STATUS, REPRODUCTIVE SUCCESS, AND HABITAT USE OF SOUTHWESTERN WILLOW FLYCATCHERS ON THE VIRGIN RIVER, UTAH, 2008-2011

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EXECUTIVE SUMMARY

The Southwestern Willow Flycatcher (*Empidonax traillii extimus*) was federally listed as endangered in 1995 due to population declines resulting from the loss and degradation of native riparian breeding habitat. In 2008 the Utah Division of Wildlife Resources (UDWR), in cooperation with the Virgin River Resource Management and Recovery Program, began monitoring Southwestern Willow Flycatcher (hereafter flycatcher) status and distribution, reproductive success, and habitat use along the upper Virgin River in the vicinity of St George, Washington County, Utah. Specific objectives were to track the abundance and distribution of breeding flycatchers, to quantify reproductive success and productivity, to identify primary causes of nest failure, to identify habitat characteristics important in nest site selection, and to identify habitat characteristics associated with successful nests. Here we present results of the first four years (2008-2011) of flycatcher monitoring, which coincided with initial effects of Tamarisk Leaf Beetle (*Diorhabda carinulata*) biocontrol on tamarisk (*Tamarix* spp.) components of riparian habitat on the upper Virgin River.

STATUS AND DISTRIBUTION

Tracking the number and distribution of flycatchers breeding in the St George study area is a central goal of UDWR flycatcher monitoring. In Chapter 2 we present results of presence-absence surveys revealing a decline in the number of territorial male flycatchers, but no overall change in the number of breeding female flycatchers (sites combined), within the St George study area between 2008 and 2011. The distribution of both territorial males and breeding females, however, varied dramatically within the St George study area over the 2008-2011 period. Specifically, numbers of both territorial male and breeding female flycatchers declined at Seegmiller Marsh and River Road Bridge between 2009 and 2010. These declines were offset by increases in numbers of territorial males and breeding females at Snipe Pond between 2009 and 2010, and at Y-Drain Marsh between 2010 and 2011. This shift in distribution within the St George study area was associated with a shift in habitat use between 2009 and 2010-2011. Sites vacated between 2009 and 2010 were dominated by larger tamarisk trees, whereas sites colonized between 2009 and 2010-2011 were dominated by Coyote Willow (*Salix exigua*) saplings and shrubs.

BREEDING BIOLOGY AND REPRODUCTIVE SUCCESS

Understanding variation in reproductive success and causes of nest failure is necessary to identify factors limiting local productivity in birds. We monitored Southwestern Willow Flycatcher nests in the St George study area from 2008 through 2011. In Chapter 3 we describe various components of flycatcher breeding biology, quantify reproductive success, and identify causes of nest failure at St George. Flycatcher breeding biology (e.g., phenology, clutch size, reproductive success) at St George was generally similar to that described elsewhere in the subspecies' range. Apparent nest success ranged from 13 % to 70 % among years, and Mayfield nest survival ranged from 25 % to 68 % among years. Apparent nest success, Mayfield nest survival, and nest productivity were notably lower in 2009 than in 2008, 2010, and 2011; annual variation was statistically significant for apparent nest success and nest productivity. In 2009, 40 % of nests failed to hatch, presumably due to effects of biocontrol-related tamarisk defoliation on nest microclimate. Flycatchers nested primarily in tamarisk-dominated habitat in 2009, and defoliation coincided, for the first time, with the peak of flycatcher breeding, primarily incubation (June). Over the four years of the study depredation was the primary cause of nest failure, accounting for 73 % of flycatcher nest failures. Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) was common, with rates ranging from 20 to 59 % of flycatcher nests parasitized among years.

HABITAT USE AND NEST SITE SELECTION

Throughout its range the Southwestern Willow Flycatcher breeds in areas that exhibit considerable variation in plant species composition, vegetation structure and floristics. To best implement recovery actions designed for local populations, identifying features of nesting habitat remains important. In Chapter 4 we compare vegetation characteristics between nesting plots and randomly-selected, non-nesting plots that were located in suitable riparian habitat. We found substantial annual variation in habitat characteristics among use sites, suggesting that over time flycatchers nested in areas with fewer trees, more Coyote Willow stems, a denser subcanopy-canopy layer and were located closer to standing water. Of the eleven habitat variables we measured, eight differed between use and non-use sites. Use sites had denser understory and subcanopy-canopy layers, greater canopy cover and height diversity, more shrub and Coyote Willow stems, fewer tree stems and were closer to water. The logistic regression model corroborated these analyses, and identified three habitat variables as important predictors of flycatcher nest sites: foliage density, number of willow stems and proximity to water.

The preference for dense foliage, presence of willows and proximity to water are typical nesting habits for the subspecies. However, one difference that appears unique to our region is an absence of trees within nesting plots. Similarities in the prevalence and distribution of tamarisk between use and non-use plots also highlight the importance of this exotic species to flycatchers in our study area. In order to improve flycatcher habitat, restoration efforts should consider multiple approaches that balance the selective removal of tamarisk with replacement by high-quality, native dominated habitat and increase access to standing water. Furthermore, to maintain the preferred structural complexity and high foliage density, consideration should be given to the rates of replacement and development of the native vegetation.

NEST SITE CHARACTERISTICS AND NEST SUCCESS

Habitat characteristics surrounding a nest are thought to influence the probability of nest success. In Chapter 5 we examine nest microhabitat characteristics and evaluate their relationship with nest success, predation and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). We found a total of 62 nests that were distributed among three nest tree species; flycatchers utilized tamarisk most often, followed by Coyote Willow, with a single nest built in Russian Olive. Nest tree selection was non-random and year dependent; given the abundance of each tree species during the 2010-2011 breeding season flycatchers sought tamarisk and avoided nesting in Coyote Willow. Nesting in tamarisk was beneficial, as individuals had higher nest success and were less likely to be depredated. However, the underlying reasons for this association were unclear as attributes of nest tree species were generally similar. Furthermore, nest attributes were similar between successful and unsuccessful nests, except in relative nest height where successful nests were lower than unsuccessful nests. Similarly, nest attributes of depredated nests were analogous to successful nests. In contrast, susceptibility to brood parasitism was similar among tree species, although we found year dependent differences in nest attributes for parasitized and nonparasitized nests. During the 2008-2009 breeding seasons parasitized nests were placed relatively lower, and located in shorter nests trees, while in 2010-2011parasitized nests were differentiated only by higher canopy cover.

Additional study is warranted to clarify the relationship between nest tree species and nest success, and should include data collection on nest concealment and identification of the primary nest predators. The importance of brood parasitism should not be overlooked and analysis of additional variables from a broader spatial scale is recommended. Where management and conservation goals include the reduction of nests lost to predation or parasitism, we suggest habitat restoration plans include selective removal of tamarisk.

CHAPTER 1
INTRODUCTION

PROJECT HISTORY

The Utah Division of Wildlife Resources (UDWR) began monitoring Southwestern Willow Flycatcher (*Empidonax traillii extimus*) status and distribution along the Virgin River in Washington County, Utah in 1995 (McDonald et al. 1995). Since its inception, however, UDWR monitoring has noted breeding activity only anecdotally, and an understanding of the factors limiting Southwestern Willow Flycatcher productivity in the area remains poor. 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 Southwestern Willow Flycatcher recovery, the Program funded UDWR in 2008 to monitor breeding activity, reproductive success, and habitat use in the area. The Washington County Habitat Conservation Plan sensitive species fund and the U.S. Fish and Wildlife Service contributed funding for the project 2009 to 2011. 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.

SOUTHWESTERN WILLOW FLYCATCHER LIFE HISTORY AND HABITAT

One of four currently recognized subspecies of the widespread Willow Flycatcher (*Empidonax traillii*), the Southwestern Willow Flycatcher (*E. t. extimus*; hereafter flycatcher) is a small (12 g) Neotropical-Nearctic migratory bird (Passeriformes: Tyrannidae) that breeds (May-August) in the southwestern United States and spends the remainder of the year in, and *en route* to and from, Central America (Unitt 1987, AOU 1998, Sedgwick 2000, Paxton et al. 2011b). During the breeding season flycatchers are lowland riparian obligates, and range throughout much of Arizona and New Mexico and southern portions of California, Nevada, Utah, and Colorado (AOU 1998, Sedgwick 2000, USFWS 2002, Paxton et al. 2008). Our work is limited to the breeding period and thus this report focuses on breeding ecology.

Male flycatchers arrive on the breeding grounds in late April – 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. Flycatchers are primarily monogamous, but polygyny is not uncommon (Pearson et al. 2006). 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). 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.

Flycatcher breeding habitat may be characterized generally by woody plant species composition as follows: native broadleaf, monotypic exotic, and mixed native-exotic (Sogge et al. 2010). 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*), seepwillow (*Baccharis* spp.), and Common Buttonbush (*Cephalanthus occidentalis*); native broadleaf habitat may contain a rare exotic component. Monotypic exotic habitat is comprised by dense stands of exotic species, such as tamarisk (saltcedar; *Tamarix ramosissima*, *T. chinensis*, hybrid *T. ramosissima* x *chinensis*) or Russian Olive (*Elaeagnus angustifolia*), and mixed native-exotic habitat includes dense mixtures of both native broadleaf and exotic species. Note, however, habitat suitability for flycatchers appears to be more related to vegetative structure than species composition (USWFS 2002).

Flycatcher breeding biology and habitat use remain little studied in the northern portion of its breeding range, including the Virgin River drainage in Utah, where nesting was first documented in 1996 (McDonald et al. 1995, Day 1998). Whitmore (1975, 1977) characterized habitat relationships of birds along the Virgin River in Utah during the breeding season and found that flycatchers, as in many parts of its breeding range, prefer patches of dense shrub and sapling growth and relatively few large trees. Beyond generalizations regarding habitat use and presence-absence survey data for breeding birds in the area, virtually nothing is known about flycatcher breeding biology, reproductive success, or nest site selection and microhabitat use in southern Utah.

THREATS AND STATUS

The Southwestern Willow Flycatcher was federally listed as endangered in 1995 due to population declines resulting from the loss, degradation, and fragmentation of riparian habitats (USFWS 1995, 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 exotic species represent another threat to riparian habitat in the southwest. Tamarisk, 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 exotic species (Hunter et al. 1988, Busch and Smith 1995, Shafroth et al. 2005). Introduced to the American west in the 1800s for erosion control, tamarisk spread rapidly along riparian corridors, irrigation ditches, and reservoir margins during the mid-1900s, and currently ranks as the third most abundant woody riparian plant species in the western U.S., where it covers an estimated 364,000 ha (Nagler et al. 2010). Although flycatchers historically nested in habitats dominated by native vegetation, approximately 25 % of known of flycatcher territories, range-wide, are currently located in tamarisk-dominated habitat (Sogge et al. 2008). In central Arizona, where 30 % of all known flycatcher territories are located, the majority (71 %) of flycatcher territories occur in mixed native-exotic habitat (Ellis et al. 2008). Mounting evidence suggests that flycatchers breeding in tamarisk-dominated habitat do not suffer negative consequences compared with flycatchers breeding in habitat dominated by native vegetation (Owen et al. 2005, Sogge et al. 2006, 2008, Paxton et al. 2007, Durst et al. 2008a, 2008b). However, rapid degradation of tamarisk-dominated habitat represents a significant threat to breeding flycatchers due to its susceptibility to wildfire (Busch and Smith 1995, Shafroth et al. 2002) and, potentially, to biocontrol efforts (Hultine et al. 2010, Paxton et al. 2011a; see below).

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). Cowbirds often reduce their hosts' reproductive success by removing host eggs, by prompting host nest abandonment, or via cowbird nestlings' competitive advantage over host nestlings for parental care (Robinson et al. 1995b). 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).

The range-wide flycatcher population consists of approximately 1000 known pairs, and an estimated population size of 1200 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 36.7 km to the Washington Fields Diversion structure in Washington County (USFWS 2005). 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.

TAMARISK LEAF BEETLES

The Tamarisk Leaf Beetle (*Diorhabda carinulata*; hereafter tamarisk beetle) is a recently-developed biocontrol agent that provides the potential for rapid, large-scale eradication of tamarisk in the western U.S. (DeLoach et al. 2000). Tamarisk beetles defoliate tamarisk trees during the growing season and tamarisk mortality occurs after repeated defoliations over multiple years (Dudley et al. 2001), with some data showing 40 % tamarisk mortality after five years of repeated defoliation (see Hultine et al. 2010). Tamarisk beetles were released at seven locations in the western U.S. in 2001 (Dudley et al. 2001) and continue to disperse, both naturally and with human assistance. Although long-term effects of tamarisk biocontrol may improve riparian habitat conditions throughout the southwest, there are potential negative short- and long-term consequences for wildlife, including the Southwestern Willow Flycatcher, as tamarisk beetles alter the condition of large areas of riparian habitat.

Tamarisk defoliation by tamarisk beetles may affect riparian birds by altering prey availability, increasing nest failure due to the loss of foliar cover, and reducing the amount of suitable habitat available (Paxton et al. 2011a). In the short term, while tamarisk beetles are actively consuming tamarisk foliage, tamarisk beetles may represent a potential food source for insectivorous birds (note, however, that consumption of tamarisk beetles by birds remains undocumented). Following defoliation and mortality of tamarisk trees, however, a decline in foliage-feeding or -dwelling arthropods will likely result in an overall decline in prey abundance for insectivorous birds. At the same time, reduced foliar cover will likely increase exposure of open-cup bird nests to predators, brood parasites, and extreme conditions (greater sun exposure, higher temperature, lower relative humidity). In the long term, bird population response to tamarisk mortality may depend on the rate and type of habitat recovery. Rapid recovery of native riparian vegetation may result in no net loss of habitat, while a significant time lag between tamarisk mortality and habitat recovery or invasion by other exotic or unsuitable plant species would likely result in a net loss of habitat (Paxton et al. 2011a).

Tamarisk beetles impacted the condition of tamarisk trees and the suitability of tamarisk-dominated habitat on the upper Virgin River over the course of this study (UDWR unpublished data) and, as a result, represent an important factor influencing the flycatcher’s distribution, reproductive success, and habitat use as described in this report. Tamarisk beetles were introduced on the Virgin River at St George in 2006, and defoliated tamarisk trees for the first time in late July – August 2008. In 2008 tamarisk defoliation occurred late in the flycatcher breeding cycle or after flycatchers had finished breeding altogether, and thus likely had little impact on flycatcher behavior. In both 2009 and 2010, however, tamarisk beetles caused two defoliation events, the first in early June, coinciding with the peak of flycatcher egg laying and incubation, and then again in late July – August. In 2011, following a winter flood and cool spring conditions, beetles caused a single defoliation event during late July – August.

During each of the defoliation events on the upper Virgin River, the condition of tamarisk trees declined dramatically and rapidly, typically within 1-2 weeks (Figure 1.1). Defoliation resulted in decreased canopy cover, increased maximum daily temperature, and decreased maximum daily relative humidity in tamarisk-dominated plots relative to native-dominated plots at flycatcher breeding sites in the Upper Virgin River study area (UDWR and U.S. Bureau of Reclamation unpublished data). Altered microhabitat and microclimate conditions may influence habitat use by and reproductive success of flycatchers. Small decreases in foliar cover, for example, may reduce habitat suitability for flycatchers (Allison et al. 2003). Utilizing data on the timing of defoliation from Colorado, and nest success from a long-term study in Arizona, Paxton et al. (2011a) developed a model predicting at least a 40 % decline in annual flycatcher population productivity. We suggest that 2008 represents a pre-tamarisk beetle baseline against which to measure subsequent flycatcher response to tamarisk beetle-related effects in 2009-2011. Although circumstantial, these data provide the first opportunity to examine how tamarisk beetle activity may affect flycatcher productivity and habitat use under natural conditions.

