State of Utah
DEPARTMENT OF NATURAL RESOURCES
Division of Wildlife Resources

STATUS, REPRODUCTIVE SUCCESS, AND HABITAT USE OF THE SOUTHWESTERN WILLOW FLYCATCHER ON THE VIRGIN RIVER, UTAH

2008-2017

Publication Number 19-19
Utah Division of Wildlife Resources
1594 W. North Temple
Salt Lake City, Utah
Mike Fowlks, Director

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Final Report
March 2019

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ACKNOWLEDGMENTS

The Utah Division of Wildlife Resources conducted Southwestern Willow Flycatcher monitoring in coordination with signatories to the Virgin River Resource Management and Recovery Program. We are grateful to Pamela Wheeler for field work assistance, Meribeth Huizinga for statistical design and analysis, and Keith Day for administrative support and unpublished data. Thanks also to Mary Anne McLeod and Anne Pellegrini of SWCA Environmental Consultants (Flagstaff, AZ), for their banding efforts in St George and providing data summaries of their monitoring in Arizona and Nevada along the lower Virgin River.

Funding for Southwestern Willow Flycatcher nest monitoring was provided by the Washington County Habitat Conservation Plan, the Virgin River Resource Management and Recovery Program, Utah Division of Wildlife Resources, and the U.S. Fish and Wildlife Service.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

From 2008 to 2017, the Utah Division of Wildlife Resources (UDWR) completed ten consecutive years of Southwestern Willow Flycatcher (*Empidonax traillii extimus*) nest monitoring along the upper Virgin River in St George, Utah. Of 16 sites surveyed in the St George study area during 2008-2017, we detected flycatchers at 13 sites and confirmed breeding at eight sites. The number of male flycatchers maintaining breeding territories ranged from seven to 16, while the number of female flycatchers ranged from seven to 12. The area of occupied breeding patches ranged from 1.3 to 22.3 ha, and averaged 5.5 ha. Vegetation occupied breeding sites was a mix of native and non-native plant species; however, at one extreme, flycatchers breeding at Seegmiller Marsh used habitat characterized by 82.1 % non-native vegetation, and in particular 80.2 % tamarisk. At the opposite extreme, flycatchers breeding at Snipe Pond and Y-Drain Marsh used habitat characterized by only 6.3 % and 12.8 % non-native (100 % tamarisk) vegetation, respectively.

We monitored 148 active Southwestern Willow Flycatcher nests from 2008 through 2017. Apparent nest success was 45 % and varied significantly among years. The lowest was observed in 2009, when only 13 % of flycatcher nests were successful. The highest nest success was observed in 2013 (80 %). Flycatchers fledged an average 1.0 ± 0.11 young per nest overall (n = 148; successful and unsuccessful nests combined). Successful nests fledged an average of 2.3 ± 0.12 young flycatchers per nest (n = 67). A total of 155 flycatchers fledged over the 10 years of this study. The number of fledglings ranged from two in 2008 to 29 in 2017. Nest predation was the primary cause of nest failure in each of the 10 years from 2008-2017, ranging from 43 % to 100 % of nest failures among years, and averaging 67 % overall (years combined).

At nesting sites, microhabitat variables differed among the 10 years of this study. Five of nine habitat variables showed significant changes over time and two variables in particular, number of tree stems and number of Coyote Willow stems, showed marked differences. From 2008 to 2014, flycatcher use sites contained fewer trees, more Coyote Willows, and had a denser subcanopy-canopy layer. However, from 2015 to 2017, use sites contained a higher number of trees, fewer Coyote Willow, and a less dense subcanopy-canopy layer. Flycatcher nests were distributed among five nest tree species. The majority of nests were located in tamarisk (n = 106) and Coyote Willow (n = 38); however, one nest was built in Russian Olive; one in Seep Willow; one in Fremont Cottonwood; and one in a Coyote Willow snag.

Flycatchers exhibited two major shifts in the use of specific breeding sites within the St George study area between 2008 and 2017 likely due to tamarisk defoliation events by Tamarisk Leaf Beetles (*Diorhabda carinulata*). The most dramatic shift occurred between 2009 and 2010 where flycatchers essentially vacated sites dominated by non-native vegetation (tamarisk) and moved to sites dominated by large native (willow) vegetation. In 2014, flycatchers shifted back to tamarisk dominated habitats due to timing of defoliation events occurring after flycatcher critical breeding stages. Our observations emphasize that flycatchers require dense foliage, nest in the mid-canopy regardless of tree species or substrate height, and are more successful in tamarisk relative to willow substrates. Where management plans include habitat restoration, we suggest maintaining some tamarisk component in the understory.

INTRODUCTION

The Southwestern Willow Flycatcher (*Empidonax traillii extimus*) was federally listed as endangered in 1995 due to population declines resulting from the loss, degradation, and fragmentation of riparian habitats (USFWS 1995, 2002). The range-wide flycatcher population consists of approximately 1,000 known pairs, and an estimated population size of 1,200 pairs (USFWS 2002). Flycatchers are known to breed along the Virgin River in southwestern Utah, where designated critical habitat extends from the Utah-Arizona state line upstream for 46.2 km to Berry Springs in Washington County (USFWS 2013). The Southwestern Willow Flycatcher Recovery Plan subsumed the Utah, Arizona, and Nevada portions of the Virgin River drainage into the Virgin Management Unit, which contains 40 known territories and requires a minimum of 100 territories for reclassification to threatened status (USFWS 2002). The recovery plan does not explicitly state recovery goals for the Utah portion of the Virgin Management Unit (Lower Colorado Recovery Unit). Nevertheless, an increase in population size proportionally similar to that mandated for the entire Virgin Management Unit would produce a minimum goal of 30 territories in Washington Co., Utah (Dobbs et al. 2012).

From 1995 to 2007, Utah Division of Wildlife Resources (UDWR) surveys documented between three and 12 potential flycatcher breeding territories annually along the upper Virgin River (McDonald et al. 1995, 1997, Day, 1998, Peterson et al. 1998, Day 1999, Porter and Day 2000, Day 2004). These surveys indicated that virtually all flycatchers breeding (potentially or confirmed) on the upper Virgin River occupied portions of two breeding sites, Riverside Marsh and Seegmiller Marsh in the city of St George. Although UDWR surveys (1995-2007) noted breeding activity only anecdotally, personnel confirmed breeding at Riverside Marsh by finding nests in 1996 and 1997 (McDonald et al. 1997, Peterson et al. 1998). Personnel also documented evidence of a breeding attempt at Seegmiller Marsh by observing copulation behavior in 1998 (Day 1998).

In 2005, the Virgin River Resource Management and Recovery Program (Program) incorporated oversight of monitoring and recovery efforts for the Southwestern Willow Flycatcher on the Virgin River in Utah. Toward the ultimate goals of identifying and implementing conservation actions aimed at flycatcher recovery, beginning in 2008 the Program funded UDWR to monitor breeding activity, reproductive success, and habitat use in the area. Additionally, the Washington County Habitat Conservation Plan sensitive species fund and the U.S. Fish and Wildlife Service contributed funding for the project. Specific goals of this work were to monitor nesting attempts, quantify reproductive success, determine causes of nest failure and effects of brood parasitism, and quantify microhabitat and vegetation characteristics associated with nest sites. UDWR conducted long-term population and habitat monitoring from 2008 to 2017 along the upper Virgin River in St George, Utah. This report summarizes work conducted by UDWR personnel from 2008 to 2017 and is a continuation of Dobbs et al. 2012.

LIFE HISTORY AND BACKGROUND

Male flycatchers migrate from Central America and arrive on the breeding grounds in late April-early May, preceding females by about one week, and establish and maintain territories using an advertising song consisting of *fitz-bew* and *britt* vocalizations (Sedgwick 2000, McCarthey 2005, Sogge et al. 2010). Females pair and settle with territorial males upon arrival, and build nests over three to seven days with no assistance from males. Females typically build small (~ 8 x 8 cm), open-cup nests in the fork or crotch of small-diameter branches of a shrub, sapling, or tree, 2-7 m above the ground (Sogge 2000, Sogge et al. 2010). Females lay one egg per day, occasionally skipping a day between eggs, to complete clutches of two to four eggs, and incubate without male assistance (Stoleson et al. 2000, Sogge et al. 2010). Barring nest failure, eggs hatch in 11-14 days, at which time both females and males provision nestlings for 10-15 days in the nest, and for an additional one to two weeks after fledging (Rourke et al. 1999). Timing of departure from the breeding grounds is poorly known, but breeding adults generally depart territories in early to mid-August (Sogge et al. 2010). Flycatchers are insectivorous during the breeding season, foraging primarily in dense vegetation and using aerial (sally) maneuvers to capture arthropods on vegetative substrates (e.g., on leaf surfaces) or in flight (Sogge 2000; authors personal observations).

Flycatcher breeding habitat may be characterized as a mosaic of relatively dense tree, sapling, and shrub growth, interspersed with more open areas, open water, or shorter, sparser vegetation along rivers, streams, reservoir margins, or other wetlands (Sogge and Marshall 2000, USFWS 2002, Sogge et al. 2010). Occupied habitat is almost always associated with still or slow-moving surface water, swampy areas, or, at the very least, saturated soil (Sogge and Marshall 2000, USFWS 2002, Allison et al. 2003, Paradzick and Woodward 2003). Plant species composition, vegetation height and density, and patch size vary greatly, but occupied sites typically consist of dense tree and shrub cover ≥ 3 m tall, dense vegetation 2-5 m above the ground, dense twig structure, and high levels of green foliage (Sogge and Marshall 2000, USFWS 2002, Allison et al. 2003, Paradzick and Woodward 2003). These riparian habitat conditions, which tend to be early successional, are ephemeral and become unsuitable as the vegetation matures and/or as flood events reset successional conditions. Low to mid-elevation native broadleaf sites may be dominated by a single species, such as Goodding's (*Salix gooddingi*) or Coyote (*S. exigua*) willows, or may be composed of a mixture of willows, Fremont Cottonwood (*Populus fremontii*), Velvet Ash (*Fraxinus velutina*), Seep Willow (*Baccharis* spp.), and Common Buttonbush (*Cephalanthus occidentalis*); native broadleaf habitat may contain a rare non-native component. Monotypic non-native habitat is comprised by dense stands of non-native species, such as tamarisk (*Tamarix ramosissima)* or Russian Olive (*Elaeagnus angustifolia*), and mixed native/non-native habitat includes dense mixtures of both native broadleaf and non-native species. Note, however, habitat suitability for flycatchers appears to be more related to vegetative structure than species composition (USWFS 2002).

Land use practices including channelization, agriculture, livestock grazing, and urbanization have directly reduced and fragmented the area of available riparian habitat (Marshall and Stoleson 2000, USFWS 2002). Water management practices such as river damming, water diversion, and groundwater pumping to facilitate flood control, irrigation agriculture, and urban development have also directly reduced potential habitat availability (Marshall and Stoleson

2000, USFWS 2002). Water management has also degraded riparian habitat indirectly by reducing the frequency and intensity of flooding events (Poff et al. 1997, Shafroth et al. 2005), and thus the potential for the establishment and regeneration of most native woody riparian species (Stromberg et al. 1991, Scott et al. 1997). Under natural flow regimes periodic flood flows recycle the dynamic characteristics of suitable flycatcher habitat by removing older trees and resetting early-successional conditions by scouring floodplain sediment, depositing seeds, and recharging groundwater (Scott et al. 1996, Stromberg 1997, Stromberg et al. 1997, Poff et al. 1997).

Invasive non-native species represent a threat to riparian habitat in the southwest. Tamarisk (saltcedar; *Tamarix ramosissima*, *T. chinensis*, hybrid *T. ramosissima* x *chinensis*), in particular, has invaded as native willows and cottonwoods have declined, resulting in a widespread shift from riparian habitats dominated by native tree species to those dominated by non-native species (Hunter et al. 1988, Busch and Smith 1995, Shafroth et al. 2005). In addition to habitat-related effects, a number of factors may negatively affect flycatcher productivity directly. Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) may reduce flycatcher reproductive success, and represents an important threat to some flycatcher populations (Marshall and Stoleson 2000, USFWS 2002, Sogge et al. 2010). Nest predation by snakes, birds, and small mammals is an important factor limiting reproductive success, and may be responsible for up to 60 % of nest failures in some flycatcher populations (Marshall and Stoleson 2000). In the midwestern U.S. both brood parasitism and nest predation rates are typically higher in more fragmented habitats (Robinson et al. 1995a, Donovan et al. 1997), emphasizing the potential importance of edge effects on breeding bird productivity in human-altered landscapes. In the landscape context of the southwestern U.S., cowbirds and their hosts are most abundant in riparian habitats and river valleys, which also tend to be used for agriculture and grazing, providing cowbird foraging habitat in close proximity to breeding flycatchers (Robinson 1999 and references therein).

METHODS

Study Area

The upper Virgin River flows west-southwest through Washington Co., Utah, from above Zion National Park to the Arizona-Utah state line southwest of St George, Utah. This reach of the Virgin River descends through a transition zone from the Colorado Plateau into the Mohave Basin and Range ecoregions. Above Hurricane, Utah the river is confined to a relatively narrow floodplain, often bound by steep canyon walls, and is characterized by narrow riparian zones, heterogeneous in-stream habitat structure (riffles, runs, pools) and primarily cobble and boulder substrates. Below Hurricane, particularly in the vicinity of St George, the river meanders through a wide floodplain and is characterized by relatively simple in-stream habitats (runs) and sandy substrates. In addition to urban development, much of the floodplain and adjacent land is used for agriculture. Irrigation return flows and municipal and storm water runoff support wetlands and associated riparian woodlands in numerous locations within this portion of the floodplain. These patches of riparian habitat are distributed along the upper Virgin River, primarily in the St George area (hereafter St George study area).

Riparian woodlands in the study area are typically mixed non-native-native, but the ratio of non-native to native vegetation varies widely among individual habitat patches. Dominant native woody species in riparian habitat in the St George study area include Coyote Willow, Fremont Cottonwood, Mule's Fat or Seep Willow, and Arrow Weed (*Pluchea sericea*), and less commonly Goodding's Willow and Velvet Ash. The dominant non-native woody species in this habitat is tamarisk or Saltcedar, but Russian Olive also represents an important component of some habitat patches. This study was conducted in the riparian habitats along an approximately 17 km reach of the Virgin River in the cities of St. George and Washington, Utah (Figure 1).

Habitat Patch Characteristics

We differentiated among occupied habitat patches (i.e., breeding sites) that were located at least 300 m apart and separated by habitat lacking one or more key elements of suitable flycatcher habitat, typically appropriate hydrological conditions. Sites were not necessarily independent, however, as there was some degree of riparian habitat connectivity among them. We delineated boundaries of individual sites based on contiguous forest cover at least 5 m tall radiating out from nest sites. We used ArcMap 10.0 and Google Earth to digitize individual site boundaries and calculate patch size.

Following the breeding season, based on results of nest monitoring, we measured vegetation and microhabitat characteristics in detail at the majority of nest sites in the study area. Thus, in addition to qualitatively categorizing the proportion of non-native to native vegetation at the patch scale (Sogge et al. 2010), we also characterized patches based on microhabitat characteristics (woody stem counts) around nest sites within those occupied habitat patches.

Population Size and Distribution

We conducted flycatcher presence-absence surveys during the breeding seasons of 2008-2017 in suitable and potentially suitable habitat in the St George study area. We conducted surveys following the standardized Southwestern Willow Flycatcher survey protocol, which partitions the breeding season into three time periods (15–31 May, 1–24 June, and 24 June–17 July) and, depending on survey goals, requires different numbers of surveys in each of the three periods (Sogge et al. 1997, 2010). At potential project locations (i.e., where restoration work was planned or tentatively planned) we conducted one survey during the first survey period and two surveys during each of the latter two survey periods (Sogge et al. 2010). At non-project related locations we generally conducted a single survey in each of the three periods. However, where we confirmed breeding activity at non-project locations, we did not necessarily conduct subsequent presence-absence surveys *per se*, but monitored breeding activity at those sites for the duration of the breeding season. We conducted successive presence-absence surveys of the same location at least five days apart, regardless of survey period.

Prior to attempting surveys we used aerial photographs to delineate survey areas and to identify survey routes providing adequate coverage of each area. During surveys we walked survey routes, stopping approximately every 30 m. At each stop we first looked and listened for flycatchers for 1-2 min, after which, if a flycatcher was not detected, we broadcasted 15-20 sec of flycatcher song (including *fitz-bew* and *britt* phrases), and then again looked and listened for responding flycatchers for an additional 1-2 min. We conducted surveys between one-half hour before sunrise and 10:00 MDT, and did not conduct surveys during periods of inclement weather. Upon confirming the presence of one or more flycatchers, we attempted to observe them from a distance and determine the number of territorial males, general locations of territory boundaries, the presence of female flycatchers, and breeding-related behaviors prior to resuming the survey. We did not broadcast the song during surveys that were conducted at currently occupied breeding sites.

Banding and Re-sighting

SWCA Environmental Consultants (Flagstaff, Arizona; hereafter SWCA) maintains a long-term banding program throughout much of the Lower Colorado River Recovery Unit, including the St George study area (McLeod and Koronkiewicz 2009). We thus attempted to re-sight color-banded flycatchers returning or dispersing to breeding sites along the Virgin River throughout the breeding seasons of 2008-2017 toward the goal of understanding flycatcher demography. Additionally, when appropriate conditions allowed, SWCA personnel placed federal metal and plastic color bands on 6-9 day old flycatcher nestlings within the St George study area.

Reproductive Success

We attempted to locate and monitor all active flycatcher nests during the 2008-2017 breeding seasons following standard methods (Martin et al. 1997, Rourke et al. 1999). We searched for nests by observing adult behavior and/or systematically searching vegetation based on behavioral cues (Martin and Geupel 1993). We generally checked nests every three to four days, but increased nest check frequency to every one to two days in anticipation of nest stage transitions. We monitored nests from a distance when possible, particularly during nest building and egg laying, but approached nests closely to observe nest contents and thus determine nest stage transition dates, clutch size, hatching success, and nest fate. We observed nest contents at nests located > 1.5 m above the ground using a mirror or small video camera lens mounted on a telescoping pole.

We considered a nest successful if it fledged at least one young flycatcher, which we determined by observing fledglings or evidence of fledglings (e.g., adults carrying food, defensive behavior) near the nest, or by observing nestlings (in the nest) within two days of the estimated fledging date (Martin et al. 1997). We considered a nest unsuccessful if (1) the nest was found empty, destroyed, or missing more than two days prior to the estimated fledging date (depredated), (2) the nest fledged a cowbird and zero flycatchers (parasitism), (3) the nest was abandoned with eggs or nestlings (abandoned), (4) the entire clutch failed to hatch after at least 18 days of incubation (infertile), or the nest failed due to (5) other or (6) unknown reasons. We included only nests observed containing at least one flycatcher egg or nestling (i.e., active nests) in estimates of reproductive success, and thus omitted nests abandoned prior to egg-laying.

NEST VARIABLES

Nest Phenology. We calculated nest initiation dates following Martin et al. (1997). Nest initiation date, or first-egg date, is defined as the date that the first host egg is laid in a nest. Because we typically found nests during the building stage, we often observed nests during egg-laying and thus estimated nest initiation dates with a high degree of accuracy. We assumed that one egg was laid per day, except where field observations suggested otherwise, which generally translated to an egg-laying period of one day less than the final number of eggs laid (clutch size). For nests found later in the nesting cycle we counted back the number of days from known nest period transition dates (hatching, fledging), from estimated nest period transition dates using average durations of incubation and nestling periods, or based on nestlings' estimated age (see *Nest Success*, below). We estimated nestling age following Paxton and Owen (2002). We also examined the general pattern of nesting phenology in the St George study area by pooling nest data among years and calculating the percentage of nests active with eggs and nestlings on each date of the breeding season.

Clutch Size. We determined clutch size when the final number of host eggs laid in a nest was known exactly, generally by observing the same number of host eggs on successive nest checks without potential interference from cowbirds. We did not assume that the number of eggs observed in a nest was equivalent to clutch size when (a) nests were found after hatching, (b) nests failed before females may have finished egg-laying, (c) cowbirds parasitized nests after flycatchers had begun egg-laying, or (d) nest contents could not be seen clearly.

Hatching Success. We measured hatching success by (a) the number of eggs hatched and (b) hatching success rate, which we calculated by dividing the number of eggs that hatched by the number of eggs present during incubation. For these metrics we included only nests that survived to the nestling period, or that survived for at least 18 days of incubation. Including nests incubated for at least 18 days allowed inclusion of nests that failed due to infertility. We tested for year effects using Kruskal-Wallis tests.

Nest Success. We estimated nest success by calculating both apparent nest success and Mayfield nest success. We calculated apparent nest success by dividing the number of successful nests by the total number of active nests monitored. We tested for variation in apparent nest success among years using a chi-square test. We also estimated nest success using the Mayfield, or exposure, method, which minimizes bias in nest success estimates associated with finding nests at different stages of the nesting cycle and thus observing nests for different periods of time (Mayfield 1961). We calculated numbers of days that nests were under observation, by nesting stage (egg-laying, incubation, nestling), following Martin et al. (1997). We considered incubation to start the day that the last host egg was laid, and the nestling period to start the day that the first host egg hatched. Where not known explicitly, we used the mid-point between nest visits to estimate when events occurred (e.g., nest stage transitions, fledging, nest failure). We calculated daily survival rates (DSR) following Mayfield (1961, 1975; see also Hensler and Nichols 1981), and calculated variance following Johnson (1979). We calculated Mayfield survival probabilities (MSP) of nests by raising DSR to the exponent of the duration (days) of each nesting period. We used average nest period durations of 2.1, 12.9, and 13.7 days for egg-laying, incubation, and nestling periods, respectively, as observed for nests with known transition dates over an eight-year period on the lower Colorado River and tributaries (McLeod and Pellegrini 2011).

Nest Productivity. We calculated nest productivity as (a) the number of flycatcher fledglings produced per active nest (overall nest productivity) and (b) the number of flycatcher fledglings produced per successful nest (successful nest productivity). We also examined annual variation in overall and successful nest productivity.

Nest Failure. We summarized causes of nest failure for each year of the study. From 2012 to 2017, we used Sony Handycam digital video cameras to record active flycatcher nests in an attempt to identify local nest predators. We used a setup consisting of a video camera that recorded continuous footage to an internal hard drive, mounted on a tripod and powered by a rechargeable portable battery or generator. Equipment was covered and/or wrapped in camouflage fabric, and placed as far from nests as possible while achieving high-quality imagery.

Brood Parasitism

We summarized rates of brood parasitism of flycatcher nests by Brown-headed Cowbirds for each year of the study. To evaluate effects of brood parasitism on nest success, we compared DSR of parasitized and non-parasitized nests. We also compared DSR and MSP of parasitized nests prior to (2008-2011) and during (2012-2017) cowbird control efforts conducted by UDWR. Control practices included addling cowbird eggs, replacing fertile cowbird eggs with infertile cowbird eggs, and capturing and removing adult cowbirds from nesting sites. Because brood parasitism may influence flycatcher productivity in ways not captured by estimations of nest success, we also asked if the number of flycatcher eggs incubated and hatched, and if the number of flycatcher fledglings produced, differed between parasitized and non-parasitized nests.

Habitat Use and Nest Site Selection

We described and measured vegetation and habitat features at sites used by nesting flycatchers from 2008 to 2017 (n = 104). At our study location female flycatchers often re-nest within spatially overlapping areas. Therefore to avoid problems associated with non-independence (pseudo-replication) we excluded nesting attempts in the same year made by the same female that exhibited spatial overlap (within 5 m radius). However, we opted to include nest attempts in the same year made by the same female that were not spatially overlapping due to a limited sample size and because success outcomes often differed among first and subsequent nesting attempts. We also included nests built by the same female in different years because females often switch mates and territories among years (UDWR unpublished data).

Vegetation and habitat features for non-use sites were measured from 2010-2017 (n = 64). Within occupied patches, non-use sites were randomly selected from a 30 x 30 m matrix of gridded points created in ARC-GIS and overlaid onto LANDSAT imagery. All non-use sites were visited prior to sampling to confirm their location within available, suitable riparian habitat containing dense, woody vegetation. To be included in the analysis non-use sites were located a minimum of 22 m from a nearby active flycatcher nest.

Vegetation characteristics measured for this study follow modified BBIRD methods from Martin et al. (1997). We measured all vegetation characteristics late in summer after flycatcher breeding activity at the nest, territory and adjacent territories had ceased (27 July-15 October for all years; most commonly mid-August to mid-September). For each use and non-use site we utilized a circular sample plot with a 5 m radius. Vegetation plots at use sites were centered on the nest tree itself, while non-use sites were centered on the randomly selected grid point. Using a total of five points, including the center of the plot and 5 m from the center of the plot in each cardinal direction, we measured canopy height (m) and percent canopy cover using a spherical densiometer (see Martin et al. 1997). We also measured vertical foliage density using a 10 m vertical pole marked with 1 m increments and recorded the number and species of each vegetation type touching the pole (Mills et al. 1991). The number and size class (diameter at breast height; dbh) of all shrubs (≤ 8 cm dbh) and the number of all trees (> 8 cm dbh) within the 5 m radius plot were also recorded. Additionally, the number of all trees (> 8 cm dbh) by species within a 5.1 m and 11 m radius plot were recorded. In many cases dead vegetation was present but could not be identified to species; instead it was classified as a snag. Snags were included in the analysis because they are a potentially important component of the habitat. For each nest we recorded the nest substrate (i.e., plant) species, nest substrate height (m), nest height (m), nest substrate diameter (cm) at breast height (dbh), and average canopy height (m) within a one meter circular radius of the nest. In addition, we measured percent canopy cover at the nest using a spherical densiometer. Relative nest height was calculated as nest height divided by nest canopy height.

For each sample plot we calculated average canopy cover and average canopy height as the mean of the five measurements recorded per plot. We also calculated two foliage density indices per plot; one for understory vegetation by summing the height categories < 3 m and averaging the five plot measurements, and one for subcanopy-canopy vegetation using the 3-10 m height categories. An average foliage height index was measured using the Shannon diversity index for foliage density height up to 10 meters, and we calculated the mean of the five plot measurements (Shannon and Weaver 1949). The number of shrub stems (≤ 8 cm dbh) and tree stems (> 8 cm dbh) for all species were summed per plot. We utilized these values to estimate plant species diversity using the Shannon diversity index (Shannon and Weaver 1949). In addition, the total number of stems of tamarisk, Coyote Willow and snags were separated for analysis because together they comprised greater than 95 % of all stem data. Last, we included a measurement of horizontal distance (m) from the center of the plot to the nearest surface water.

Nest Site Characteristics and Nest Success

Prior to analysis we opted to split the data file into three sections based on year, 2008-2009, 2010-2014, and 2015-2017. Separate analyses indicated a significant year effect that was associated with two important biological events: release of Tamarisk Leaf Beetles (*Diorhabda carinulata*) and shifts in habitat use by flycatchers. We opted to include all nest attempts made by, presumably, the same females in these analyses due, in part, to a limited sample size and because nest fates often differed among first and subsequent nesting attempts. Further, because few flycatchers in the St George study area were banded, identification of individuals was often not possible. We also assumed that nests built in the same territories in different years were independent.

