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Author(s) :Lisa A. Ellis, Shaylon D. Stump, and Dominique M. Weddle

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Southwestern Willow Flycatcher Population and Habitat Response to Reservoir Inundation

LISA A. ELLIS,[1,2] *Research Biologist, Arizona Game & Fish Department, 5000 W Carefree Highway, Phoenix, AZ 85086, USA*
SHAYLON D. STUMP, *Research Biologist, Arizona Game & Fish Department, 5000 W Carefree Highway, Phoenix, AZ 85086, USA*
DOMINIQUE M. WEDDLE, *Research Biologist, Arizona Game & Fish Department, 5000 W Carefree Highway, Phoenix, AZ 85086, USA*

ABSTRACT One of the largest known populations of the federally endangered southwestern willow flycatcher (*Empidonax traillii extimus*) occurs at Roosevelt Lake, Arizona, USA. Modifications to Roosevelt Dam, completed in 1996, raised the height of the dam and resulted in a high probability of willow flycatcher habitat inundation within the reservoir's conservation pool. We collected habitat measurements and monitored 922 willow flycatcher nests from 1996 to 2006 to investigate effects of inundation on willow flycatcher habitat and subsequent changes in nest success, productivity, and distribution. Inundation of willow flycatcher habitat at Roosevelt Lake occurred in 2005, changing the location and amount of suitable breeding habitat and significantly altering habitat structure (e.g., thinner vegetation, more canopy gaps) of formally occupied nest sites. The willow flycatcher population at Roosevelt Lake decreased 47% from 209 territories in 2004 to 111 territories in 2006 in response to habitat changes. Willow flycatchers made fewer nesting attempts and nest success rates were significantly lower during inundation (2005 and 2006: 45%) than preinundation (1996–2004: 57%). Combined, these factors negatively affected the population's productivity during inundation. Although inundation caused extensive vegetation die-off, we did observe regeneration of vegetation in some areas at Roosevelt Lake in 2006. The Roosevelt Lake population remains one of the largest willow flycatcher populations in the state and territory numbers remain high enough that the population may not suffer long-term effects if sufficient suitable habitat continues to exist during the cycle of inundation and regeneration. Reservoir managers may be able to develop dam management guidelines that reduce damage to habitat, encourage habitat growth, and mimic the dynamic nature of unaltered riparian habitat. These guidelines can be implemented, as appropriate, at reservoirs throughout the willow flycatcher's range. (JOURNAL OF WILDLIFE MANAGEMENT 73(6):946–954; 2009)

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KEY WORDS *Empidonax traillii extimus*, nest success, productivity, reservoir inundation, riparian habitat, Roosevelt Lake, southwestern willow flycatcher.

The federally endangered southwestern willow flycatcher (*Empidonax traillii extimus*) is a riparian-obligate breeder occurring in a wide range of elevations from sea level in California to >2,500 m in Arizona (USA; U.S. Fish and Wildlife Service [USFWS] 1995). Whereas other subspecies of the willow flycatcher may breed away from surface water (Bent 1942, King 1955, McCabe 1991), the southwestern subspecies only breeds near surface water or saturated soil along rivers and streams, reservoirs, cienegas, and other wetlands in the southwestern United States and northern Mexico (Sogge and Marshall 2000; USFWS 2002, 2005; Allison et al. 2003; Paradzick and Woodward 2003). The southwestern willow flycatcher (willow flycatcher) breeds in riparian tree and shrub communities that vary in vegetation height and structure, patch size, and species composition, but most breeding flycatchers are found in patches of dense contiguous vegetation or a mosaic of dense vegetation interspersed with multiple small openings (creating a mosaic of forest and openings; Sogge and Marshall 2000; USFWS 2002, 2005; Allison et al. 2003; Paradzick and Woodward 2003).

Riparian habitat in which the willow flycatcher breeds is dynamic and recycles naturally when hydrologic and geomorphic features are intact (reviewed in Poff et al. 1997). As willow flycatcher habitat matures past suitability, drought, fire, and scouring floods assist in habitat recycling by clearing older unsuitable trees and snags. Habitat is then renewed by sediment and seed deposition (by floods or partial inundation), periodic inundation, and groundwater recharge (Periman and Kelly 2000; Sogge and Marshall 2000; USFWS 2002, 2005; Allison et al. 2003). Over the past century, this natural cycling and associated habitat continuity has been disrupted by modifications to natural flow regimes due to groundwater pumping, flood control projects, water diversions, and dam operations (Poff et al. 1997; Periman and Kelly 2000; Marshall and Stoleson 2000; USFWS 2002, 2005). Although willow flycatchers are well-adapted to ephemeral conditions, up to 90% of their historical riparian habitat has been lost, altered, or degraded (Governor's Riparian Habitat Task Force 1990, Ohmart 1994). Remaining habitat patches are smaller, more isolated, and more susceptible to stochastic events; thus, willow flycatchers are more prone to local extirpation.