REPORT PURPOSE AND ORGANIZATION

Here we synthesize results of Southwestern Willow Flycatcher monitoring conducted by UDWR from 2008 through 2011. The report is organized among six chapters, each covering a distinct component of the study. This introductory chapter provides background information on the flycatcher, its biology and habitat, threats to recovery and current status, tamarisk beetles, and our project itself. Chapter two, “Status and Distribution,” describes survey work by which we monitored the number and distribution of flycatchers in the Upper Virgin River study area. Chapter three, “Breeding Biology and Reproductive Success,” provides a summary of breeding biology and life history traits quantified during the study, and examines annual variation in reproductive success, causes of nest failure, and effects of brood parasitism on reproductive success. Chapter four, “Habitat Use and Nest Site Selection,” examines changes in microhabitat (vegetation) characteristics at flycatcher nests over the study period, and provides a comparison of microhabitat characteristics at flycatcher nests with those at randomly-selected sites to address whether or not flycatchers show selectivity of microhabitat characteristics when choosing nest site locations. Chapter five, “Nest Site Characteristics and Nest Success,” compares various components of flycatcher nest sites between successful and unsuccessful nests, as well as parasitized and nonparasitized nests, and examines the use of available nest substrates given their availability in occupied habitat. Finally, based on results presented throughout the report, chapter six identifies management recommendations.

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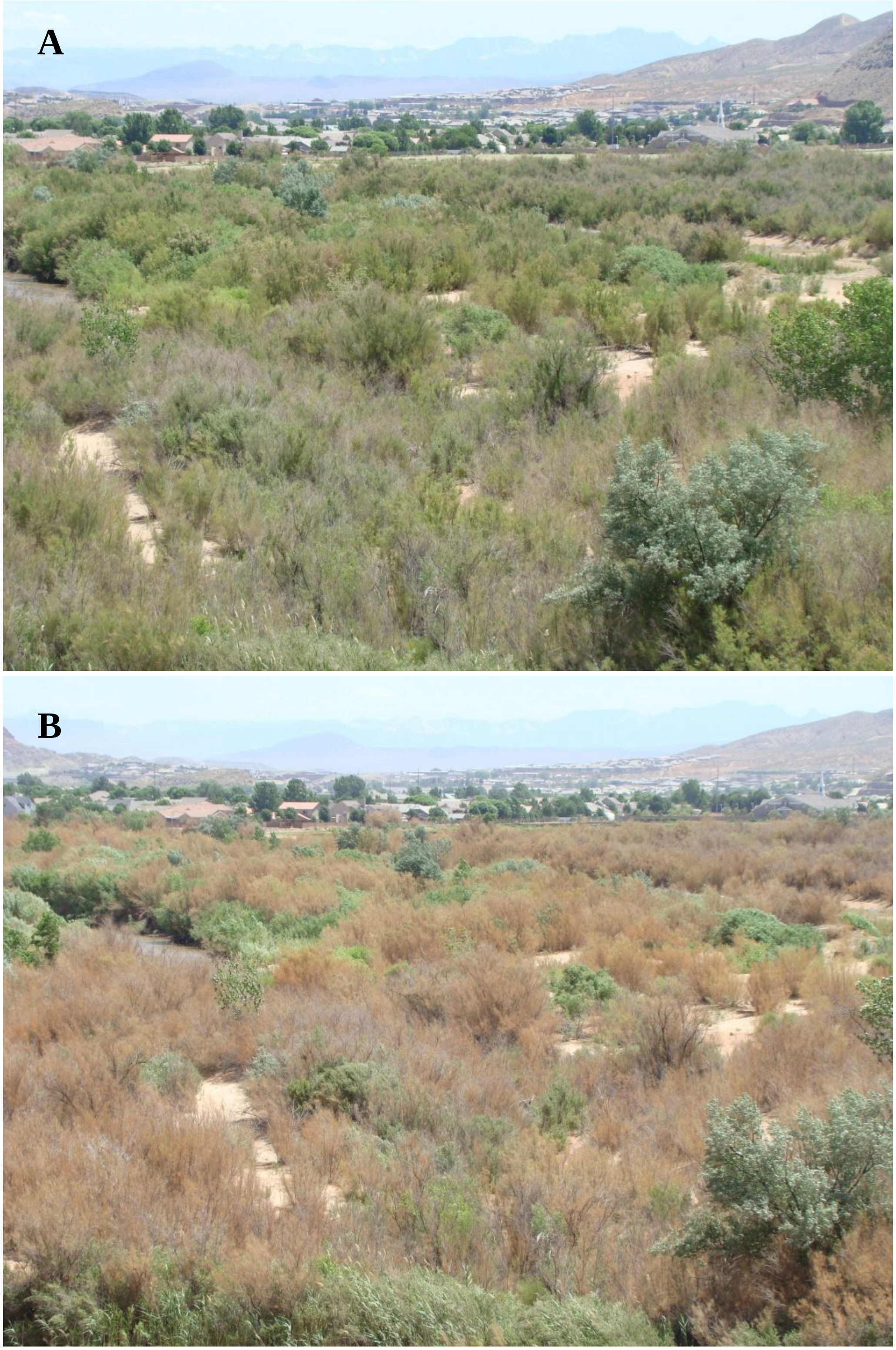

Figure 1.1. Virgin River floodplain near St. George, Washington County, Utah (A) prior to tamarisk beetle defoliation on 2 June 2010, and (B) following tamarisk beetle defoliation on 17 June 2010.

CHAPTER 2
STATUS AND DISTRIBUTION

INTRODUCTION

The Southwestern Willow Flycatcher, *Empidonax traillii extimus*, reaches the northern limit of its breeding range in southern Utah, where a region of intergradation with the more northern subspecies *E. t. adastus* occurs along a transition zone from more xeric, low elevation deserts to the south and more mesic, high elevation habitats to the north (Paxton et al. 2008). Prior to 1995 knowledge of Southwestern Willow Flycatcher status and distribution in Utah was limited to historical breeding season records from the San Juan and Colorado rivers, Kanab Creek, and the Virgin River (USFWS 2002). Coincident with the federal listing of the flycatcher as endangered (USFWS 1995) and widespread standardized survey efforts (Tibbitts et al. 1994), UDWR initiated annual surveys in southern Utah in 1995 (McDonald et al. 1995). Prior to UDWR surveys only 28 records of Willow Flycatchers, including both potentially breeding Southwestern Willow Flycatchers and migrant Willow Flycatchers of other subspecies (e.g., *E. t. adastus*), were documented for the Virgin River in Utah (hereafter upper Virgin River; McDonald et al. 1995).

From 1995 to 2007 UDWR surveys documented between three and 12 potential Southwestern Willow Flycatcher (hereafter 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, UDWR unpublished data). These surveys indicated that virtually all flycatchers breeding (potentially or confirmed) on the upper Virgin River occupied portions of 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).

Understanding the status, distribution, and annual variation in the flycatcher population on the upper Virgin River is essential for tracking recovery in the Virgin Management Unit (Lower Colorado Recovery Unit; USFWS 2002). UDWR continued long-term population monitoring during the 2008-2011 period by conducting presence-absence surveys in suitable and potentially suitable habitat along the upper Virgin River. In this chapter we describe annual variation in the number and distribution of territorial male and breeding female flycatchers, and discuss factors that likely influenced patterns of distribution among years.

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 exotic-native, but the ratio of exotic 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 (*Salix exigua*), Fremont Cottonwood (*Populus fremontii*), Mule's Fat (*Baccharis* spp.), and Arrow Weed (*Pluchea sericea*), and less commonly Goodding's Willow (*Salix gooddingi*), and Velvet Ash (*Fraxinus velutina*). The dominant exotic woody species in this habitat is tamarisk or Saltcedar (e.g., *Tamarix ramosissima*), but Russian Olive (*Elaeagnus angustifolia*) also represents an important component of some habitat patches.

PRESENCE-ABSENCE SURVEYS

We conducted flycatcher presence-absence surveys during the breeding seasons of 2008–2011 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 (2010-2011 only; 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 (Chapter 3). 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 broadcast 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.

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 to digitize individual site boundaries and calculate patch size.

Following the breeding season, based on results of nest monitoring (Chapter 3), we measured vegetation and microhabitat characteristics in detail at the majority of nest sites in the study area (Chapter 4). Thus, in addition to qualitatively categorizing the proportion of exotic 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 (Chapter 4).

RESULTS

FLYCATCHER NUMBERS AND DISTRIBUTION

Of nine sites surveyed in the St George study area during 2008–2011, we detected flycatchers at seven sites and confirmed breeding at six sites (Table 2.1). The number of male flycatchers maintaining breeding territories in the St George study area declined over the four-year period, most strongly between 2009 and 2011, during which numbers dropped from 15 to seven individuals (Figure 2.2). The number of female flycatchers breeding in the study area, however, remained stable over the same period, ranging from eight to 10 individuals (Figure 2.2). The percentage of unpaired males remaining on territory into June varied among years, ranging from 14 % to 50 % (Figure 2.3).

The distribution of territorial males and breeding females shifted among individual sites in the St George study area from 2008 to 2011 (Figures 2.4, 2.5). The number of territorial males at Seegmiller Marsh, for example, declined from 10 to zero between 2008 and 2011 (Figure 2.4). The Seegmiller Marsh decline was offset somewhat by males colonizing Snipe Pond (2010) and Y-Drain Marsh (2011), two sites not previously known to host breeding flycatchers (Figure 2.4). Note that, although Snipe Pond and Riverside East were not surveyed prior to 2009, anecdotal observations indicated that flycatchers were not present at either site in 2008.

Breeding females also exhibited a shift in distribution within the St George study area, similar to that observed for territorial males (Figure 2.5). Again, the number of females breeding at Seegmiller Marsh decreased over 2008-2011, with the most dramatic decline occurring between 2009 and 2010 (Figures 2.5, 2.6). Concomitant with the decrease in females using Seegmiller Marsh, females colonized Snipe Pond in 2010 and continued breeding there in 2011 (Figures 2.5, 2.7).

The decline 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 this study, 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 in the seven years preceding this study (Figure 2.8; Day 2004, UDWR unpublished data). In 2011 zero male flycatchers established territories at Seegmiller Marsh.

BREEDING SITES

Six sites in the St George study area were occupied by breeding flycatchers during at least one year of this study. 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 both Seegmiller Marsh and Riverside Marsh, as well as at Y-Drain Marsh. In addition to a fish barrier at Seegmiller Marsh, these beaver dams serve to maintain relatively constant water levels in wetlands at these three sites. Despite beaver activity at Riverside East and Snipe Pond, these two sites have widely fluctuating water levels subject to daily variation in irrigation schedules. The wetland at River Road Bridge is maintained by a relatively constant flow of water from a natural spring. All of these sites are bound by the Virgin River and some configuration of agricultural land and urban development.

The area of occupied breeding patches ranged from 2.0 to 25.5 ha, and averaged 8.4 ha (Table 2.2). 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 exotic plant species (Table 2.2). 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 (Chapter 4). These data showed that, at one extreme, flycatchers breeding at Seegmiller Marsh used habitat characterized by 82.1 % exotic vegetation, and in particular 80.2 % tamarisk (Figure 2.9). At the opposite extreme, flycatchers breeding at Snipe Pond and Y-Drain marshes used habitat characterized by only 6.3 % and 12.8 % exotic (100 % tamarisk in both cases) vegetation, respectively (Figure 2.9). Riverside Marsh, Riverside East, and River Road Bridge ranged from 60:40 to 70:30 native:exotic vegetation (Figure 2.9).

DISCUSSION

Southwestern Willow Flycatchers exhibited a dramatic shift in the use of specific breeding sites within the St George study area between 2008 and 2011. The most dramatic shifts occurred between sites dominated by exotic (tamarisk) and native (willow) vegetation, suggesting that a shift in habitat use was responsible for the observed distributional pattern (see Chapter 4). That is, while flycatchers utilized mixed native-exotic habitat patches throughout 2008-2011, flycatchers vacated the tamarisk-dominated Seegmiller Marsh and colonized the willow-dominated Snipe Pond between 2009 and 2010. Although very few flycatchers in the St George study were color-banded, at least one (color-banded) female moved from Seegmiller Marsh in 2009 to Snipe Pond in 2010.

The 2009-2010 shift between breeding sites and habitat types in the St George study area coincided with increasingly severe tamarisk defoliation by Tamarisk Leaf Beetles (*Diorhabda* *carinulata*; hereafter tamarisk beetles) over the 2008-2011 period. More specifically, the timing of the shift between 2009 and 2010 followed a dramatic decline in flycatcher reproductive success in 2009, the first year that defoliation coincided with peak flycatcher breeding (Chapter 3). Although tamarisk beetles defoliated tamarisk in the St George study area first in 2008, the July-August timing of that event occurred late in the flycatcher breeding season and thus likely had little impact on flycatcher behavior and reproductive success. In contrast, tamarisk beetles defoliated tamarisk during early June in 2009, which coincided with flycatcher egg laying and incubation and appears to have negatively affected flycatcher reproductive success (Chapter 3). The timing of these events suggests that flycatchers may have shifted between Seegmiller Marsh and Snipe Pond as a result of deteriorating habitat suitability at Seegmiller Marsh, and in tamarisk-dominated habitat generally, between 2009 and 2010.

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Table 2.1. Southwestern Willow Flycatcher presence-absence survey effort and detections among sites and years in the St George study area (x = surveys conducted with no detections; d = surveys conducted and flycatcher(s) detected; B = surveys conducted and breeding confirmed).

Survey site	2008	2009	2010	2011
Riverside Marsh[1]	B	B	B	B
Riverside East		B	B	B
River Road Bridge	B	B	B	x
Schmutz Drain		d	d	x
Seegmiller Marsh	B	B	B	x
Y-Drain Marsh[2]	X	x	x	B
Snipe Pond		B	B	B
Mad Dog Pond				x
Below WFD			x	x

[1] Site traditionally referred to as Duck Pond-Willow Grove.

[2] Site combined with Seegmiller Marsh on survey data sheets.

Table 2.2. Area and habitat classification of occupied Southwestern Willow Flycatcher breeding sites in the St George study area, 2008-2011.

Site	Area (ha)	Patch-scale habitat category[1]
Riverside Marsh	9.3	Mixed native-exotic, mostly exotic (50-90 % exotic)
Riverside East	2.0	Mixed native-exotic, mostly native (50-90 % native)
River Road Bridge	2.8	Mixed native-exotic, mostly exotic (50-90 % exotic)
Schmutz Drain	5.7	Mixed native-exotic, mostly native (50-90 % native)
Seegmiller Marsh	25.5	Mixed native-exotic, mostly exotic (50-90 % exotic)
Y-Drain Marsh	8.1	Mixed native-exotic, mostly native (50-90 % native)
Snipe Pond	5.3	Mixed native-exotic, 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 exotic plants (mostly native; 50-90 % native); (3) Mixed native and exotic plants (mostly exotic; 50-90 % exotic); (4) Exotic/introduced plants (entirely or almost entirely; > 90 % exotic).