First, we tested if flycatchers chose nest trees in proportion to their availability. We considered all stems that were ≥ 1 cm dbh, as flycatcher nests were not found in vegetation with a diameter < 1 cm. A composite stem count for each plant species was calculated by summing the number of stems present in all nest site plots. We then compared the use of each nest tree species given the availability of each species among all nesting plots using chi-square tests with an applied Yates continuity correction. Second, we tested for associations between nest tree species and the number of nests that were successful or unsuccessful, successful or depredated, and nests parasitized by cowbirds and those not parasitized. In the first case we did not differentiate among the causes of nest failure, which included: abandonment, failure to hatch, depredation or brood parasitism. However, in the subsequent test we included only nests that were confirmed to be lost as a result of predation. Next, we measured differences in nest microhabitat variables between nest tree species. Finally, we measured differences in microhabitat variables between nests that were either: successful or unsuccessful, successful or depredated, and nests that were parasitized by cowbirds or those that were not parasitized using independent sample *t*-tests or Mann-Whitney *U*-tests.

RESULTS

Breeding Sites

During the duration of this study, flycatchers occupied eight breeding sites along the Virgin River (Figure 1, Table 1). With the exception of Brinton Pond which is spring fed, all breeding sites are bound by the Virgin River and some configuration of agricultural land and urban development. Seegmiller Marsh and Riverside Marsh are both isolated oxbow ponds in the Virgin River floodplain, and each receives agricultural irrigation return flows and municipal and storm water runoff. Both Seegmiller Marsh and Riverside Marsh are large complexes of wetlands and riparian forest of variable composition and structure. Dams constructed by American Beavers (*Castor canadensis*) impound water at Seegmiller Marsh, Riverside Marsh, and Y-Drain Marsh. In addition to a fish barrier at Seegmiller Marsh, the beaver dams serve to maintain relatively constant water levels in wetlands at these sites. Despite beaver activity at Riverside East, Snipe Pond, and Schmutz Drain, water levels widely fluctuate with daily variation in irrigation schedules.

The area of occupied breeding patches ranged from 1.3 to 22.3 ha, and averaged 5.5 ha (Table 2). At the scale of the habitat patch, vegetation at each of the occupied breeding sites in the St George study area was a mix of native and non-native plant species (Table 2). As observed elsewhere in the breeding range (USFWS 2002, Sogge et al. 2010), however, flycatchers in the St George study area often clustered territories in small portions of occupied patches and thus left large portions of those patches unoccupied. In addition to qualitatively classifying vegetation at the patch scale, we quantitatively characterized vegetation at occupied sites based on woody plant species stem counts in the immediate vicinity of nest sites. These data showed that, at one extreme, flycatchers breeding at Seegmiller Marsh used habitat characterized by 82.1 % non-native vegetation, and in particular 80.2 % tamarisk (Figure 2). At the opposite extreme, flycatchers breeding at Snipe Pond and Y-Drain Marsh used habitat characterized by only 6.3 % and 12.8 % non-native (100 % tamarisk) vegetation, respectively (Figure 2). Riverside Marsh, Riverside East, and Schmutz Drain ranged from 60:40 to 75:25 native:non-native vegetation (Figure 2).

Population Size and Distribution

We detected flycatchers at 13 of 16 sites surveyed in the St George study area during 2008-2017 (Table 1). The number of male flycatchers maintaining breeding territories in the St George study area averaged 9.7 individuals each season (range 7-16). Territorial males declined between 2009 and 2011, during which numbers dropped from 18 to seven individuals; however, between 2013 and 2014 the numbers increased from seven to 13 (Figure 3). A second decline in males occurred between 2015 and 2017, during which numbers dropped from 11 to eight individuals. The number of female flycatchers breeding in the study area averaged 9.2 individuals each season (range 7-12). Breeding females remained relatively stable between 2008 and 2012, ranging from eight to 10 individuals. A decline was observed between 2012 and 2013, during which numbers dropped from 10 to seven; however, from 2013 to 2014 the numbers increased from seven to 12 individuals. A relatively stable number of females continued from 2015 to 2017. The percentage of unpaired males remaining on territory into June varied among years, ranging from 0 % in 2013 to 50 % in 2008 (Figure 4).

The distribution of territorial males and breeding females shifted among individual sites in the St George study area during 2008-2017 (Figures 5, 6). The number of territorial males at Seegmiller Marsh, for example, declined from 18 during 2008-2009 to three during the 2010-2013 breeding seasons, and increased to 16 during the 2014-2017 breeding seasons (Figure 5). Additionally, at Seegmiller Marsh, the number of active nests declined from 14 during 2008-2009, to two during the 2010-2013 breeding seasons, and to 22 during the 2014-2017 breeding seasons (Figures 7, 8, 9). Throughout the same time periods the number of active nests at Snipe Pond shifted from zero (2008-2009) to 22 (2010-2013) to one (2014-2017) (Figures 10, 11, 12). In 2014, two territorial males and one female were observed at Schmutz Drain, which represented the first and only record of flycatchers colonizing this site (2008-2017). Additionally, in 2017, one male and one female flycatcher colonized Brinton Pond.

Breeding females exhibited a shift in distribution within the St George study area similar to that observed for territorial males (Figure 6). The number of females breeding at Seegmiller Marsh decreased between 2008-2009 (n = 10) and 2010-2013 (n = 2) and increased during 2014-2017 (n = 17) (Figure 6). Concomitant with the decrease in females using Seegmiller Marsh and River Road Bridge, females increased at Snipe Pond and Y-Drain Marsh between 2010 and 2013 and colonized Schmutz Drain in 2014.

The dramatic decline and subsequent dramatic increase in the number of flycatchers breeding at Seegmiller Marsh was particularly noteworthy given the importance of the site over the previous 10-15 years. One of only two sites known to support breeding flycatchers prior to 2008, Seegmiller Marsh has represented the flycatcher’s stronghold in the region since 1995, when UDWR initiated surveys on the upper Virgin River. An average of six male flycatchers maintained breeding territories at Seegmiller Marsh annually between 2001 and 2009 (Figure 13;

Day 2004, UDWR unpublished data). The average declined to <1 between 2010 and 2013; including zero male flycatchers with established territories in 2011 and 2013. However, during 2014-2017 an average of four male flycatchers maintained breeding territories at Seegmiller Marsh.

Banding and Re-sighting

Prior to 2010, very few flycatchers were color-banded or re-sighted in the St George study area. However, during the 2010-2017 breeding seasons, 47 individuals were re-sighted (several were duplicate re-sites from multiple years), 40 of which were confirmed as previously occupying the Virgin River in St George, Utah. Additionally, during the 2010-2017 breeding seasons in the St George study area, five adults and 27 nestlings were color-banded by SWCA personnel at five separate breeding sites (Table 3). With the exception of one flycatcher that was banded at the Mesquite West site (2009), it is assumed that all re-sights were birds banded in the St George study area.

Reproductive Success

We monitored 148 active Southwestern Willow Flycatcher nests in the St George study area during 2008-2017. Active nests were comprised by 72 initial nesting attempts, 62 renesting attempts following failed nests, and 14 double-brood nests following successful nests (Table 4). We documented an additional 38 flycatcher nests not known to ever contain flycatcher eggs (i.e. inactive). Of the 62 renesting attempts following nest failures, 40, 14, six, and two were second, third, fourth, and fifth re-nesting attempts, respectively. Forty-seven percent of females attempted at least one renest following failed nests, and 14 % of females attempted double-brood nests following successful nests (Table 5).

Males and females typically maintained socially monogamous pairs, but we observed 11 cases of social polygyny from 2008 to 2017 (Table 6). Social polygyny occurred at Riverside Marsh (2009, 2014), Riverside East (2010), Seegmiller Marsh (2015, 2017), Snipe Pond (2011), and Y-Drain Marsh (2015, 2016, 2017). At Seegmiller Marsh in 2017, one male was observed in a polygynous relationship with three females. Similar to other flycatcher populations (Pearson et al. 2006), it is assumed that a small portion of paired and unpaired male flycatchers in the St George study area participated in extra-pair fertilizations from 2008 to 2017.

Nest Phenology

Average nest initiation date (first-egg date) for first nest attempts was 14 June ± 1.4 days (range 28 May - 19 July; n = 69) over the 10 years of this study. Average nest initiation date for re-nest attempts was 1 July ± 1.5 days (range 9 June - 29 July; n = 68). Nest initiation dates for renest attempts following predation events ranged from 22 June to 27 July (n = 34), and nest initiation dates for double-brood attempts following successful nests ranged from 5 July to 29 July (n = 14). The timing of initial nesting attempts and renesting/double-brooding attempts resulted in a bimodal distribution of flycatcher breeding activity during six breeding seasons (2009, 2010, 2012, 2014, 2015, and 2017); however, over the combined 10 years, flycatcher breeding activity was distributed uniformly throughout the breeding season (Figure 14). The latest fledging date observed in the St George study area was 23 August. The late May-early June start of the flycatcher breeding season is notably later than that of other ecologically-similar coexisting species (e.g., Yellow Warbler, *Setophaga petechia*) at St George (authors personal observations).

Clutch Size and Hatching Success

Mean clutch size was 3.05 ± 0.08 eggs (range 1-4; n = 78) overall, (Table 7). Clutch size for first nest attempts was 3.2 ± 0.09 eggs (range 1-4; n = 48) and 2.8 ± 0.13 eggs (range 1-4; n = 30) for renest attempts. A total of 209 flycatcher eggs successfully hatched over the 10 years of this study. The lowest number of eggs hatched in one breeding season was eight in 2009 and the highest number was 34 in 2017. Average hatching success was 54.15 % (range 22.2 % - 87.5 %). The number of flycatcher eggs that hatched successfully varied significantly among years, as did hatching success rate (Figure 15). Both the number of eggs hatched and hatching success rate was lowest in 2009.

Nest Success

Apparent nest success for flycatchers in the St George study area was 45 % during 2008-2017. Apparent nest success varied significantly among years (Figure 16). In 2008, 70 % of nests successfully fledged at least one young flycatcher. Apparent nest success dropped dramatically in 2009, when only 13 % of flycatcher nests were successful. In 2010, 2011, and 2012, 30-37 % of flycatcher nests successfully fledged. The highest nest success was observed in 2013 (80 %) and 2017 (71 %), respectively (Figure 16). The probability of a nest surviving to fledge at least one young flycatcher (Mayfield survival probability; MSP) was 64 % in 2008, but declined to 25-27 % from 2009 to 2011 (Table 8). Estimates of Mayfield nest success and apparent nest success were quite different in 2009, 2011, and 2012, but followed the same general trend over the 2008-2017 period (Figure 16). Although not statistically significant, DSR appeared to vary somewhat among years (Table 8), consistent with annual variation in apparent nest success. A summary of individual breeding site nest success can be found in Appendix A.

Nest Productivity

Flycatchers fledged an average 1.0 ± 0.11 young per nest overall (n = 148; successful and unsuccessful nests combined) over the 10 years of this study. Overall nest productivity, however, varied significantly among years and was significantly lower in 2009 than all other years (Figure 17). Successful nests fledged an average of 2.3 ± 0.12 young flycatchers per nest (n = 67) over the 10-year period. A total of 155 flycatchers fledged during 2008-2017. The number of fledglings ranged from two in 2009 to 29 in 2017 (Figure 18).

Nest Failure

Nest predation was the primary cause of nest failure in each of the 10 years from 2008-2017, ranging from 43 % to 100 % of nest failures among years (Table 9, Figure 19) and averaging 67 % overall (years combined). Nest predation occurred during egg-laying (17 %), incubation (43 %), and nestling (40 %) periods. Flycatchers abandoned nine nests after eggs failed to hatch (for at least 18 days, i.e. infertile); six of which occurred during the 2009 breeding season (Table 9).

Brood parasitism directly caused flycatcher nest failure at 13 active nests (8.9 %; n = 148) and accounted for 16 % of nest failures overall (years combined), ranging from 0 % to 50 % (Table 9). Causes of failure included nest abandonment by the flycatchers following the appearance of a Brown-headed Cowbird egg; cowbird nestlings outcompeting and killing young flycatchers in the nest; and depredation due to cowbird activity in and around nests (drawing attention to nest). Five flycatcher nests failed when the female abandoned during egg-laying, seemingly in response to interactions with Brown-headed Cowbirds. Four flycatcher nests failed when the female abandoned during incubation with the appearance of a cowbird egg in the nest. Once in 2014 and once in 2016, adult flycatchers were observed feeding cowbird fledglings.

In addition to the above active nests used in nest success calculations, we also observed 38 flycatcher nests with no flycatcher eggs or nestlings. Female flycatchers presumably abandoned these nests during building or prior to egg-laying, although it is possible that some were depredated if egg-laying and depredation events both occurred between nest monitoring visits. Note that omission of such depredated nests from nest success calculations inflates nest success estimates and underestimate nest predation rates.

Brood Parasitism

Brood parasitism rates ranged from 14 % to 63 % of active nests (nests confirmed to contain flycatcher eggs or nestlings) from 2008-2017 (Table 4), and averaged 39 % overall (years combined).

Daily survival rates of parasitized nests (DSR = 0.952 ± .007) were lower than non-parasitized nests (DSR = 0.980 ± 0.003). The probability of a nest surviving to fledge a young flycatcher (MSP) was 25 % for parasitized nests and 56 % for non-parasitized nests. Apparent nesting success versus parasitism rates by breeding sites can be observed in Appendix B. Because cowbirds often remove flycatcher eggs at parasitized nests, cowbirds may have also directly reduced flycatcher fecundity. In 2012, we initiated cowbird management practices (e.g. addling, replacing fertile eggs with infertile eggs) at active flycatcher nests. Daily survival rates of parasitized nests prior to management practices (2008-2011) was 0.943 ± .013. Following the initiation of cowbird management (2012-2017), DSR of parasitized flycatcher nests increased to 0.958 ± .008. Additionally, the probability of a parasitized nest surviving to fledge a young flycatcher (MSP) increased from 19 % (2008-2011) to 29 % (2012-2017). We addled and returned cowbird eggs at five active flycatcher nests. We replaced fertile cowbird eggs with infertile cowbird eggs at seven flycatcher nests. We removed cowbird nestlings (1-2 d) from two active flycatcher nests.

The number of flycatcher eggs that were incubated and hatched successfully, as well as hatching success rate, did not differ between parasitized and non-parasitized nests, although parasitized nests tended to contain fewer of each than did non-parasitized nests (Figure 20). However, the number of flycatcher fledglings produced was significantly lower at parasitized nests than at non-parasitized nests (Figure 20).

We observed numerous flycatcher-cowbird interactions near flycatcher nests during nest-building, which we suspect prompted flycatchers to abandon, relocate, and rebuild several nests.

Abandoning and rebuilding nests represents an indirect effect of cowbirds not captured by nest success estimates (such nests were omitted from calculations of nest success, measures of fecundity, and brood parasitism rates because they were not observed containing flycatcher eggs). We observed six nests where a female flycatcher responded to brood parasitism by burying a cowbird egg beneath the nest lining, thus avoiding incubating the cowbird egg.

In addition to cowbird management efforts via egg disturbance during incubation, we initiated a pilot cowbird removal project in the St George study area in 2013. We acquired and used two previously constructed cowbird traps from the U.S. Bureau of Reclamation (Boulder City, NV). In 2013, we operated one trap at Snipe Pond from June 4 to July 17 and one trap at Y-Drain Marsh from June 21 to July 18. We removed a total of 53 cowbirds, including 31 (22 males and 9 females) from Snipe Pond and 22 (13 males and 9 females) from Y-Drain Marsh. From 2014 through 2016, we operated one trap at Riverside Marsh and one trap at Schmutz Drain. Traps were operated from as early as April 20 (2016) to as late as August 13 (2015). We removed 99 cowbirds (48 males, 43 females, and 8 juveniles) from Riverside Marsh and 113 cowbirds (60 males, 34 females, and 19 juveniles) from Schmutz Drain over the three years combined. In 2017, we operated one trap at Riverside Marsh from May 2 to June 30 and one trap at Y-Drain Marsh from May 2 to July 20. We removed a total of 59 cowbirds, including 23 (16 males and 7 females) from Riverside Marsh and 36 (20 males, 13 females, and 3 juveniles) from Y-Drain Marsh.

Habitat Use and Nest Site Selection

At use sites, microhabitat variables differed among the 10 years of this study (Table 10). Five of nine habitat variables showed significant changes over time and two variables in particular, number of tree stems and number of Coyote Willow stems, showed marked differences. From 2008 to 2014, flycatchers use sites contained fewer trees, more Coyote Willows, and had a denser subcanopy-canopy layer. However, from 2015 to 2017, use sites contained a higher number of trees, fewer Coyote Willow, and a less dense subcanopy-canopy layer.

Habitat variables around nest sites differed from non-use sites in nearly all of the aspects measured here (Table 11). Comparisons revealed that 6 of 9 variables were significantly different between use and non-use sites. In general, use sites typically had denser understory and subcanopy-canopy layers, greater canopy cover and height, more shrub and Coyote Willow stems, and fewer tree stems. It is assumed that these variables are significant predictors in nest site selection and that the likelihood of a site being used for nesting increased with greater foliage density, number of willow stems and proximity to water.

Use sites contained a higher density of stems between three and seven meters, and fewer stems in the eight meter height category (Figure 21). In addition, we found that there were more smaller stems of all species in use than non-use sites, although there were more large trees in non-use areas relative to use areas (Figure 22). Among the dominant vegetation types, non-use sites contained more tamarisk trees (> 8 cm), along with two size classes of snags (Figures 23, 24). In contrast, use sites contained more small Coyote Willow stems relative to non-use sites (Figure 25). In general flycatchers preferred habitats containing a dense mid-canopy layer containing more live vegetation, and in particular Coyote Willow.

Nest Site Characteristics and Nest Success

We located a total of 148 Southwestern Willow Flycatcher nests that were distributed among five nest tree species. The majority of nests were located in tamarisk (n = 106) and Coyote Willow (n = 38); however, one nest was built in Russian Olive; one in Seep Willow; one in Fremont Cottonwood; and one in a Coyote Willow snag (Table 12). During the 2008-2009 and 2015-2017 breeding seasons, flycatchers nested in areas where tamarisk was the dominant live plant species, and utilized nest tree substrates proportionally. However, from 2010 to 2014, nest trees were not selected in proportion to availability (Table 12). Beginning in 2010 and continuing through 2014, flycatchers nested in areas containing substantially more willow stems, although, as a nest substrate Coyote Willow was generally avoided, while tamarisk was utilized significantly more often relative to its availability. We found a similar pattern in the data sets between nest tree species and nest success. There was no difference in nest success among nest tree species in 2008-2009 ($\chi^2_2 = 0.6$, $P = 0.74$). Yet in 2010-2011 flycatchers nesting in tamarisk trees were more likely to successfully fledge one or more offspring, while those nesting in Coyote Willow were more likely to fail ($\chi^2_1 = 5.8$, $P = 0.016$). Moreover, the number of nests that failed specifically as a result of depredation also differed among nest tree species in 2010-2011 ($\chi^2_1 = 5.7$, $P = 0.017$), but not in 2008-2009 ($\chi^2_2 = 1.6$, $P = 0.44$; Figure 26). Nests built in tamarisk were depredated less often than those placed in Coyote Willow. In 2015-2017, only three flycatcher nests were built in Coyote Willow, of which none successfully fledged a young. Regardless of these differences, there was no relationship between nest tree species and nests parasitized by Brown-headed Cowbirds in either dataset (Figure 27).

The mean height of all nests in 2008-2009 was 2.9 ± 1.2 m, 2.6 ± 0.2 m in 2010-2014, and 2.9 ± 0.2 m in 2015-2017 (Tables 13, 14). Nest height was variable among the nest tree species and was significantly different in 2008-2009 ($t_{3.41} = -3.22$, $P = 0.04$).

The mean distance to habitat edge in 2008-2009 was 33.9 ± 10.1 m, 18.0 ± 2.2 m in 2010-2014, and 23.9 ± 3.5 m in 2015-2017 (Tables 13, 14). The mean distance to water in 2008-2009 was 17.4 ± 4.5 m, 2.9 ± 1.0 m in 2010-2014, and 10.0 ± 4.3 m in 2015-2017. Both variables exhibited significant differences among the varying breeding season periods (Table 14).

We found that the majority of nest site characteristics did not differ with nest outcome or parasitism rate (Table 15, Figures 28, 29). In most cases, flycatcher nests that failed to fledge any offspring, versus nests that produced one or more fledges were similar with respect to the substrate variables. The only exception was relative nest height during 2008-2009 and 2015-2017. Nests that failed were located significantly higher than successful nests (Table 15). In spite of this difference, nests that failed as a direct result of predation had similar microhabitat characteristics as those that were successful.

Nests parasitized by Brown-headed Cowbirds differed from non-parasitized nests in only a few nest attributes (Table 16). These results were year dependent such that in 2008-2009 and 2015-2017, nests containing a brood parasite were placed relatively lower, and in smaller, shorter nest trees compared to nests that did not contain a cowbird (Table 16). However, in 2010-2014 these differences were absent.

DISCUSSION

Southwestern Willow Flycatchers exhibited two major shifts in the use of specific breeding sites within the St George study area between 2008 and 2017. The most dramatic shift occurred between 2009 and 2010 where flycatchers essentially vacated sites dominated by non-native vegetation (tamarisk) and moved to sites dominated by large native (willow) vegetation, suggesting that a shift in habitat use was responsible for the observed distributional pattern. That is, while flycatchers utilized mixed native/non-native habitat patches throughout 2008-2009 and 2014-2017, flycatchers vacated the tamarisk-dominated Seegmiller Marsh and used the willow-dominated Snipe Pond and Riverside East from 2010 through 2013 breeding seasons.

The shift initiated in 2014 between breeding sites and habitat types in the St George study area coincided with the later tamarisk defoliation events (Figure 30) by Tamarisk Leaf Beetles over the 2011-2017 period. More specifically, flycatchers shifted back to tamarisk dominated habitats due to defoliation events occurring after flycatcher critical breeding period (i.e. laying, incubating) and thus likely having little impact on flycatcher behavior and reproductive success. Additionally, tamarisk which has not been defoliated is structurally more complex than willow and offer increase levels of protection from predators. Thus flycatchers potentially prefer to nest in tamarisk which could result in an increase in reproductive success. The timing of these events suggests that flycatchers may have shifted between Snipe Pond and Seegmiller Marsh as a result of lack of concealment from predators at the willow-dominant Snipe Pond.

Breeding ecology of Southwestern Willow Flycatchers on the upper Virgin River at St George was generally similar to that described elsewhere in the subspecies' range. Nest initiation (first-egg) date was slightly later in our study area (mean 14 June, range 28 May – 19 July) than in the Gila River drainage in Arizona (mean 10 June, range 14 May – 17 August; Ellis et al. 2008), likely due to the more northern location of our study area at St George, Utah. Mean clutch size in our study area was 3.05 eggs overall, which is slightly higher but similar to that documented in Arizona (2.8 eggs; Ellis et al. 2008) and elsewhere (Stoleson et al. 2000 and references therein). Flycatcher reproductive success varies greatly among sites and among years. Annual apparent nest success during 2008-2017 at St George averaged 45 % and ranged from 13 % to 80 %, and was thus within the range documented elsewhere in the subspecies' range. On the lower Virgin River in Nevada, for example, annual apparent nest success averaged 39 % (range 0-82 %) and 45 % (range 0-70 %) at Mesquite and Mormon Mesa, respectively, from 1996 to 2010 (McLeod and Pellegrini 2011).

Several measures of Southwestern Willow Flycatcher reproductive success varied among years at St George between 2008 and 2017. Following a high nesting success rate in 2008, apparent nest success, hatching success, and nest productivity dropped considerably during the 2009 breeding season. A steady increase was observed over the next several years until a dramatic increase was observed in 2013. Each of these metrics then decreased until 2017 but none lower than the 2009 levels. Concomitant with this pattern of annual variation in reproductive success, Tamarisk Leaf Beetles defoliated tamarisk to various degrees each year, and thereby altered the overall condition of riparian habitat, in the St George study area over the course of this study. The beetles were released at St George in 2006 and defoliated tamarisk for the first time in late July 2008, late in the flycatcher breeding cycle or after the majority of flycatchers were finished nesting. Hence, tamarisk defoliation likely did not affect breeding flycatchers significantly in 2008, which we consider a “pre-beetle” year from the flycatchers’ perspective. In 2009 beetles defoliated tamarisk in early-mid June, during the peak of flycatcher egg-laying and incubation. Because most flycatchers nested in tamarisk-dominated habitat in 2008 and 2009, potential impacts of beetle-related habitat alteration were high in 2009. Although beetles defoliated tamarisk early in the flycatcher breeding season again in 2010, flycatchers shifted to nesting in more native-dominated mixed native/non-native habitat in 2010 and 2011. The year 2009 was thus the only year in which flycatchers nested in habitat dominated by defoliated tamarisk. These patterns suggest that beetle-induced tamarisk defoliation contributed to low nesting success in 2009, an hypothesis that is supported, most notably, by flycatchers’ significantly lower hatching success in 2009 than all other monitoring years (2010-2017). Increased temperature in defoliated tamarisk habitat may have exceeded flycatchers’ embryonic thermal tolerance in 2009, thereby reducing hatching success (*sensu* Webb 1987). Indeed, nearly half of nest failures in 2009 resulted from hatching failure. During the duration of this study, hatching failure rarely contributed to nest failure in any year except 2009.

Following exceptionally low reproductive success in 2009 and the subsequent shift in habitat use from tamarisk to more native-dominated nesting sites, Mayfield nest success (i.e., nest survival probability) remained low until the dramatic increase in 2013 which represents the year with highest nesting success rate of this study. Low nest survival between 2010 to 2012 was likely driven, in part, by increased nest predation rates in native-dominated sites. Because we monitored flycatcher nests during only a single “pre-beetle” year (2008), it is difficult to evaluate the significance of flycatchers’ reduced reproductive success relative to baseline variation in reproductive success prior to beetle-induced habitat alteration. Nevertheless, nest survival probability was consistently depressed following the flycatchers shift from tamarisk-dominated to native-dominated mixed native/non-native habitat following 2009 and maintained higher reproductive success as they shifted back to tamarisk-dominated habitat in 2014. We suggest that, in the context of mixed native/non-native habitat, tamarisk may improve, or may be associated with some habitat component that improves flycatcher nest success. Structural complexity, for example, is higher where tamarisk occurs in the understory of native-dominated habitat. Increased structural habitat complexity may impede nest predators’ search efforts (e.g., by increasing nest concealment) or reduce the likelihood of nest discovery (e.g., by increasing the number of potential nest sites), thereby increasing nest success (Martin and Roper 1988, Martin 1992, 1993, Chalfoun and Martin 2009).