Reservoir inundation can cause a major loss of habitat close to the river or reservoir (Baxter and Glaude 1980, Reitan and Thingstad 1999). The extent to which inundation affects habitat is dependent upon timing, degree, and length of inundation (reviewed in Gill 1970; Warren and Turner 1975, Stevens and Waring 1985, Reitan and Thingstad 1999). Loss or degradation of habitat due to reservoir inundation can cause declines in some bird populations, species richness, and nesting success, although some species (e.g., shorebirds, waterfowl) may benefit from improved feeding conditions (Fleshman and Kaufman 1984, Reitan and Thingstad 1999). Willow flycatchers are riparian-obligate breeders that frequently associate with

[1] *E-mail: lisa_ellis@fws.gov*
[2] *Present address: United States Fish and Wildlife Service, Sacramento Field Office, 2800 Cottage Way, Sacramento, CA 95825, USA*

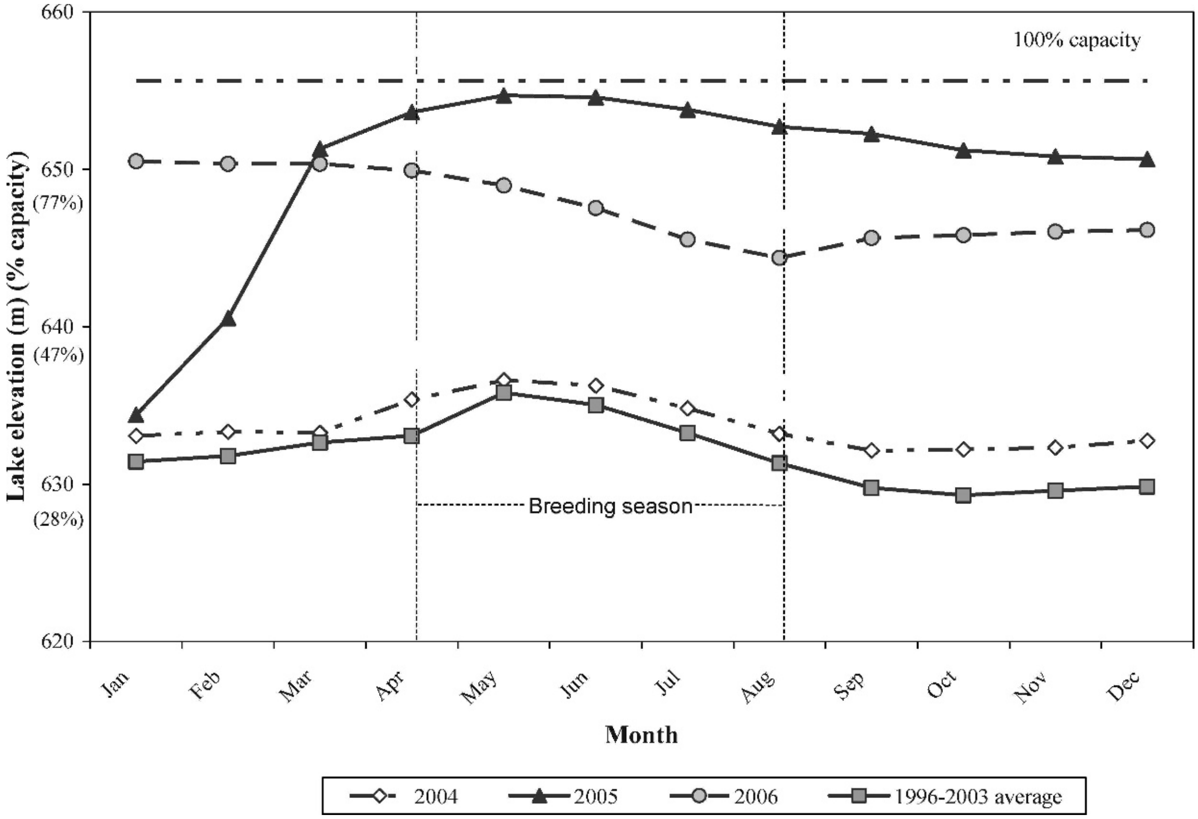

Figure 1. Average monthly reservoir elevations for Roosevelt Lake in central Arizona, USA, for 2004, 2005, 2006, and average lake elevation from 1996 to 2003 (T. Skarupa, Salt River Project, personal communication). Each point represents elevation of the reservoir on the first day of each month.

reservoirs and, therefore, could experience habitat loss due to inundation.

As natural riparian habitat declines in the Southwest, human-made reservoirs are becoming more important breeding habitat for riparian birds. One of the largest populations of willow flycatchers occurs at Roosevelt Lake, a reservoir in Arizona. The population likely plays an important role in regional population dynamics and genetic diversity, and may serve as a source population to smaller populations (USFWS 1996). The first record of willow flycatchers and suitable habitat at the reservoir is from 1993 when willow flycatcher surveys began (Muiznieks et al. 1994). Since then, riparian habitat suitable for willow flycatcher nesting developed within the conservation pool, primarily near the inflows. Modifications to Roosevelt Dam occurred in 1996 and raised the height of the dam 23 m, increasing the top of the conservation pool from 651 m to 656 m. Water levels at Roosevelt Lake fluctuated in the 1990s and early 2000s, but remained well below capacity due to low rainfall (Fig. 1).