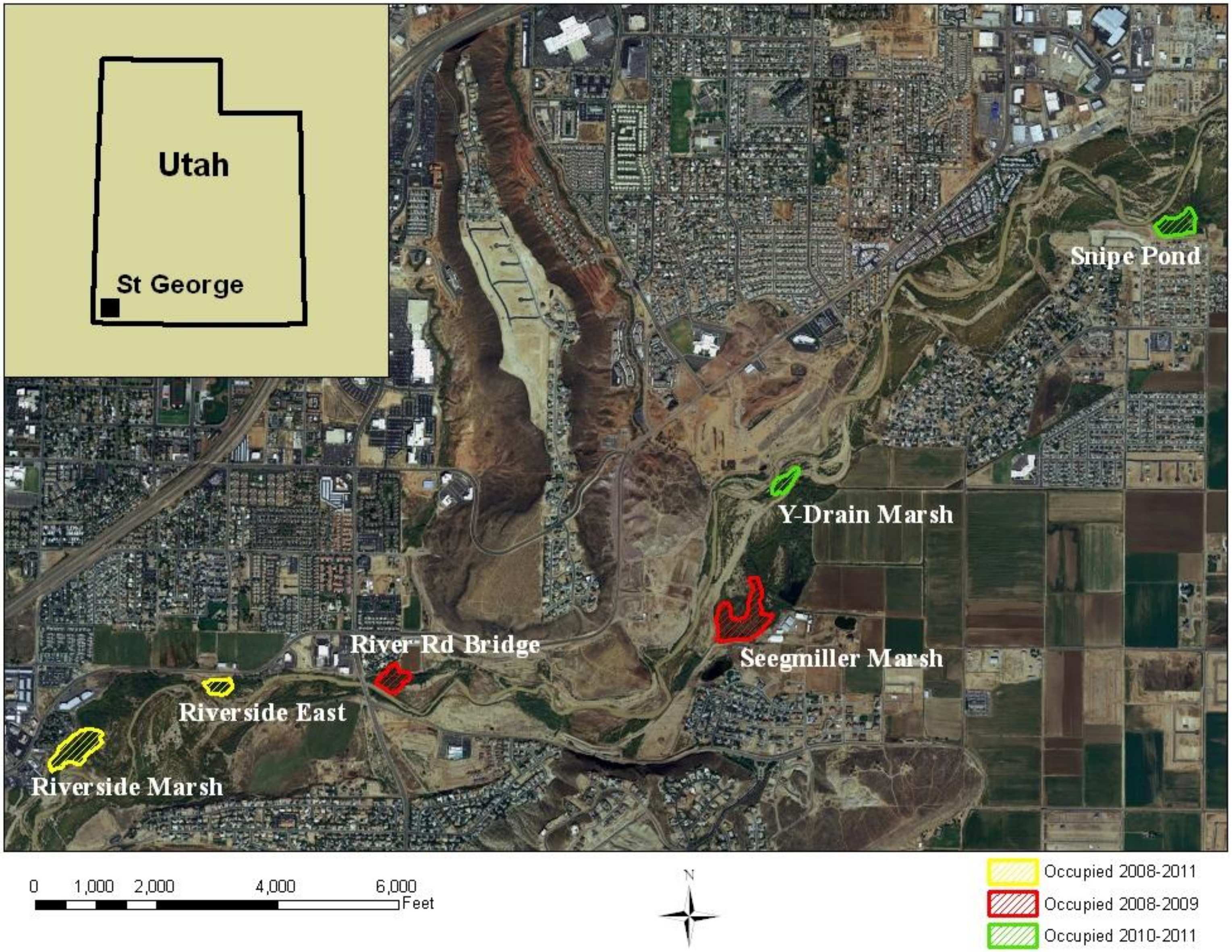

Figure 2.1. The St George study area is located on the upper Virgin River in the vicinity of St George, Washington Co., Utah.

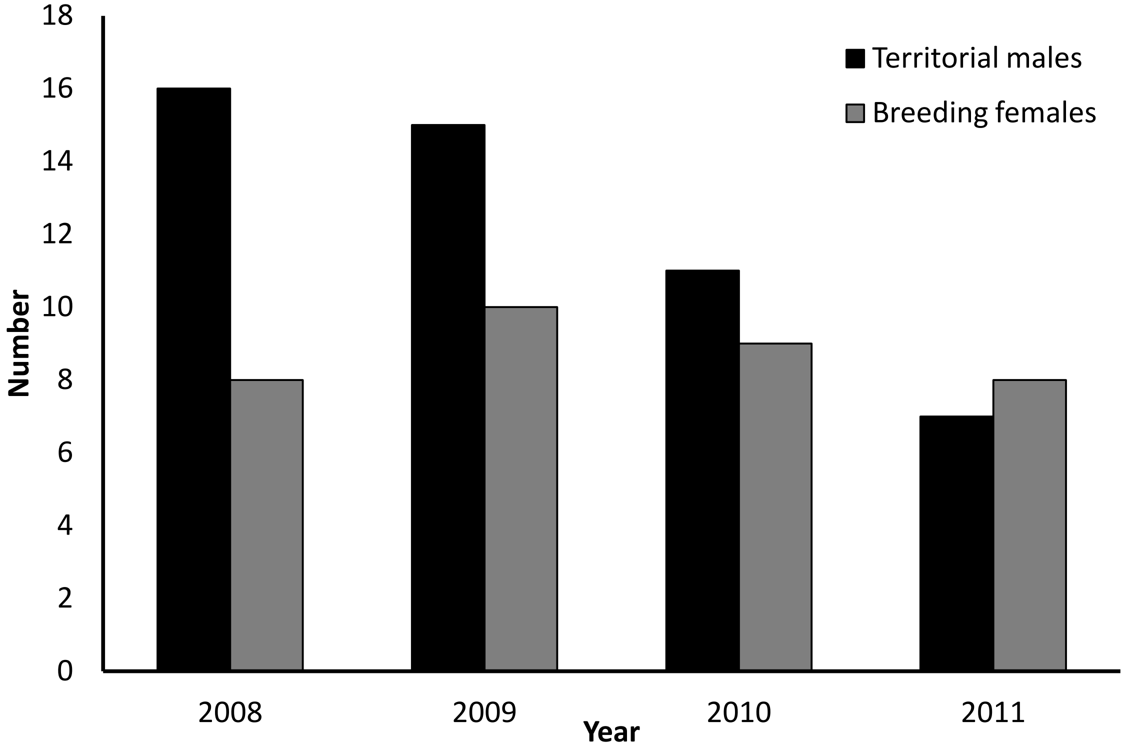

Figure 2.2. The number of territorial male flycatchers declined, while the number of breeding females remained stable, in the St George study area from 2008-2011.

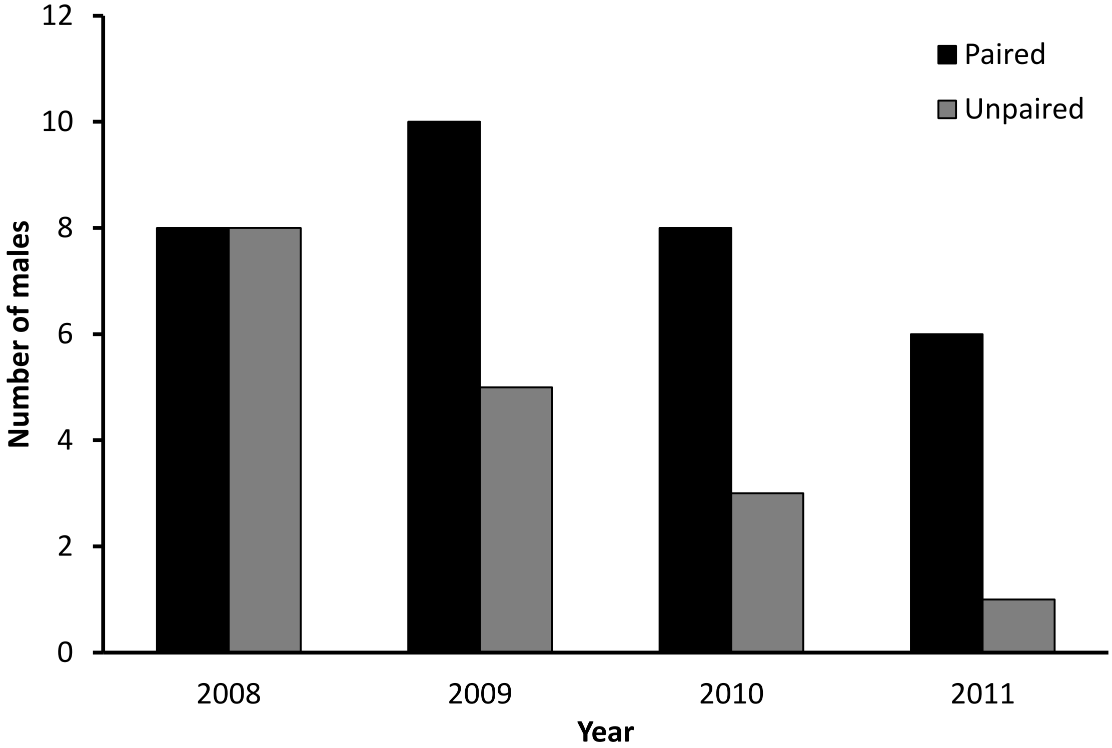

Figure 2.3. The number of paired and unpaired male flycatchers maintaining territories in the St George study area was even in 2008, but paired males outnumbered unpaired males in all subsequent years.

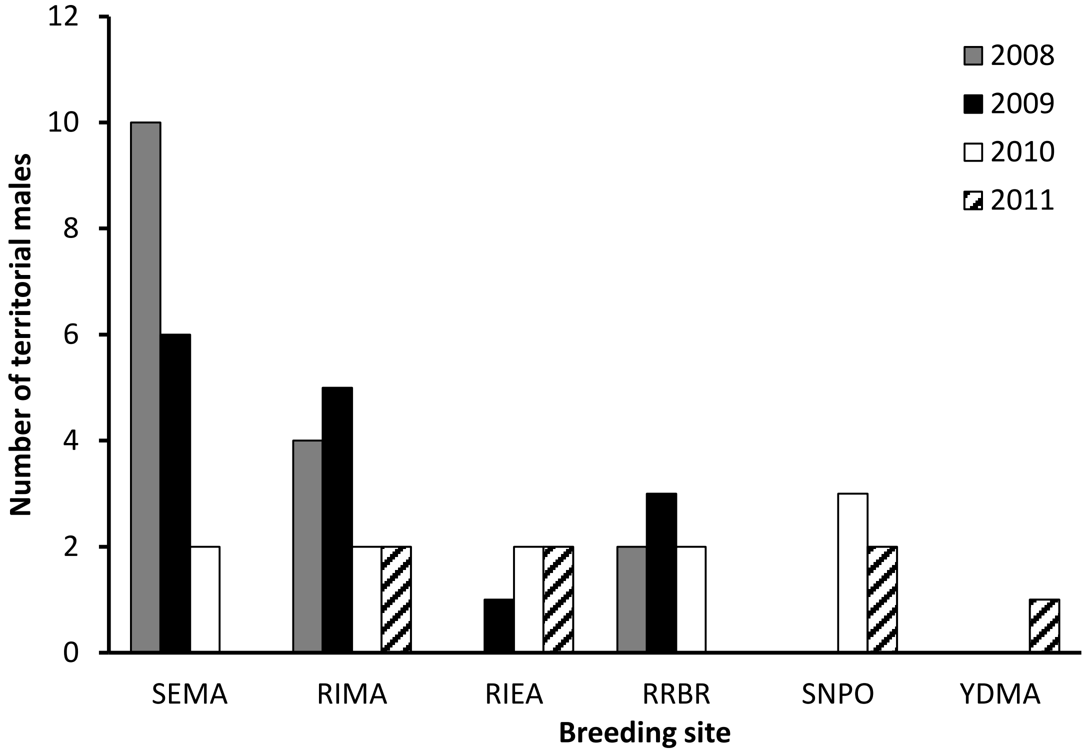

Figure 2.4. The number and distribution of territorial male flycatchers changed over the 2008–2011 period, marked by declines at Seegmiller Marsh (SEMA) and increases at Snipe Pond (SNPO). Territorial male flycatchers also occupied Riverside Marsh (RIMA), Riverside East (RIEA), River Road Bridge (RRBR), and Y-Drain Marsh (YDMA).

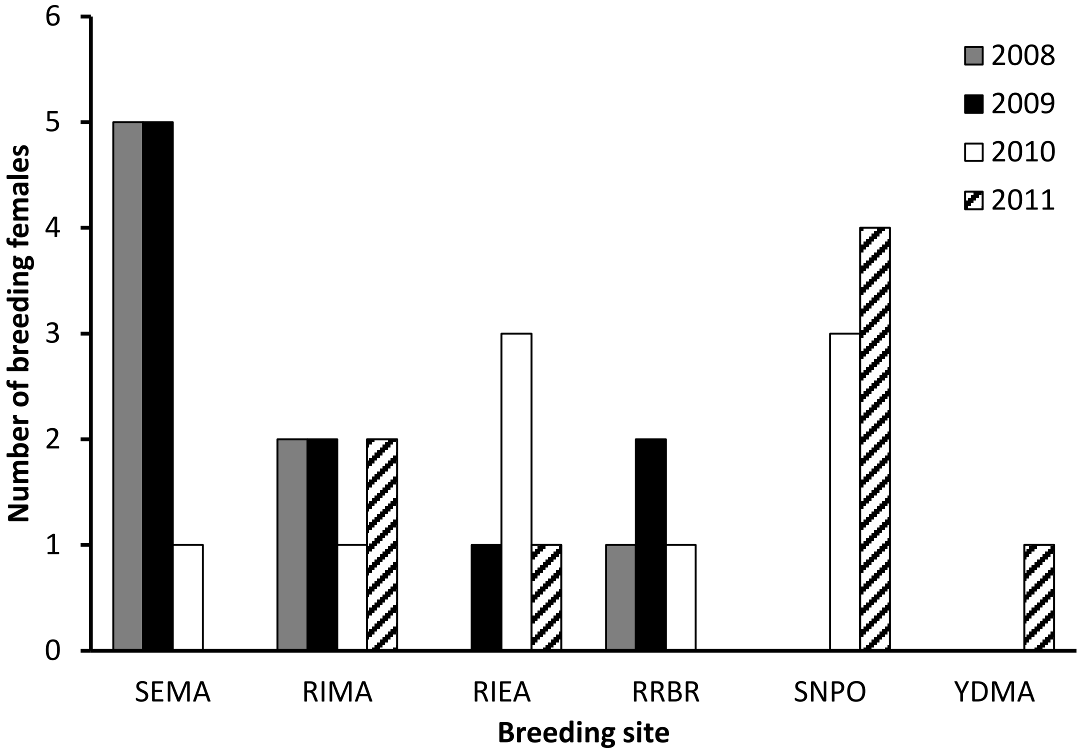

Figure 2.5. The distribution of breeding female flycatchers shifted over the 2008 – 2011 period, declining at Seegmiller Marsh (SEMA) and increasing at Snipe Pond (SNPO). See Figure 1 for additional breeding site abbreviations.