As in the majority of the flycatcher’s range (Sogge 2000, Ellis et al. 2008, McLeod and Pellegrini 2011), nest predation was the primary cause of flycatcher nest failure at St George. To date, however, we have not observed any nest predation events and, hence, do not know which species depredate flycatcher nests in the study area. However, in 2015, a video camera recording of an active flycatcher nest at Y-Drain Marsh captured footage of an adult Cooper’s Hawk (*Accipiter cooperii*) perching next to and observing a flycatcher nest containing eggs only. The hawk left the nest unharmed but we assume that it is a potential nest predator for flycatchers in the St George study area, especially if there are nestlings present. At Roosevelt Lake and along the San Pedro and Gila rivers in Arizona, where workers employed time-lapse video cameras to monitor nest predation, Cooper's Hawk was the most important predator of Southwestern Willow Flycatcher nests (Ellis et al. 2008). Additional avian species video-documented depredating flycatcher nests were Western Screech-Owl (*Megascops kennicottii*) and Yellow-breasted Chat (*Icteria virens*), and workers also observed Yellow-breasted Chat, Brown-headed Cowbird, and Great-tailed Grackle (*Quiscalus mexicanus*) depredating flycatcher nests (Ellis et al. 2008). In the same study, Ellis et al. (2008) also video-documented Common Kingsnake (*Lampropeltis getula*) and Gopher Snake (*Pituophis catenifer*) depredating flycatcher nests. In Nevada, on the lower Virgin River and along Pahranagat Wash, video photography has documented Bewick's Wren (*Thryomanes bewickii*), Brown-headed Cowbird, and Common Kingsnake depredating Southwestern Willow Flycatcher nests (see McLeod and Pellegrini 2011). All of these bird and reptile species occur in the St George study area, and Cooper's Hawk, Bewick's Wren, Yellow-breasted Chat, Brown-headed Cowbird, and Great-tailed Grackle are common breeding species at flycatcher breeding sites in the St George study area. Additional potential flycatcher nest predators in the study area include various species of birds and reptiles, and numerous mammals including various rodent species, Western Spotted (*Spilogale gracilis*) and Striped (*Mephitis mephitis*) skunks, Northern Raccoon (*Procyon lotor*), and the domestic cat (*Felis catus*). Identification of species depredating flycatcher nests in the St George study area may have important management implications and should be a priority for future work. High rates of nest predation by raccoons or domestic cats, for example, may merit the implementation of predator control and/or, for domestic cats, public outreach programs.

Brood parasitism of flycatcher nests was common and was associated with reduced flycatcher reproductive success in the St George study area. Overall, 39 % of active flycatcher nests were parasitized by cowbirds over the 10 years of this study, and as many as 63 % of active flycatcher nests were parasitized in a single year. Range-wide, brood parasitism rates of flycatcher nests vary widely (0-80 %); where rates are high, parasitism may exert a strong negative effect on flycatcher productivity (Whitfield and Sogge 1999, Kus and Whitfield 2005). At St George, the likelihood of surviving to fledge a young flycatcher was only 25 % for parasitized flycatcher nests, compared with 56 % for non-parasitized flycatcher nests. In addition, we suspect that cowbirds often delayed flycatcher nesting by causing flycatchers to relocate nests during nest building and egg-laying. Nest abandonment, prior to egg-laying, was often associated with observations of cowbirds interacting with flycatchers at or near nests. Such behavior is not captured by the various metrics of reproductive success, but may be associated with reduced fecundity. Female flycatchers that abandon, relocate, and rebuild nests multiple times may experience reduced opportunities to successfully breed due to increasingly limited time or energetic resources as the breeding season progresses.

Brood parasitism may represent an important factor limiting flycatcher productivity in small or isolated populations (Unitt 1987, USFWS 1995), such as the flycatcher population at St George. Observed brood parasitism rates at St George exceeded the 20-30 % rate suggested as a threshold to trigger active cowbird management (i.e., adult cowbird control) in flycatcher breeding areas (USFWS 2002). Cowbird control has proven to be an effective management tool at other flycatcher breeding areas. At the South Fork Kern River in California, for example, the parasitism rate of flycatcher nests declined from 65 % prior to cowbird control to 22 % during cowbird control. More importantly, flycatcher nest success increased from 23 % prior to cowbird control to 39 % during cowbird control (Whitfield et al. 1999).

We implemented a pilot study in 2013 to investigate the feasibility and effectiveness of cowbird control efforts along the Virgin River in St George; specifically, if cowbird removal is associated with reductions in brood parasitism rates, nest success, and productivity at flycatcher nests and at nests of the ecologically similar and more common Yellow Warbler. Between 2013 and 2017, we removed a total of 324 cowbirds (315 adult, 9 juvenile) from three breeding sites using previously acquired and constructed cowbird traps from the U.S. Bureau of Reclamation (Boulder City, NV). Additionally, in 2012, we initiated the practice of addling or replacing fertile cowbird eggs with infertile eggs at active flycatcher nests. It is difficult to assess the effectiveness of our cowbird control efforts in decreasing the overall population of adult cowbirds at trapping sites. However, by monitoring flycatcher nests we were able to determine if parasitism rates decrease during active cowbird removal. In 2016, cowbird control efforts were not in place at Y-Drain Marsh and five of six flycatcher nests (83 %) were parasitized. However, in 2017, cowbird control efforts were active and only one of four flycatcher nests (25 %) was parasitized. Coupled with dramatic declines in parasitism rates during three years of cowbird control at Schmutz Drain (2014-2016), these data suggest that trapping and removing adult cowbirds can increase the nesting success and overall productivity of breeding riparian bird species (i.e. flycatchers and warblers).

We found significant annual variation in some aspects of Southwestern Willow Flycatcher habitat use in the St George study area. More specifically, relative to 2008-2009, from 2010-2014 flycatchers nested in areas with denser understories, that were closer to water, that contained more shrubs and willows, and that contained fewer trees. However, from 2015 to 2017, use sites contained a higher number of trees, fewer Coyote Willow, and a less dense subcanopy-canopy layer. Two related events occurred that provide the most plausible explanation for these observed differences: tamarisk defoliation by Tamarisk Leaf Beetles and changes in flycatcher patch occupancy. During the study period, the release of tamarisk beetles directly altered study site vegetation, causing widespread tamarisk foliage-browning and defoliation. Beetle activity was first observed in this area in 2008 and occurred after flycatchers had largely completed breeding activities (late July – August). Although the timing of beetle activity fluctuates among years, the greatest level of beetle activity coincided with the flycatcher breeding period during 2009-2010. Flycatchers in our study area nest in patches that differ in vegetation composition, which can be categorized into one of three types: non-native tamarisk dominated, mixed native/non-native, and native dominated areas. Beetle activity varies among patch types and falls along a continuum; the severity of defoliation increases as the vegetation composition becomes tamarisk dominated. More specifically, in tamarisk dominated areas, browning and defoliation substantially reduced canopy cover, green foliage, and mean daily minimum humidity levels, and considerably increased mean daily maximum air temperatures relative to native dominated areas (UDWR and U.S. Bureau of Reclamation unpublished data). Such drastic differences in microhabitat conditions are likely to have consequences on nest site selection, as well as flycatcher reproductive success (Pelech and Hannon 1995, Martin 1998, Sogge et al. 2008, Paxton et al. 2011).

Flycatchers have occupied the Seegmiller Marsh complex since at least the mid-1990's. However, we observed only a single pair at this site in 2010, no pairs in 2011, one pair in 2012, and no pairs utilized Seegmiller Marsh for breeding in 2013. Instead, we observed flycatchers at Riverside East and Snipe Pond, which were previously unoccupied breeding sites. This is noteworthy because Seegmiller Marsh is tamarisk dominated, while Riverside East and Snipe Pond are dominated by native vegetation, particularly Coyote Willow. This shift in patch occupancy is likely related to the observed differences in habitat variables described here, particularly the increase in the number of willows and the decrease in the number of tamarisk.

Three variables were considered important predictors of flycatcher use sites: distance to nearest water, understory canopy density, and number of willow stems. This indicates that flycatchers at our study sites, during specific breeding seasons, established nests in dense thickets containing willows, above or nearby standing water. Collectively our results match the qualitative description and previous studies detailing Southwestern Willow Flycatcher nesting habitats (Brown 1988, Sogge and Marshall 2000, Allison et al. 2003, Stoleson and Finch 2003, Dockens and Ashbeck 2005, Paradzick 2005). Relatively few studies have quantified patterns of habitat selection in Southwestern Willow Flycatchers (Allison et al. 2003, Stoleson and Finch 2003, Paradzick 2005). Our results largely corroborate previous work and highlight the importance of dense foliage, high densities of willow stems and proximity to water, despite substantial differences in species composition among the study areas. Earlier studies also have found that flycatchers utilize areas with taller canopies (Allison et al. 2003, Stoleson and Finch 2003, Paradzick 2005); we also observed this pattern, as canopy height was taller at use compared to non-use sites. However, both Allison et al. (2003) and Stoleson and Finch (2003) found that nest sites contained more trees. In contrast, we found flycatchers used areas with fewer trees, while Paradzick (2005) noted flycatchers selected against large trees (> 25 cm dbh), primarily nesting in young trees. Both Allison et al. (2003) and Paradzick (2005) also found that flycatchers nested in areas containing more medium sized stem classes of vegetation, 2.5-8 cm and 5.5-15 cm, respectively. Yet our study found flycatchers utilized areas containing smaller stem size classes, those < 8 cm. This among site variation in plant species composition and floristics, as well as nest placement suggests that flycatchers exhibit some degree of plasticity in nest site selection, provided that vegetative structure is similar among sites, an idea that is gaining traction (Sogge and Marshall 2000, USFWS 2002, Sogge et al. 2008).

In our study area, Southwestern Willow Flycatchers utilized non-native tamarisk as the primary nest substrate (plant) species, in spite of the availability of native Coyote Willow. This selective use of tamarisk as a nest tree species is not uncommon among Southwestern Willow Flycatcher populations breeding in stands of mixed native and non-native vegetation (Sogge and Marshall 2000, Owen and Sogge 2002, Allison et al. 2003, Paradzick 2005, Sogge et al. 2008). However, during specific breeding seasons, flycatchers at our sites underutilized willows as a nesting substrate; this is surprising considering flycatchers often breed in sites where willow is the dominant plant species (Sogge and Marshall 2000, Sogge et al. 2001). Although Coyote Willow stems are collectively the most numerous stem species in our study area as well, the breeding sites differ in vegetation composition; these areas (as mentioned previously) are categorized as non-native tamarisk dominated, mixed native/non-native, and native dominated areas. When viewed in this context, flycatchers at our location behaved in a similar manner to those found elsewhere (Sogge and Marshall 2000, Sogge et al. 2001). Individuals nesting in native dominated sites utilized willow more frequently, although not proportionately, while those present in mixed or non-native dominated areas primarily nested in tamarisk. Collectively, our results are consistent with studies that have documented the rejection of willows as nest substrates when alternative substrates are available (Stoleson and Finch 1999, Paradzick et al. 2000, Sogge 2000, Sogge et al. 2001, USFWS 2002, Stoleson and Finch 2003, McCreedy and Heath 2004).

This study identifies nest microhabitat features that make flycatchers vulnerable to nest failure, depredation and brood parasitism. Our results indicate that nest tree species was associated with differences in nest outcome. Despite the availability of native Coyote Willow, most flycatchers sought out non-native tamarisk trees as preferred nest substrates. Although most individuals avoided nesting in willow, those that did were more susceptible to nest failure and depredation. This variation is not easily explained; only one microhabitat feature, substrate dbh, differed among nest tree species, and relative nest height was the only nest attribute that differed with nest outcome. Brood parasitism was not associated with nest tree species *per se*, but based on the year of analysis, parasitized nests were relatively lower, in shorter substrate, and under higher canopy cover.

To our knowledge, this study is the first to demonstrate that for flycatchers, nesting in willow is associated with a higher risk of depredation. The underlying reasons for this association are unclear. Southwestern Willow Flycatchers may select nest sites based on the nest tree species itself, or because of correlated microhabitat characteristics that increase nest success, conceal nests from predators or reduce parasitism by Brown-headed Cowbirds (Martin 1992, Whitfield and Sogge 1999, Sogge 2000, Heckscher 2004, Brodhead et al. 2007, Stumpf et al. 2011). Predation is the single largest cause of nest failure in our population. Therefore, during nest site selection females should favor patches that reduce the risk of predation through increased nest concealment or by impeding the search efficiency of potential predators (Martin 1993). Flycatchers demonstrate a strong preference for nesting in dense foliage and complex vegetation, a behavior consistent with both the nest concealment and the predator mobility hypothesis (Sogge 2000, USFWS 2002). While our study measured a number of nest scale microhabitat characteristics and none of the variables differed between successful and depredated nests, nest concealment was not measured specifically. Nest concealment, while difficult to quantify, nevertheless likely influenced nest predation rates in this study. Moreover, the identification of the major nest predators has not been documented at our site, and the community of potential predators is vast (USFWS 2002, UDWR unpublished data). To better understand the relationship between depredation and nest substrate selection, further study of microhabitat variables, including nest concealment, and identification of the primary nest predators is warranted.

Brood parasitism by Brown-headed Cowbirds is an important factor contributing to Southwestern Willow Flycatcher population declines (Whitfield and Sogge 1999, Uyehara et al. 2000). The rate of parasitism is incredibly variable across breeding locales (Uyehara et al. 2000), and, despite this threat, relatively few studies have measured the structure and floristics of the habitat surrounding the nest (Brodhead et al. 2007, Stumpf et al. 2011). Consistent with our results, Brodhead et al. (2007) found nests placed in willows were more susceptible to parasitism, although this was only significant for a single year. Moreover, they found parasitized nests were built lower in the tree and in shorter trees; however, these results are confounded by nest tree species (Brodhead et al. 2007). At the Cliff-Gila study site most flycatchers nest in

Boxelder (*Acer negundo*), a tree with a substantially higher canopy, (e.g. parasitized and non-parasitized nest tree heights along the Gila River were 12.2 m and 14.1 m, respectively; Brodhead et al. 2007).

Aside from the risks of predation and parasitism, flycatchers may selectively build nests in tamarisk and avoid willows for a number of reasons. Among them, tamarisk provides a dense vegetative structural component to the understory, a characteristic preferred by all subspecies of flycatchers regardless of the composition of the plant species community (Sogge and Marshall 2000, USFWS 2002). Indeed, this structural component differs between nest sites and non-use sites. Moreover, among nest sites, understory vegetation at native dominated sites is more open and the branching structural complexity is lower relative to mixed and non-native dominated sites. Yet, the benefits of nesting in areas containing tamarisk may be more closely related to characteristics measured at a larger spatial scale, rather than the localized scale surrounding the nest (Hatten and Paradzick 2003, Hatten et al. 2010). Other studies of flycatchers have documented the importance of patch area, distance to edge and distance to water on breeding densities, nest fate and rates of brood parasitism (Sedgwick and Knopf 1992, Hatten and Paradzick 2003, Brodhead et al. 2007, Hatten et al. 2010, Stumpf et al. 2011).

Alternatively, the selection of nest sites in tamarisk may be related to the availability or proximity to food resources (Sedgwick and Knopf 1992, Durst et al. 2008). Flycatchers are generalist insectivores and consume a broad array of insect taxa (Drost et al. 2003, Durst 2004, Durst et al. 2008), including Tamarisk Leaf Beetle larvae (authors personal observations). Studies indicate that insect abundance and flycatcher diet vary among habitat patch type (DeLoach et al. 2000, Drost et al. 2003, but see Durst 2004, Durst et al. 2008), but this variation has not translated to differences in physiological condition of flycatchers (Owen and Sogge 2002). Instead, diet variation may reflect annual changes in insect abundance, with total insect abundance as the best predictor of flycatcher productivity (Drost et al. 2003, Durst 2004, Durst et al. 2008). This relationship is not inconsequential given the patterns of tamarisk defoliation by Tamarisk Leaf Beetles. The long-term effects of changes in vegetation structure and food abundance on flycatcher nest site selection and productivity remain to be seen (Paxton et al. 2011).

The nest placement attributes reported here are similar to previous studies documenting variation in nest site selection for Southwestern Willow Flycatchers (Stoleson and Finch 1999, Sogge 2000, Stoleson and Finch 2003, Paradzick 2005). Our observations emphasize that flycatchers require dense foliage, nest in the mid-canopy regardless of tree species or substrate height, and are more successful in tamarisk relative to willow substrates. Where management plans include habitat restoration, we suggest that maintaining some tamarisk component in the understory may reduce nest failure due to depredation. Additionally, we recommend that collection of additional data related to microhabitat characteristics, including nest concealment and identification of the major nest predators.

The removal and eradication of tamarisk has recently been the focus of many riparian restoration efforts, particularly in the southwest (Sogge et al. 2008, Paxton et al. 2011). Tamarisk is prolific, and when left unchecked growth typically results in monotypic stands of extremely dense vegetation. Tamarisk has also been implicated as a factor leading to the decline of some southwestern bird species, including Southwestern Willow Flycatchers (Hunter et al. 1988). Yet studies are revealing that not all bird species respond in a similar manner to the presence of tamarisk (Shafroth et al. 2005, Sogge et al. 2008, van Riper III et al. 2008), and flycatchers may actually seek out sites containing tamarisk (Owen and Sogge 2002, Allison et al. 2003, Paradzick 2005). Furthermore, the use of tamarisk as a nesting substrate and its prevalence and distribution throughout all of the sites in our study area clearly highlight the importance of tamarisk in our study area. Flycatchers prefer the structurally complex, dense understory growth that tamarisk provides, but they also preferentially nest in areas containing willows and open water. Such a conclusion has ramifications on habitat restoration. Our data indicate that restoration efforts that completely eliminate tamarisk in order to improve flycatcher habitat may in fact have negative consequences for flycatchers. Large-scale efforts designed to eradicate tamarisk using either biocontrol agents or mechanical removal may greatly reduce vegetative cover and foliage density, potentially rendering a site unsuitable for nesting flycatchers. Therefore, our results suggest restoration efforts should consider multiple approaches that balance selective tamarisk removal with replacement by high-quality, spatially variable habitat, and increased access to open water. Consideration should also be given to the rate of replacement and development of native vegetation, particularly in the desert southwest where water is scarce and native vegetation grows slowly (Sogge et al. 2008, Paxton et al. 2011).

MANAGEMENT RECOMMENDATIONS

1. *Continue to monitor Southwestern Willow Flycatcher reproductive success in the St George study area*.

   Results of flycatcher nest monitoring during the 2008-2017 period were confounded by effects of Tamarisk Leaf Beetles. Baseline or “pre-beetle” conditions occurred during only a single season (2008), after which beetle activity dramatically altered flycatcher habitat conditions and, apparently, flycatcher productivity and habitat use. As a result, the factors influencing flycatcher nest success in the St George study area are changing, and our understanding of those factors remains incomplete. Additional flycatcher nest monitoring is necessary to identify conservation actions that may minimize or mitigate factors limiting flycatcher productivity under these conditions.

2. *Continue to quantify microhabitat and vegetation characteristics at Southwestern Willow Flycatcher nest sites in the St George study area.*

   Flycatchers dramatically altered their habitat use over the 2008-2017 period, apparently due to deteriorating habitat conditions resulting from the defoliation of tamarisk by Tamarisk Leaf Beetles. Quantitative habitat data will continue to be necessary to understand ongoing flycatcher response to seasonal and annual variation in tamarisk vigor and overall habitat condition at St George. Further, quantitative habitat data may be of critical importance in flycatcher habitat management as the condition of tamarisk continues to change and as habitat restoration efforts increase availability of potentially suitable native habitat. Detailed understanding of how flycatchers use available habitat and respond to habitat restoration efforts may have particularly important implications for the design and implementation of habitat restoration plans.

3. *Continue efforts to reduce numbers of adult Brown-headed Cowbirds at occupied Southwestern Willow Flycatcher sites in the St George study area*.

   Cowbird control programs, intended to reduce the numbers of breeding adult cowbirds via trapping and euthanasia, have proven to be effective tools in the management of endangered bird species, including the Southwestern Willow Flycatcher (Whitfield et al. 1999, Kus and Whitfield 2005). Brood parasitism rates of flycatchers observed at St George led to the implementation of cowbird control in 2013 according to the Southwestern Willow Flycatcher recovery plan (USFWS 2002). Cowbird control is further justified by data showing that brood parasitism significantly reduces flycatcher productivity in the St George study area. We recommend the continuation of a cowbird control program involving cowbird traps located at multiple (e.g., $\geq$2) flycatcher breeding sites in the St George study area. Monitoring cowbird abundance, brood parasitism rates of host nests, and host nest success and productivity prior to and during cowbird control will be a critical component of a cowbird control program. Flycatcher nest success and productivity data collected during 2008-2017 (this report) includes a pre-cowbird control baseline and post-cowbird control implementation comparison.

4. *Continue efforts to identify nest predators of Southwestern Willow Flycatchers in the St George study area*.

   Ongoing efforts to identify the species that depredate flycatcher nests in the St George study area may have important management implications and should be a priority for future work. Nest predation by mammals is often higher in fragmented habitats and urban landscapes, and thus may be high in the St George study area. High rates of nest predation by raccoons or cats, for example, may merit the implementation of seasonal predator control and/or, for domestic cats, public outreach programs. We recommend that video photography of flycatcher nests during incubation and nestling periods to document nest predators continue.

5. *Continue to enhance and restore potentially suitable Southwestern Willow Flycatcher breeding habitat in the St George study area*.

   Habitat suitability currently limits flycatcher population growth range-wide (USFWS 2002), and may limit flycatcher population size in the St George study area. The Virgin River Program, UDWR, and their partners are currently engaged in restoring and enhancing flycatcher habitat on the upper Virgin River. These efforts primarily involve reducing tamarisk cover, replanting native species characteristic of flycatcher habitat, increasing surface water availability at potential breeding sites, and monitoring project sites for vegetation and hydrologic conditions appropriate for flycatcher habitat development and maintenance. We recommend that such restoration efforts continue, in addition to small-scale habitat enhancement projects. Enhancement projects could include removing 20-30% of tamarisk cover or selectively removing patches (e.g. 5 m radius) of tall, old-growth willow stands from potential breeding sites.

6. *Provide long-term protection of flycatcher breeding habitat through floodplain property acquisition and protection.*

   Seven of eight flycatcher breeding sites in the St George study area are associated with off-channel wetlands supported by municipal and storm water runoff and/or irrigation return. As agricultural areas continue to be converted to housing developments in the St George area, the availability of both irrigation return and storm water runoff may change. We recommend securing long-term water availability to flycatcher breeding habitat through planning documents, conservation agreements or easements, and acquisition of property and/or water rights.

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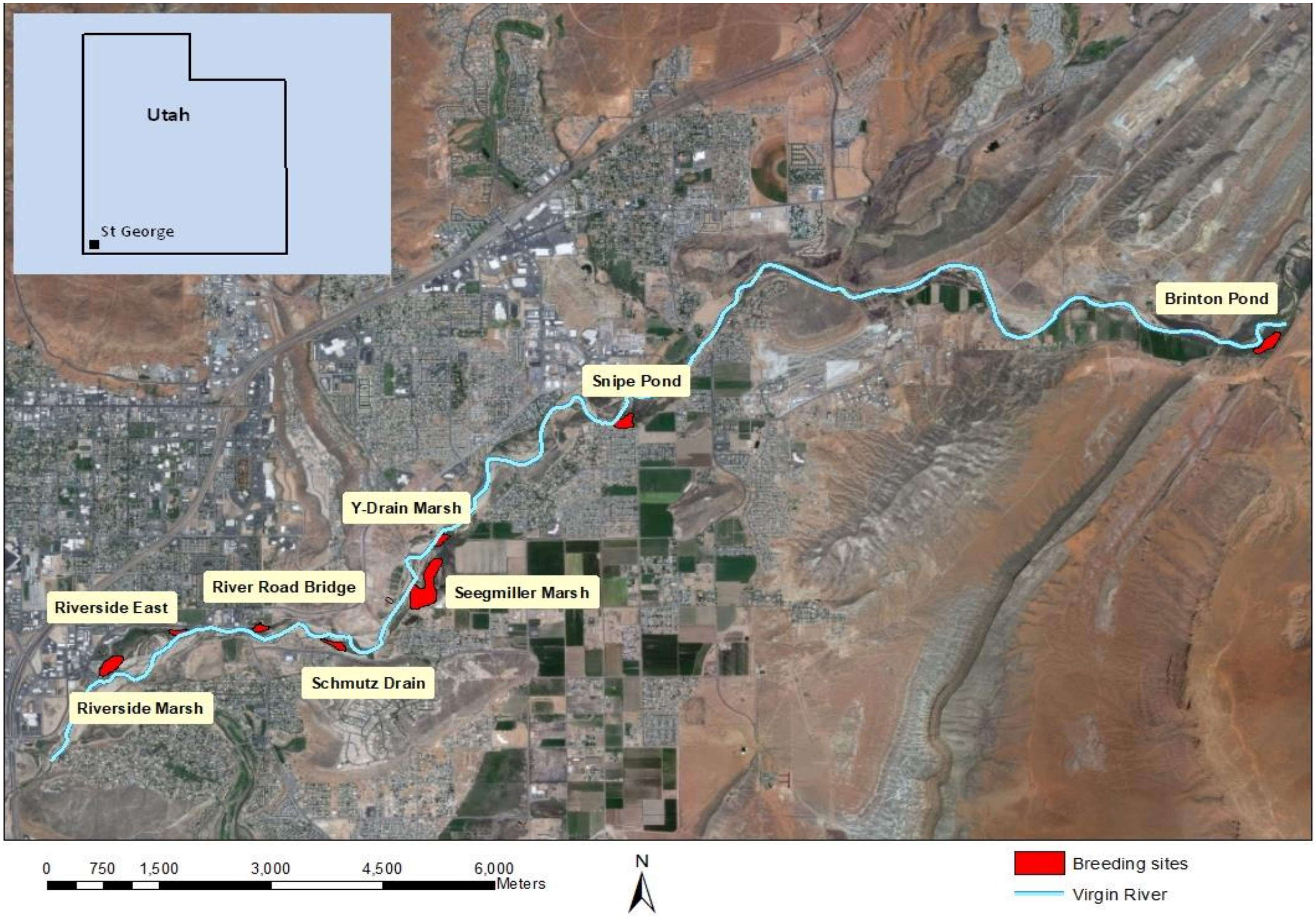


Figure 1. The St George study area located on the upper Virgin River in the vicinity of St George, Washington Co., Utah.

Table 1. Presence-absence survey sites for Southwestern Willow Flycatcher in the St George study area, Washington Co., Utah (x = survey conducted, oc = occupied by breeding flycatchers, WFD = Washington Fields Diversion).

Site	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
Riverside Marsh	x - oc	x - oc	x - oc	x - oc	x - oc	x - oc	x - oc	x - oc	x - oc	x
Riverside East	-	x - oc	x - oc	x - oc	x - oc	x - oc	x	x	x	x
River Rd Bridge	x - oc	x - oc	x - oc	x	x	x	x	x	-	-
Seegmiller Marsh	x - oc	x - oc	x - oc	x	x - oc	x	x - oc	x - oc	x - oc	x - oc
Schmutz Drain	-	x	x	x	x	x	x - oc	x	x	x
Y-Drain Marsh	-	-	-	x - oc	x - oc	x - oc	x - oc	x - oc	x - oc	x - oc
Snipe Pond	-	x	x - oc	x - oc	x - oc	x	x - oc	x - oc	x	x
Riverside Restoration[1, 2]	-	-	-	-	-	x	x	x	x	x
Springs Pond Outflow[2]	-	-	-	-	-	-	-	-	x	x
Rio Virgin Estates (JD 6)[2]	-	-	-	-	-	-	-	-	x	x
Mad Dog Pond[2]	-	-	-	x	x	-	x	x	x	x
Below WFD[2]	-	-	x	x	x	-	-	-	-	-
Brinton Pond[2]	-	-	-	x	-	-	-	-	-	x - oc
Above WFD[2]	-	-	-	-	-	-	-	-	x	x - oc
Santa Clara Confluence[2]	-	-	-	-	-	-	x	x	x	x
Sand Wash	-	-	-	-	-	-	x	x	x	x

[1]Historically (2003-2011) included and classified as a large portion of Riverside Marsh; however, following extensive nonnative removal in 2011-2012, the area was reclassified and established as a separate site.