Inundation of riparian habitat within the new conservation pool of Roosevelt Lake occurred in May 2005 when the reservoir filled to 655 m (96% capacity; Fig. 1). As a result, the reservoir completely or partially inundated almost all habitat occupied in 2004, rendering formally occupied habitat largely unsuitable in 2005, which caused a dramatic change in the quantity, quality, and distribution of available habitat. Our objectives were to document changes in habitat and subsequent changes in willow flycatcher distribution, nest success, and productivity as a result of reservoir inundation.

STUDY AREA

We conducted our study at 2 breeding areas in central Arizona: Salt River and Tonto Creek (Fig. 2). Salt River and Tonto Creek were located approximately 25 km apart (distance varied based on reservoir elevation) and were the primary inflows to Roosevelt Lake, a reservoir, on the Tonto National Forest in Gila County. The Salt River study area was a perennial 15-km reach of the river that flowed into the southeastern end of Roosevelt Lake. The Tonto Creek study area was a 16-km reach of creek that flowed into the northwestern end of Roosevelt Lake; flows were intermittent and dependent on spring snowmelt and summer monsoon rains, causing it to frequently dry late in the breeding season. Study areas were comprised of United States Forest Service (Tonto National Forest) and private land.

Each study area was composed of numerous discrete vegetation patches that varied in vegetation composition and age. Riparian habitat was classified as Sonoran Riparian Deciduous Forest (Minckley and Brown 1994) and habitat composition ranged from monotypic stands of native broadleaf trees, to stands of mixed native and exotic, to nearly monotypic stands of exotic tamarisk (*Tamarix ramosissima*).

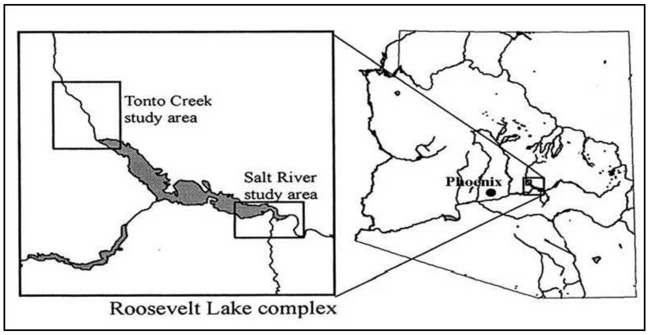

Figure 2. Location of southwestern willow flycatcher study areas at the Roosevelt Lake complex (Tonto Creek and Salt River study areas) in central Arizona, USA, 1996–2006.

METHODS

Surveys and Movement

Each year (1996–2006), we surveyed all suitable breeding habitat (Sogge and Marshall 2000; USFWS 2002, 2005; Allison et al. 2003; Paradzick and Woodward 2003) within each study area for which we obtained landowner permission. Surveys followed a standardized tape-playback protocol using the willow flycatcher's song to elicit responses (Tibbitts et al. 1994, Sogge et al. 1997). We performed one tape-playback survey at each site in each of the following 3 survey periods: 15–31 May, 1–21 June, and 22 June–10 July. We performed surveys ≥ 5 days apart, from 1 hour prior to sunrise to 1000 hours, the time of day when birds were most active.

In accordance with survey protocol, we noted general habitat characteristics at each study area, including predominance of native or exotic vegetation, predominant tree species, and average canopy height.

We identified territories based on these surveys and collected Universal Transverse Mercator coordinates of all territories. We created maps in ArcGIS 9.2 to depict changes in willow flycatcher territory distribution in 2004, 2005, and 2006 in response to inundation in 2005 and continuing inundation and postinundation habitat changes in 2006.

Nest Monitoring

We located and monitored nests each year (1996–2006) using the Southwestern Willow Flycatcher Nest Monitoring Protocol (Rourke et al. 1999). Once we detected a willow flycatcher on a survey, we located nests by watching adults return to a nest or by systematically searching suspected nest areas. We monitored nests every 2–4 days. During incubation, we observed nest contents directly using a mirror-pole or miniature video camera. After hatching, we confirmed the number of nestlings using these same techniques. When nests were too high for the use of a mirror-pole or camera, we visually confirmed the number of nestlings with binoculars (i.e., beaks visible above rim of the nest). Once we confirmed nestlings, we observed nests from a distance to reduce the risk of attracting predators or causing premature fledging. If we observed no activity at a previously active nest, we checked the nest directly to determine nest contents and searched the general area to locate possible fledglings or evidence of depredation.