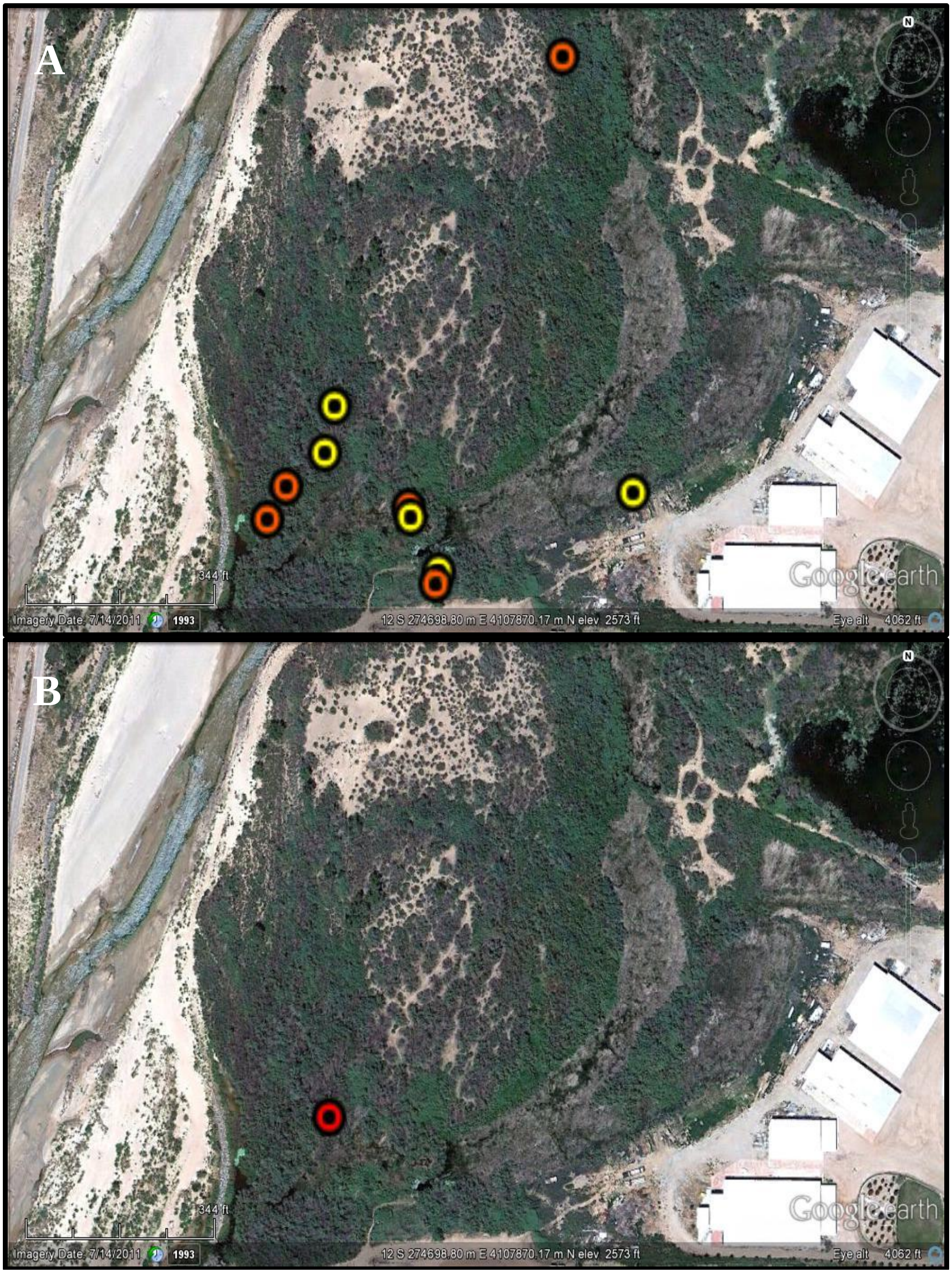

Figure 2.6. The number of flycatchers breeding at Seegmiller Marsh decreased between (A) 2008-2009 and (B) 2010-2011. Symbols represent locations of first nest attempts within years (symbol colors).

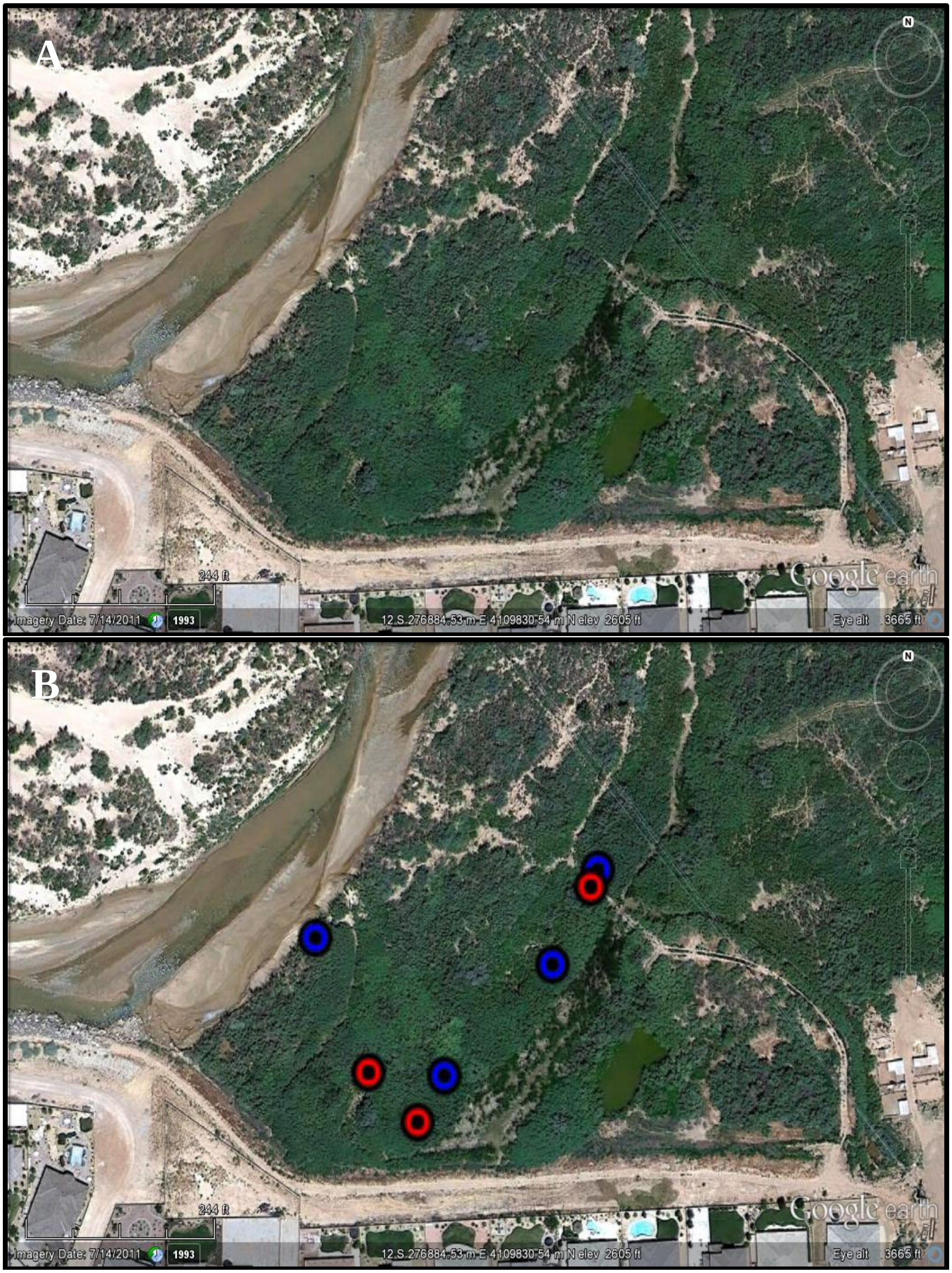

Figure 2.7. The number of flycatchers breeding at Snipe Pond increased between (A) 2008-2009 and (B) 2010-2011. Symbols represent locations of first nest attempts within years (symbol colors).

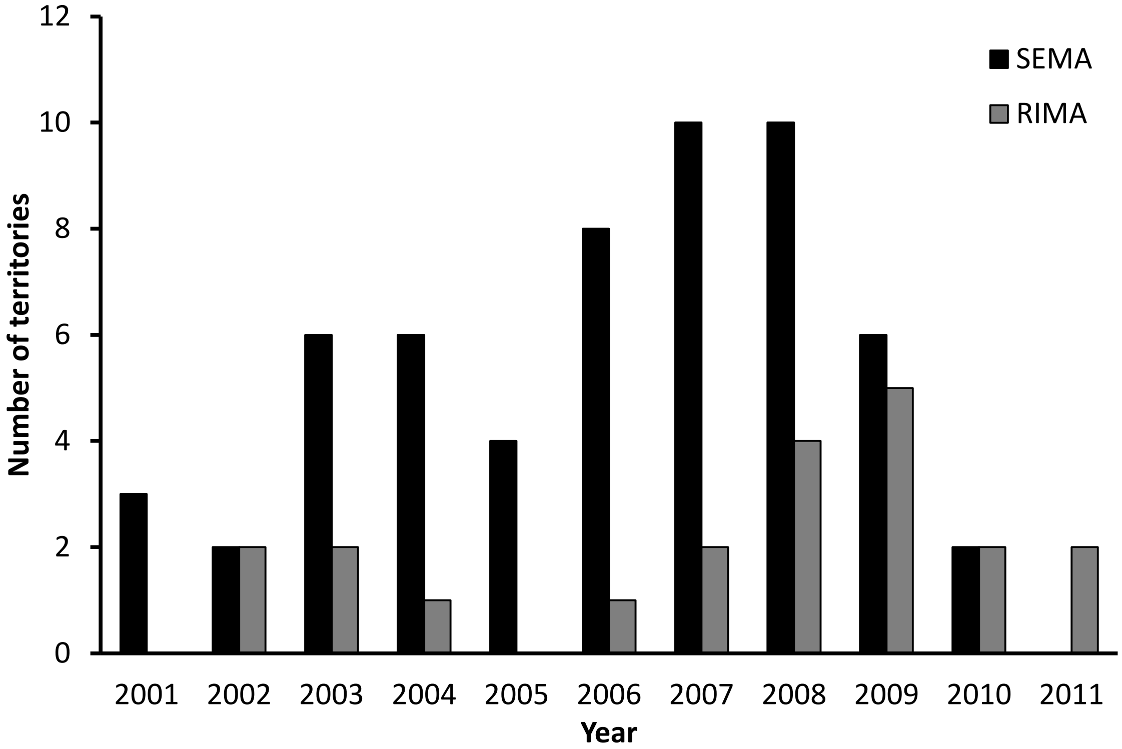

Figure 2.8. Numbers of flycatcher territories at Seegmiller Marsh (SEMA) and Riverside Marsh (RIMA) varied among years (2001-2011).

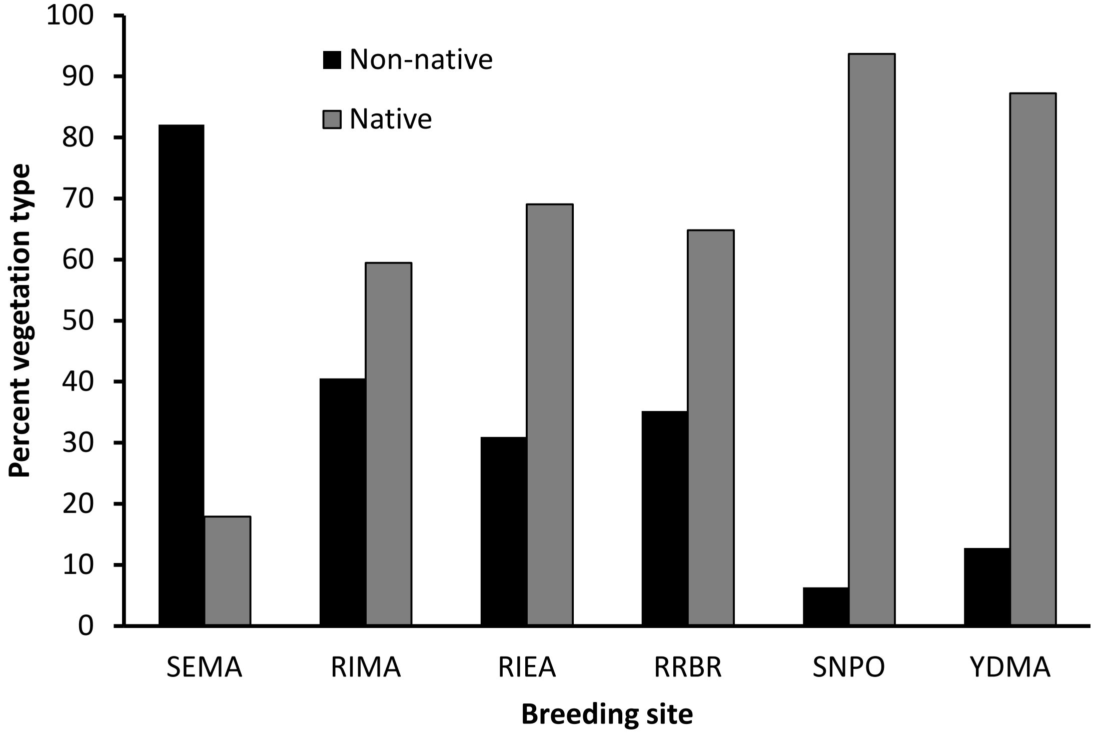

Figure 2.9. Exotic and native vegetation composition of occupied areas within breeding patches varied strongly among patches, with Seegmiller Marsh (SEMA) dominated by exotics, Riverside Marsh (RIMA), Riverside East (RIEA), and River Road Bridge (RRBR) more evenly mixed exotic-native, and Snipe Pond (SNPO) and Y-Drain Marsh (YDMA) dominated by natives. Tamarisk and Coyote Willow comprised 97.5 % and 95.2 % of exotic and native vegetation, respectively, over all sites.

CHAPTER 3
BREEDING BIOLOGY AND REPRODUCTIVE SUCCESS

INTRODUCTION

Understanding the demographic factors that influence Southwestern Willow Flycatcher population growth is paramount to identifying and implementing appropriate conservation actions and recovery efforts (USFWS 2002). Demographic data analysis combined with detailed knowledge of the natural history, breeding biology, and behavior of flycatchers may provide important insight into the factors influencing productivity. These data may be particularly important for the management of small or isolated populations, which may be more prone than large populations to effects of limiting factors such as nest predation and brood parasitism. Demographic data are currently unavailable for the small population of Southwestern Willow Flycatchers breeding on the upper Virgin River at St George, Utah. Moreover, virtually all aspects of the life history, nesting biology and behavior of flycatchers breeding in the St George study area, at the northern edge of the subspecies' range, remain unknown.

Southwestern Willow Flycatchers (hereafter flycatchers) migrate from Central America to the breeding grounds in the southwestern United States during April-June. Older male flycatchers arrive on the breeding grounds from one to several weeks before females and younger males, as early as late April in some locations (McCarthey 2005, Sogge et al. 2010). Males establish and defend territories using advertising *fitz-bew* song and agonistic behavior (Sedgwick 2000, Sogge et al. 2010). Territory size is highly variable and may range from 0.06 to 2.3 ha (0.15-5.68 ac), depending on population density, habitat quality, and other factors (Sogge et al. 2010 and references therein). Range-wide, for first nest attempts, egg-laying typically occurs from late-May to mid-June, and nestlings may be present from late May to early August; fledglings leave nests from mid-June to mid-August (Sogge et al. 2010). Following pair formation, females build small (~ 8 x 8 cm), open-cup nests, typically 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). Once nests are complete, females lay one egg per day, occasionally skipping a day between eggs, and subsequently incubate a clutch of 3-4 eggs (first nest attempts) for 12-13 days. Both parents provision nestlings for 12-15 days in the nest, and fledglings for up to two weeks after leaving the nest. 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).

Female flycatchers typically produce a single brood per year, if successful, but will renest multiple times following nest failure. Occasionally, a female may produce a second clutch following a successful nest (double-brooding). Flycatchers are facultatively polygynous, with socially monogamous pairs (one male mated with one female) often engaging in extra-pair mating (Pearson et al. 2006). Social polygyny, in which one male has two to four breeding females in his territory, also occurs and may be common in some populations (Davidson and Allison 2003). Some males fail to attract even one female and remain unpaired and territorial, while additional unpaired males adopt a floater strategy by remaining nonterritorial and surreptitiously seeking extra-pair copulations from females paired within territorial males' territories (Paxton et al. 2007, Sogge et al. 2010).