[2]Identified as a potential breeding site and thus included in presence-absence surveys.

Table 2. Area and habitat classification of occupied Southwestern Willow Flycatcher breeding sites in the St George study area, 2008-2017.

Site	Area (ha)	Patch-scale habitat category[1]
Riverside Marsh[2]	3.2	Mixed native/non-native, mostly non-native (50-90 % non-native)
Riverside East	2.0	Mixed native/non-native, mostly native (50-90 % native)
River Road Bridge	2.8	Mixed native/non-native, mostly non-native (50-90 % non-native)
Schmutz Drain	4.7	Mixed native/non-native, mostly native (50-90 % native)
Seegmiller Marsh	22.3	Mixed native/non-native, mostly non-native (50-90 % non-native)
Y-Drain Marsh[3]	1.3	Mixed native/non-native, mostly native (50-90 % native)
Snipe Pond	5.3	Mixed native/non-native, mostly native (50-90 % native)
Brinton Pond	2.7	Mixed native/non-native, mostly native (50-90 % native)

[1] Habitat classification of the entire habitat patch, following Sogge et al. (2010): (1) native broadleaf plants (entirely or almost entirely; > 90 % native); (2) Mixed native and non-native plants (mostly native; 50-90 % native); (3) Mixed native and non-native plants (mostly non-native; 50-90 % non-native); (4) Non-native/introduced plants (entirely or almost entirely; > 90 % non-native).

[2] Total area was much reduced from previous years (2003-2011) due to division of the site and formation of the Riverside Restoration site (4.6 ha).

[3] Total area was much reduced due to habitat loss (2.3 ha) from the construction of the Mall Drive Bridge in 2014.

Table 3.Total number of Southwestern Willow Flycatchers color-banded by SWCA personnel in the St George study area, 2010-2017.

Year	Site	Adults	Nestlings[1]
2010	Riverside Marsh	1	2
2010	Riverside East	2	3
2011	Snipe Pond	2	1
2013	Riverside Marsh	0	3
2013	Y-Drain Marsh	0	10
2015	Riverside Marsh	0	1
2015	Seegmiller Marsh	0	4
2017	Seegmiller Marsh	0	3
Total		**5**	**27**

[1] Banded nestlings were 6-9 days old.

Table 4. Number of active nests monitored, number of re-nest and double-brood nest attempts, and number (percentage) of successful nests and nests parasitized by Brown-headed Cowbirds in the St George study area, 2008-2017.

Year	Site	Total Active Nests[1]	Re-nest / Double-brood Attempts[2]	Successful Nests (%)[3]	Parasitized Nests (%)[4]
2008	Seegmiller Marsh	6	0/1	5 (83)	0
	Riverside Marsh	3	0/1	1 (33)	2 (66)
	River Road Bridge	1	0	1 (100)	1 (100)
	Total	**10**	**0/2**	**7 (70)**	**2 (20)**
2009	Seegmiller Marsh	8	2/1	1 (12)	2 (25)
	Riverside Marsh	3	1/0	0	1 (33)
	Riverside East	1	0	1 (100)	1 (100)
	River Road Bridge	3	1/0	0	2 (66)
	Total	**15**	**4/1**	**2 (13)**	**6 (40)**
2010	Seegmiller Marsh	1	0	1 (100)	0
	Riverside Marsh	1	0	1 (100)	0
	Riverside East	8	4/1	3 (38)	1 (13)
	River Road Bridge	3	2/0	1 (33)	2 (66)
	Snipe Pond	7	4/0	0 (0)	2 (29)
	Total	**20**	**10/1**	**6 (30)**	**5 (25)**
2011	Riverside Marsh	6	4/0	1 (17)	4 (67)
	Riverside East	2	0/1	2 (100)	0
	Snipe Pond	8	4/0	2 (25)	5 (63)
	Y-Drain Marsh	1	0	1 (100)	1 (100)
	Total	**17**	**8/1**	**6 (35)**	**10 (59)**
2012	Riverside Marsh	5	3/0	1 (20)	3 (60)
	Riverside East	2	1/0	1 (50)	2 (100)
	Seegmiller Marsh	1	0	1 (100)	0
	Y-Drain Marsh	4	2/1	2 (50)	0
	Snipe Pond	7	6/1	2 (29)	4 (57)
	Total	**19**	**12/2**	**7 (37)**	**9 (47)**
2013	Riverside Marsh	2	1/0	2 (100)	0
	Riverside East	1	0	1 (100)	0
	Y-Drain Marsh	7	2/1	5 (71)	2 (29)
	Total	**10**	**3/1**	**8 (80)**	**2 (20)**
2014	Riverside Marsh	6	2/1	4 (67)	4 (67)
	Seegmiller Marsh	6	3/1	3 (50)	4 (67)
	Y-Drain Marsh	3	2/0	2 (67)	1 (33)
	Snipe Pond	1	0/0	0 (0)	1 (100)
	Total	**16**	**7/2**	**9 (56)**	**10 (63)**
2015	Riverside Marsh	7	3/1	3 (43)	4 (57)
	Seegmiller Marsh	4	0/0	4 (100)	1 (25)
	Y-Drain Marsh	6	4/0	1 (17)	1 (17)
	Total	**17**	**7/1**	**8 (47)**	**6 (35)**
2016	Riverside Marsh	1	0	0	0
	Seegmiller Marsh	3	0	3 (100)	0
	Y-Drain Marsh	6	4/0	1 (17)	5 (83)
	Total	**10**	**4/0**	**4 (40)**	**5 (50)**
2017	Seegmiller Marsh	9	2/2	6 (67)	1 (11)
	Y-Drain Marsh	4	2/0	3 (75)	1 (25)
	Brinton Pond	1	0	1 (100)	0
	Total	**14**	**4/2**	**10 (71)**	**2 (14)**
Overall Total		**148**	**59/13**	**67 (45)**	**57 (39)**

[1] Active nests are defined as those confirmed containing at least one flycatcher egg or nestling.

[2] Renest and double-brood attempts are those following unsuccessful and successful nesting attempts, respectively.

[3] Successful nests produced at least one young flycatcher; the percentage of successful nests is the number of successful nests divided by the total number of active nests (i.e., apparent nest success).

[4] Parasitized nests are nests confirmed containing at least one flycatcher egg and at least one cowbird egg, regardless of nest fate.

Table 5. Percentages and number (n) of females that renested at least once following nest failure and that attempted double-brood nests following successful nests in the St George study area, 2008-2017.

Year	Females renesting	Females double-brooding
2008	0 % (0)	25 % (2)
2009	40 % (4)	10 % (1)
2010	67 % (6)	11 % (1)
2011	63 % (5)	13 % (1)
2012	70 % (7)	20 % (2)
2013	43 % (3)	14 % (1)
2014	50 % (6)	17 % (2)
2015	50 % (5)	10 % (1)
2016	38 % (3)	0 % (0)
2017	50 % (5)	20 % (2)
Overall	**47 % (43)**	**14 % (13)**

Table 6. Percentages and number (n) of socially polygynous Southwestern Willow Flycatcher males, females, and nests in the St George study area, 2008-2017.

Year	Polygynous males	Polygynous females	Polygynous nests[1]
2008	0	0	0
2009	7 % (1)	20 % (2)	20 % (3)
2010	9 % (1)	22 % (2)	25 % (5)
2011	14 % (1)	38 % (3)	29 % (5)
2012	0	0	0
2013	0	0	0
2014	8 % (1)	17 % (2)	6 % (1)
2015	27 % (3)	60 % (6)	47 % (8)
2016	10 % (1)	25 % (2)	50 % (5)
2017	38 % (3)	70 % (7)	79 % (11)
Overall	**10 % (11)**	**26 % (24)**	**26 % (38)**

[1] Nests (including renests) built by polygynous females.

Table 7. Mean ± SE (range; n [nests]) nest initiation date, clutch size, number of eggs hatched, and number of young fledged by Southwestern Willow Flycatchers in the St George study area, 2008-2017.

	First nest attempts	Renest attempts	All nest attempts (combined)
Nest initiation date[1]	14 June ± 1.4 days (28 May – 19 July, n = 69)	1 July ± 1.5 days (9 June – 29 July, n = 68)	22 June ± 1.2 days (28 May – 29 July, n = 137)
Clutch size[2]	3.2 ± 0.09 eggs (1-4, n = 48)	2.8 ± 0.13 eggs (1-4, n =30)	3.1 ± 0.08 eggs (1-4, n = 78)
No. eggs hatched[3]	2.3 ± 0.15 eggs (0-4, n = 59)	1.9 ± 0.17 eggs (0-4, n = 44)	2.1 ± 0.11 eggs (0-4, n = 103)
No. young fledged[4]	1.6 ± 0.18 young (0-4, n = 59)	1.4 ± 0.20 young (0-4, n = 44)	1.5 ± 0.13 young (0-4, n =103)

[1] Date first flycatcher egg was laid. [2] Known clutch size (see METHODS).

[3] For nests surviving to the nestling stage or for ≥ 18 days of incubation.[4] For successful nests only.

Table 8. Daily survival rates and Mayfield survival probabilities for Southwestern Willow Flycatcher nests monitored in the St George study area, 2008-2017.

Year	Nest period	Nest losses	Exposure days[1]	Daily Survival Rate[2]	Mayfield Survival Probability[3]
2008	Laying	0	8	1.000	1.000
	Incubation	2	79	0.975	0.718
	Nestling	1	106	0.991	0.878
	All periods combined	*3*	*193*	*0.984*	***0.638***
2009	Laying	3	31	0.903	0.808
	Incubation	6	187	0.968	0.657
	Nestling	4	59	0.932	0.382
	All periods combined	*13*	*277*	*0.953*	***0.252***
2010	Laying	1	31	0.968	0.933
	Incubation	7	168	0.958	0.578
	Nestling	6	118	0.949	0.489
	All periods combined	*14*	*317*	*0.956*	***0.274***
2011	Laying	3	26	0.885	0.773
	Incubation	6	114	0.947	0.498
	Nestling	2	90	0.978	0.735
	All periods combined	*11*	*230*	*0.952*	***0.245***
2012	Laying	3	30	0.900	0.802
	Incubation	7	163	0.957	0.568
	Nestling	2	94	0.979	0.745
	All periods combined	*12*	*287*	*0.958*	***0.294***
2013	Laying	1	17	0.941	0.880
	Incubation	1	85	0.988	0.858
	Nestling	0	96	1.000	1.000
	All periods combined	*2*	*198*	*0.990*	***0.747***
2014	Laying	1	32	0.969	0.936
	Incubation	3	192	0.984	0.816
	Nestling	3	152	0.980	0.761
	All periods combined	*7*	*376*	*0.981*	***0.583***
2015	Laying	0	37	1.000	1.000
	Incubation	7	199	0.965	0.630
	Nestling	2	142	0.986	0.823
	All periods combined	*9*	*378*	*0.976*	***0.501***
2016	Laying	2	22	0.909	0.819
	Incubation	1	106	0.991	0.885
	Nestling	3	77	0.961	0.580
	All periods combined	*6*	*205*	*0.971*	***0.426***
2017	Laying	0	27	1.000	1.000
	Incubation	1	172	0.994	0.928
	Nestling	3	164	0.982	0.777
	All periods combined	*4*	*363*	*0.989*	***0.728***

[1] Number of days a nest was exposed to potential nest failure.

[2] Daily survival rate (DSR) is the probability that a nest will survive from one day to the next.

[3] Mayfield survival probability (MSP) is the probability that a nest will survive to fledge at least one young flycatcher; MSP = $(DSR)^d$, where *d* is the average duration (days) of the nesting period (egg-laying, incubation, nestling).

Table 9. Total numbers of failed nests, and numbers (percentages) of nest failures due to predation, hatching failure, abandonment, and Brown-headed Cowbirds in the St George study area, 2008-2017. Note, between 2012 and 2017 UDWR personnel conducted cowbird control management practices.

Year	Site	Total nest failures[1]	Cause of nest failure: Predation (%)	Infertile (%)[2]	Abandoned (%)	Parasitism (%)[3]
2008	Seegmiller Marsh	1	1 (17)	0	0	0
	Riverside Marsh	2	1 (33)	0	1 (33)	0
	Total	**3**	**2 (67)**	**0**	**1 (33)**	**0**
2009	Seegmiller Marsh	7	4 (50)	3 (38)	0	0
	Riverside Marsh	3	1 (33)	2 (66)	0	0
	River Rd Bridge	3	2 (66)	1 (33)	0	0
	Total	**13**	**7 (54)**	**6 (46)**	**0**	**0**
2010	Riverside East	5	4 (80)	0	0	1 (20)
	River Rd Bridge	2	2 (100)	0	0	0
	Snipe Pond	7	7 (100)	0	0	0
	Total	**14**	**13 (93)**	**0**	**0**	**1 (7)**
2011	Riverside Marsh	5	5 (100)	0	0	0
	Snipe Pond	6	3 (50)	1 (17)	0	2 (33)
	Y-Drain Marsh	0	0	0	0	0
	Total	**11**	**8 (73)**	**1 (9)**	**0**	**2 (18)**
2012	Riverside Marsh	4	2 (50)	0	0	2 (50)
	Riverside East	1	0	0	0	1 (100)
	Y-Drain Marsh	2	1 (50)	1 (50)	0	0
	Snipe Pond[4]	5	2 (40)	0	0	2 (40)
	Total	**12**	**5 (42)**	**1 (8)**	**0**	**5 (42)**
2013	Y-Drain Marsh	2	2	0	0	0
	Total	**2**	**2 (100)**	**0**	**0**	**0**
2014	Riverside Marsh	2	1 (50)	0	0	1 (50)
	Seegmiller Marsh	3	1 (33)	1 (33)	0	1 (33)
	Y-Drain Marsh	1	0	0	0	1 (100)
	Snipe Pond	1	1 (100)	0	0	0
	Total	**7**	**3 (43)**	**1 (14)**	**0**	**3 (43)**
2015	Riverside Marsh[5]	4	2 (50)	0	1 (25)	0
	Y-Drain Marsh[5]	5	4 (80)	0	0	0
	Total	**9**	**6 (67)**	**0**	**1 (11)**	**0**
2016	Riverside Marsh	1	1 (100)	0	0	0
	Y-Drain Marsh	5	2 (40)	0	0	3 (60)
	Total	**6**	**3 (50)**	**0**	**0**	**3 (50)**
2017	Seegmiller Marsh	3	3 (100)	0	0	0
	Y-Drain Marsh	1	1 (100)	0	0	0
	Total	**4**	**4 (100)**	**0**	**0**	**0**
Overall Total		**81**	**53 (65)**	**9 (11)**	**2 (4)**	**14 (17)**

[1]Includes only active nests (nests confirmed to contain at least one flycatcher egg or nestling).
[2]Nests in which eggs failed to hatch after at least 18 days of incubation.
[3]Represents direct effects of parasitism only (cowbird nestling caused death of flycatcher nestling).
[4]Nest failure was caused by American Beaver (*Castor canadensis*) cutting down the nest tree.
[5]Cause of failure for nest was not determined.

Table 10**.** Comparisons of habitat variables among years for Southwestern Willow Flycatcher nest sites. Values are given as mean ± SE.

Variable	2008 (n = 9)	2009 (n = 12)	2010 (n = 13)	2011 (n = 12)	2012 (n = 14)	2013 (n = 8)	2014 (n = 10)	2015 (n = 8)	2016 (n = 7)	2017 (n = 5)
Average canopy cover (%)	91.5 ± 3.1	92.4 ± 3.0	92.4 ± 1.9	93.8 ± 1.7	93.6 ± 1.0	91.0 ± 2.3	91.9 ± 1.4	91.5 ± 1.9	91.5 ± 1.6	88.8 ± 5.2
Average canopy height (m)	6.2 ± 0.2	5.8 ± 0.3	5.8 ± 0.3	6.2 ± 0.2	6.1 ± 0.3	6.4 ± 0.4	5.4 ± 0.2	6.1 ± 0.3	5.7 ± 0.2	6.8 ± 0.2
Foliage density 0-3 m	18.4 ± 1.5	19.6 ± 1.3	15.8 ± 2.3	15.5 ± 2.0	13.1 ± 1.7	12.0 ± 1.6	14.8 ± 2.3	12.6 ± 1.5	15.3 ± 2.6	14.2 ± 2.2
Foliage density 3-10 m	15.9 ± 1.2	12.7 ± 1.7	22.4 ± 2.9	24.8 ± 1.7	26.4 ± 2.5	33.8 ± 8.2	18.9 ± 2.8	17.2 ± 2.5	18.6 ± 4.1	18.5 ± 5.3
Total shrub stems (≤8 cm dbh)	348.1 ± 56.2	236.5 ± 49.1	432.2 ± 57.1	577.8 ± 95.1	424.4 ± 71.6	433.3 ± 46.6	497.2 ± 101.2	325.3 ± 46.8	313.7 ± 63.4	241.0 ± 61.1
Total tree stems (>8 cm dbh)	6.0 ± 1.4	4.7 ± 1.2	1.1 ± 0.6	0.6 ± 0.4	0.9 ± 0.3	2.1 ± 1.4	0.3 ± 0.2	2.5 ± 1.0	4.3 ± 1.1	4.0 ± 0.8
Total snag stems	249.6 ± 62.1	92.8 ± 24.1	58.2 ± 12.9	127.2 ± 19.7	107.9 ± 23.0	100.6 ± 14.8	195.3 ± 53.1	120.1 ± 21.4	123.4 ± 14.6	139.4 ± 45.6
Total tamarisk stems	78.1 ± 10.9	56.2 ± 12.3	104.5 ± 32.1	55.4 ± 14.3	28.5 ± 6.3	46.4 ± 14.0	78.0 ± 18.1	51.9 ± 9.4	76.7 ± 11.1	56.0 ± 17.3
Total willow stems	20.4 ± 18.3	76.4 ± 44.9	249.5 ± 43.7	391.8 ± 74.8	278.9 ± 55.2	276.5 ± 43.5	199.3 ± 46.3	144.9 ± 24.4	62.6 ± 34.2	36.0 ± 14.8

Table 11. Comparisons of habitat variables between Southwestern Willow Flycatcher nest sites and non-use sites, 2008-2017. Values are given as mean ± SE.

Variable	Use Sites (n = 98)	Non-use Sites (n = 64)
Average canopy cover (%)	91.9 ± 2.3	78.1 ± 5.7
Average canopy height (m)	6.0 ± 0.3	5.2 ± 0.6
Foliage density 0-3 m	15.1 ± 1.9	15.1 ± 2.5
Foliage density 3-10 m	20.9 ± 3.3	10.0 ± 2.2
Total shrub stems (≤8 cm dbh)	382.9 ± 64.8	298.4 ± 65.9
Total tree stems (>8 cm dbh)	2.7 ± 0.9	2.0 ± 0.9
Total snag stems	131.5 ± 29.1	106.3 ± 22.2
Total tamarisk stems	63.2 ± 14.6	60.2 ± 21.6
Total willow stems	173.6 ± 40.0	78.0 ± 42.0

Table 12. Southwestern Willow Flycatcher nests, total number of available stems, and percent occurrence of each species within nest sites for each plant species.

	2008-2009 [a]		2010-2014 [b]		2015-2017 [c]	
Plant Species	Nests and % occurrence	Stems and % occurrence	Nests and % occurrence	Stems and % occurrence	Nests and % occurrence	Stems and % occurrence
Tamarisk	21 (84%)	1556 (23%)	49 (60%)	3618 (13%)	36 (88%)	1232 (20%)
Coyote Willow	3 (12%)	1238 (18%)	33 (40%)	16875 (60%)	2 (5%)	1777 (29%)
Russian Olive	1 (4%)	30 (< 1%)	--	73 (< 1%)	--	6 (< 1%)
Seep Willow	--	86 (1%)	--	696 (2%)	1 (2%)	500 (8%)
Fremont Cottonwood	--	0	--	3 (< 1%)	1 (2%)	33 (1%)
Velvet Ash	--	112 (2%)	--	34 (< 1%)	--	0
Snag	--	3825 (56%)	--	6799 (24%)	1 (2%)	2522 (42%)
Total	**25 (100%)**	**6847 (100%)**	**82 (100%)**	**28098 (100%)**	**41 (100%)**	**6070 (100%)**

[a] Flycatchers utilized nest tree substrates proportionally
[b] Nest trees were not selected in proportion to availability
[c] Flycatchers utilized nest tree substrates proportionally

Table 13. Comparisons of nest tree variables among years for Southwestern Willow Flycatcher. Values are given as mean ± SE.

Variable	2008 (n = 10)	2009 (n = 15)	2010 (n = 20)	2011 (n = 17)	2012 (n = 19)	2013 (n = 10)	2014 (n = 16)	2015 (n = 17)	2016 (n = 10)	2017 (n = 14)
Average nest height (m)	3.0 ± 0.2	2.8 ± 0.2	2.4± 0.2	2.7 ± 0.2	2.7 ± 0.1	2.7 ± 0.2	2.7 ± 0.1	2.8 ± 0.2	3.0 ± 0.2	3.0 ± 0.3
Maximum nest height (m)	4.8	4.6	3.7	4.2	3.5	3.9	3.6	4.9	4.3	4.3
Minimum nest height (m)	2.3	1.5	1.7	1.7	1.4	1.7	1.5	1.3	2.3	1.6
Average substrate height (m)	5.9 ± 0.5	5.1 ± 0.5	4.2 ± 0.3	4.4 ± 0.3	4.6 ± 0.3	4.2 ± 0.2	4.3 ± 0.6	4.2 ± 0.6	5.7 ± 0.3	5.1 ± 0.4
Average canopy height (m)	6.6 ± 0.2	5.9 ± 0.3	5.8 ± 0.3	6.1 ± 0.3	6.3 ± 0.3	7.0 ± 0.5	5.4 ± 0.2	6.6 ± 0.4	6.2 ± 0.2	7.9 ± 1.8
Average distance to habitat edge (m)	28.4 ± 6.1	39.3 ± 14.0	28.6 ± 2.7	11.9 ± 1.9	16.7 ± 1.9	13.9 ± 2.5	19.0 ± 1.9	24.8 ± 2.7	17.0 ± 1.4	30.0 ± 6.3
Average distance to water (m)	21.8 ± 5.2	12.9 ± 3.8	3.7 ± 0.8	2.7 ± 0.9	1.9 ± 0.7	1.7 ± 0.7	4.7 ± 1.7	1.4 ± 0.5	11.0 ± 3.2	17.7 ± 9.3

Table 14. Southwestern Willow Flycatcher nest site variables among varying breeding season periods. Values are given as mean ± SE.

	2008-2009		2010-2014		2015-2017	
Variable	Average	Range	Average	Range	Average	Range
Nest height (m)	2.9 ± 1.2	1.5 - 4.8	2.6 ± 0.2	1.5 - 3.9	2.9 ± 0.2	1.3 - 4.9
Substrate height (m)	5.5 ± 0.5	2.1 - 8.5	4.3 ± 0.3	2.4 - 6.8	5.0 ± 0.4	2.2 - 6.9
Canopy height (m)	6.3 ± 0.3	3.8 - 8.5	6.1 ± 0.3	3.1 - 9.5	6.9 ± 0.8	5.2 - 15.0
Canopy cover (%)	92.0 ± 3.0	64.9 - 99.8	92.5 ± 1.7	69.9 - 96.0	90.6 ± 2.9	68.4 - 95.8
Distance to habitat edge (m)*****	33.9 ± 10.1	5.0 - 230.0	18.0 ± 2.2	2.0 - 59.0	23.9 ± 3.5	10.0 - 77.0
Distance to water (m)*****	17.4 ± 4.5	0.0 - 47.0	2.9 ± 1.0	0.0 - 19.0	10.0 ± 4.3	0.0 - 109.0

*Significant differences observed among the varying breeding seasons

Table 15. Southwestern Willow Flycatcher nest site microhabitat characteristics for successful and unsuccessful nests. Values are given as mean ± SE.

	2008-2009		2010-2014		2015-2017	
Variable	Successful	Unsuccessful[a]	Successful	Unsuccessful[a]	Successful	Unsuccessful[a]
Nest height (m)	2.8 ± 0.2	3.0 ± 0.2	2.6 ± 0.1	2.7 ± 0.1	2.7 ± 0.2	3.1 ± 0.2
Canopy height (m)	6.6 ± 0.2	6.0 ± 0.3	6.2 ± 0.2	6.0 ± 0.2	6.9 ± 0.7	6.5 ± 0.3
Distance to habitat edge (m)	26.6 ± 4.8	39.6 ± 13.3	18.6 ± 1.7	18.1 ± 1.8	26.9 ± 4.3	22.2 ± 2.4
Distance to water (m)	15.0 ± 4.6	17.3 ± 4.2	3.0 ± 0.6	2.8 ± 0.7	12.7 ± 6.3	5.5 ± 1.5

[a] Includes multiple causes of nest failure, including: depredation, parasitism, failure to hatch and abandonment

Table 16. Southwestern Willow Flycatcher nest site microhabitat characteristics for parasitized and non-parasitized nests. Values are given as mean ± SE.