We considered a nest successful if we documented any of 4 conditions 1) we visually confirmed ≥ 1 young fledging from the nest or located near the nest; 2) we observed adults feeding fledglings; 3) parents behaved as if dependant young were nearby (defensive behavior or ad agitated) when the nest was empty; or 4) we observed nestlings in the nest within 2 days of the estimated fledge date (fledging considered to occur at 12 days; Rourke et al. 1999). Based on observations of willow flycatcher nestlings successfully fledging at 10 days of age during our study, we assumed that nestlings successfully fledged if we observed them in the nest within 2 days of the estimated fledge date. We did not uphold this assumption if subsequent visits to the territory provided evidence that fledging did not occur (e.g., building or incubation dates for a renest contradicted the estimated fledge date). We considered the first 2 of these 4 conditions confirmed fledging, whereas we considered the last 2 presumed fledging; we designated all as successful for our analyses.

We considered a nest to have failed if we documented any of 5 outcomes: 1) we found the nest empty or destroyed >2 days prior to the estimated fledge date (depredated); 2) the nest fledged no willow flycatcher young but contained brown-headed cowbird (*Molothrus ater*) eggs or young (parasitized); 3) the female deserted the nest with eggs or nestlings remaining (deserted); 4) the female incubated the entire clutch unsuccessfully for >20 days (infertile); or 5) the nest failed due to other reasons such as weather or human disturbance (other). We designated an unknown outcome if we could not determine success or failure (generally due to infrequent visits to a nest).

We performed 2 sets of analyses: 1) we compared nests in noninundated habitat with nests in partially inundated habitat in 2005 and 2006 (we pooled yr to increase sample size); and 2) we compared nests preinundation (1996–2004) with nests during inundation (2005–2006). For each set of analyses, we compared simple nest success (excluding nests with unknown outcomes), first-egg day, clutch size, and productivity (no. of fledges/nest with known outcome) of nests using chi-square tests (nest success) and *t*-tests (other variables). We also compared productivity of successful nests using a *t*-test. We were not able to determine some variables (e.g., first-egg day, clutch size) for all nests because of the stage the nest was in when we located the nest (i.e., during the nestling stage). The first set of tests allowed us to examine effects of inundation on individual nests, whereas the second set of tests allowed us to examine overall effects of inundation at a landscape scale.

We examined whether nesting in inundated habitat increased the rate of brown-headed cowbird parasitism or the proportion of failed nests that were depredated by comparing nests in noninundated habitat and nests in partially inundated habitat in 2005 and 2006 using chi-square tests. We repeated the analyses comparing nests preinundation (1996–2004) and nests during inundation (2005–2006).

Table 1. Habitat variables measured at southwestern willow flycatcher nest sites in 2004 (preinundation) and in 2006 (during inundation), Roosevelt Lake, Arizona, USA.

Variable	Definition
Nest ht	Distance (m) from the ground to the rim of the nest
Ht of nest tree	Ht (m) of the tree where the nest was built
Dbh of nest tree	Dbh (cm) of nest tree
Distance to water	Horizontal distance (m) from nest to water or saturated soil
Distance to canopy gap	Horizontal distance (m) from nest to the nearest $\geq$1-m^2 gap in canopy foliage at the ht of the nest
Ht of canopy	Estimated average ht (m) of the top of the canopy within an 11.3-m radius of the nest
% canopy cover	Average of % canopy cover measured with a densiometer 1 m N and 1 m S from the nest
Distance to nearest broadleaf	Horizontal distance (m) from nest to the edge of the nearest broadleaf tree (i.e., native deciduous tree such as cottonwood or willow)

Because we pooled years and identification of all individuals was not possible, there is a lack of independence of some observations. Paxton et al. (2007) conducted a study concurrent with ours and estimate an average return rate of 55% and detection probability of 78% of this willow flycatcher population; therefore, many birds were present for multiple years of our study.

Habitat and Vegetation Characteristics

We collected vegetation data at nest sites in 2004 (Table 1). In 2006, we returned to accessible 2004 nest sites that inundated in 2005 and remeasured variables to determine the degree to which inundation changed the nest site. These variables captured habitat components that would have been affected by inundation (i.e., distance to water, distance to nearest canopy break, ht of canopy, % canopy cover, and distance to nearest broadleaf tree). We selected these variables, with the exception of distance to water, as indicators of vegetation density, which has been found to be a strong predictor of willow flycatcher occupancy (Hatten and Paradzick 2003, Paxton et al. 2007). We also included some variables we believed would not change substantially over the course of 1 year due to natural causes (i.e., ht of nest, ht of nest tree, and dbh of nest tree) as a way to determine whether differences were due to observer error. We selected these variables because their physical characteristics did not lend them to change at an accelerated rate due to inundation. We were not able to remeasure all variables at all 2004 nest sites because some nests washed away and some nest trees had fallen.