Here we summarize the breeding biology of Southwestern Willow Flycatchers on the upper Virgin River at St George, Utah from 2008-2011. Our goals were (1) to describe basic components of breeding biology (e.g., nesting phenology), (2) to quantify demographic variables (e.g., clutch size, nest success) and annual variation therein, (3) to describe causes of nest failure and, more specifically, to quantify nest predation rates, and (4) to evaluate the importance of brood parasitism on nest success and productivity. Regarding the latter, we address a number of questions aimed at understanding the importance of brood parasitism on flycatcher reproductive success at St George, including: (i) what is the brood parasitism rate and does it vary annually? (ii) does brood parasitism influence nest success or nest productivity? (iii) does brood parasitism vary seasonally?

METHODS

We attempted to locate and monitor all active flycatcher nests during the 2008-2011 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.

VARIABLES AND STATISTICAL ANALYSIS

We pooled nests from individual sites within the St George study area for all statistical analyses. We conducted statistical analyses in R (R Development Core Team 2010), except for nest daily survival rate data, which we analyzed using program CONTRAST (Hines and Sauer 1989). We adjusted α for pairwise comparisons using a sequential Bonferroni correction (Rice 1989). We report mean ± SE for summary statistics unless otherwise specified.

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 tested for year effects on nest initiation date, for first nest attempts only, using a Kruskal-Wallis test. 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. We tested for year effects on clutch size using a Kruskal-Wallis test and examined effects of nest initiation date on clutch size (years combined) using linear regression. We also examined if clutch size differed between first nest and renest attempts using a Kruskal-Wallis test.

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, and conducted pairwise comparisons using Mann-Whitney U tests. To evaluate seasonal effects, we used linear regression to determine if the number of eggs hatched or hatching success rate varied with nest initiation date.

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 conducted linear contrasts of DSR among groups (Hines and Sauer 1989) to test for differences in nest success associated with nest stage, year, and brood parasitism. 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 examined annual variation in overall and successful nest productivity using Kruskal-Wallis tests, and conducted pairwise comparisons using Mann-Whitney U tests where appropriate.

Nest Failure. We summarized causes of nest failure for each year of the study.

Brood Parasitism. We summarized rates of brood parasitism of flycatcher nests by Brown-headed Cowbirds for each year of the study, and tested for year effects using a chi square test. To evaluate effects of brood parasitism on nest success, we compared DSR of parasitized and nonparasitized nests (see *Nest Success*, above). 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 nonparasitized nests. We used linear regression to test whether the number of cowbird eggs laid per flycatcher nest varied with flycatcher nest initiation date.

RESULTS

We monitored 62 active Southwestern Willow Flycatcher nests in the St George study area from 2008 through 2011. Active nests were comprised by 35 initial nesting attempts, 22 renesting attempts following failed nests, and five double-brood nests following successful nests (Table 3.1). We documented an additional 11 flycatcher nests not known to ever contain flycatcher eggs. Of the 22 renesting attempts following nest failures, 15, six, and one were second, third, and fourth re-nesting attempts, respectively. Forty-three percent of females attempted at least one renest following failed nests, and 14 % of females attempted double-brood nests following successful nests (Table 3.2).

Males and females typically maintained socially monogamous pairs, but we observed three cases of social polygyny, one in each of three years of the four year study (Table 3.3). Social polygyny occurred at Riverside Marsh (2009), Riverside East (2010), and Snipe Pond (2011).

NEST PHENOLOGY

Average nest initiation date (first-egg date) for first nest attempts was 13 June ± 1.8 days (range 28 May - 6 July; $n = 32$) over the four years of this study, and did not differ among years ($F_{1,30} = 0.01$, $P = 0.93$). Nest initiation dates for renest attempts following predation events ranged from 23 June to 24 July ($n = 22$), and nest initiation dates for double-brood attempts following successful nests ranged from 5 July to 19 July ($n = 5$). The timing of initial nesting attempts and renesting/double-brooding attempts resulted in a bimodal distribution of flycatcher breeding activity (Figure 3.1). The latest fledging date observed in the St George study area was 21 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

Mean clutch size was 2.87 ± 0.13 eggs (range 1-4; $n = 31$) overall, and did not vary among years ($\chi^2_3 = 2.19$, $P = 0.53$). Clutch size declined seasonally ($F_{1,29} = 20.01$, $P < 0.001$; Figure 3.2) and, not unrelated, clutch size for first nest attempts was significantly larger than for renest attempts ($U = 166$, $P = 0.03$; Table 3.6).

HATCHING SUCCESS

The number of flycatcher eggs that hatched successfully varied significantly among years ($\chi^2_3 = 8.2$, $P = 0.04$), as did hatching success rate ($\chi^2_3 = 9.36$, $P = 0.02$). Both the number of eggs hatched and hatching success rate tended to be lower in 2009 than in 2008, 2010, or 2011 (Table 3.7, Figure 3.3).

NEST SUCCESS

Apparent Nest Success. Apparent nest success varied significantly among years ($\chi^2_3 = 8.80$, $P = 0.03$; Figure 3.4). 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 and 2011, 30-35 % of flycatcher nests successfully fledged.

Mayfield Nest Success. Daily survival rates (DSR) of flycatcher nests did not vary significantly among periods (laying, incubation, nestling) of the nesting cycle ($\chi^2_2 = 1.83$, $P = 0.39$; Table 3.3), and we thus pooled data from all three periods for subsequent analyses. Although not statistically significant at α level 0.05, DSR appeared to vary somewhat among years ($\chi^2_3 = 6.88$, $P = 0.07$; Table 3.4), consistent with annual variation in apparent nest success. 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 3.4). Estimates of Mayfield nest success and apparent nest success were quite different in 2009 and 2011, but followed the same general trend over the 2008-2011 period (Figure 3.4).

NEST PRODUCTIVITY

Flycatchers fledged an average 0.7 ± 0.14 young per nest overall ($n = 62$; successful and unsuccessful nests combined) over the four years of the study. Overall nest productivity, however, varied significantly among years ($\chi^2_3 = 10.16$, $P = 0.02$), and was significantly lower in 2009 than in 2008, 2010, or 2011 (Table 3.7, Figure 3.5).

Successful nests fledged an average 2.1 ± 0.18 young flycatchers per nest ($n = 21$) over the four-year period. Although it followed the same annual pattern as overall nest productivity (Figure 3.5), nest productivity at successful nests did not vary significantly among years ($\chi^2_3 = 4.2$, $P = 0.24$).

NEST FAILURE

Nest predation was the primary cause of nest failure in each of the four years of this study, ranging from 54 % to 93 % of nest failures among years (Table 3.5) and averaging 73 % overall (years combined). Nest predation occurred during egg-laying (23 %), incubation (43 %), and nestling (34 %) periods. We did not actually observe any nest predation events during this study, and thus did not identify any flycatcher nest predators. Flycatchers abandoned seven nests after eggs failed to hatch (for at least 18 days); six of these seven infertile nests occurred during 2009 (Table 3.5). Brood parasitism directly caused flycatcher nest failure at three (5 %) active nests ($n = 62$); in these cases the cowbird nestling killed the flycatcher nestlings by outcompeting them for parental care or by causing direct physical harm. One flycatcher nest failed when the female abandoned during egg-laying, seemingly in response to interactions with Brown-headed Cowbirds.

In addition to the above active nests used in nest success calculations, we also observed 11 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 20 % to 59 % of active nests (nests confirmed to contain flycatcher eggs or nestlings) over the four years of this study (Table 3.1), and averaged 37 % overall (years combined). Brood parasitism rates did not vary among years ($\chi^2_3 = 5.99$, $P = 0.11$).

Daily survival rates of parasitized nests (DSR = 0.943 ± .01) were lower than nonparasitized nests (DSR = 0.968 ± 0.007), although the difference was not statistically significant at $\alpha = 0.05$ ($\chi^2_1 = 3.01$, $P = 0.08$). The probability of a nest surviving to fledge a young flycatcher (MSP) was 19 % for parasitized nests and 39 % for nonparasitized nests. Because cowbirds often remove flycatcher eggs at parasitized nests, cowbirds may have also directly reduced flycatcher fecundity. The number of flycatcher eggs that were incubated ($U = 425$, $P = 0.41$) and hatched successfully ($U = 132$, $P = 0.23$), as well as hatching success rate ($U = 138$, $P = 0.14$), did not differ between parasitized and nonparasitized nests, although parasitized nests tended to contain fewer of each than did nonparasitized nests (Figure 3.6). However, the number of flycatcher fledglings produced was significantly lower at parasitized nests than at nonparasitized nests ($U = 575.5$, $P = 0.03$; Figure 3.6). There was no relationship between the number of cowbird eggs per flycatcher nest and nest initiation date ($F_{1,57} = 2.74$, $P = 0.10$), suggesting that parasitism rates did not vary seasonally.

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 a single nest where a female flycatcher responded to brood parasitism by burying a cowbird egg beneath the nest lining, thus avoiding incubating the cowbird egg.

DISCUSSION

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 13 June, range 28 May – 24 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 2.8 eggs overall, which is 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 2008-2011 at St George averaged 37.6 % and ranged from 13 % to 70 %, 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. Apparent nest success, hatching success, and nest productivity were notably high in 2008 and declined dramatically in 2009. Each of these metrics increased in 2010-2011, but none rebounded to 2008 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 (Chapter 4), 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-exotic habitat in 2010 and 2011 (Chapter 4). 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 in 2008, 2010, or 2011. 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. Although reproductive success did not return to pre-2009 levels when flycatchers shifted to nesting in more native-dominated mixed native-exotic habitat in 2010 and 2011, 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 (Chapter 4), Mayfield nest success (i.e., nest survival probability) remained low in 2010 and 2011. Low nest survival probability was driven, in part, by increased nest predation rates in 2010 and 2011. 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 has been consistently depressed since flycatchers shifted from tamarisk-dominated to native-dominated mixed native-exotic habitat following 2009. We suggest that, in the context of mixed native-exotic habitat, tamarisk may improve, or may be associated with some habitat component that improves, flycatcher nest success (see also Chapter 5). 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. 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 (*Accipiter cooperii*) 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 Brown-headed Cowbirds, for example, may merit the implementation of a cowbird control program (see below). 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, 37 % of active flycatcher nests were parasitized by cowbirds over the four years of this study, and as many as 59 % 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 19 % for parasitized flycatcher nests, compared with 39 % for nonparasitized 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). Results presented in this report, including both high rates of parasitism and negative effects of parasitism on flycatcher nest success, indicate that the implementation of a cowbird control program at flycatcher breeding areas in the St George study area may be warranted.

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Table 3.1. 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, 2008-2011.

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	-	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	-	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	-	1 (100)	0
	Riverside Marsh	1	-	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	-	1 (100)	1 (100)
	Total	**17**	**8/1**	**6 (35)**	**10 (59)**
Overall Total		**62**	**22/5**	**21 (34)**	**23 (37)**

[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 3.2. Percentages (*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, 2008-2011.

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)
Overall	**43 % (15)**	**14 % (5)**

Table 3.3. Percentages (*n*) of socially polygynous Southwestern Willow Flycatcher males, females, and nests in the St George study area, 2008-2011.

Year	Polygynous males	Polygynous females	Polygynous nests[1]
2009	7 % (1)	20 % (2)	20 % (3)
2010	9 % (1)	22 % (2)	25 % (5)
2011	14 % (1)	38 % (3)	29 % (5)

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

Table 3.4. Daily survival rates and Mayfield survival probabilities for Southwestern Willow Flycatcher nests monitored in the St George study area, 2008-2011.

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***

[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 3.5. 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, 2008-2011.

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
	River Rd Bridge	0	0	0	0	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
	Riverside East	0	0	0	0	0
	River Rd Bridge	3	2 (66)	1 (33)	0	0
	Total	**13**	**7 (54)**	**6 (46)**	**0**	**0**
2010	Seegmiller Marsh	0	0	0	0	0
	Riverside Marsh	0	0	0	0	0
	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
	Riverside East	0	0	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)**
Overall Total		**41**	**30 (73)**	**7 (17)**	**1 (2)**	**3 (7)**

[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 nestlings).

Table 3.6. 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, 2008-2011.

	First nest attempts	Renest attempts	All nest attempts (combined)
Nest initiation date[1]	14 June ± 2.0 days (28 May – 6 July, *n* = 32)	6 July ± 1.5 days (23 June – 24 July, *n* = 27)	24 June ± 1.9 days (28 May – 24 July, *n* = 59)
Clutch size[2]	3.1 ± 0.11 eggs (2-4, *n* = 18)	2.5 ± 0.24 eggs (1-4, *n* =13)	2.9 ± 0.12 eggs (1-4, *n* = 31)
No. eggs hatched[3]	2.2 ± 0.28 eggs (0-4, *n* = 20)	1.4 ± 0.34 eggs (0-3, *n* = 12)	1.9 ± 0.22 eggs (0-4, *n* = 32)
No. young fledged[4]	2.2 ± 0.22 young (1-3, *n* = 13)	2.0 ± 0.33 young (1-3, *n* = 8)	2.1 ± 0.18 young (1-3, *n* =21)

[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 3.7. Mann-Whitney test *P*-values for pairwise comparisons between years for the number of Southwestern Willow Flycatcher eggs hatched, hatching success rates, and the number of flycatcher fledglings produced in the St George study area, 2008-2011. Italicized and bolded *P*-values indicate statistical significance prior to and following sequential Bonferroni adjustment (adjusted α = 0.008) for multiple tests, respectively.

Year comparison	Eggs hatched	Hatching success	Young fledged
2008-2009	0.055	*0.024*	**0.002**
2008-2010	0.234	0.199	0.033
2008-2011	0.627	0.413	0.126
2009-2010	*0.032*	*0.025*	0.196
2009-2011	*0.041*	*0.031*	0.106
2010-2011	0.296	0.509	0.646

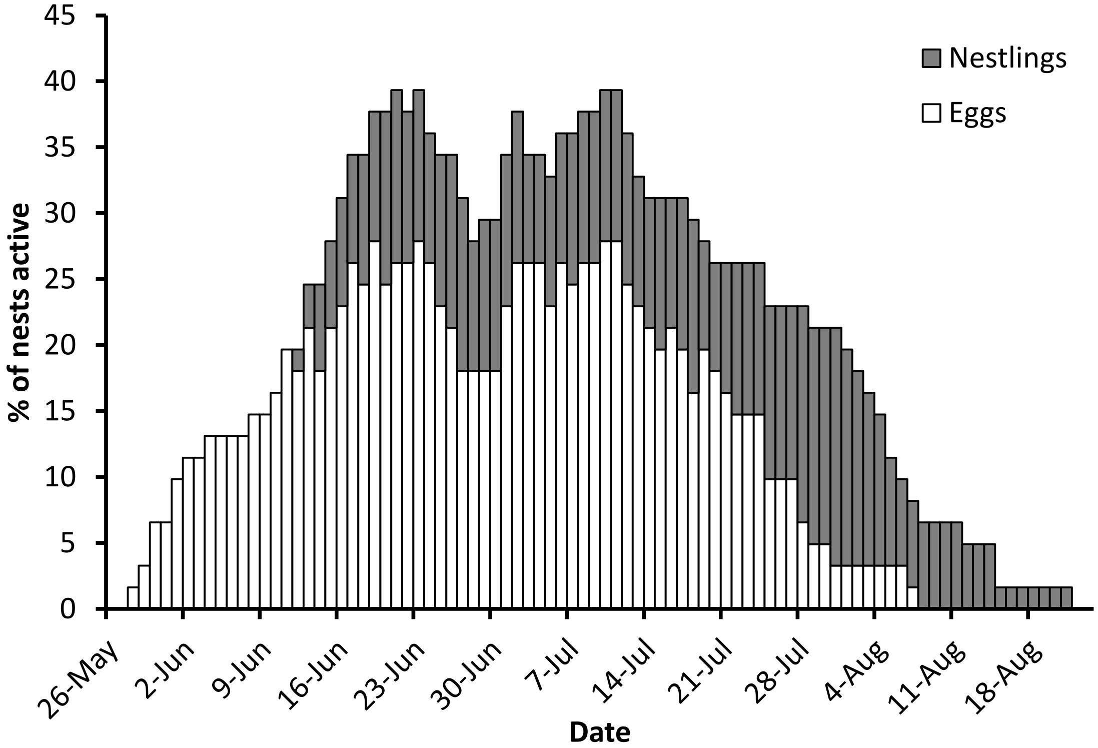

Figure 3.1. Southwestern Willow Flycatcher breeding phenology in the St George study area, 2008-2011 (years combined; *n* = 61 nests).