	2008-2009		2010-2014		2015-2017	
Variable	Parasitized (n = 8)	Non-parasitized (n = 17)	Parasitized (n = 23)	Non-parasitized (n = 40)	Parasitized (n = 6)	Non-parasitized (n = 14)
Nest height (m)	2.5 ± 0.1	3.1 ± 0.2	2.7 ± 0.1	2.4 ± 0.1	2.6 ± 0.4	2.9 ± 0.2
Substrate height (m)	4.3 ± 0.7	5.9 ± 0.4	4.7 ± 0.3	4.2 ± 0.2	4.1 ± 0.5	5.3 ± 0.3
Substrate dbh (cm)	6.5 ± 2.9	7.3 ± 1.1	3.4 ± 0.5	3.6 ± 0.9	4.6 ± 0.9	5.1 ± 0.7
Canopy height (m)	6.6 ± 0.3	6.0 ± 0.3	6.2 ± 0.3	6.2 ± 0.2	5.8 ± 0.2	7.2 ± 0.6
Canopy cover (%)	98.3 ± 0.8	96.2 ± 1.3	93.7 ± 0.9	92.2 ± 1.1	90.4 ± 2.4	91.0 ± 2.0

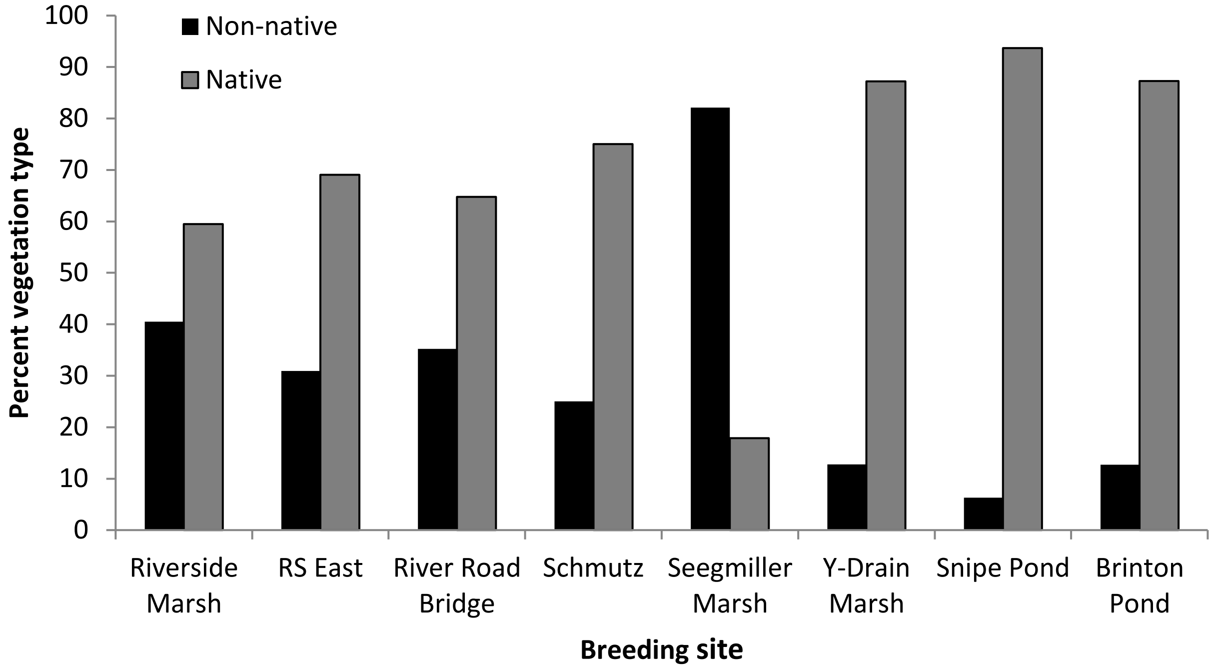


Figure 2. Non-native and native vegetation composition of occupied areas within breeding patches varied strongly among patches, with Seegmiller Marsh dominated by non-natives; Riverside Marsh, Riverside East, and Schmutz Drain more evenly mixed non-native-native; and Y-Drain Marsh and Snipe Pond dominated by natives. Tamarisk and Coyote Willow comprised 97.5 % and 95.2 % of non-native and native vegetation, respectively, over all sites.

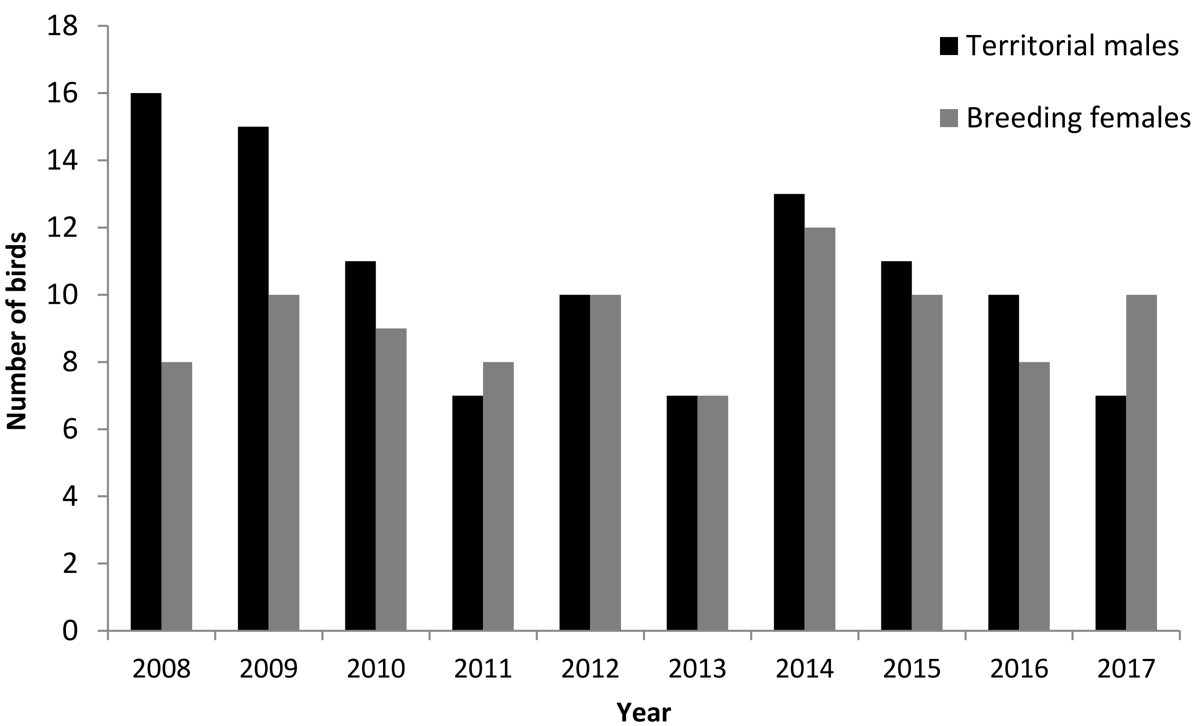


Figure 3. Total number of territorial male flycatchers and breeding female flycatchers in the St George study area, 2008-2017.

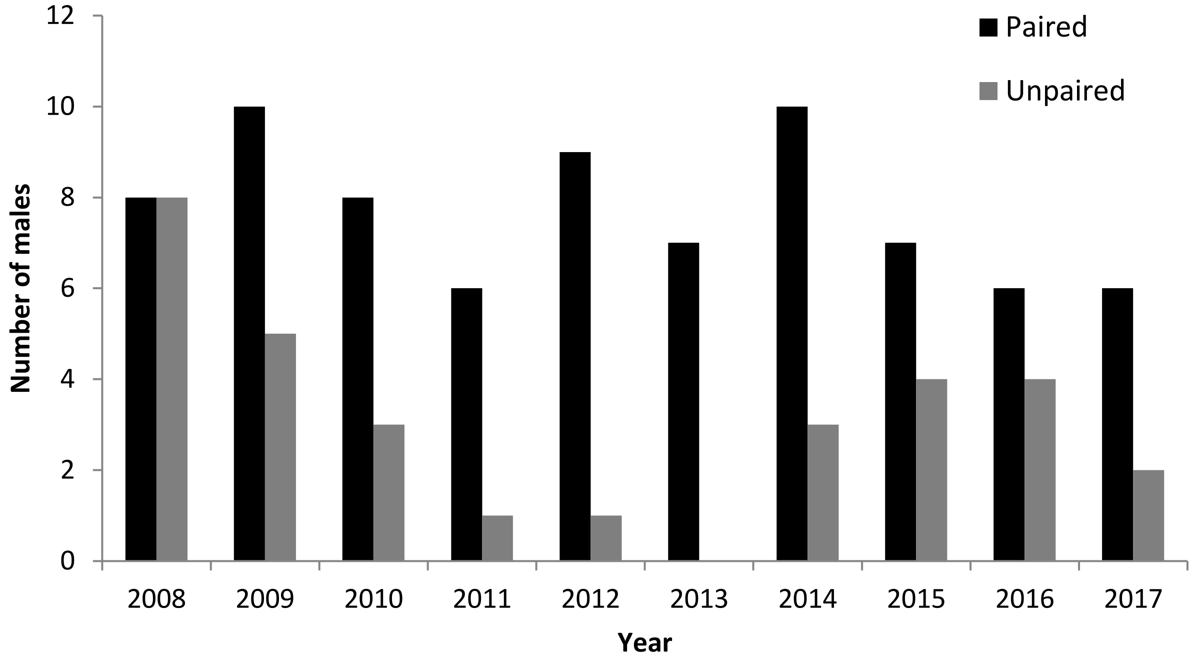


Figure 4. The number of paired and unpaired male flycatchers maintaining territories in the St George study area, 2008-2017.

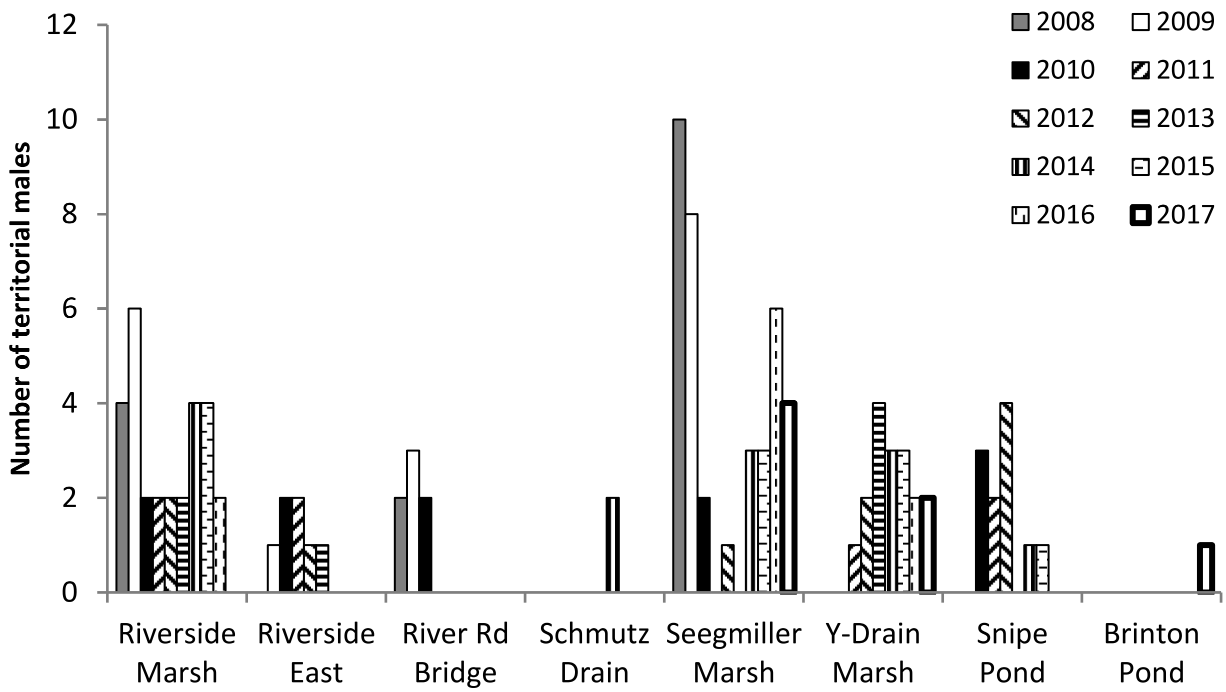


Figure 5. The total number and distribution of territorial male flycatchers at breeding sites in the St George study area, 2008-2017.

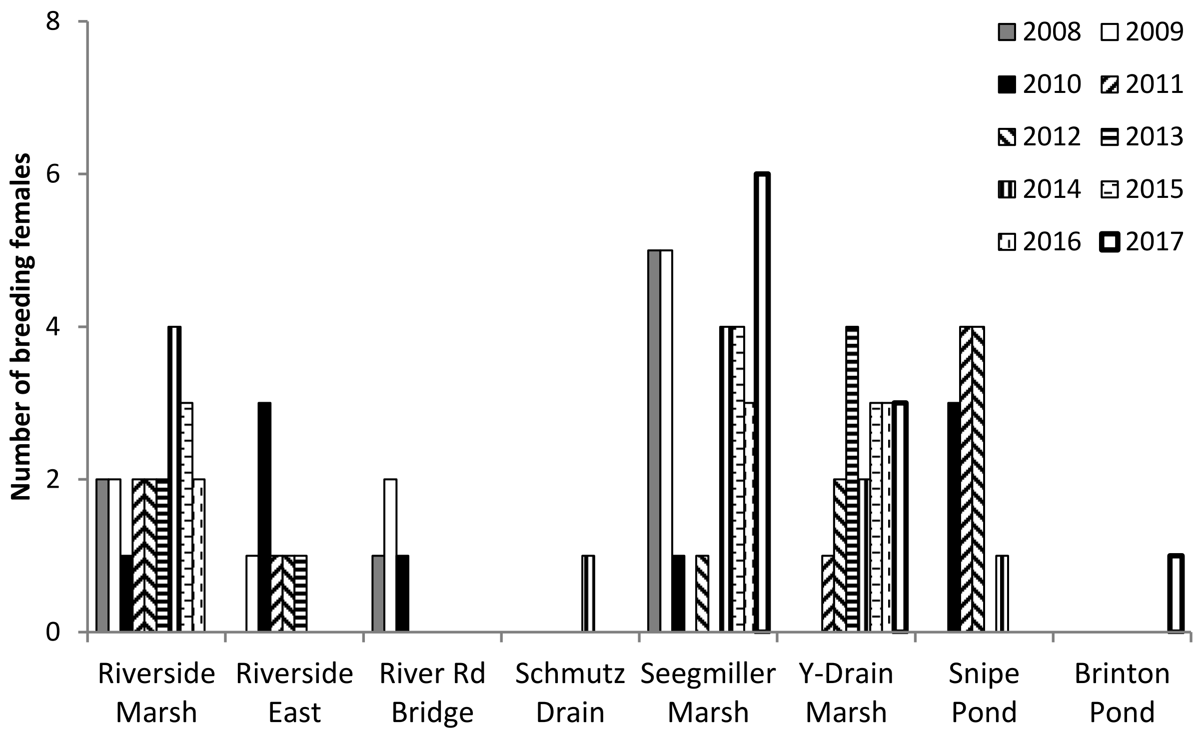


Figure 6. The total number and distribution of breeding female flycatchers at breeding sites in the St George study area, 2008-2017.

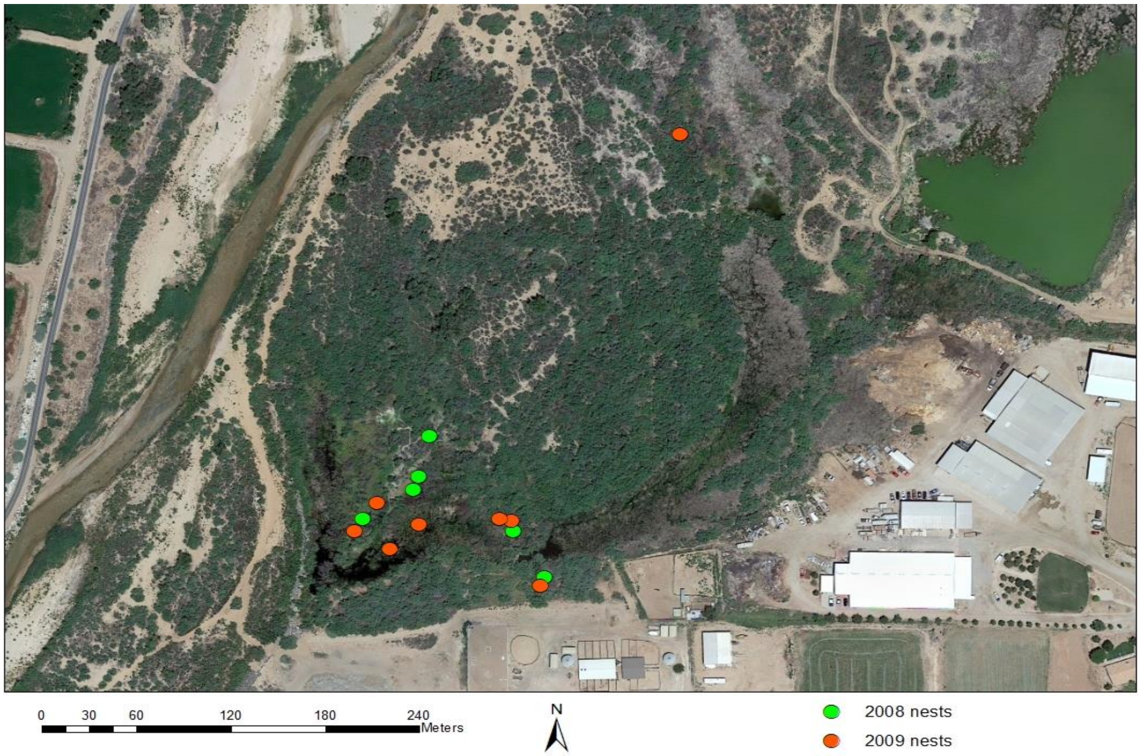


Figure 7. Total number (n = 14) and location of active flycatcher nests at Seegmiller Marsh during the 2008 and 2009 breeding seasons.

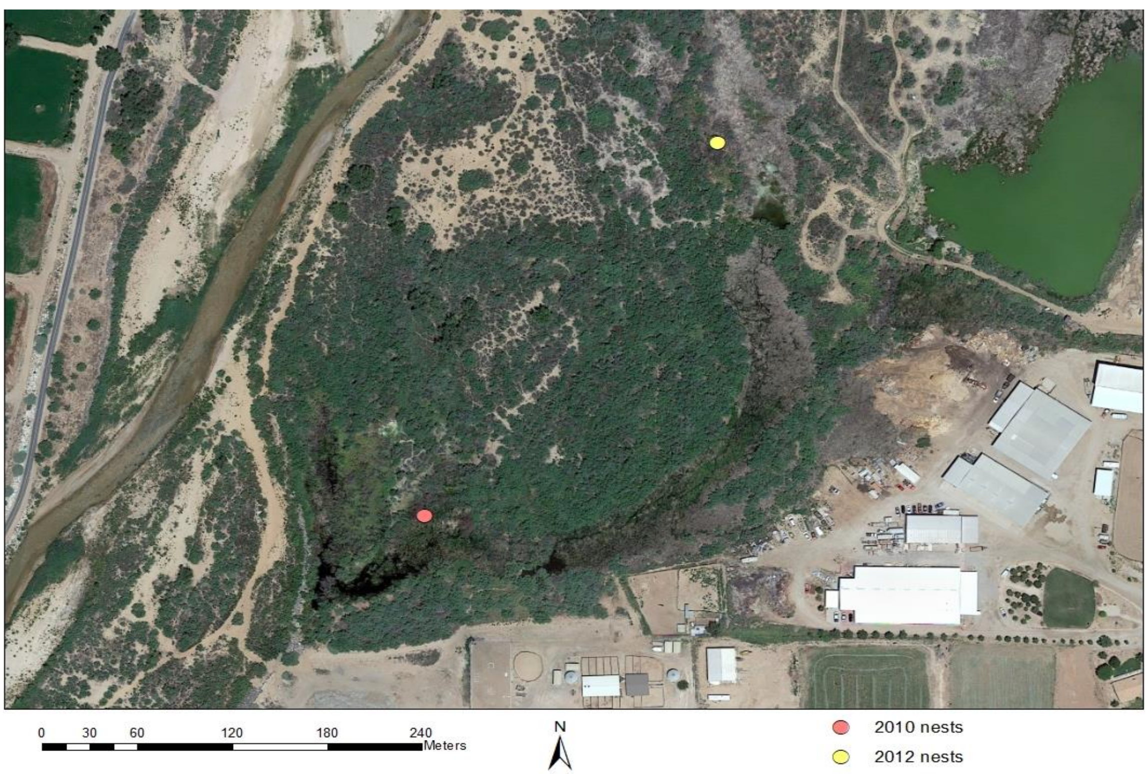


Figure 8. Total number (n = 2) and location of active flycatcher nests at Seegmiller Marsh between the 2010 and 2013 breeding seasons.

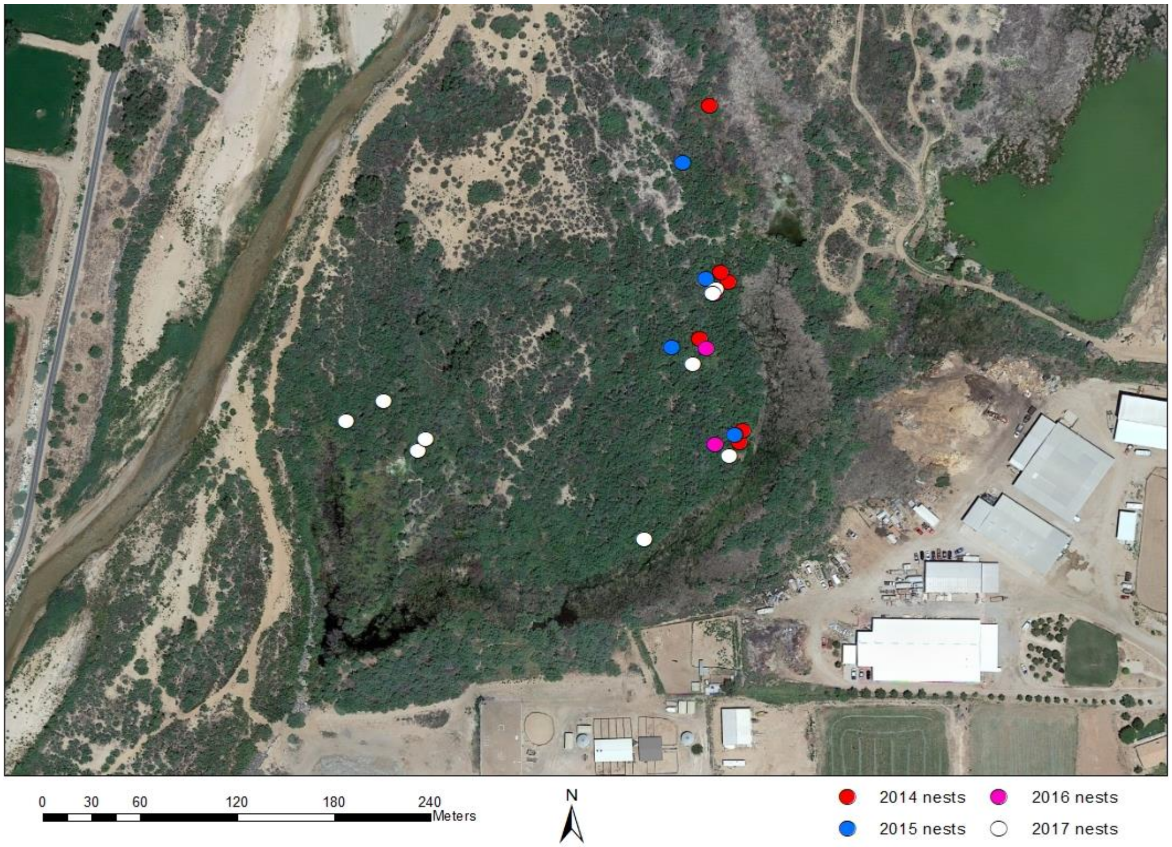


Figure 9. Total number (n = 22) and location of active flycatcher nests at Seegmiller Marsh between the 2014 and 2017 breeding seasons.

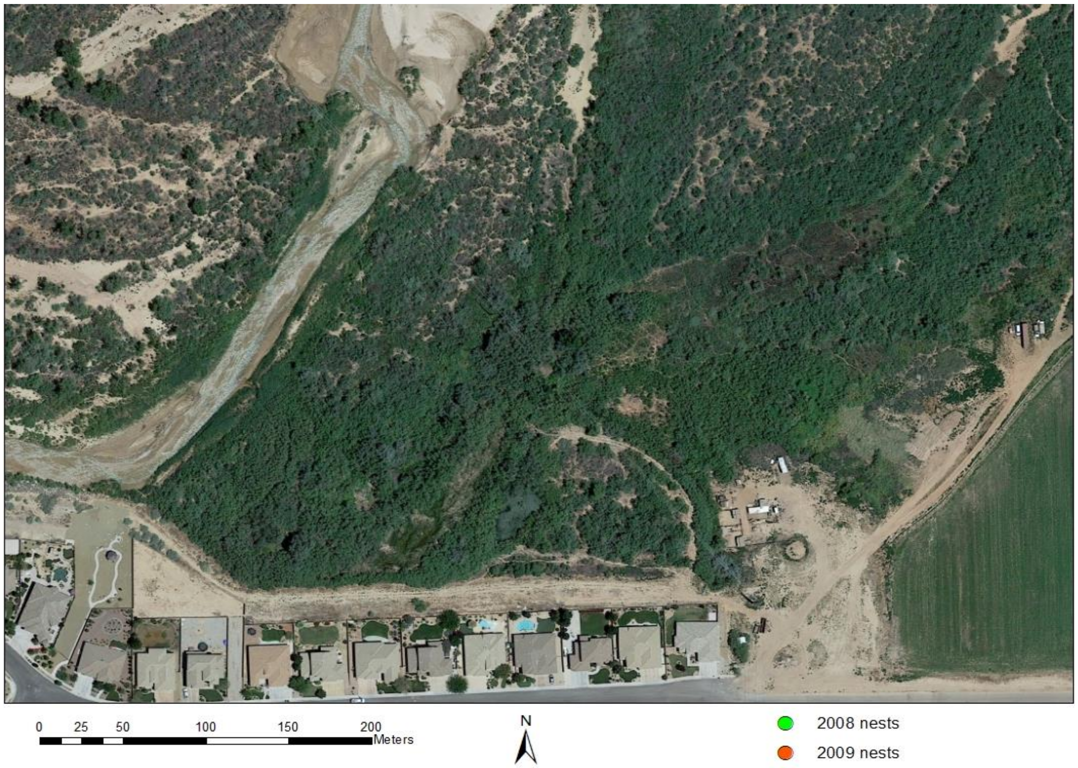


Figure 10. Total number (n = 0) and location of active flycatcher nests at Snipe Pond during the 2008 and 2009 breeding seasons.

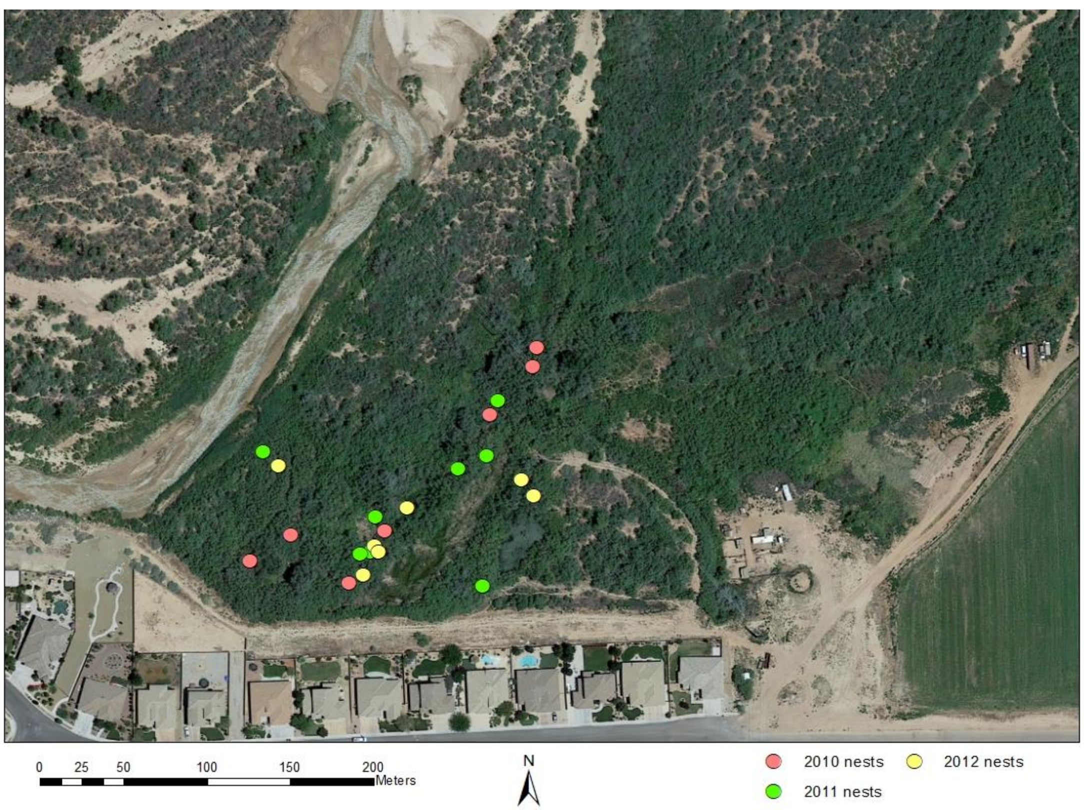


Figure 11. Total number (n = 22) and location of active flycatcher nests at Snipe Pond between the 2010 and 2013 breeding seasons.