We compared measurements collected from 2004 nests with measurements taken in 2006 at the same nest sites using paired *t*-tests. Tests were 2-tailed for variables that we did not expect to differ and 1-tailed for variables for which we had a directional prediction. We predicted no change in height of nest, height of nest tree, or diameter at breast height of nest tree. We predicted decreases in distance to water, distance to nearest canopy break, and percent of canopy cover and an increase in distance to nearest broadleaf tree. We intended for measurements of distance to nearest canopy break, percent of canopy cover, and distance to nearest broadleaf tree to capture decreases in habitat density, cover, and presence of native species. In 2006, inundation caused extensive vegetation die-off, which resulted in the nearest broadleaf tree being >30 m away and difficult to detect. Therefore, we recorded >30 m, which caused our sample size for distance to broadleaf tree to be small. By changing the >30 m to 30 m (as a min.) we were able to test our 1-tailed prediction.

RESULTS

Surveys and Movement

Number of territories at the reservoir decreased 27% from 209 territories in 2004 to 153 territories in 2005. The number of territories at the reservoir decreased again in 2006 by 27% from 153 territories in 2005 to 111 territories in 2006. Overall, from 2004 to 2006, willow flycatcher territories decreased 47% at Roosevelt Lake (Salt River study area: 64%, Tonto Creek study area: 12%).

During inundation in 2005, willow flycatchers at both the Salt River and Tonto Creek study areas moved to habitat upstream of areas occupied prior to inundation (Figs. 3, 4).

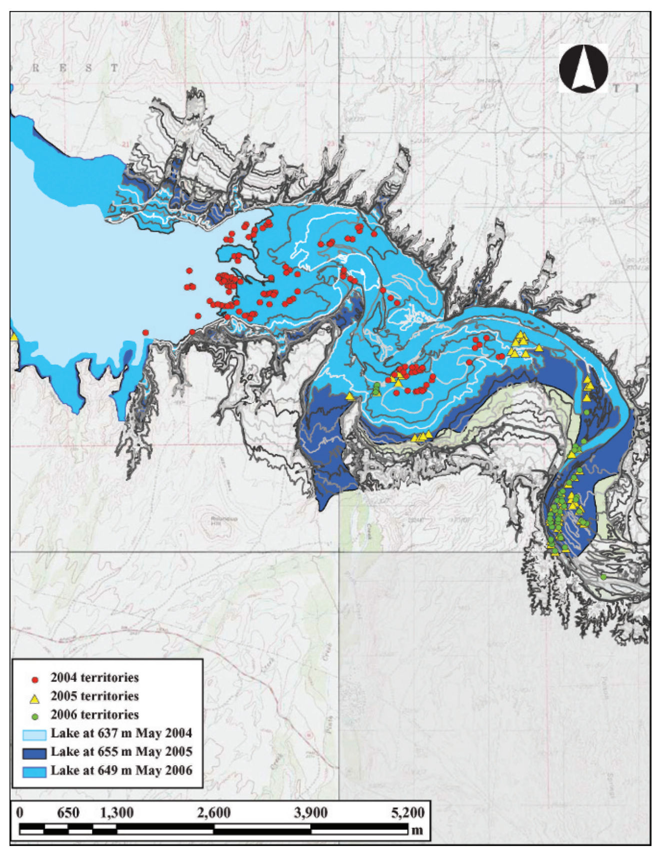

Figure 3. The Salt River study area at the Roosevelt Lake complex in central Arizona, USA, and approximate reservoir levels and southwestern willow flycatcher territory locations during 2004, 2005, and 2006.

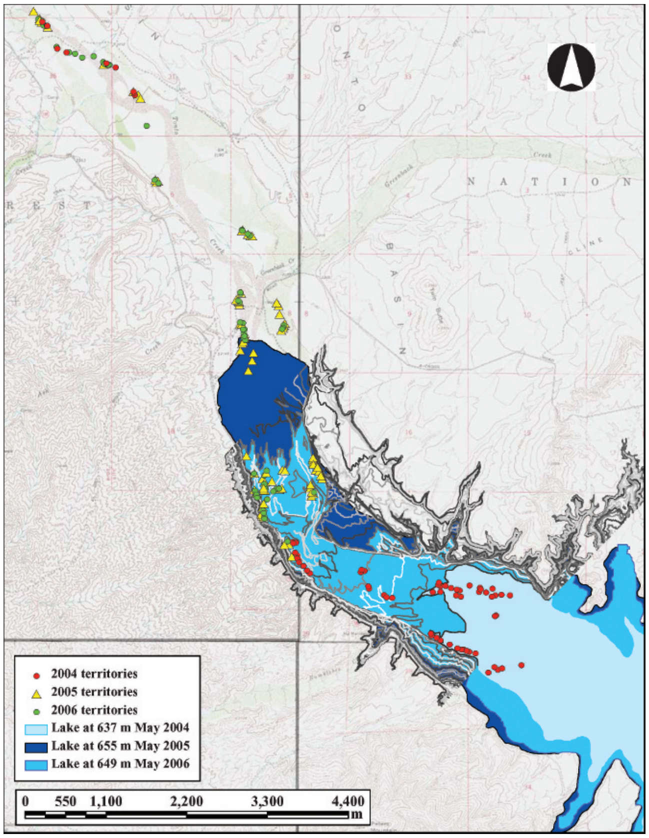

Figure 4. Tonto Creek study area at the Roosevelt Lake complex in central Arizona, USA, and approximate reservoir levels and southwestern willow flycatcher territory locations during 2004, 2005, and 2006.