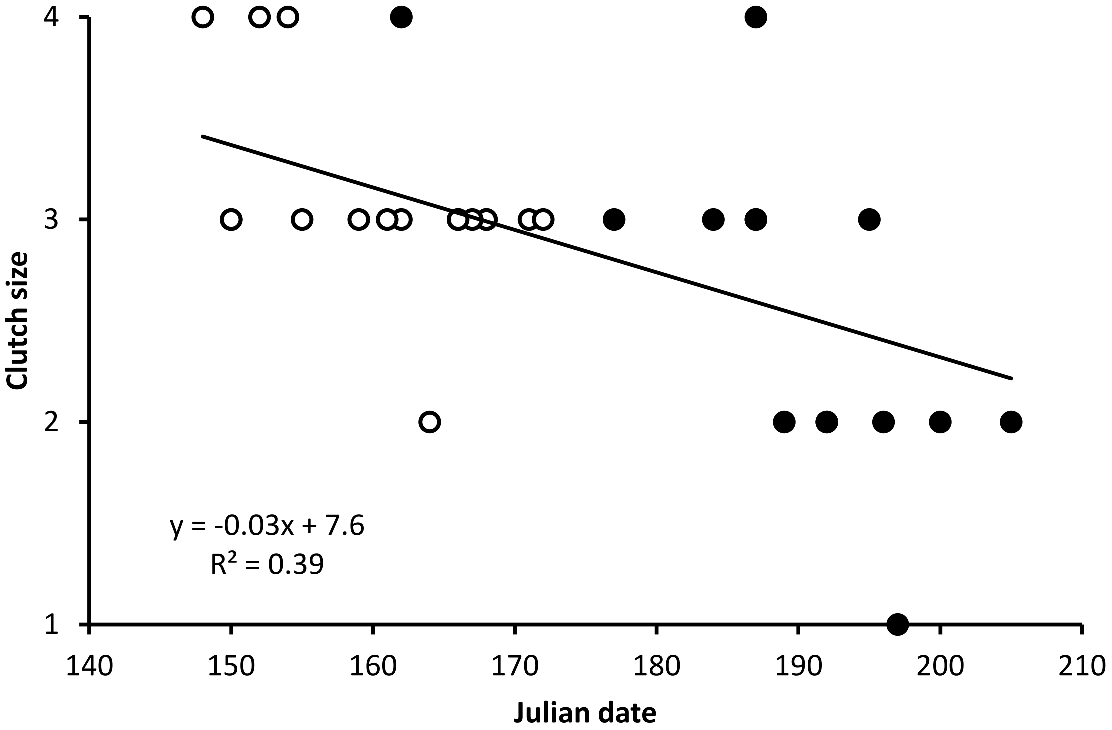

Figure 3.2. Southwestern Willow Flycatcher clutch size declined seasonally. Open and closed symbols represent first nest attempts and renest attempts, respectively. Julian date 140 = 20 May.

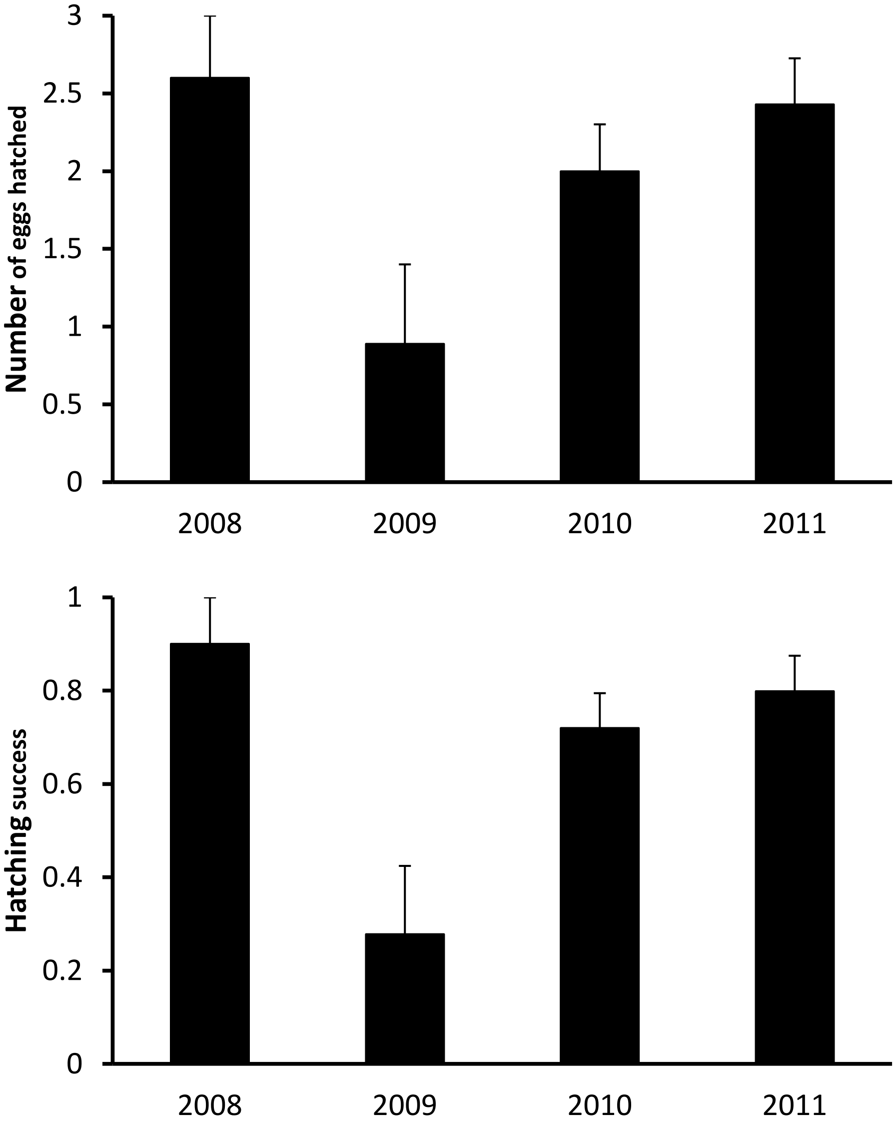

Figure 3.3. Mean (± SE) number of eggs hatched (upper) and hatching success rate (lower) for Southwestern Willow Flycatchers in the St George study area, 2008-2011.

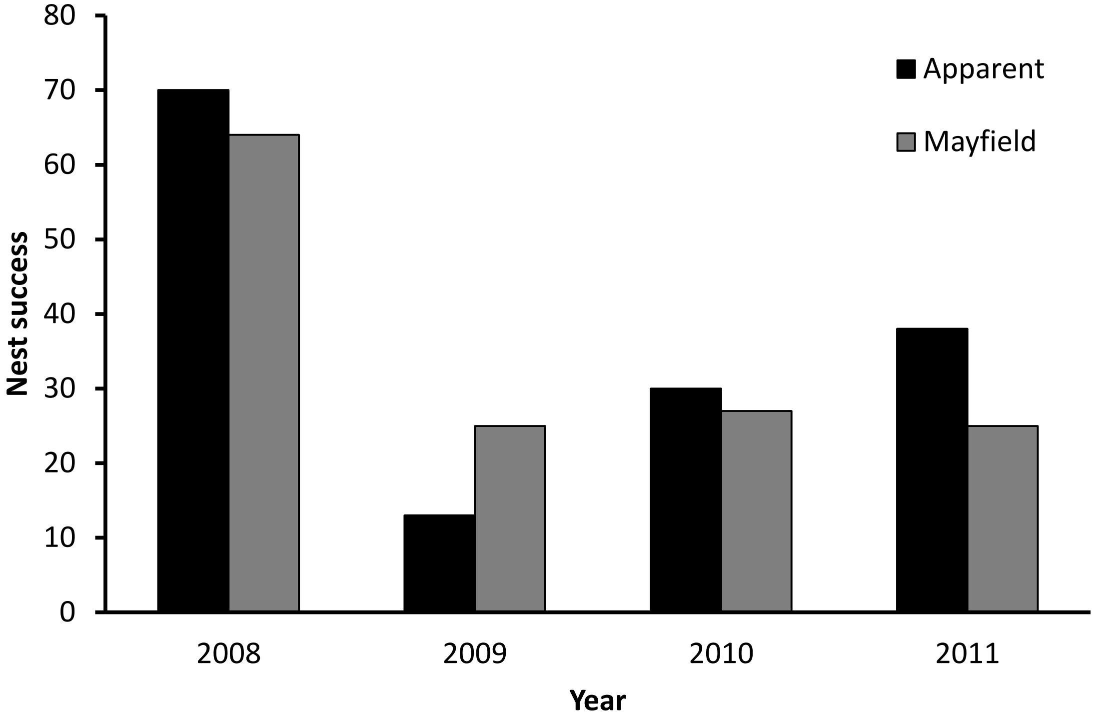

Figure 3.4. Apparent nest success (percentage of nests successfully fledging ≥ one flycatcher) and Mayfield survival probability (percent probability of nests surviving to fledge ≥ one flycatcher) of Southwestern Willow Flycatcher nests in the St George study area, 2008-2011.

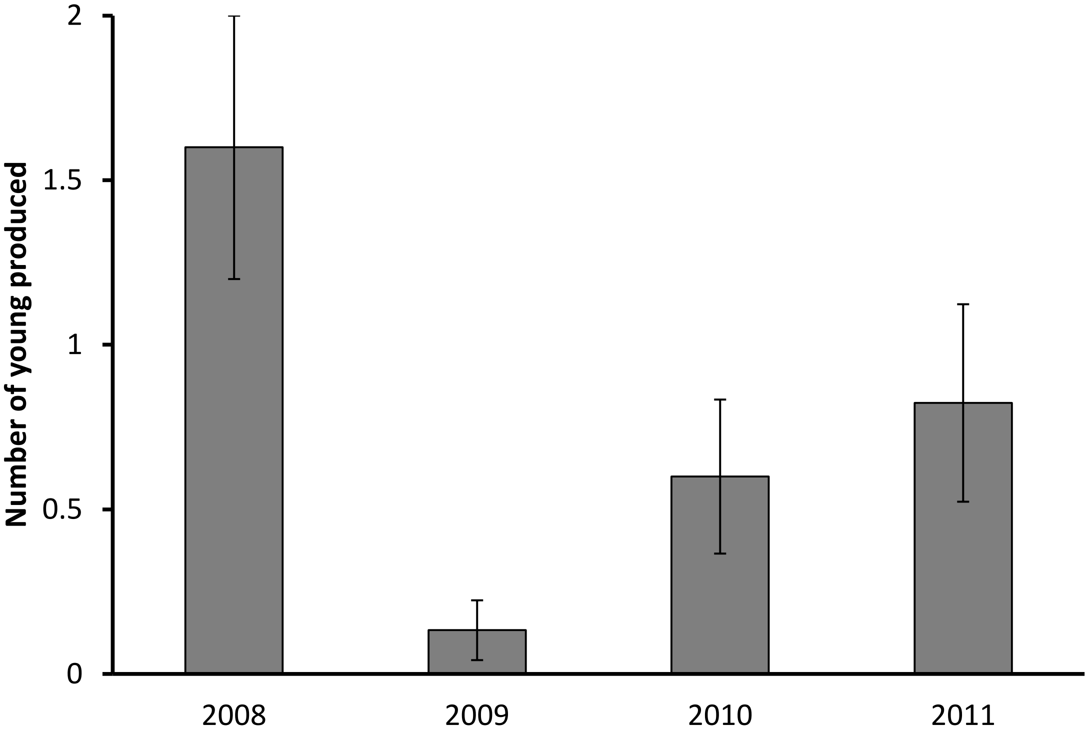

Figure 3.5. Mean (± SE) number of young Southwestern Willow Flycatchers produced per nest (successful and unsuccessful nests combined) in the St George study area, 2008-2011.

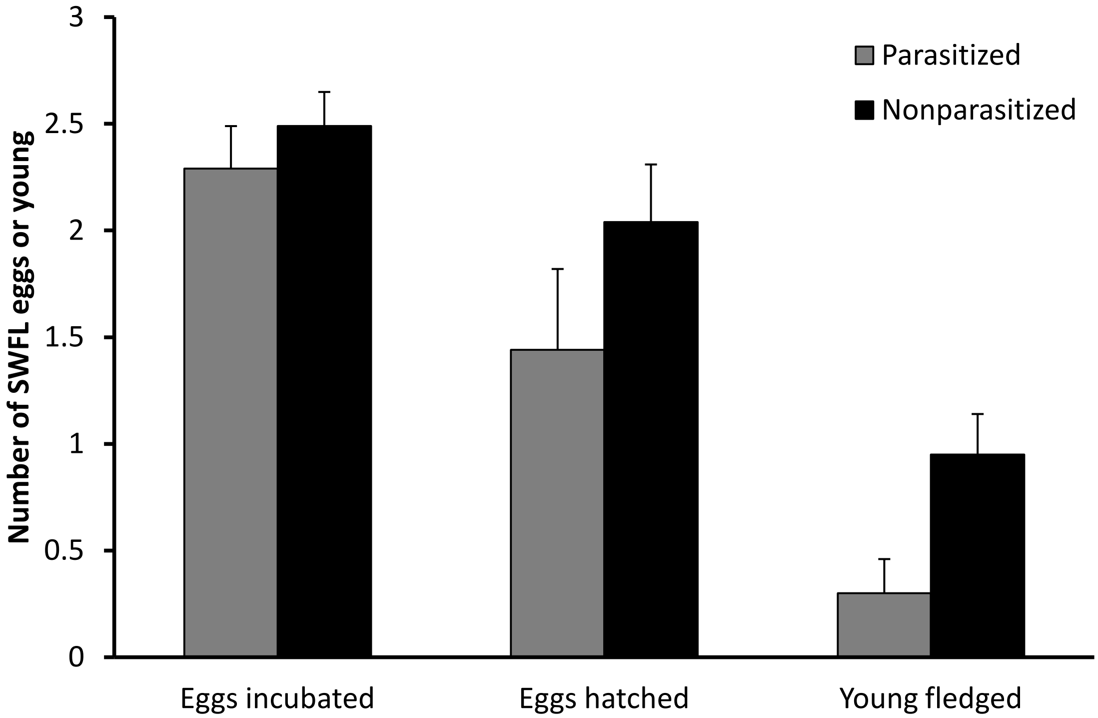

Figure 3.6. Mean (± SE) number of Southwestern Willow Flycatcher (SWFL) eggs incubated and successfully hatched in, and young successfully fledged from, flycatcher nests parasitized by and not parasitized by Brown-headed Cowbirds in the St George study area, 2008-2011.

