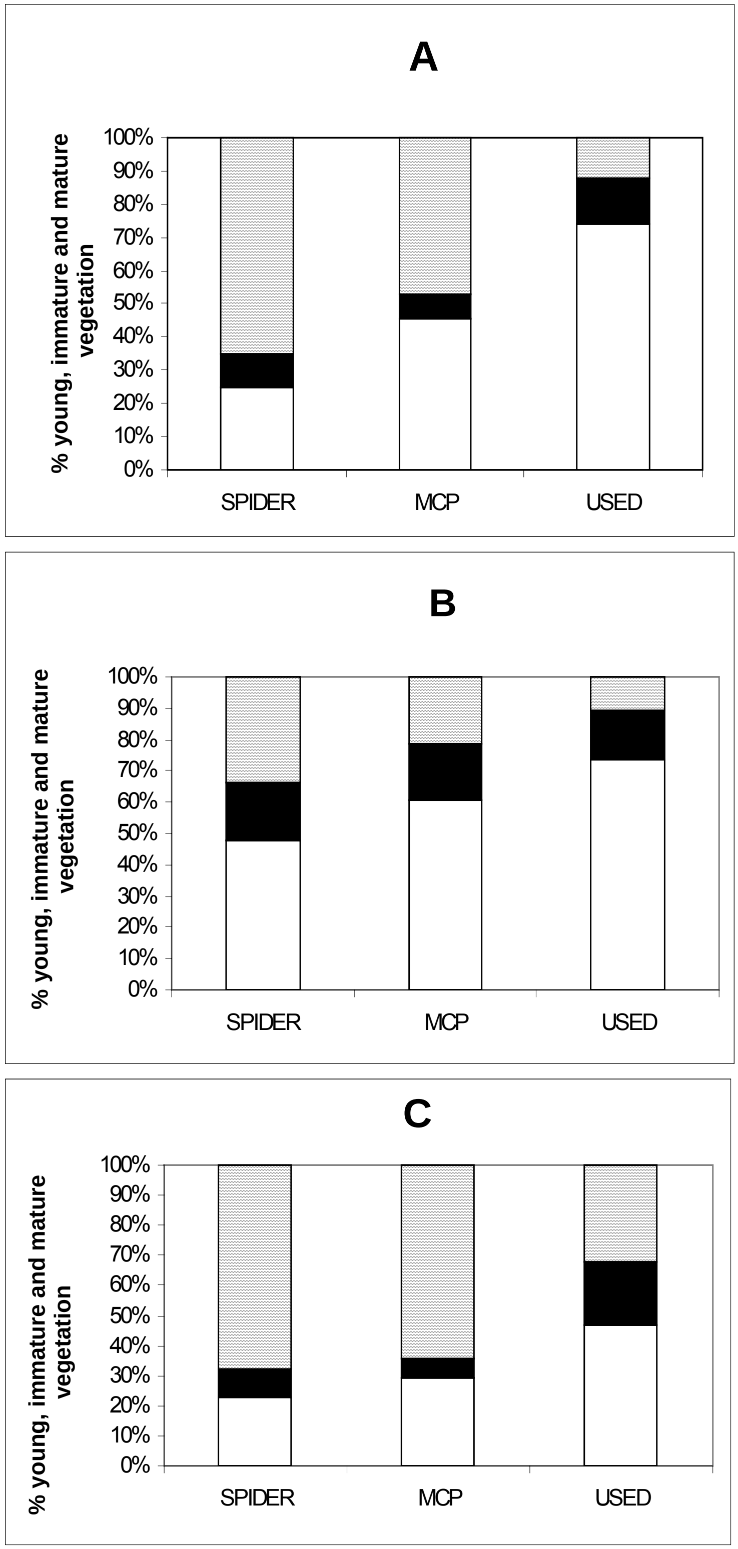

Figure 7. The amount of young (hatched), immature (black) and mature (white) riparian vegetation available in the area defined by spider distance and MCP versus the percentage of vegetation types used by male Southwestern Willow Flycatchers in the pre-nesting (A), nesting (B) and post-nesting periods (C).