Habitat closest to the reservoir that supported most willow flycatcher territories in 2004 was inundated and supported zero territories in 2005. Habitat upstream of the reservoir was partially inundated and territory numbers decreased in 2005. Willow flycatchers occupied habitat even farther upstream for the first time or for the first time since the early 2000s, presumably due to the presence of wet channels and moist soil.

In 2006, willow flycatcher territories continued to decline in habitat closest to the reservoir. As in 2005, inundated habitat did not support willow flycatchers. Territory numbers also generally declined in partially inundated habitat. Willow flycatchers continued to occupy habitat farthest from the reservoir that did not inundate.

Nest Monitoring

In 2004, we monitored 131 nest attempts at Roosevelt Lake. In 2005, this number increased slightly to 136 then declined in 2006 to 82. Using ArcGIS 9.2, we estimated that 73% of the 2004 Roosevelt Lake nests (75% of Salt River, 70% of Tonto Creek territories) were in locations inundated in 2005 based on the May 2005 reservoir elevation (T. Skarupa, Salt River Project, personal communication). In 2005, 63% of nests were located in partially inundated areas at the time they were built (95% of Salt River territories and 40% of Tonto Creek territories). In 2006, 12% of nests were located in partially inundated areas when built (15% of Salt River territories and 10% of Tonto Creek territories).

During inundation (2005 and 2006), we detected no difference in the proportion of successful nests in noninundated habitats (47.5%, $n = 118$) and nests in partially inundated habitat (42.5%, $n = 94$; $\chi^2_1 = 0.51$, $P = 0.48$). However, a higher proportion of nests were successful preinundation (1996–2004: 56.6%, $n = 680$) than during inundation (2005–2006: 45.2%, $n = 212$; $\chi^2_1 = 8.36$, $P = 0.004$).

We detected no difference between the first-egg day (16 Jun vs. 17 Jun, $P = 0.83$), clutch size (2.7 vs. 2.8 eggs, $P = 0.37$), productivity of all nests (1.1 vs. 1.0 fledges, $P = 0.46$), or productivity of successful nests (2.4 vs. 2.4 fledges, $P = 0.82$) during inundation for nests in noninundated habitats and nests in partially inundated habitat (Table 2). We detected no difference between the first-egg day (17 Jun vs. 16 Jun, $P = 0.84$) or clutch size (2.8 vs. 2.8 eggs, $P = 0.67$) between preinundation (1996–2004) and during inundation nests (2005–2006; Table 3). All nests produced more fledglings (1.4 vs. 1.1 fledglings, $P = 0.003$) preinundation than during inundation, but we detected no difference (2.5 vs. 2.4 fledglings, $P = 0.47$) for successful nests between preinundation and during inundation (Table 3).

We detected no difference between the rate of parasitism of nests in noninundated habitat (4.9%, $n = 118$) and nests in partially inundated habitat during inundation years (2005 and 2006: 5.3%, $n = 94$; $\chi^2_1 = 0.01$, $P = 0.94$). We detected no difference between the proportion of failed nests that were depredated between nests in noninundated habitat (71.0%, $n = 62$) and nests in partially inundated habitat (81.5%, $n = 54$; $\chi^2_1 = 1.74$, $P = 0.18$). We detected no difference between the rate of parasitism of preinundation nests (1996–2004: 4.4%, $n = 680$) and during inundation nests (2005–2006: 4.6%, $n = 212$; $\chi^2_1 = 0.1$, $P = 0.64$). We also detected no difference between the proportion of failed nests that were depredated between preinundation nests (77.3%, $n = 295$) and during inundation nests (75.9%, $n = 116$; $\chi^2_1 = 0.09$, $P = 0.76$).

Habitat and Vegetation Characteristics

We found no differences in height of nest (average difference of 0.46 m, $P = 0.21$), height of nest tree (average difference of 0.7 m, $P = 0.11$), or diameter at breast height of nest tree (average difference of 0.12 m, $P = 0.66$) between 2004 and 2006 measurements at 2004 nest sites (Table 4). Distance to water (average difference of 184.1 m, $P < 0.001$), distance to nearest canopy break (average difference of 6.2 m, $P < 0.001$), height of canopy (average difference of 2.04 m, $P < 0.001$), and percent of canopy cover (average difference of 59.4%, $P < 0.001$) were less in 2006 than in 2004. Distance to nearest broadleaf tree was an average of 14 m more in 2006 than in 2004 ($P < 0.001$).

DISCUSSION

From 1996 to 2006, we documented changes in willow flycatcher distribution, nest success, productivity, and habitat as these variables related to the 2005 inundation of

Table 2. Univariate *t*-tests on nesting variables comparing southwestern willow flycatcher nests in noninundated habitat and nests in partially inundated habitat during 2005 and 2006, Roosevelt Lake, Arizona, USA.