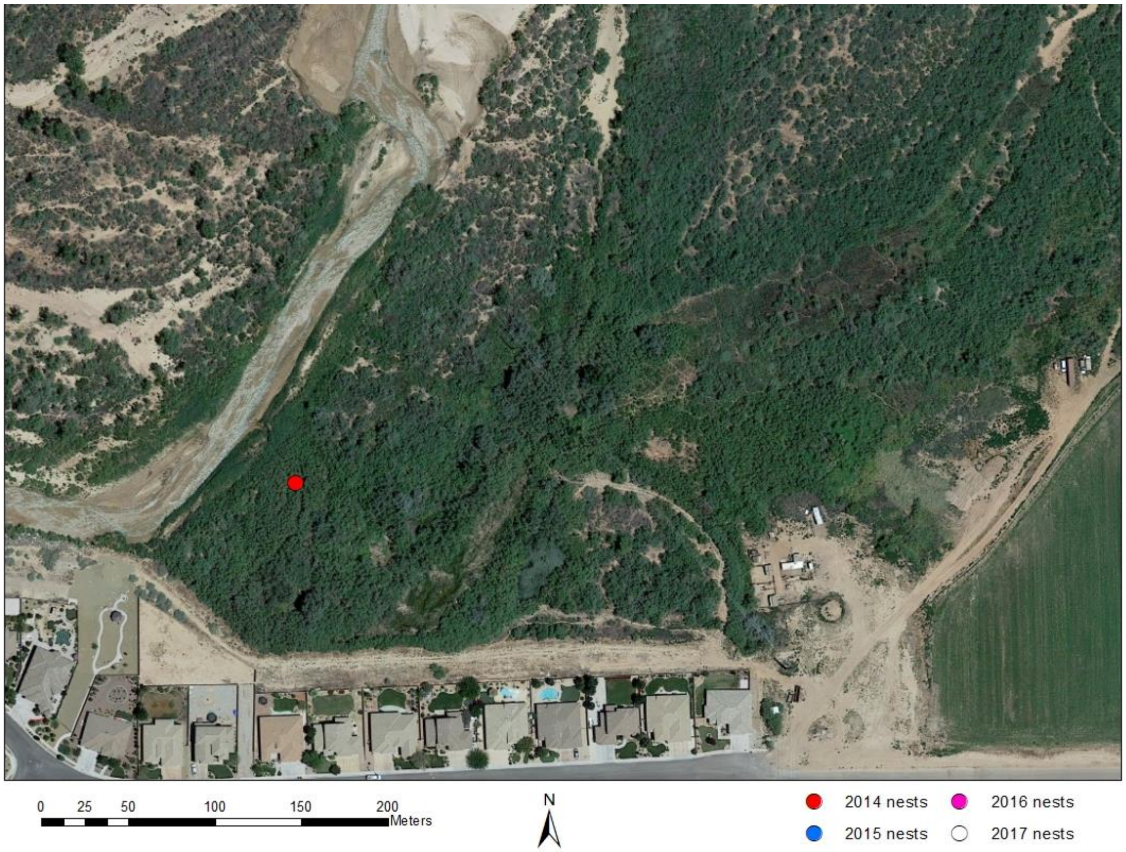


Figure 12. Total number (n = 1) and location of active flycatcher nests at Snipe Pond between the 2014 and 2017 breeding seasons.

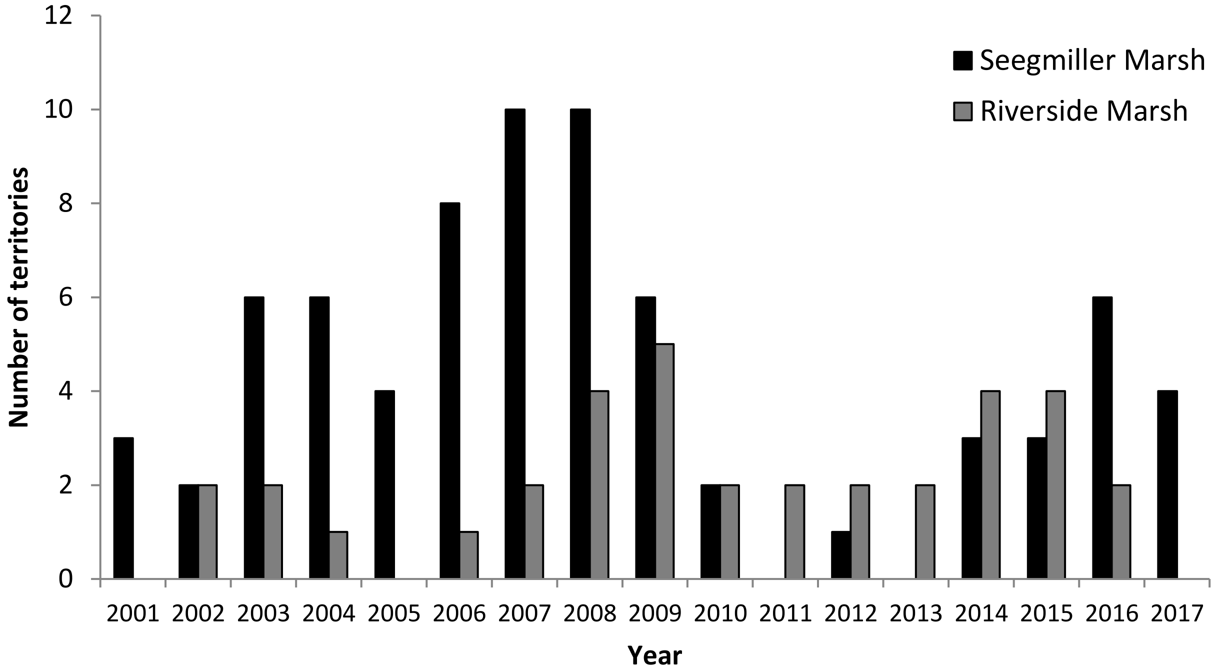


Figure 13. Number of flycatcher territories at Seegmiller Marsh and Riverside Marsh from 2001-2017.

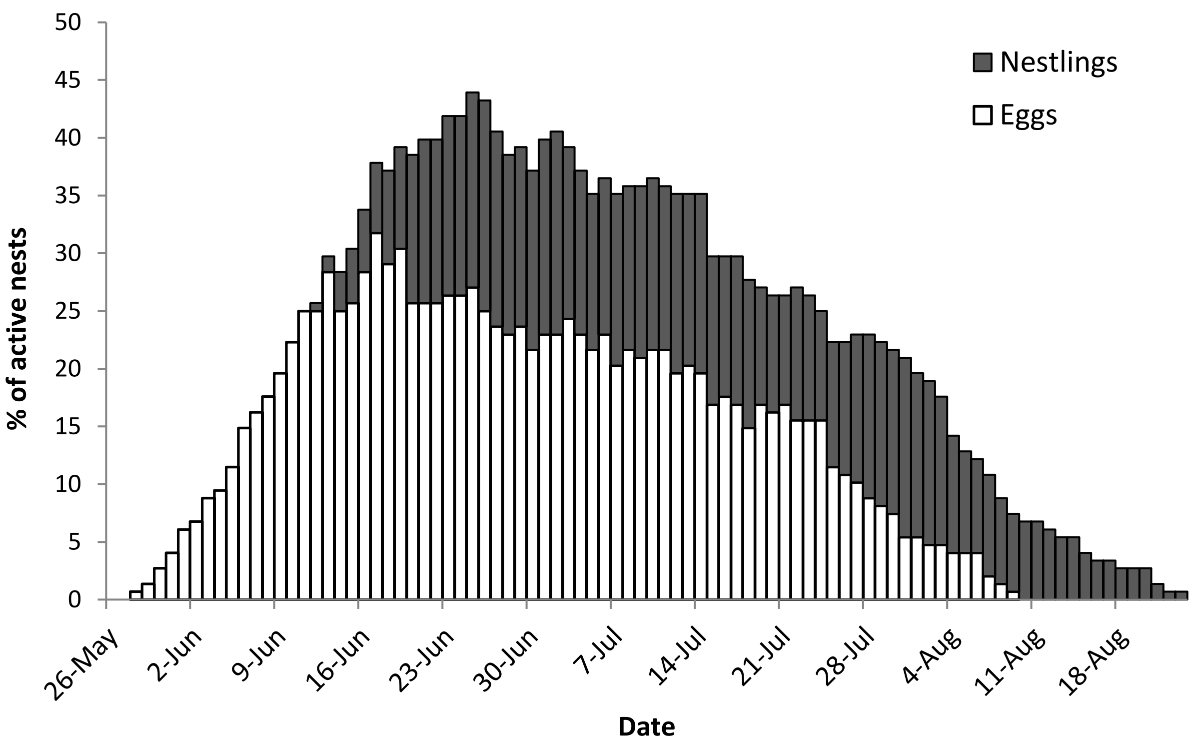
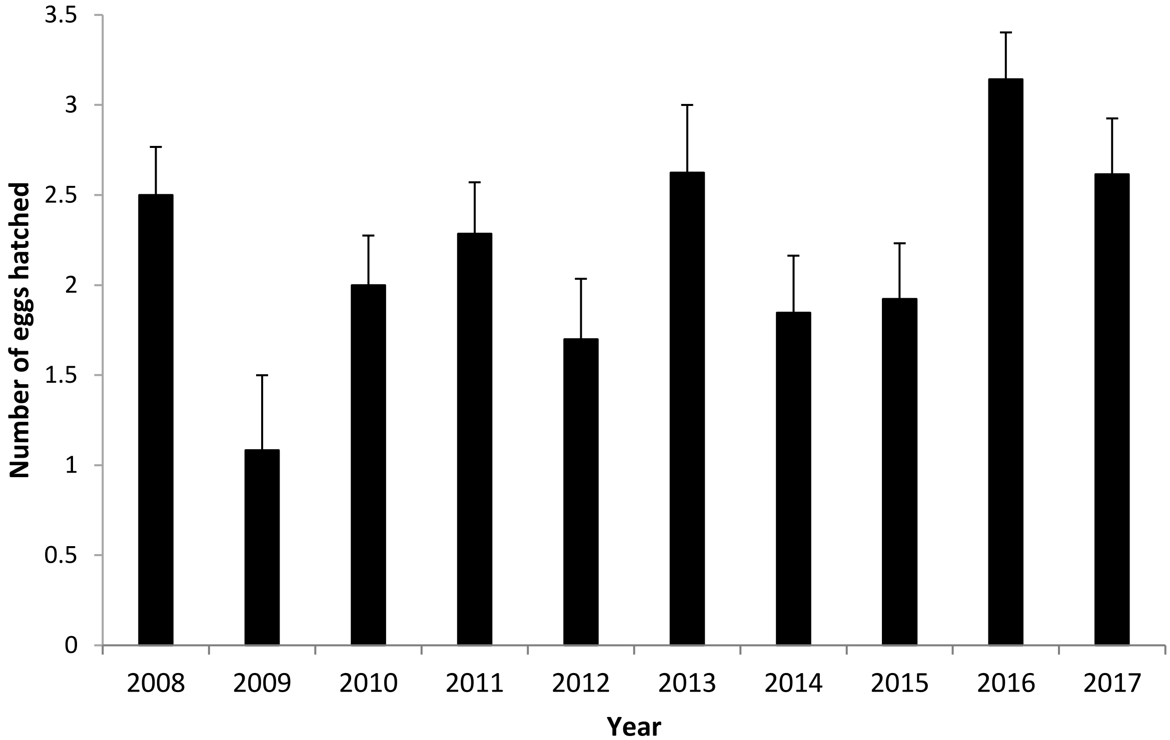


Figure 14. Southwestern Willow Flycatcher breeding phenology in the St George study area, 2008-2017 (years combined; n = 148 nests).



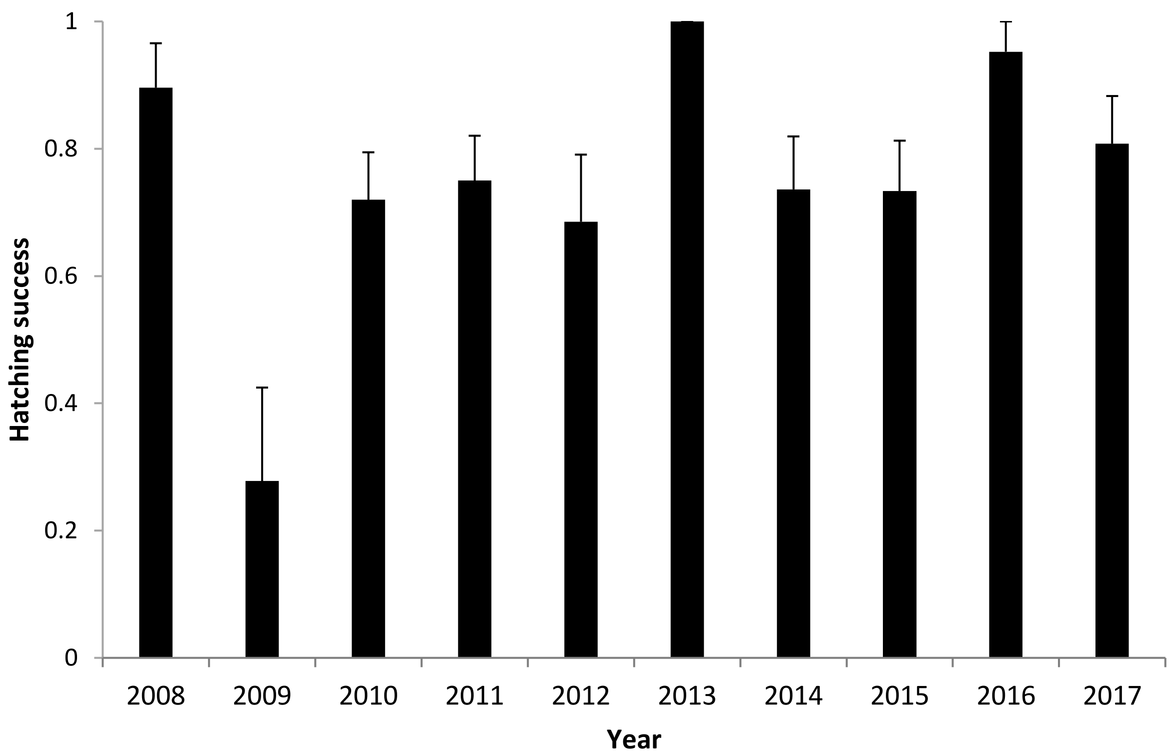


Figure 15. Mean (± SE) number of eggs hatched (upper) and hatching success rate (lower) for Southwestern Willow Flycatchers in the St George study area, 2008-2017.

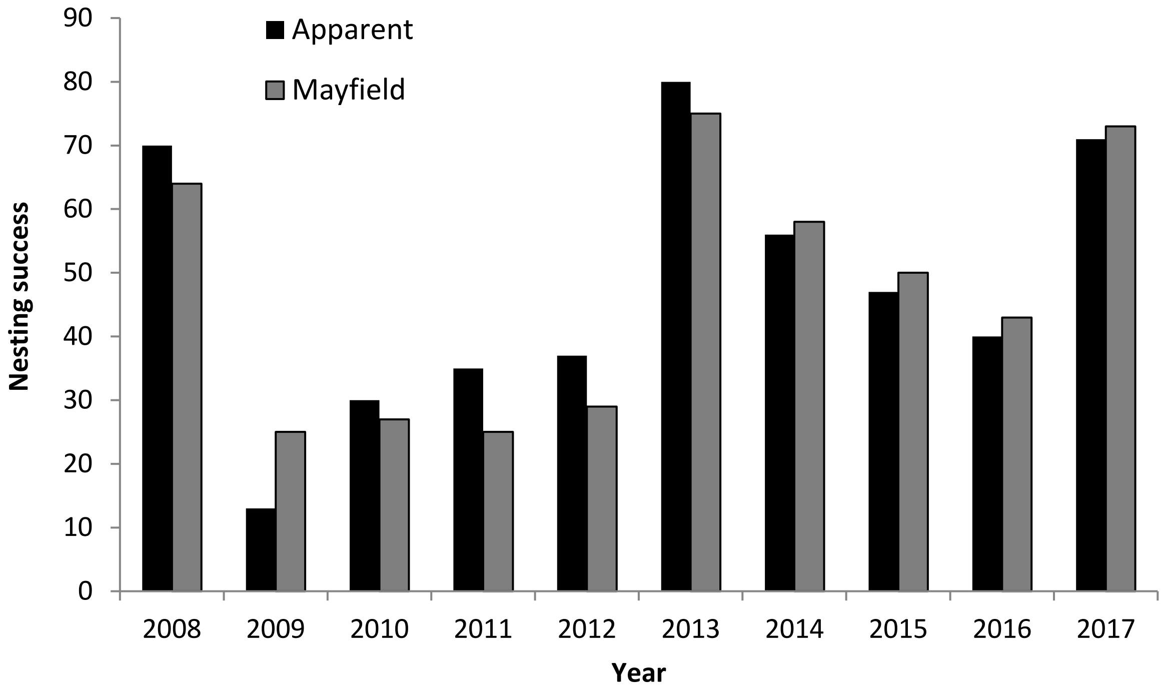


Figure 16. Apparent nest success (percentage of nests successfully fledging ≥ one flycatcher) and Mayfield survival probability (percent probability of nests surviving to fledge ≥ one flycatcher) of Southwestern Willow Flycatcher nests in the St George study area, 2008-2017.

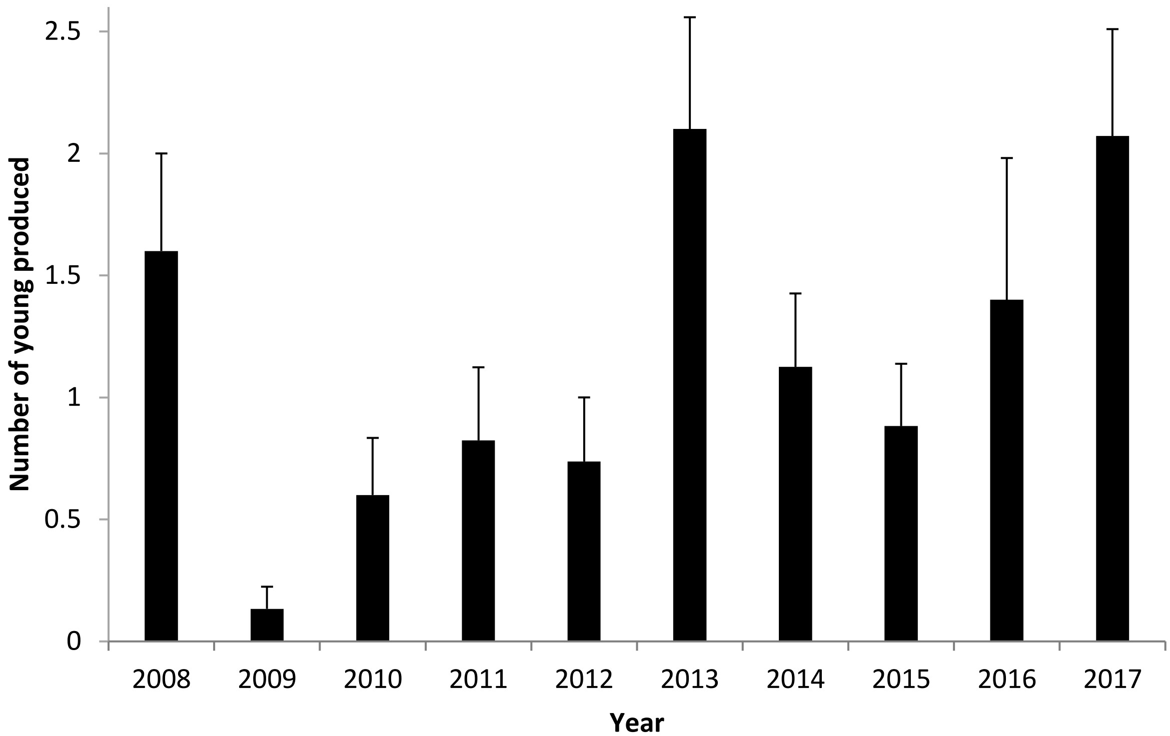


Figure 17. Mean (± SE) number of young Southwestern Willow Flycatchers produced per nest (successful and unsuccessful nests combined) in the St George study area, 2008-2017.

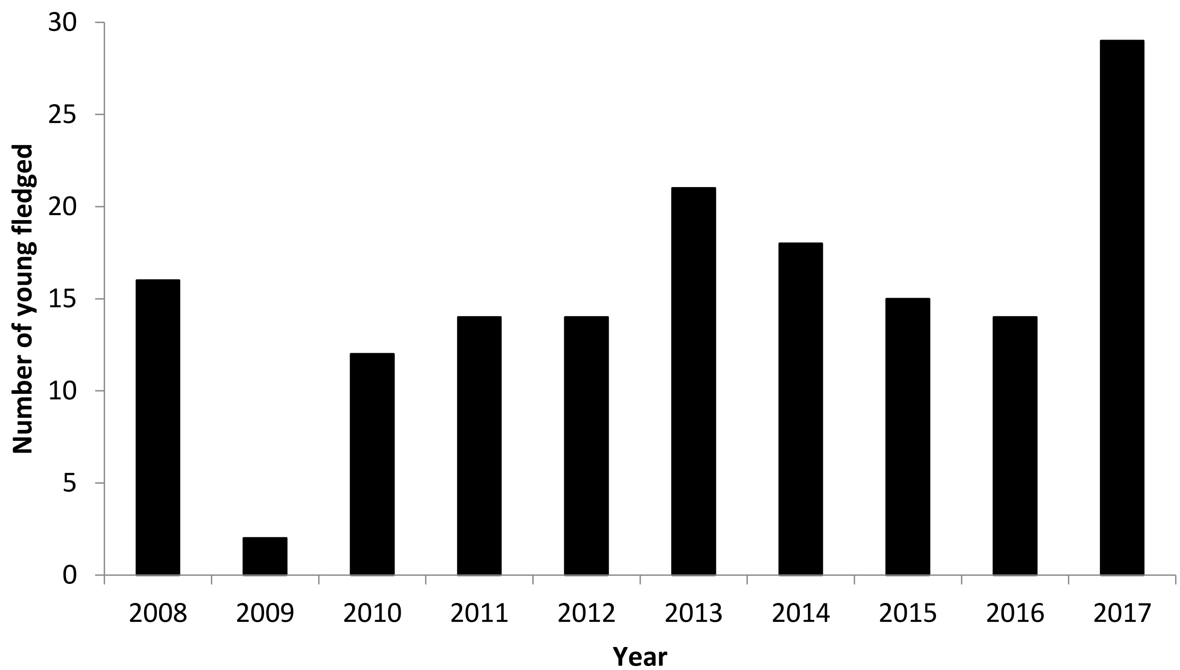


Figure 18. Total number of young Southwestern Willow Flycatchers produced in the St George study area, 2008-2017.

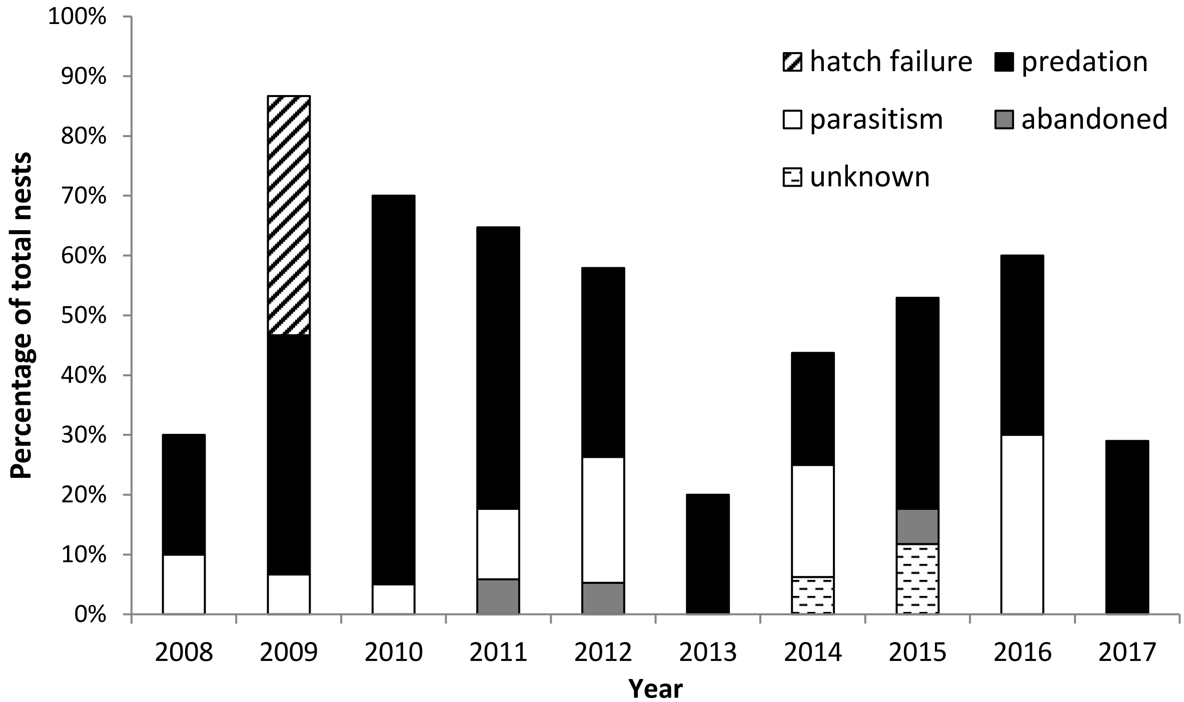


Figure 19. Total number (percentage) of unsuccessful nests and cause of failure of Southwestern Willow Flycatchers in the St George study area, 2008-2017.