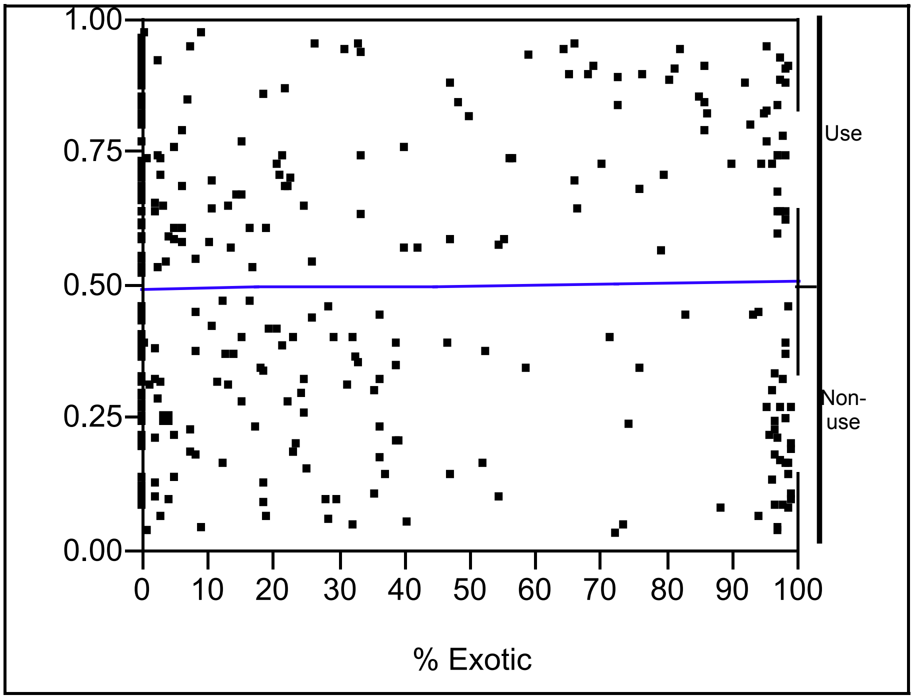

Figure 8. Proportional probability that a point was random versus a bird location relative to percent of vegetation canopy comprised of exotic saltcedar. The X-Axis indicates the percent of exotic within the canopy and the Y-axis shows the probability of finding a nesting Southwestern Flycatcher at each exotic canopy composition. The logistic regression model was not significant (P= 0.8576).

Table 1. Stage within the breeding season, available mature habitat type, and percentage of each habitat used and available is listed. Only significant availability is shown for each habitat type. The X^2 for both Spider and MCP availabilities are given. Selection is given for significant availability only and the P value. NS= Not significant. Dashes indicate habitat not available.

STAGE	Available Mature Types	n=	Percentage of Native used	Percentage of Native Available	Percentage of Exotic used	Percentage of Exotic Available	Percentage of Mixed used	Percentage of Mixed Available	X^2 SPIDER	X^2 MCP	SELECTION
Pre-nesting	Native, Exotic or Mix	1	88.73%	62.62% Spider	1.41%	19.81% Spider	9.86%	17.57% Spider	22.28	1.81	SPIDER P <0.0001 Native; MCP NS
Pre-nesting	Native or Mix	2	13.54%	61.26% Spider	—	—	86.46%	38.74% Spider	27.4928	3.83	SPIDER P <0.0001 Mix, MCP NS
Nesting	Native or Mix	3	35.57%	49.57% Spider	—	—	64.34%	50.42% Spider	11.08	9.91	SPIDER P= 0.0009 Mix, MCP P=0.0016 Mix
Nesting	Exotic or Mix	1	—	—	86.21%	61.48% Spider; 63.55% MCP	13.79%	38.52% Spider; 36.45% MCP	7.48	6.429	SPIDER P= 0.006 Exotic, MCP P= 0.011 Exotic
Post-nesting	Native, Exotic or Mix	3	9.88%	39.05% Spider; 21.19% MCP	0	26.89% Spider; 10.78% MCP	90.12%	34.06% Spider; 68.03% MCP	114.16	19.43	SPIDER and MCP P< 0.0001 Mix
Post-nesting	Exotic or Mix	1	—	—	71.43%	NS	28.57%	NS	0.07	0.275	Both NS P> 0.05

Appendix 1

Table 1. Home range sizes based on fixed Kernel 95% and 50% contours, longest distance moved between points and mean distance between consecutive points. Bird #, Year tracked and Breeding Stage are also given.

			Fixed Kernel			
Breeding Stage	**Year**	**Bird #**	**95% (in ha)**	**50% (in ha)**	**Longest distance between points (in meters)**	**Mean (+- SE) of consecutive movements**
Pre-nesting	2003	WIFL 1	1.07	0.28	819	63 (16)
	2003	WIFL 2	0.97	0.20	390	67 (12)
	2004	WIFL 51	0.27	0.05	62	20
	2004	WIFL 52	65.44	10.42	722	239
	2004	WIFL 53	0.18	0.02	42	18
	2004	WIFL 54	0.27	0.05	99	21
Nesting	2003	WIFL 11	0.10	0.02	33	16 (1)
	2003	WIFL 14	0.24	0.03	115	27 (3)
	2003	WIFL 17	0.97	0.16	144	44 (5)
	2003	WIFL 21	0.51	0.07	89	34 (22)
	2003	WIFL 22	0.60	0.04	76	35 (3)
	2003	WIFL 23	0.76	0.11	127	38 (7)
	2003	WIFL 32	0.27	0.04	170	24 (4)
	2004	WIFL 62	0.32	0.05	99	26
	2004	WIFL 63	0.15	0.01	40	18
	2004	WIFL 64	0.16	0.03	37	14
	2004	WIFL 65	0.26	0.05	123	22
	2004	WIFL 66	0.26	0.03	50	18
Post-nesting	2003	WIFL 41	3.91	0.46	1129	94 (22)
	2004	WIFL 71	4.07	0.62	190	83
	2004	WIFL 72	176.34	47.4	2341	161
	2004	WIFL 73	32.63	4.69	1275	175
	2004	WIFL 74	360.05	46.43	2851	756
Floater	2003	WIFL 31	7.57	1.79	549	91 (14)

Appendix 2: Locations and home range estimates for tele-metered Southwestern Willow Flycatchers at Roosevelt Lake, AZ

The following pages contain home range information for flycatchers telemetered in 2003 and 2004 at Roosevelt Lake, Arizona. Home ranges are shown with the fixed kernel method for male flycatchers with at least 28 locations collected. The fixed kernel method was calculated using 95% and 50% contours. The 95% kernel contour is shown in the solid blue color, and the 50% kernel contour is shown in the solid green color. Bird locations are shown with a circle containing a black dot. The location of active nests (active while the flycatcher was being tracked) is indicated by a purple star. The 2003 and 2004 Willow Flycatcher territories are shown with the small red flag. The birds are shown by breeding stage with pre-nesting first, nesting second, and post-nesting third and the floater last. Home ranges are followed by movement patterns. Movement patterns for all birds that moved over 600 m are shown with graduated colors by time.