	Noninundated			Partially inundated					
Variable	**Mean**	**Half-width of 95% CI**	***n***	**Mean**	**Half-width of 95% CI**	***n***	***t***	**df**	***P***
First-egg day	16 Jun	3.0 days	65	17 Jun	4.2 days	39	0.22	102	0.83
Clutch size	2.7	0.1	104	2.8	0.2	76	0.89	178	0.37
Fledges of all nests	1.1	0.2	118	1	0.2	94	−0.75	210	0.46
Fledges of successful nests	2.4	0.2	56	2.4	0.2	40	−0.23	94	0.82

Roosevelt Lake. Although the number and location of territories varied among years, the most drastic redistribution of willow flycatcher territories at Roosevelt Lake occurred following inundation. In 2005, inundation displaced willow flycatchers from the most recently occupied habitat within the conservation pool to habitat that was either partially inundated (with some exposed vegetation) or farther upstream to noninundated habitat. Further, we observed the largest declines in territory numbers and nesting attempts as a result of habitat inundation. The number of territories declined by 27% from 2004 to 2005, and another 27% from 2005 to 2006 (total decline of 47% from 2004 to 2006). Along with fewer nesting attempts, the probability of nests being successful was lower during inundation, which negatively affected the population's productivity.

Knopf and Sedgwick (1987) documented a 1-year lag effect in population numbers of brown thrashers (*Toxostoma rufum*) and rufous-sided towhees (*Pipilo erythrophthalmus*) following habitat inundation. Knopf and Sedgwick (1987) theorized that birds that returned the year of inundation either failed to find suitable habitat to breed or had a failed nesting attempt and then dispersed that year or the following year to areas outside their study area. This dispersion could account for the continued decrease in willow flycatchers in 2006. The decrease in nesting attempts from 2005 to 2006 could also account for the decrease in willow flycatcher numbers. After inundation of Isabella Reservoir in California, Fleshman and Kaufman (1984) documented several species of birds being confined to smaller territories with less food, which caused reduced nesting attempts and nesting success. Past reproductive success of willow flycatchers and other species influences site fidelity, with successful individuals being more likely to return to the same breeding area (Harvey et al. 1979, Burger 1982, Blancher and Robertson 1985, Sedgwick 2004, Paxton et al. 2007). Therefore, we would expect willow flycatchers to disperse from previously occupied sites following the increase in failed nesting attempts during inundation.

In 2006, we began to observe effects of long-term inundation on habitat. Because winter precipitation within the Salt and Verde watersheds in 2006 was among the lowest on record (Western Regional Climate Center 2007), reservoir levels dropped at Roosevelt Lake throughout the winter. Reservoir levels continued to drop throughout the breeding season and reached a low of 63% capacity (646 m) in August 2006, down from a high of 96% (655 m) in May 2005 (T. Skarupa, personal communication). As reservoir levels dropped, stands of dead trees were exposed or partially exposed in previously inundated areas, indicating that most species were not able to survive inundation >1 year.

Large portions of vegetation died in 2006 at several partially inundated sites that were occupied in 2005. In some areas, the tamarisk understory died, whereas small patches of Goodding's willow (*Salix gooddingii*) overstory survived. At many of our sites, tamarisk seemed more susceptible to postinundation die-off compared to native vegetation. Other studies (e.g., Stromberg et al. 1993, Stromberg 1997, Gladwin and Roelle 1998) support this observation (but see Warren and Turner 1975, Sprenger et al. 2001). Vandersande et al. (2001) found that during controlled greenhouse experiments, native riparian species (Fremont cottonwood [*Populus fremontii*], Gooding's willow, and seep willow [*Baccharis salicifolia*]) suffered fewer negative effects from inundation than did tamarisk; all tamarisk plants were unable to remain upright after 58 days and had the lowest root and shoot mass. Stromberg et al. (1993) found native trees were favored following inundation on the Hassayampa River because they were larger and situated on slightly higher floodplains, a possible explanation for our observation of nonnative vegetation die-off at Roosevelt Lake. Most studies acknowledge that in addition to the length and depth of inundation, other factors such as tree size and location on floodplain, factor into response to inundation (reviewed in Gill 1970; Warren and Turner 1975, Stevens and Waring 1985, Stromberg et al. 1993, Reitan and Thingstad 1999).

Table 3. Univariate *t*-tests on nesting variables comparing southwestern willow flycatcher nests preinundation (1996–2004) and during inundation (2005–2006), Roosevelt Lake, Arizona, USA.

	Preinundation			During inundation					
Variable	**Mean**	**Half-width of 95% CI**	***n***	**Mean**	**Half-width of 95% CI**	***n***	***t***	**df**	***P***
First-egg day	17 Jun	1.6 days	396	16 Jun	2.4 days	104	0.2	498	0.84
Clutch size	2.8	0.1	630	2.8	0.1	180	−0.43	808	0.67
Fledges of all nests	1.4	0.1	680	1.1	0.2	212	2.93	890	0.003
Fledges of successful nests	2.5	0.1	385	2.4	0.2	96	0.73	479	0.47

Table 4. Paired *t*-tests on variables at southwestern willow flycatcher nest sites during 2004 (preinundation) and 2006 (during inundation), Roosevelt Lake, Arizona, USA.