CHAPTER 4
HABITAT USE AND NEST SITE SELECTION

INTRODUCTION

A variety of habitat characteristics influence distribution, reproductive success and survival of birds (Martin and Roper 1988, Holway 1991, Martin 1998). For endangered species, a critical goal of management is to understand the suite of characteristics that constitute suitable habitat, and how to differentiate suitable from unsuitable habitat. Management of endangered bird populations often requires recognition, protection and restoration of suitable habitats. However, implementing such actions can be difficult, especially for sensitive species with limited ranges and strict habitat preferences. The endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*), is one such species, a riparian obligate that prefers dense, wooded areas near slow-moving or standing water (Sogge and Marshall 2000). Throughout its range the Southwestern Willow Flycatcher (hereafter flycatcher) has undergone population declines, resulting in its listing as an endangered species in 1995 (USFWS 1995). Numerous factors have been attributed to these declines, including loss or degradation of habitat, introduction of exotic species (*Tamarix* spp.), and water management practices that have altered the natural flow regime (Marshall and Stoleson 2000). Given the myriad of problems facing the flycatcher, data related to habitat suitability collected throughout the sub-species range continues to be important for developing and implementing conservation and recovery measures.

In order to inform managers and to evaluate recovery plans tailored to local populations, a clear understanding of the habitat characteristics used in nest site selection remains important. Several studies have documented habitat preferences of Southwestern Willow Flycatchers, concluding that nests are built in dense patches of vegetation near surface water (Brown 1988, Sogge and Marshall 2000, Allison et al. 2003, Paradzick and Woodward 2003, Stoleson and Finch 2003, Paradzick 2005). However, even among desert riparian habitats of the southwest, particular habitat variables such as species composition, canopy structure, nest placement and nest tree appear to be site specific (Brown 1988, Sogge and Marshall 2000, Allison et al. 2003, Stoleson and Finch 2003, Paradzick 2005). Such regional variation in nesting habits and the diversity of habitats flycatchers occupy suggest that data collected locally provide the most valuable insight for the enhancement of suitable habitat and, ultimately, recovery of local populations.

Here we describe and measure vegetation characteristics in areas used by Southwestern Willow Flycatchers as nesting plots and in non-use plots along the upper Virgin River in southern Utah. This area supports a small breeding population of flycatchers and is located near the northern edge of the subspecies range (Paxton et al. 2008). Our goals were to identify specific variables that describe areas used by locally breeding flycatchers and to provide insight about general features to assist managers with habitat restoration projects. More specifically, our objectives were to test for: (i) among year differences in flycatcher use sites, (ii) differences in habitat characteristics between use and non-use sites and (iii) preferences in nest site selection by Southwestern Willow Flycatchers.

METHODS

STUDY AREA

This study was conducted in the riparian habitats along an approximately 11 km reach of the Virgin River in the cities of St. George and Washington, Utah. Similar to other streams of the desert southwest, the Virgin River is characterized by relatively low flows punctuated by large spring runoff peaks and late summer/early autumn storm driven flow spikes. Large fluctuations in discharge are also accompanied by considerable variation in sediment load and lead to unstable channel substrates. As a result, large marsh complexes have been created in detached oxbows and depressions. Most marsh areas support a mixture of native and exotic plant species; however, in a few locations native woody species continue to dominant the plant community. Dominant native woody species include: Fremont Cottonwood (*Populus fremontii*), Coyote Willow (*Salix exigua*), Goodding's Willow (*S. gooddingi*), Velvet Ash (*Fraxinus velutina*) and Mule's Fat (*Baccharis salicifolia*). The two most prolific woody exotic species are tamarisk (*Tamarix* spp.) and Russian Olive (*Elaeagnus angustifolia*). Vegetative structure at our site varies depending upon substrate and water conditions. Sandy areas susceptible to scouring tend to have little to no woody cover, with available cover being short and sparse, while higher elevation sites (e.g., berms, banks) have more fully developed, stable soils that support denser, taller plants. Saturated soils, inundated areas and some bankside locations also support dense stands of cattail (*Typha* spp.) and Common Reed (*Phragmites australis*). Most habitat patches are less than 10 ha in area.

MICROHABITAT AND VEGETATION SAMPLING

We described and measured vegetation and habitat features at sites used by nesting flycatchers from 2008 to 2011 ($n = 52$). 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 2010-2011 ($n = 28$). 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). For each use and non-use site we utilized a circular sample plot with a 5 meter 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 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. 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 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 ten 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.

STATISTICAL ANALYSES

All data were tested for violations of normality and transformed when necessary. First, we compared the use of nest tree species given availability within nesting plots using chi-square tests with an applied Yates continuity correction. Next, for nest sites only, we tested for differences in habitat variables among years using ANOVA or with Kruskal-Wallis chi-square tests when the data could not be normalized. When significant differences were detected among years, we conducted between-year comparisons using Mann-Whitney *U*-tests and applied a sequential Bonferroni adjustment for multiple comparisons (Rice 1989). We went on to test for differences in habitat variables between use and non-use sites using either independent sample *t*-tests or, when data were not normally distributed, Mann-Whitney *U*-tests. While testing for differences between use and non-use sites we restricted use site data to 2010 and 2011 because non-use site data were collected only during these years. We combined data from individual breeding sites within the St George study area for all analyses.

To identify habitat variables that were important in nest site selection we conducted logistic regression. Habitat variables included in the regression analysis were selected *a priori* based on flycatcher biology and because they had been demonstrated to be important in other studies (Allison et al. 2003, Stoleson and Finch 2003). More specifically, we expected flycatchers to utilize areas with dense, heterogeneous vegetation containing numerous stems, high canopy cover, numerous willow stems and in close proximity to water. In addition, any habitat variables that were similar between use and non-use sites based on the univariate analyses were excluded ($P > 0.1$). These habitat variables were entered into an automated model selection procedure (Calcagno and de Manzancourt 2010, Calcagno 2011). Instead of identifying a single best fitting model, we chose a multimodel approach by weighting a set of candidate models and calculating model-averaged predictions, unconditional variance estimates, 95% confidence intervals and Akaike weights of variables. All models were ranked according to Akaike Information Criteria with a second order bias correction for small sample sizes (AIC_c, Burnham and Anderson 2002, 2004). For inclusion into the candidate set of most parsimonious models we used a rescaled value of AIC_c, $\Delta AIC_c = AIC_{ci} - AIC_{cbest}$, which measures the difference in AIC_c values between the current (AIC_{ci}) and the model with the lowest AIC_c (AIC_{cbest}). Models with substantial support ($\Delta AIC_c \leq 2$) to explain variation in the empirical data were included in the candidate model set (Burnham and Anderson 2002, 2004). Akaike weights (w_i) for models and variables were also included; more specifically, Akaike weights are normalized and sum to one when a variable appears in each of the models included in the candidate set. The variable with the largest Akaike weight is estimated to be the most important, while the variable with the smallest summed Akaike weight is estimated to be the least important predictor variable (Burnham and Anderson 2002, 2004). Variables with a summed Akaike weight of 0.8 were considered important variables, thereby balancing the overall risk of type I versus type II errors (Calcagno and de Manzancourt 2010). Collectively the multimodel approach is more desirable than making inferences from a single best model because it estimates more robust parameter values and predictions from multiple models with substantial support. Moreover, model-averaged estimates provide a more honest measure of precision and reduce bias relative to a single selected best model (Burnham and Anderson 2002, 2004).

Last, we also conducted a series of *post-hoc* analyses that measured structural differences between use and non-use sites. More specifically, we used Mann-Whitney *U*-tests to measure differences in each one meter height category that comprised the vertical height density estimates, and examined differences in size classes of all stems and for the three dominant vegetation types (e.g. tamarisk, snags, Coyote Willow). These analyses were conducted as *post-hoc* tests because we had no *a priori* hypotheses regarding differences between use and non-use sites for these specific variables, and because we felt additional insight about habitat structural complexity would benefit future restoration projects.

Reported values are presented as mean ± SE. All data analyses were conducted using program R and the model selection procedure utilized the glmulti procedure (R Development Core Team 2010, Calcagno and de Manzancourt 2010, Calcagno 2011).

RESULTS

At use sites, microhabitat variables differed among the four years of this study (Table 4.1) Six of the 12 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. When examined more closely, the between year differences highlight similarities between 2008-2009 and 2010-2011 (Table 4.2). Over time, flycatchers use sites contained fewer trees, more Coyote Willows, had a denser subcanopy-canopy layer, and after 2008 were closer to standing water.

Habitat variables around nest sites differed from non-use sites in nearly all of the aspects measured here (Table 4.3).The univariate comparisons revealed that eight of the 11 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 diversity, more shrub and Coyote Willow stems, fewer total tree stems and were closer to water. The logistic regression analysis identified three of these variables as significant predictors in nest site selection; each of the ten models comprising the candidate model set contained distance to nearest water, understory canopy density and number of Coyote Willow stems as important predictor variables (Tables 4.4 and 4.5). Percent canopy cover appeared in seven of the top ten models and could also be interpreted as a marginally important predictor of nest site selection. Although parameter estimates were variable among models, the model averaging procedure corroborated the univariate analyses, indicating that the likelihood of a site being used for nesting increased with greater foliage density, number of willow stems and proximity to water.

The results of the *post-hoc* tests of habitat structure revealed that all height categories between three and eight meters were significantly different between use and non-use sites (Table 4.6). Use sites contained a higher density of stems between three and seven meters, and fewer stems in the eight meter height category (Figure 4.1). 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 (Table 4.7). Among the dominant vegetation types, non-use sites contained more tamarisk trees (> 8 cm), along with two size classes of snags (Figures 4.2 and 4.3). In contrast, use sites contained more small Coyote Willow stems relative to non-use sites (Figure 4.4). In general flycatchers preferred habitats containing a dense mid-canopy layer containing more live vegetation, and in particular Coyote Willow.

DISCUSSION

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, in 2010-2011 flycatchers nested in areas with a denser understory, that were closer to water, that contained more shrubs and willows, and that contained fewer trees. Two related events occurred that provide the most plausible explanation for these observed differences: tamarisk defoliation by Tamarisk Leaf Beetles (*Diorhabda carinulata*) and changes in flycatcher patch occupancy. First, during the study period the release of tamarisk beetles directly altered study site vegetation, causing widespread tamarisk foliage-browning and defoliation (Chapter 2). 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 2009-2011. Flycatchers in our study area nest in patches that differ in vegetation composition, which can be categorized into one of three types: exotic tamarisk dominated, mixed native-exotic, and native dominated areas (Chapter 2). 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).

During this same time period we also observed a second, confounding event: a change in flycatcher occupancy among patches. Flycatchers have occupied the Seegmiller Marsh complex since at least the mid-1990's. In 2010, however, we observed only a single pair at this site, and in 2011 no pairs utilized this site for breeding (Chapter 2). Instead, during 2010-2011 we observed a shift to a new, previously unoccupied patch, Snipe Pond. This is noteworthy because Seegmiller Marsh is tamarisk dominated, while Snipe Pond is dominated by native vegetation, particularly Coyote Willow (Chapter 2). 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.

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 established nests in dense thickets containing willows, above or nearby standing water. The results of the univariate analyses also indicated a number of other habitat variables differed between use and non-use sites; among them canopy cover, height diversity and number of shrubs and trees. 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. One conspicuous difference among these studies and ours is that earlier studies have found flycatchers utilize areas with taller canopies (Allison et al. 2003, Stoleson and Finch 2003, Paradzick 2005); surprisingly, we did not observe this pattern, as canopy height was similar between use and non-use sites. In addition, 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).

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 (Chapter 5). 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).

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Table 4.1. Comparisons of habitat variables among years for Southwestern Willow Flycatcher nest sites. Values are given as mean ± SE and bold values indicate significant differences among years (*P*<0.05).

Variable	2008 (*n* = 9)	2009 (*n* = 12)	2010 (*n* = 13)	2011 (*n* = 12)	Test Statistic	*P*-value
Average canopy cover (%)	91.5 ± 3.1	92.4 ± 3.0	92.4± 1.9	93.8 ± 1.7	$\chi^2_3 = 4.9$	0.18
Average canopy height (m)	6.2 ± 0.2	5.8 ± 0.3	5.8 ± 0.3	6.2 ± 0.2	$F_{3,4\ 2} = 0.6$	0.56
Foliage density 0-3 m	18.4 ± 1.5	19.6 ± 1.3	15.8 ± 2.3	15.5 ± 2.0	$F_{3,42} = 1.1$	0.35
Foliage density 3-10 m	15.9 ± 1.2	12.7 ± 1.7	22.4 ± 2.9	24.8 ± 1.7	$F_{3,42} = 7.3$	**< 0.001**
Foliage height diversity	1.6 ± 0.1	1.5 ± 0.1	1.4 ± 0.1	1.4 ± 0.04	$F_{3,42} = 2.1$	0.12
Plant species diversity	0.67 ± 0.08	0.81 ± 0.1	0.84 ± 0.1	0.83 ± 0.06	$F_{3,42} = 0.7$	0.58
Total shrub stems (≤8 cm dbh)	348.1 ± 56.2	236.5 ± 49.1	432.2 ± 57.1	577.8 ± 95.1	$\chi^2_3 = 12.8$	**0.005**
Total tree stems (>8 cm dbh)	6.0 ± 1.4	4.7 ± 1.2	1.1 ± 0.6	0.6 ± 0.4	$\chi^2_3 = 20.4$	**< 0.001**
Total snag stems	249.6 ± 62.1	92.8 ± 24.1	58.2 ± 12.9	127.2 ± 19.7	$\chi^2_3 = 14.0$	**0.003**
Total tamarisk stems	78.1 ± 10.9	56.2 ± 12.3	104.5 ± 32.1	55.4 ± 14.3	$\chi^2_3 = 2.2$	0.54
Total willow stems	20.4 ± 18.3	76.4 ± 44.9	249.5 ± 43.7	391.8 ± 74.8	$\chi^2_3 = 21.6$	**< 0.001**
Distance to nearest water (m)	21.5 ± 5.9	14.6 ± 4.5	3.7 ± 0.8	2.9 ± 1.0	$\chi^2_3 = 12.5$	**0.006**

Table 4.2. Comparisons of a subset of habitat variables between years for Southwestern Willow Flycatcher nest sites. Reported values are *P*-values and bold values indicate significant differences between years after sequential Bonferroni adjustment.

Year Comparison	Foliage density 3-10 m	Total shrub stems	Total tree stems	Total snag stems	Total willow stems	Distance to nearest water (m)
2008-2009	0.75	0.05	0.50	0.02	0.63	0.36
2008-2010	0.17	0.32	**0.002**	**0.001**	**0.003**	**0.004**
2008-2011	0.03	0.11	**<0.001**	0.13	**<0.001**	**0.002**
2009-2010	**0.008**	0.01	**0.009**	0.33	**0.009**	0.16
2009-2011	**0.001**	**0.001**	**0.002**	0.22	**0.001**	0.06
2010-2011	0.83	0.27	0.51	**0.009**	0.17	0.28

Table 4.3. Univariate comparisons of habitat variables between Southwestern Willow Flycatcher nest sites and non-use sites. Values are given as mean ± SE and bold values indicate significant differences between sites.