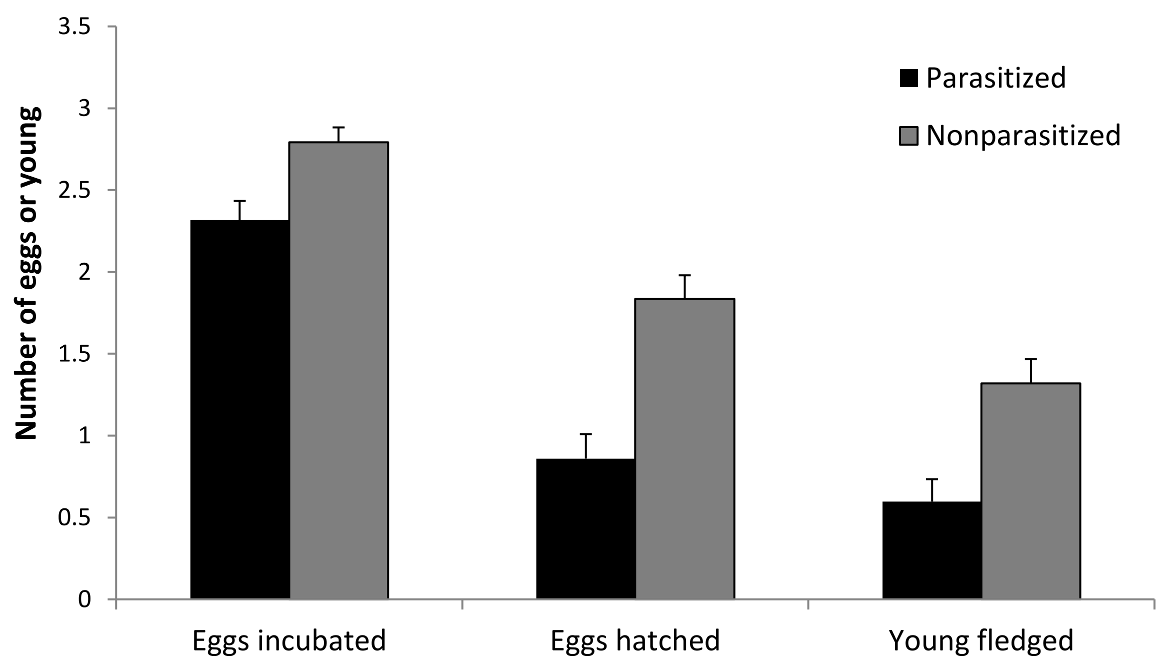


Figure 20. Mean number of Southwestern Willow Flycatcher eggs incubated and successfully hatched in, and young successfully fledged from, flycatcher nests parasitized by and not parasitized by Brown-headed Cowbirds in the St George study area, 2008-2017.

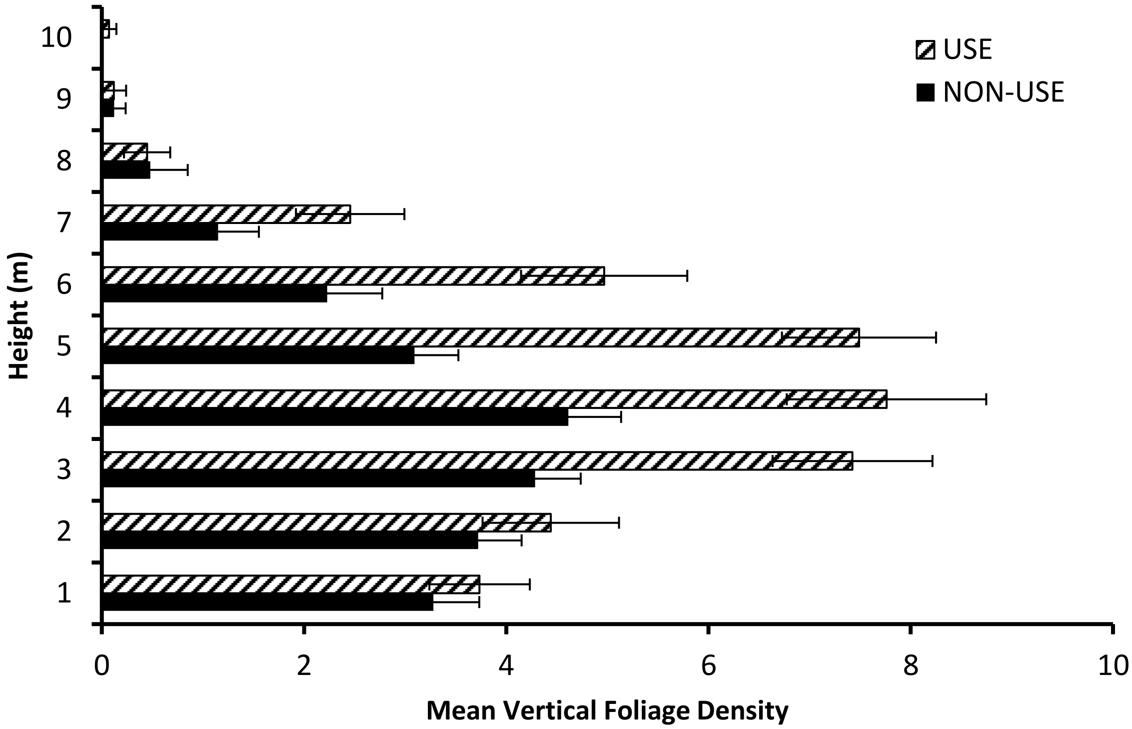


Figure 21. Mean vertical foliage density between Southwestern Willow Flycatcher use and non-use sites (2008-2011).

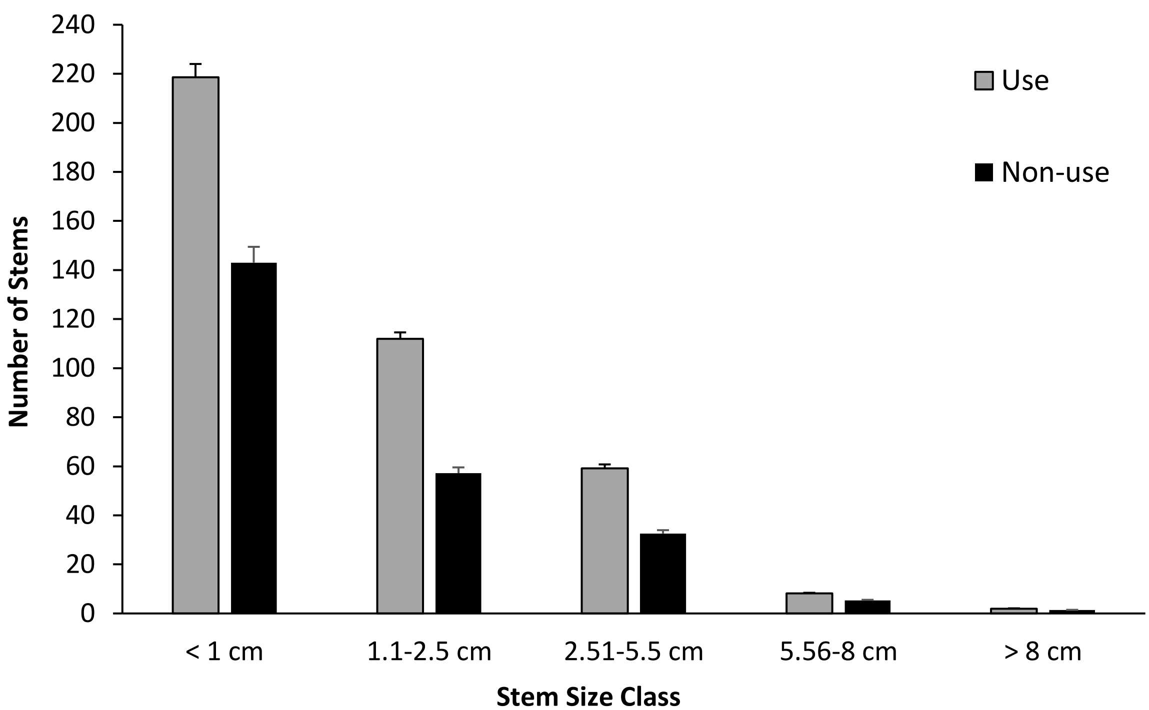


Figure 22. Total number of stems distributed by size class (cm) between Southwestern Willow Flycatcher use and non-use sites, 2008-2017.

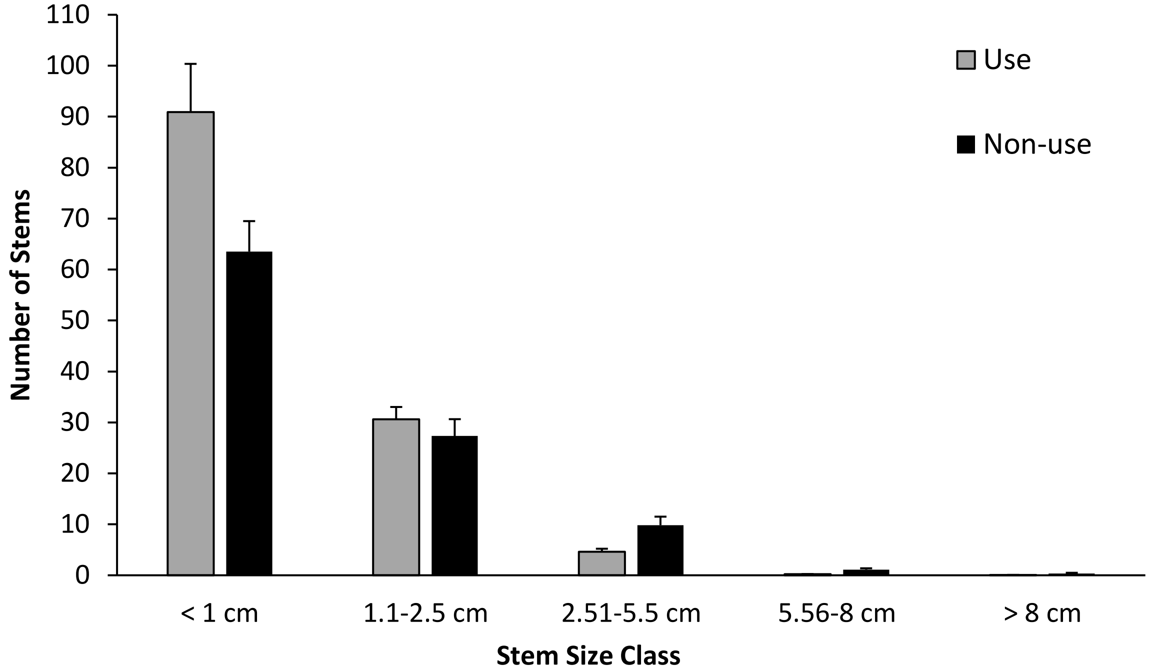


Figure 23. Number of snag stems distributed by size class (cm) between Southwestern Willow Flycatcher use and non-use sites, 2008-2017.

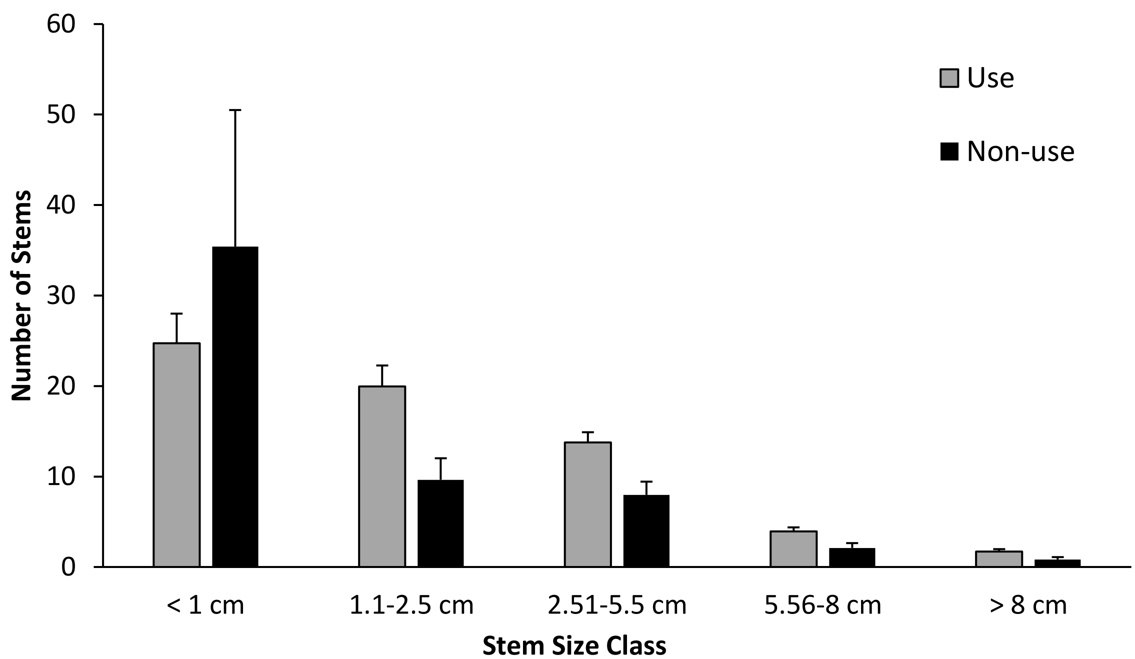


Figure 24. Number of tamarisk stems distributed by size class (cm) between Southwestern Willow Flycatcher use and non-use sites, 2008-2017.

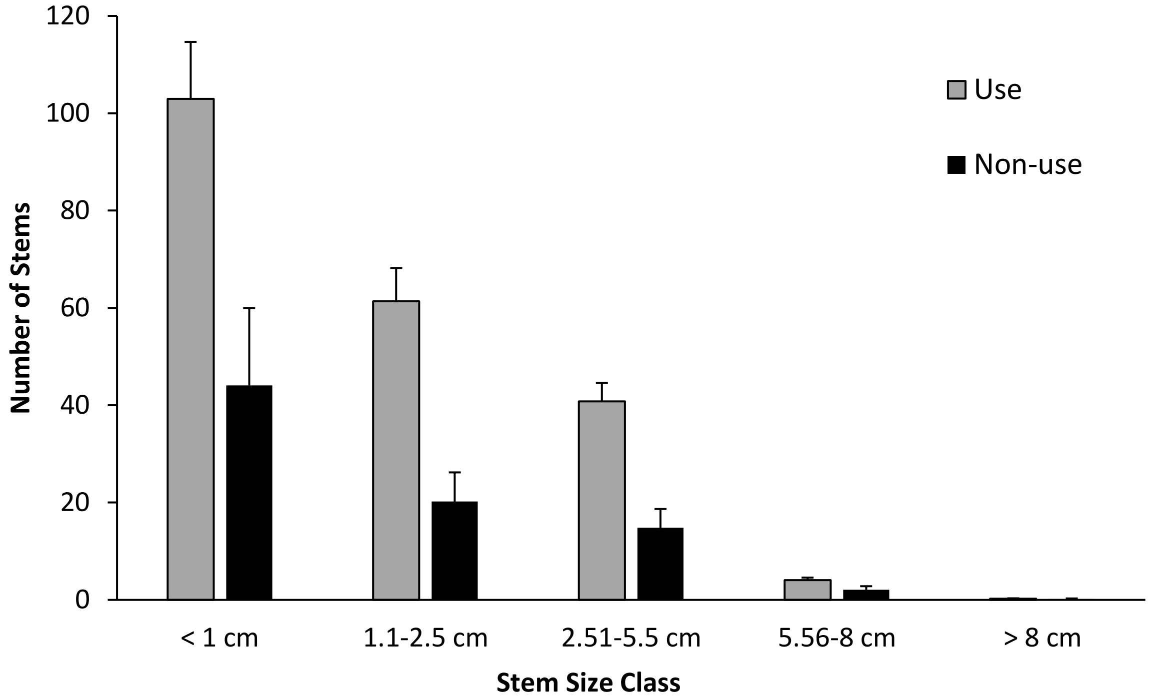


Figure 25. Number of willow stems distributed by size class (cm) between Southwestern Willow Flycatcher use and non-use sites, 2008-2017.

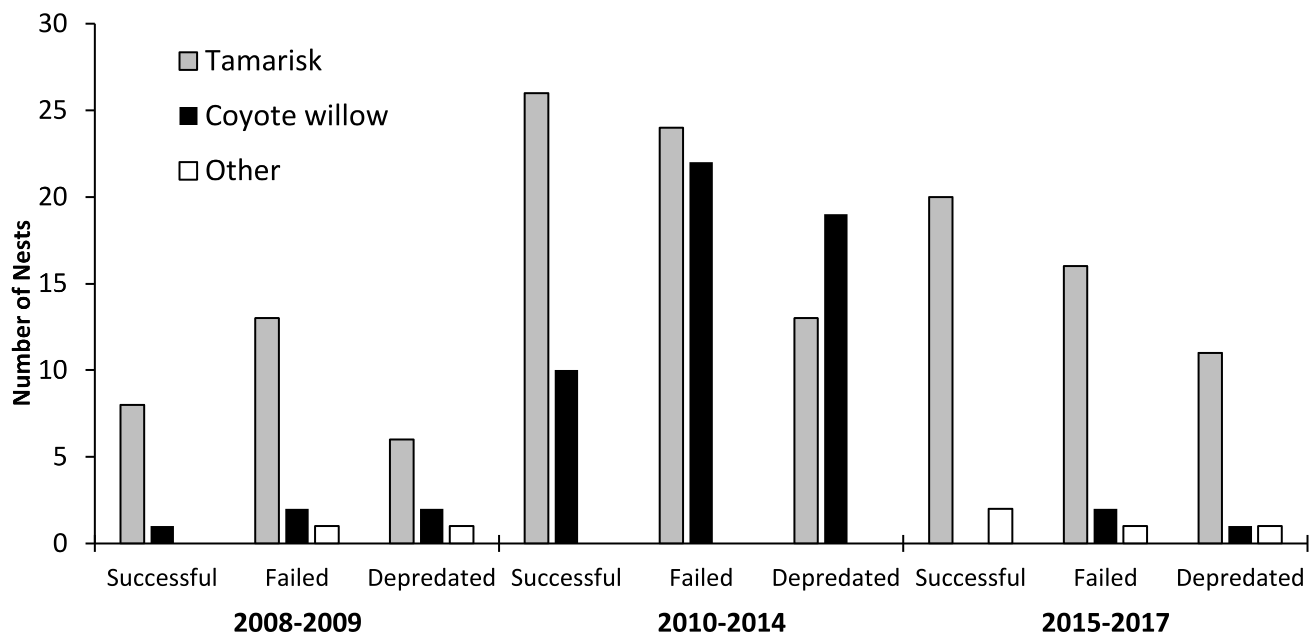


Figure 26. Fate of Southwestern Willow Flycatcher nests by substrate tree. Failed nests include depredation, parasitism, failure to hatch and abandonment. Depredation was the leading cause of failed nests. Other substrates include Russian Olive, Seep Willow, Fremont Cottonwood, and snag.

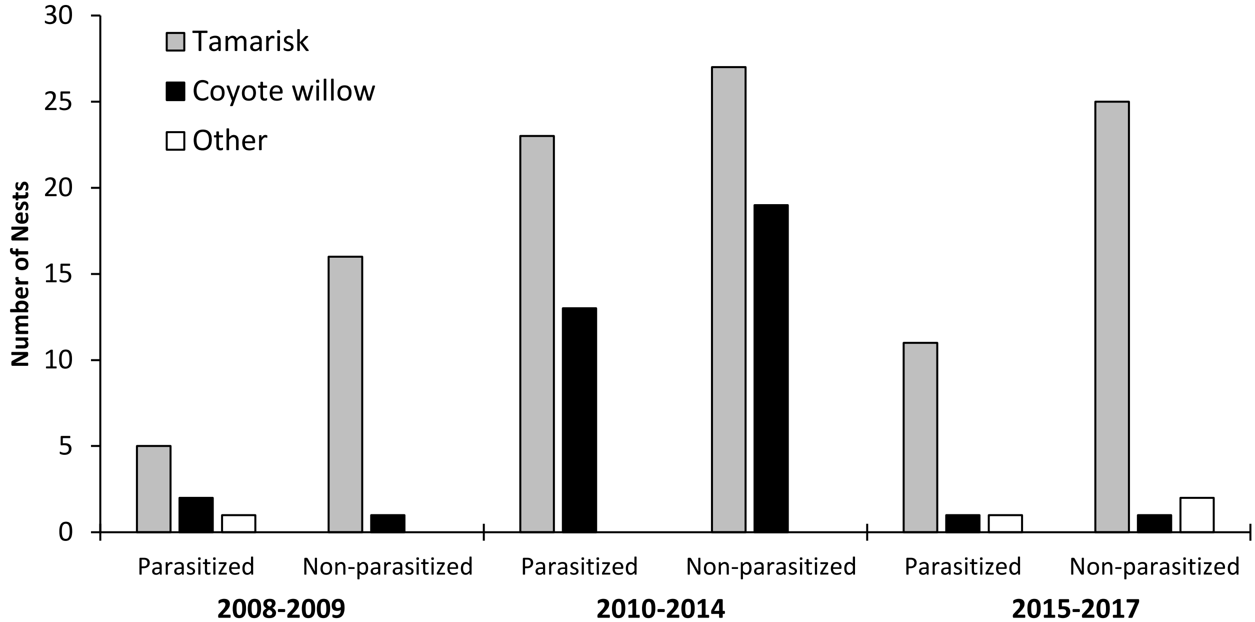


Figure 27. Number of Southwestern Willow Flycatcher nests parasitized by Brown-headed Cowbirds by substrate tree.

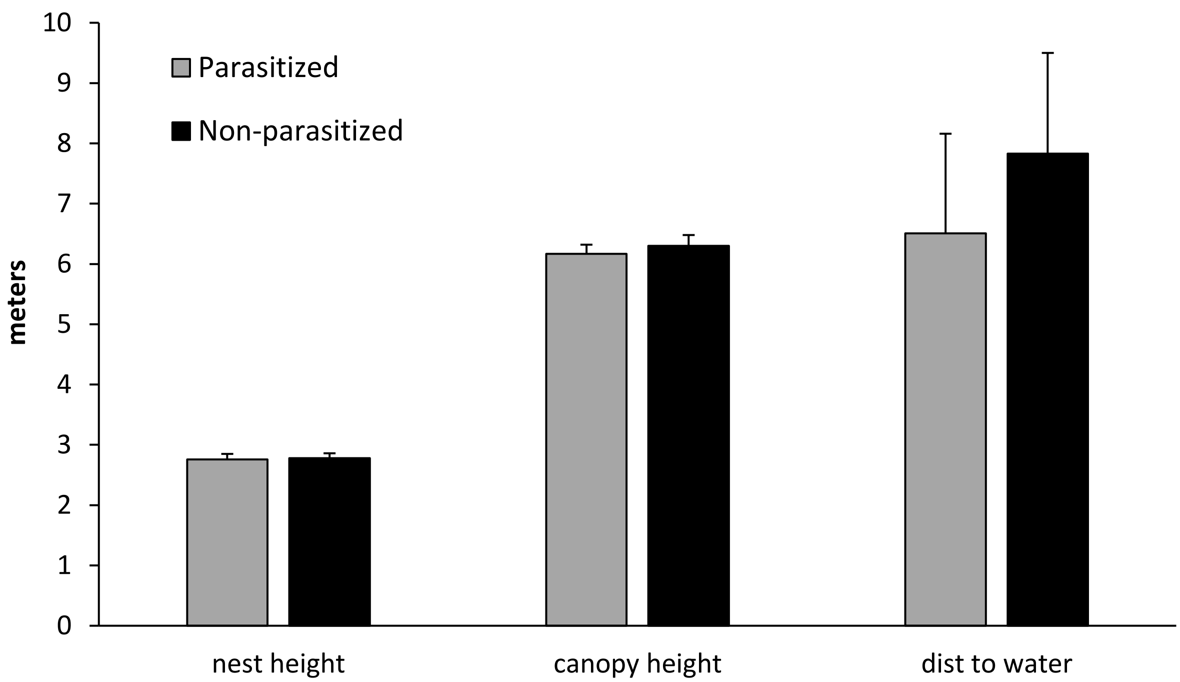


Figure 28. Southwestern Willow Flycatcher nest site microhabitat characteristics for parasitized and non-parasitized nests, 2008-2017.

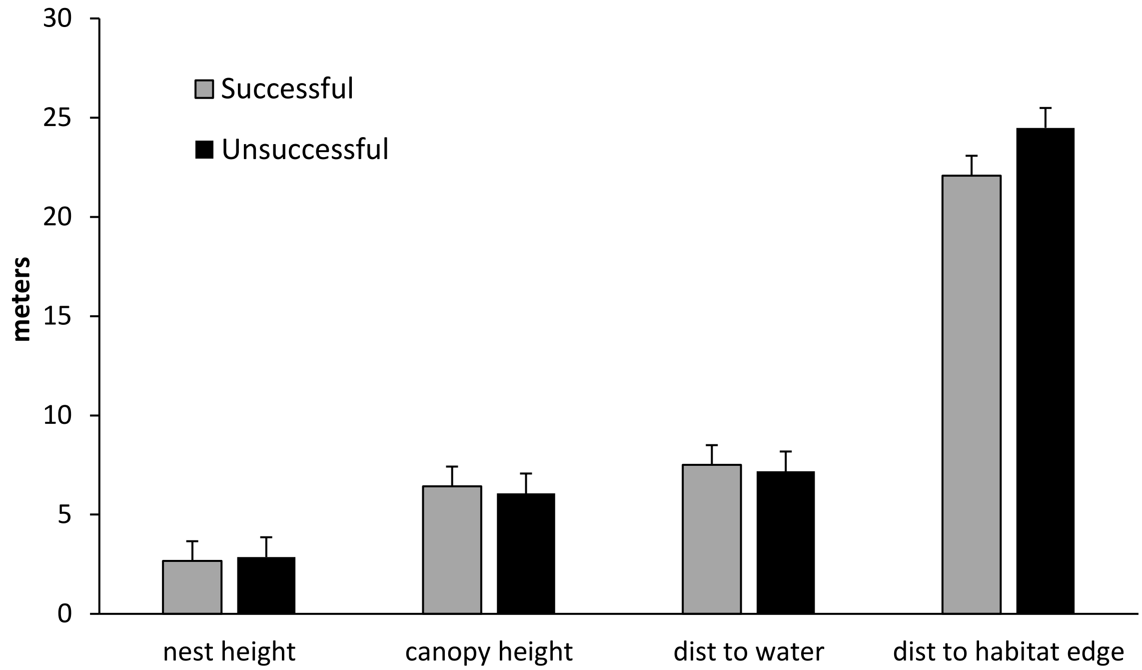


Figure 29. Southwestern Willow Flycatcher nest site microhabitat characteristics for successful and unsuccessful nests, 2008-2017.