Variable	*n*	Yr	$\bar{x}$	Half-width of 95% CI	Mean difference	Half-width of 95% CI of mean difference	*t*	df	*P*
Nest ht	9	2004	4.1	0.9	0.46	0.8	−1.36	8	0.21
		2006	3.7	0.8					
Ht of nest tree	14	2004	7.9	1	0.7	1.1	−1.73	13	0.11
		2006	7	1.7					
Dbh of nest tree	13	2004	8.8	2.2	0.12	0.6	−0.45	12	0.66
		2006	8.7	2.5					
Distance to water	20	2004	187.6	4.9	184.1	71.1	−5.41	19	<0.001
		2006	3.5	3					
Distance to canopy gap	30	2004	8.4	1.9	6.2	2.8	−4.58	29	<0.001
		2006	2.2	1.8					
Ht of canopy	29	2004	7.7	0.5	2.04	1	−4.04	28	<0.001
		2006	5.7	1					
% canopy cover	29	2004	95.1	1.4	59.4	12.9	−9.4	28	<0.001
		2006	35.7	13.2					
Distance to nearest broadleaf	29	2004	6	2.2	−14.0	4.4	6.53	28	<0.001
		2006	20	5					

In addition to changes in the location of suitable habitat available to willow flycatchers at Roosevelt Lake, habitat structure also changed. Because of inundation, we found that habitat at 2004 nest sites following inundation was thinner with less canopy cover, more canopy gaps, a lower canopy, and lower tree density than preinundation. Fleshman and Kaufman (1984) observed similar decreases in tree density, percent canopy cover, tree species diversity, and tree height following inundation at Isabella Reservoir in California. More data are necessary to fully assess long-term effects of inundation on changes in habitat structure at Roosevelt Lake.

Although inundation caused extensive vegetation die-off, we did observe regeneration of vegetation in some areas at Roosevelt Lake in 2006. At the Salt River study area, tamarisk began to regenerate at some sites that were partially inundated in 2005 when water levels dropped in the summer and autumn of 2005. By the end of the 2006 breeding season, tamarisk had grown to approximately 1.5 m in height at these sites. In parts of Salt River Inflow, native vegetation began to regenerate after water levels dropped in spring 2006. At the Tonto Creek study area, water levels also continued to drop in spring 2006 and Goodding's willow started to regenerate (approx. 0.5 m in ht by the end of the breeding season). Spring drawdown at Roosevelt Lake seems to be more conducive to native species regeneration. Stromberg et al. (1993) and Levine and Stromberg (2001) suggest that native vegetation is favored over tamarisk to regenerate if germination sites are moistened only during spring and become dry during summer. However, we noted that some of the new willow growth at the Tonto Creek study area died as drying occurred in late summer.

During a 2007 site visit, we observed that some young native vegetation persisted in areas associated with large willow trees that had survived inundation. This rapid regeneration of habitat at the reservoir is encouraging because willow flycatchers have occupied riparian habitat as young as 2–3 years in Arizona (L. Ellis, Arizona Game and Fish Department, unpublished data).

Flooding along a river is generally followed by a period of habitat regeneration that causes constant shifting in the location and age of riparian habitat (Poff et al. 1997). Although natural flooding events along free-flowing rivers may destroy large areas of vegetation and encourage habitat regeneration, they do not typically result in long-term inundation. Compared to a flood in a river system, habitat loss due to inundation is more expansive and continually high water levels postpone habitat regeneration. Floods that occur along river systems also scour vegetation and deposit woody debris in the river channel (Poff et al. 1997, Stromberg 2001), but are not expected to leave large amounts of standing dead vegetation in the habitat. However, at the reservoir, stands of dead trees remained after water levels receded, which may also hinder habitat regeneration. As the reservoir level receded, we observed habitat develop within the conservation pool at the water's edge. This cycle may repeat itself as the reservoir fills and empties, providing habitat for willow flycatchers in varying quantity and quality. However, if reservoir levels remain high, habitat regeneration will be postponed, further impacting willow flycatchers breeding at the reservoir.

MANAGEMENT IMPLICATIONS

Short-term effects of inundation at Roosevelt Lake include reduced nesting attempts and nest success leading to reduced productivity of willow flycatchers at the reservoir. Declines in available habitat and reduced productivity may result in a population reduction at Roosevelt Lake in the long term. Management problems may exist due to the lack of information regarding the long term effects of inundation and the population's ability to recover following a large-scale inundation event. Ultimately, manipulation of rivers via dam building has impacted the stability and structure of the associated riparian habitat with a ripple effect on the demographics of wildlife; the extent of impacts is largely unknown.

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