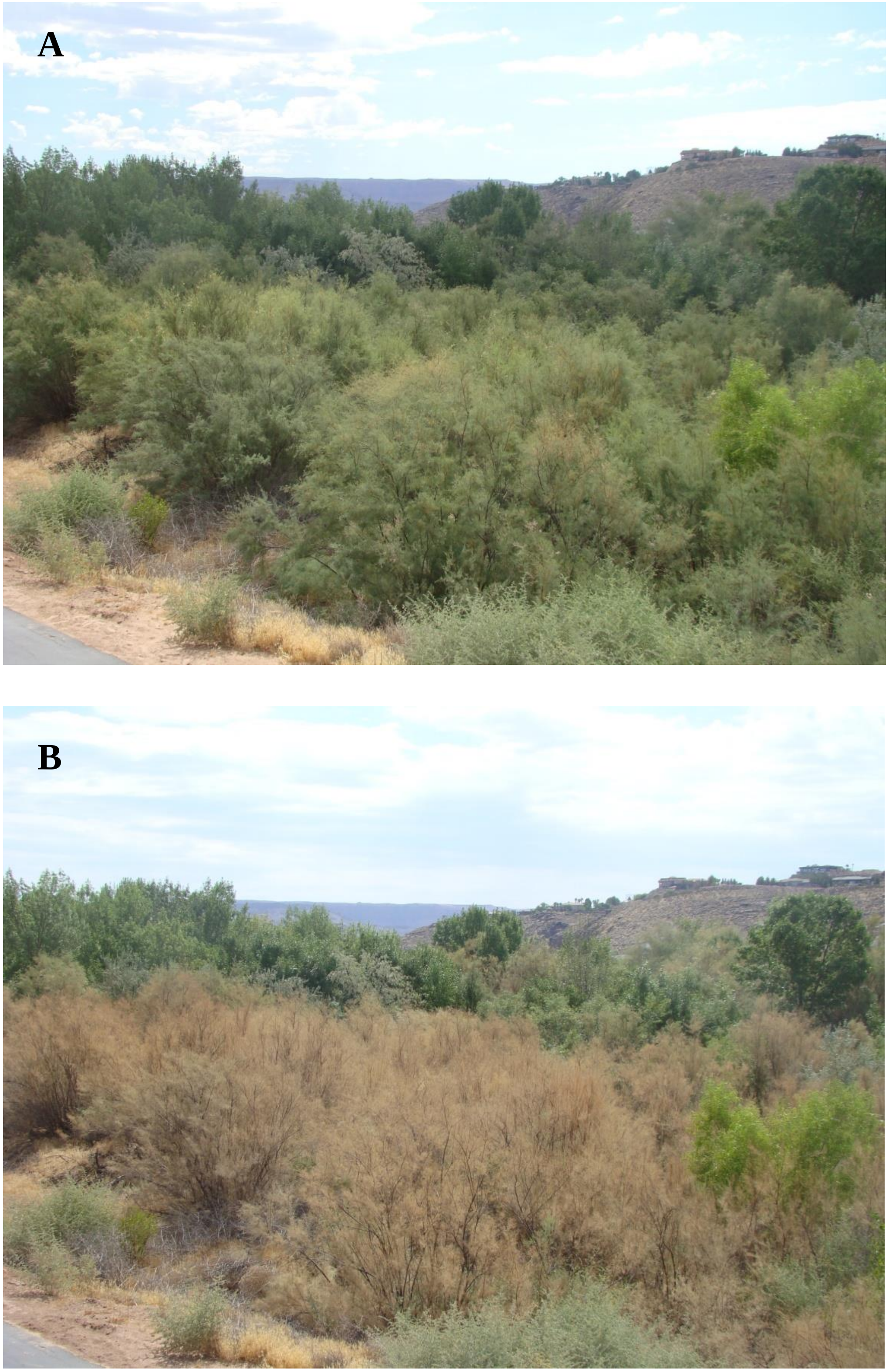


Figure 30. River Road Bridge breeding site in St. George, Washington County, Utah, (A) prior to tamarisk beetle defoliation on 11 July 2014, and (B) following tamarisk beetle defoliation on 25 July 2014.

APPENDICES

Appendix A. Summary of breeding site success during 2008-2017, including site name, number of active nests, observation days, nest losses, daily survival rate (DSR), Mayfield success, apparent success, number of nests parasitized, and parasitism rate. Note: Schmutz Drain is not included due to the absence of any active flycatcher nests.

Table A.1. Number of active nests, observation days, nest losses, daily survival rate (DSR), Mayfield success, apparent success, number of nests parasitized, and parasitism rate at Riverside Marsh, 2008-2017.

Year	Active nests	Observation days	Nest losses	DSR	Mayfield success	Apparent success	Parasitized nests	Parasitism rate
2008	3	27	2	92.6%	11.0%	33.3%	1	33.3%
2009	3	44	3	93.2%	13.2%	0.0%	1	33.3%
2010	1	29	0	100.0%	100.0%	100.0%	0	0.0%
2011	6	50	5	90.0%	4.9%	16.7%	4	66.7%
2012	5	69	4	94.2%	18.0%	20.0%	3	60.0%
2013	2	55	0	100.0%	100.0%	100.0%	0	0.0%
2014	6	165	2	98.8%	70.5%	66.7%	4	66.7%
2015	7	138	4	97.1%	43.0%	42.9%	4	57.1%
2016	1	23	1	95.7%	27.9%	0.0%	0	0.0%
2017	0	-	-	-	-	-	-	-
All	**34**	**600**	**21**	**96.5%**	**36.0%**	**38.2%**	**17**	**50.0%**

Table A.2. Number of active nests, observation days, nest losses, daily survival rate (DSR), Mayfield success, apparent success, number of nests parasitized, and parasitism rate at Riverside East, 2008-2017.

Year	Active nests	Observation days	Nest losses	DSR	Mayfield success	Apparent success	Parasitized nests	Parasitism rate
2008	0	-	-	-	-	-	-	-
2009	1	30	0	100.0%	100.0%	100.0%	1	100.0%
2010	8	136	5	96.3%	34.1%	37.5%	1	12.5%
2011	2	58	0	100.0%	100.0%	100.0%	0	0.0%
2012	2	34	1	97.1%	42.5%	50.0%	2	100.0%
2013	1	28	0	100.0%	100.0%	100.0%	0	0.0%
2014	0	-	-	-	-	-	-	-
2015	0	-	-	-	-	-	-	-
2016	0	-	-	-	-	-	-	-
2017	0	-	-	-	-	-	-	-
All	**14**	**286**	**6**	**97.9%**	**54.4%**	**57.1%**	**4**	**28.6%**

Table A.3. Number of active nests, observation days, nest losses, daily survival rate (DSR), Mayfield success, apparent success, number of nests parasitized, and parasitism rate at River Road Bridge, 2008-2017.

Year	Active nests	Observation days	Nest losses	DSR	Mayfield success	Apparent success	Parasitized nests	Parasitism rate
2008	1	22	0	100.0%	100.0%	100.0%	1	100.0%
2009	3	68	3	95.6%	27.4%	0.0%	2	66.7%
2010	3	36	2	94.4%	19.4%	33.3%	2	66.7%
2011	0	-	-	-	-	-	-	-
2012	0	-	-	-	-	-	-	-
2013	0	-	-	-	-	-	-	-
2014	0	-	-	-	-	-	-	-
2015	0	-	-	-	-	-	-	-
2016	0	-	-	-	-	-	-	-
2017	0	-	-	-	-	-	-	-
All	**7**	**126**	**5**	**96.0%**	**31.3%**	**28.6%**	**5**	**71.4%**

Table A.4. Number of active nests, observation days, nest losses, daily survival rate (DSR), Mayfield success, apparent success, number of nests parasitized, and parasitism rate at Seegmiller Marsh, 2008-2017.

Year	Active nests	Observation days	Nest losses	DSR	Mayfield success	Apparent success	Parasitized nests	Parasitism rate
2008	6	144	1	99.3%	81.9%	83.3%	0	0.0%
2009	8	135	7	94.8%	21.7%	12.5%	2	25.0%
2010	1	25	0	100.0%	100.0%	100.0%	0	0.0%
2011	0	-	-	-	-	-	-	-
2012	1	27	0	100.0%	100.0%	0.0%	0	0.0%
2013	0	-	-	-	-	-	-	-
2014	6	137	3	97.8%	53.0%	50.0%	4	66.7%
2015	4	102	0	100.0%	100.0%	100.0%	1	25.0%
2016	3	89	0	100.0%	100.0%	100.0%	0	0.0%
2017	9	221	3	98.6%	67.6%	66.7%	1	11.1%
All	**38**	**880**	**14**	**98.4%**	**63.1%**	**63.2%**	**8**	**21.1%**

Table A.5. Number of active nests, observation days, nest losses, daily survival rate (DSR), Mayfield success, apparent success, number of nests parasitized, and parasitism rate at Y-Drain Marsh, 2008-2017.

Year	Active nests	Observation days	Nest losses	DSR	Mayfield success	Apparent success	Parasitized nests	Parasitism rate
2008	0	-	-	-	-	-	-	-
2009	0	-	-	-	-	-	-	-
2010	0	-	-	-	-	-	-	-
2011	1	11	0	100.0%	100.0%	100.0%	1	100.0%
2012	4	82	2	97.6%	49.2%	50.0%	0	0.0%
2013	7	115	2	98.3%	60.4%	71.4%	2	28.6%
2014	3	62	1	98.4%	62.7%	66.7%	1	33.3%
2015	6	138	5	96.4%	34.7%	16.7%	1	16.7%
2016	6	93	5	94.6%	20.5%	16.7%	5	83.3%
2017	4	113	1	99.1%	77.5%	75.0%	1	25.0%
All	**31**	**614**	**16**	**97.4%**	**46.9%**	**48.4%**	**11**	**35.5%**

Table A.6. Number of active nests, observation days, nest losses, daily survival rate (DSR), Mayfield success, apparent success, number of nests parasitized, and parasitism rate at Snipe Pond, 2008-2017.

Year	Active nests	Observation days	Nest losses	DSR	Mayfield success	Apparent success	Parasitized nests	Parasitism rate
2008	0	-	-	-	-	-	-	-
2009	0	-	-	-	-	-	-	-
2010	7	91	7	92.3%	10.1%	0.0%	2	28.6%
2011	8	111	6	94.6%	20.3%	25.0%	5	62.5%
2012	7	75	5	93.3%	13.8%	28.6%	4	57.1%
2013	0	-	-	-	-	-	-	-
2014	1	12	1	91.7%	8.2%	0.0%	1	100.0%
2015	0	-	-	-	-	-	-	-
2016	0	-	-	-	-	-	-	-
2017	0	-	-	-	-	-	-	-
All	**23**	**289**	**19**	**93.4%**	**14.2%**	**17.4%**	**12**	**52.2%**

Table A.7. Number of active nests, observation days, nest losses, daily survival rate (DSR), Mayfield success, apparent success, number of nests parasitized, and parasitism rate at Brinton Pond, 2008-2017.

Year	Active nests	Observation days	Nest losses	DSR	Mayfield success	Apparent success	Parasitized nests	Parasitism rate
2008	0	-	-	-	-	-	-	-
2009	0	-	-	-	-	-	-	-
2010	0	-	-	-	-	-	-	-
2011	0	-	-	-	-	-	-	-
2012	0	-	-	-	-	-	-	-
2013	0	-	-	-	-	-	-	-
2014	0	-	-	-	-	-	-	-
2015	0	-	-	-	-	-	-	-
2016	0	-	-	-	-	-	-	-
2017	1	29	0	100.0%	100.0%	100.0%	0	0.0%
All	**1**	**29**	**0**	**100.0%**	**100.0%**	**100.0%**	**0**	**0.0%**

Appendix B. The number of active Southwestern Willow Flycatcher nests, nesting success, and parasitism rates by breeding sites during 2008-2017.

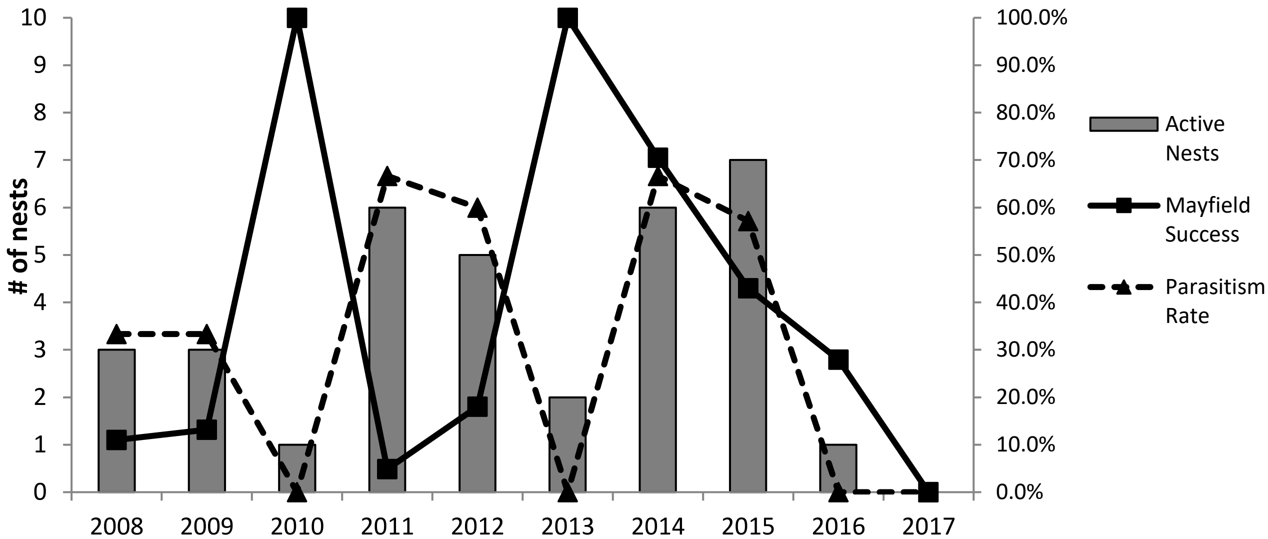


Figure B.1. Number of active Southwestern Willow Flycatcher nests, nesting success, and parasitism rates at Riverside Marsh, 2008-2017.

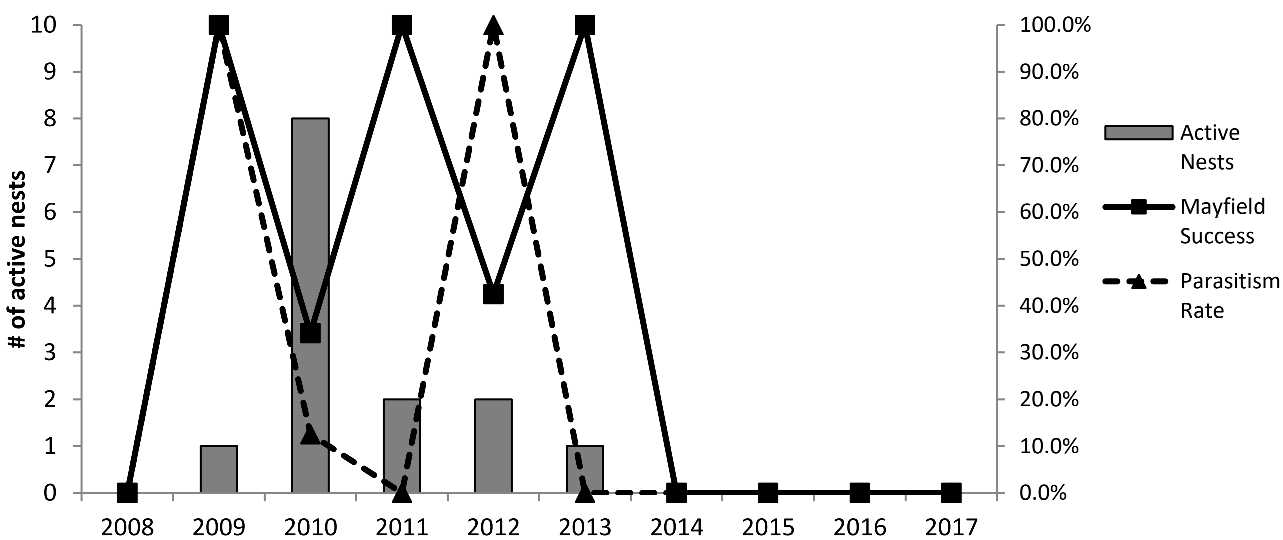


Figure B.2. Number of active Southwestern Willow Flycatcher nests, nesting success, and parasitism rates at Riverside East, 2008-2017.

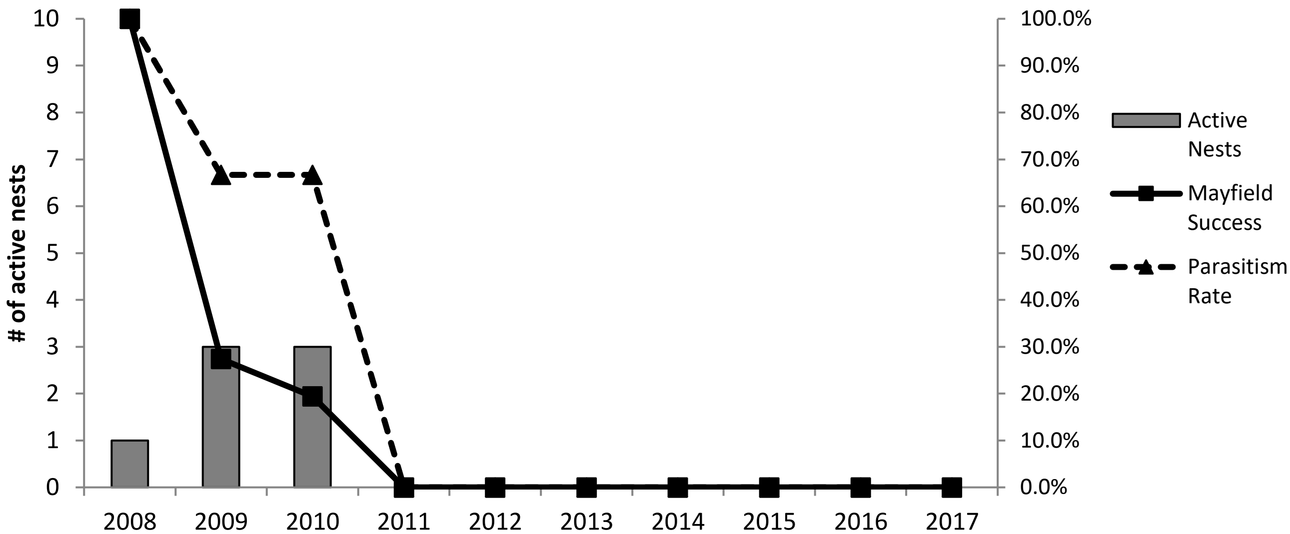


Figure B.3. Number of active Southwestern Willow Flycatcher nests, nesting success, and parasitism rates at River Road Bridge, 2008-2017.

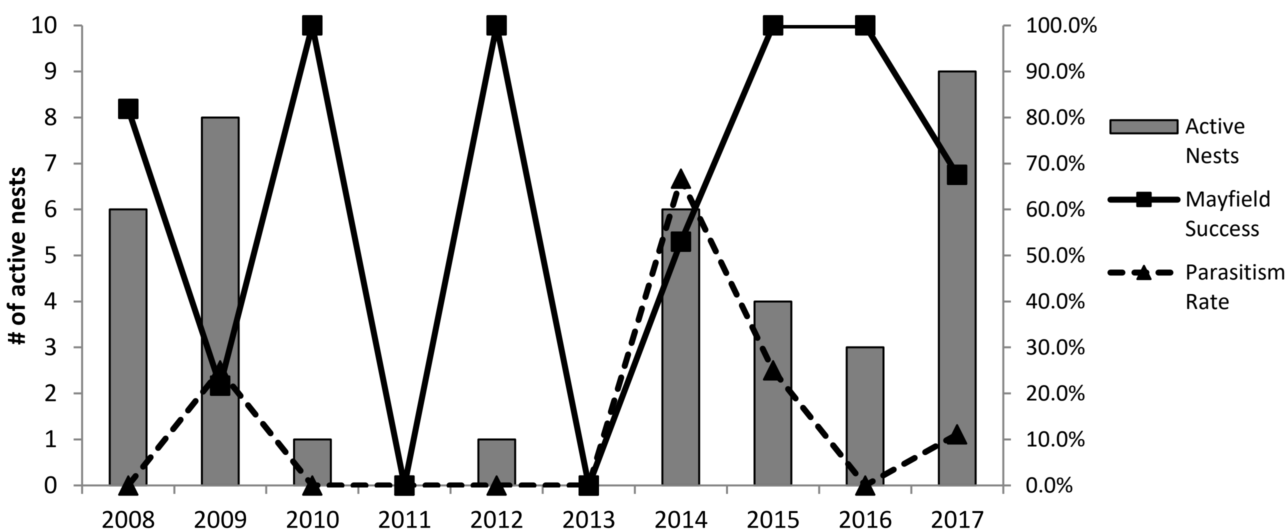


Figure B.4. Number of active Southwestern Willow Flycatcher nests, nesting success, and parasitism rates at Seegmiller Marsh, 2008-2017.

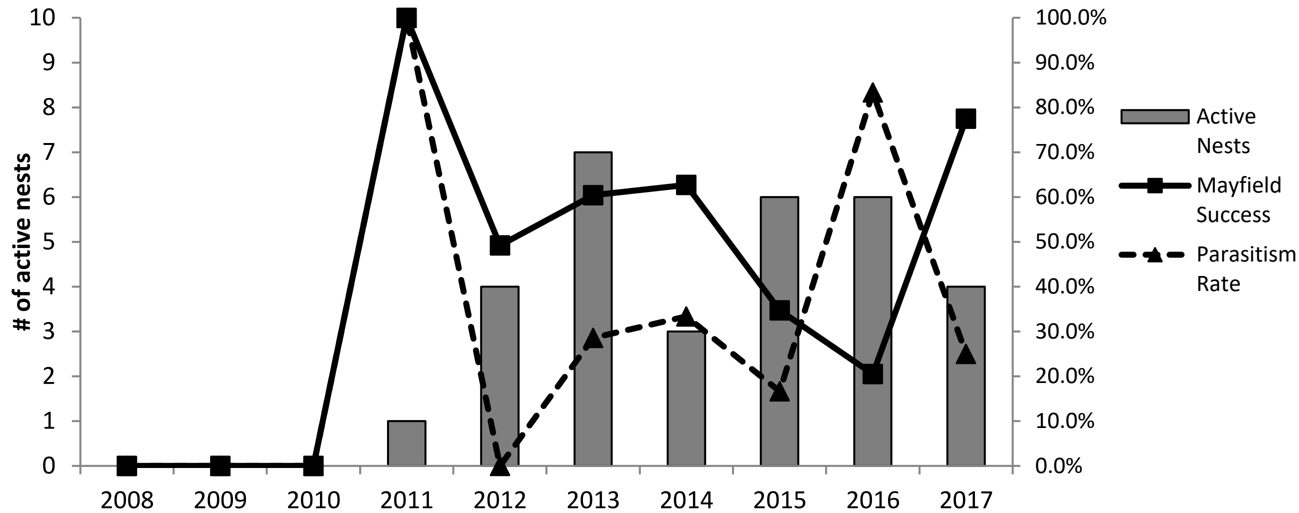


Figure B.5. Number of active Southwestern Willow Flycatcher nests, nesting success, and parasitism rates at Y-Drain Marsh, 2008-2017.

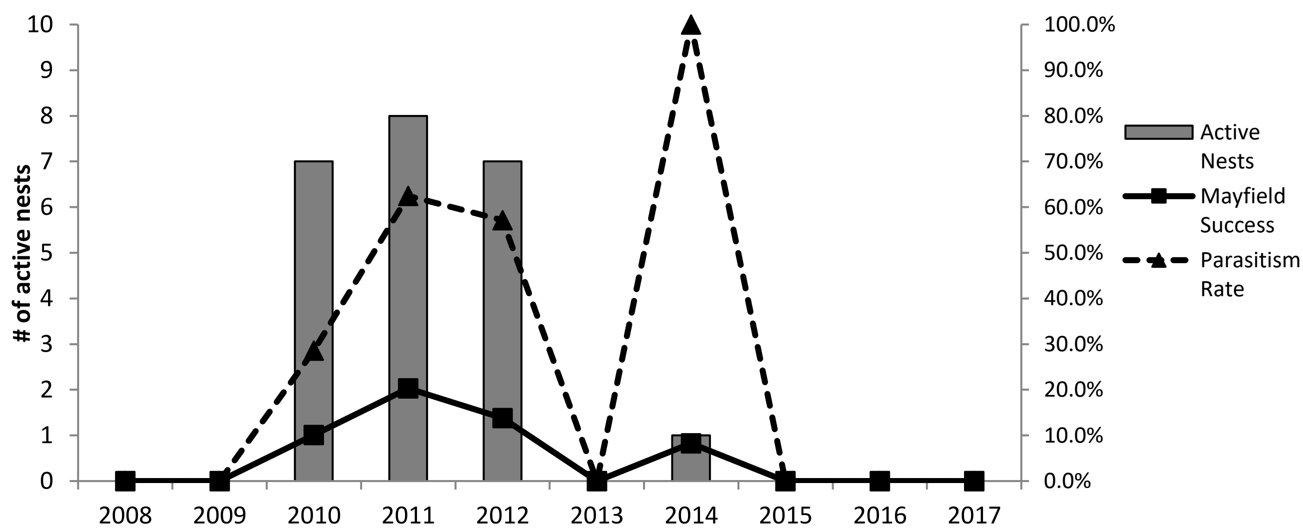


Figure B.6. Number of active Southwestern Willow Flycatcher nests, nesting success, and parasitism rates at Snipe Pond, 2008-2017.

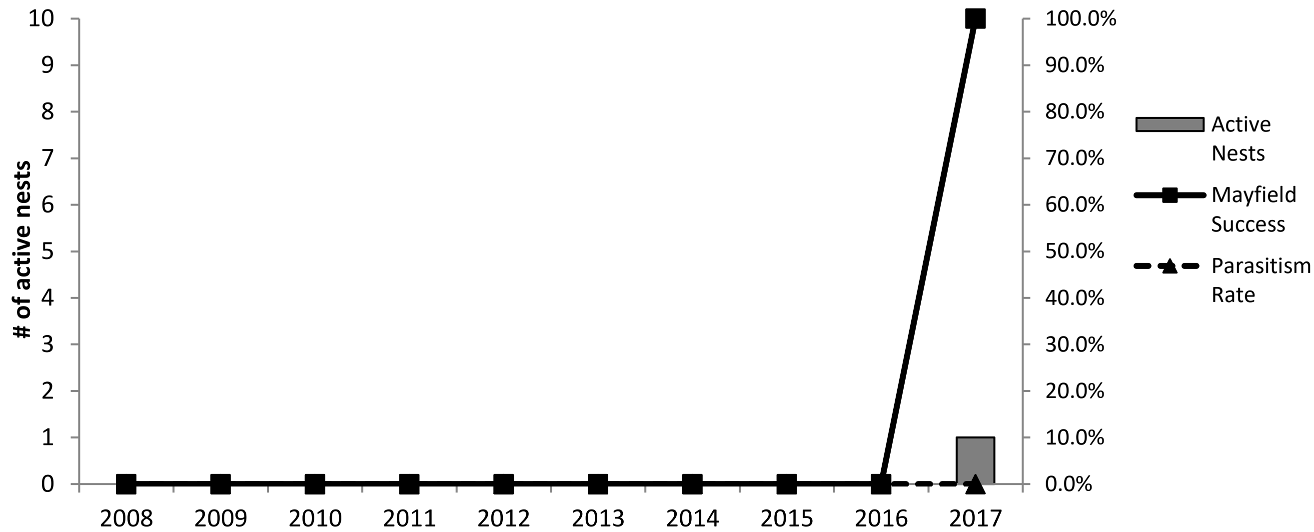


Figure B.7. Number of active Southwestern Willow Flycatcher nests, nesting success, and parasitism rates at Brinton Pond, 2008-2017.