Variable	Use Sites ($n = 25$)	Non-use Sites ($n = 28$)	Test Statistic	P-value
Average canopy cover (%)	93.1 ± 1.3	86.7 ± 2.0	$U = 155.5$	**< 0.001**
Average canopy height (m)	5.9 ± 0.2	5.5 ± 0.2	$t_{51} = -1.8$	0.07
Foliage density 0-3 m	15.7 ± 1.5	11.5 ± 1.1	$U = 230.5$	**0.03**
Foliage density 3-10 m	23.6 ± 1.7	11.8 ± 1.6	$U = 118$	**< 0.0001**
Foliage height diversity	1.4 ± 0.03	1.2 ± 0.05	$U = 168$	**< 0.001**
Plant species diversity	0.84 ± 0.06	0.88 ± 0.04	$t_{45} = 0.6$	0.55
Total shrub stems (≤8 cm dbh)	502.1 ± 55.3	244.7 ± 24.1	$U = 125.5$	**< 0.0001**
Total tree stems (>8 cm dbh)	0.8 ± 0.3	3.3 ± 0.6	$U = 543$	**< 0.001**
Total snag stems	91.3 ± 13.3	101.6 ± 11.9	$U = 393$	0.45
Total tamarisk stems	80.9 ± 18.4	59.5 ± 9.0	$U = 319.5$	0.59
Total willow stems	317.8 ± 44.02	69.0 ± 22.5	$U = 91$	**< 0.0001**
Distance to nearest water (m)	3.3 ± 0.7	43.8 ± 6.6	$U = 628.5$	**< 0.0001**

Table 4.4. Candidate set of logistic regression models ranked by Akaike's Information Criteria with second order bias correction (AIC_c) used to predict habitat variables important in nest site selection. Only models within two AIC_c units greater than the best model (ΔAIC_c) were considered for inclusion in the candidate set. Akaike weights (w_i) were computed as the standardized difference in AIC_c between a model and the top model. *K* indicates the number of parameters in each model.

Rank	Model	*K*	AIC_c	ΔAIC_c	w_i
1	Intercept + Willow stems + Understory foliage density - Canopy cover - Distance to water	5	30.887	0.000	0.149
2	Intercept + Willow stems + Understory foliage density - Canopy cover - Distance to water + Canopy height	6	31.002	0.115	0.141
3	Intercept + Willow stems + Understory foliage density - Distance to water	4	31.047	0.160	0.138
4	Intercept + Willow stems + Understory foliage density + Mid-story foliage density - Canopy cover - Distance to water	6	31.364	0.478	0.117
5	Intercept + Willow stems + Understory foliage density - Canopy cover - Distance to water - Foliage height diversity	6	31.856	0.970	0.092
6	Intercept - Shrub stems + Willow stems + Understory foliage density - Canopy cover - Distance to water + Canopy height	7	31.901	1.015	0.090
7	Intercept - Shrub stems + Willow stems + Understory foliage density - Canopy cover - Distance to water	6	32.261	1.374	0.075
8	Intercept - Shrub stems + Willow stems + Understory foliage density + Mid-story foliage density - Canopy cover - Distance to water	7	32.278	1.391	0.074
9	Intercept - Shrub stems + Willow stems + Understory foliage density - Distance to water	5	32.388	1.502	0.070
10	Intercept - Tree stems + Willow stems + Understory foliage density - Distance to water	5	32.915	2.029	0.054

Table 4.5. Model-averaged parameter estimates, unconditional variance estimates, 95% confidence intervals and Akaike weights (w_i) from the logistic regression. Estimates were calculated from the candidate set of ten models, and terms with Akaike weights of 0.8 or greater were considered important.

Variable	Estimate	Unconditional Variance	95% CI	Times Present in Top Models	w_i
Intercept	10.6	± 160.8	-14.6, 35.8	10	1
Average canopy cover (%)	-0.2	± 0.04	-0.6, 0.2	7	0.74
Average canopy height (m)	0.3	± 0.37	-0.9, 1.5	2	0.23
Distance to nearest water (m)	-0.4	± 0.05	-0.8, 0.05	10	1
Foliage density 0-3 m	0.4	± 0.06	-0.1, 0.9	10	1
Foliage density 3-10 m	0.02	± 0.002	-0.1, 0.1	2	0.2
Foliage height diversity	0.6	± 1.6	-1.9, 3.1	1	0.1
Total shrub stems (≤ 8 cm dbh)	-0.003	± 0.000	-0.02, 0.01	4	0.3
Total tree stems (>8 cm dbh)	-0.01	± 0.001	-0.07, 0.04	1	0.05
Total willow stems	0.02	± 0.000	-0.01, 0.04	10	1

Table 4.6. *Post-hoc* univariate comparisons of mean vertical foliage density between Southwestern Willow Flycatcher use sites and non-use sites shown by height class. Bold values indicate significant differences between sites.

Height Class (m)	Test Statistic	*P*-value
1	*U* = 292	0.31
2	*U* = 319.5	0.59
3	*U* = 160.5	**< 0.001**
4	*U* = 206	**0.01**
5	*U* = 116.5	**< 0.001**
6	*U* = 181.5	**0.003**
7	*U* = 234.5	**0.04**
8	*U* = 125.5	**< 0.001**
9	*U* = 361	0.64

Table 4.7. *Post-hoc* univariate comparisons of stem density distributed by size class between Southwestern Willow Flycatcher use and non-use sites. Values are given as mean ± SE and bold values indicate significant differences between sites.

Species	Size Class	Use Sites	Non-Use Sites	Test Statistic	*P*-value
All Stems	< 1 cm	274.4 ± 42.2	122.2 ±14.3	*U* = 174	**0.002**
	1.1-2.5 cm	149.4 ± 15.3	79.2 ± 11.4	*U* = 141.5	**< 0.001**
	2.51-5.5 cm	72.1 ± 6.7	35.1 ± 4.1	*U* = 110.5	**< 0.001**
	5.56-8 cm	6.2 ± 1.1	8.2 ± 1.9	*U* = 383	0.56
	> 8 cm	0.8 ± 0.3	3.3 ± 0.6	*U* = 543	**< 0.001**
Snag	< 1 cm	69.4 ± 11.9	59.7 ± 8.0	*U* = 344.5	0.93
	1.1-2.5 cm	21.0 ± 3.8	30.3 ± 5.5	*U* = 419.5	0.22
	2.51-5.5 cm	0.8 ± 0.2	9.9 ± 2.9	*U* = 526	**0.001**
	5.56-8 cm	0.04 ± 0.04	1.3 ± 0.5	*U* = 452	**0.008**
	> 8 cm	0 ± 0	0.4 ± 0.2	*U* = 387.5	0.10
Tamarisk	< 1 cm	41.5 ± 10.0	19.7 ± 3.2	*U* = 269	0.15
	1.1-2.5 cm	26.2 ± 7.3	19.7 ± 3.7	*U* = 337	0.82
	2.51-5.5 cm	11.0 ± 2.3	14.5 ± 2.7	*U* = 395.5	0.42
	5.56-8 cm	1.9 ± 0.5	3.4 ± 0.6	*U* = 454	0.06
	> 8 cm	0.4 ± 0.2	2.3 ± 0.5	*U* = 497	**0.002**
Willow	< 1 cm	154.2 ± 29.7	29.0 ± 10.3	*U* = 112.5	**< 0.001**
	1.1-2.5 cm	99.8 ± 14.3	25.8 ± 11.1	*U* = 99.5	**< 0.001**
	2.51-5.5 cm	59.7 ± 7.9	10.6 ± 3.9	*U* = 73.5	**< 0.001**
	5.56-8 cm	3.9 ± 1.0	3.4 ± 1.9	*U* = 264.5	0.09
	> 8 cm	0.1 ± 0.06	0.3 ± 0.1	*U* = 375	0.43

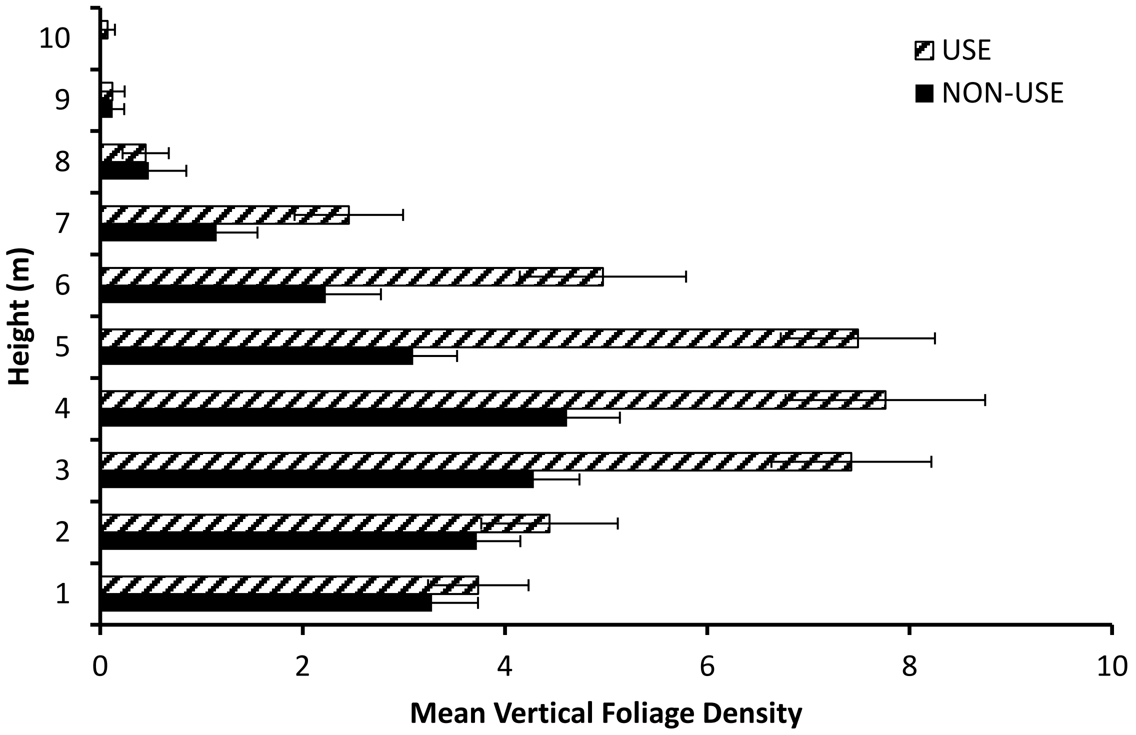

Figure 4.1. Mean vertical foliage density between Southwestern Willow Flycatcher use and non-use sites.

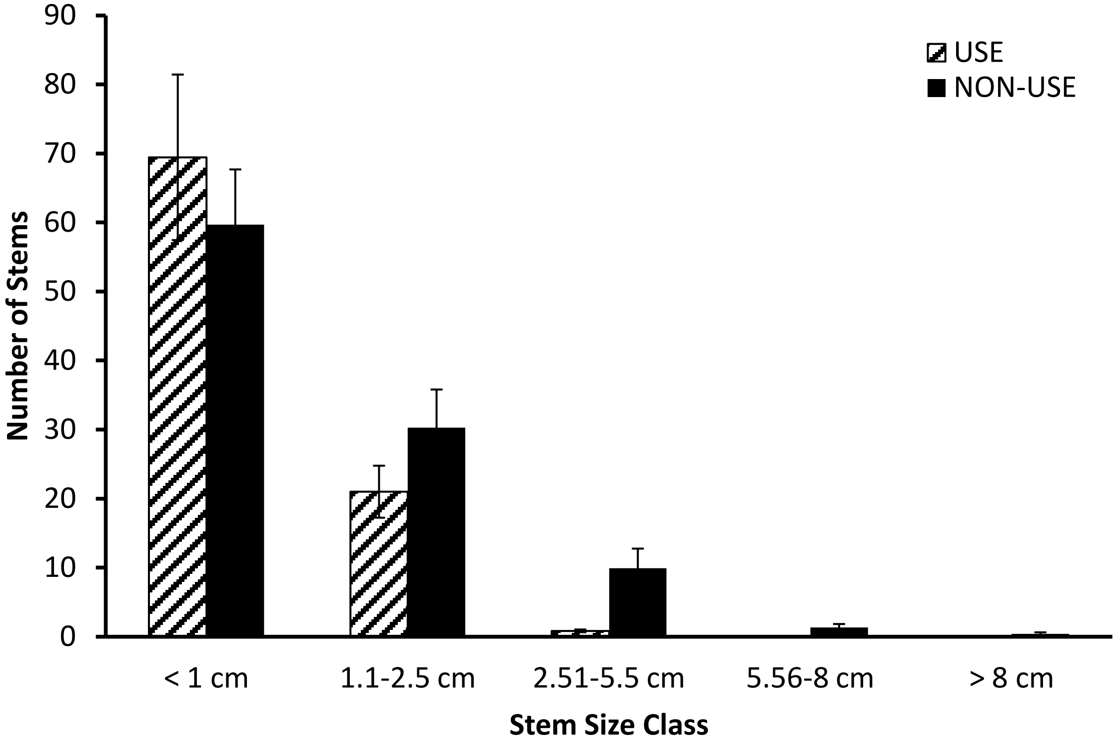

Figure 4.2. Number of snag stems distributed by size class (cm) between Southwestern Willow Flycatcher use and non-use sites.

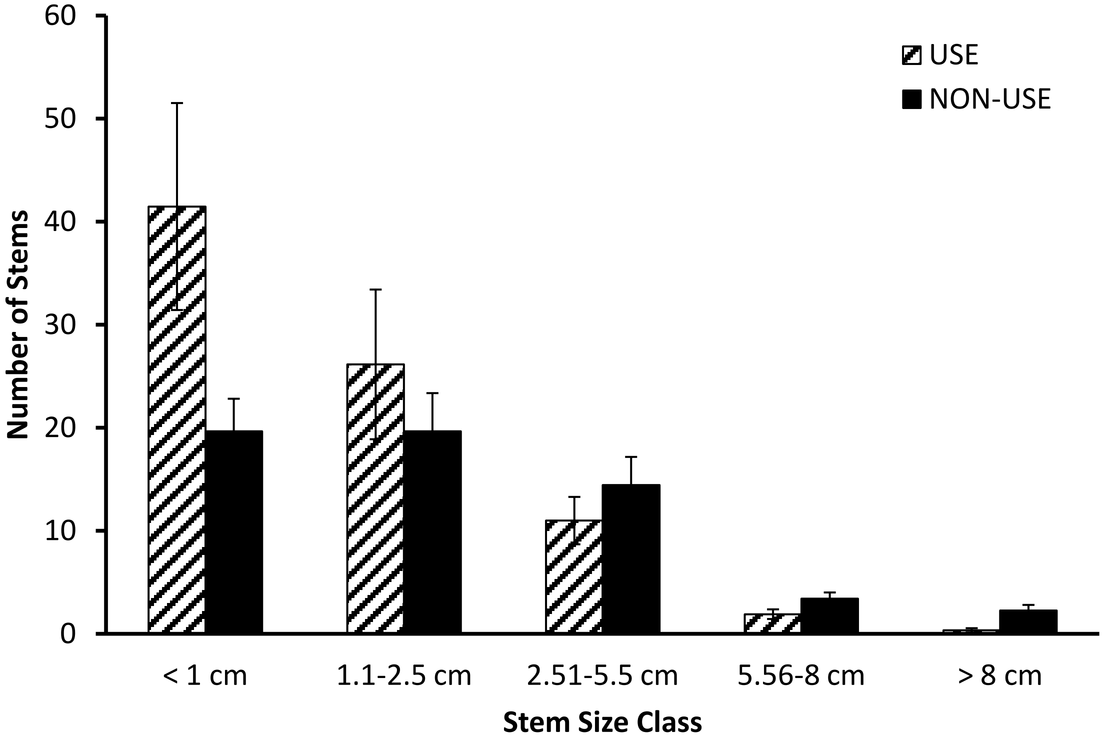

Figure 4.3. Number of tamarisk stems distributed by size class (cm) between Southwestern Willow Flycatcher use and non-use sites.

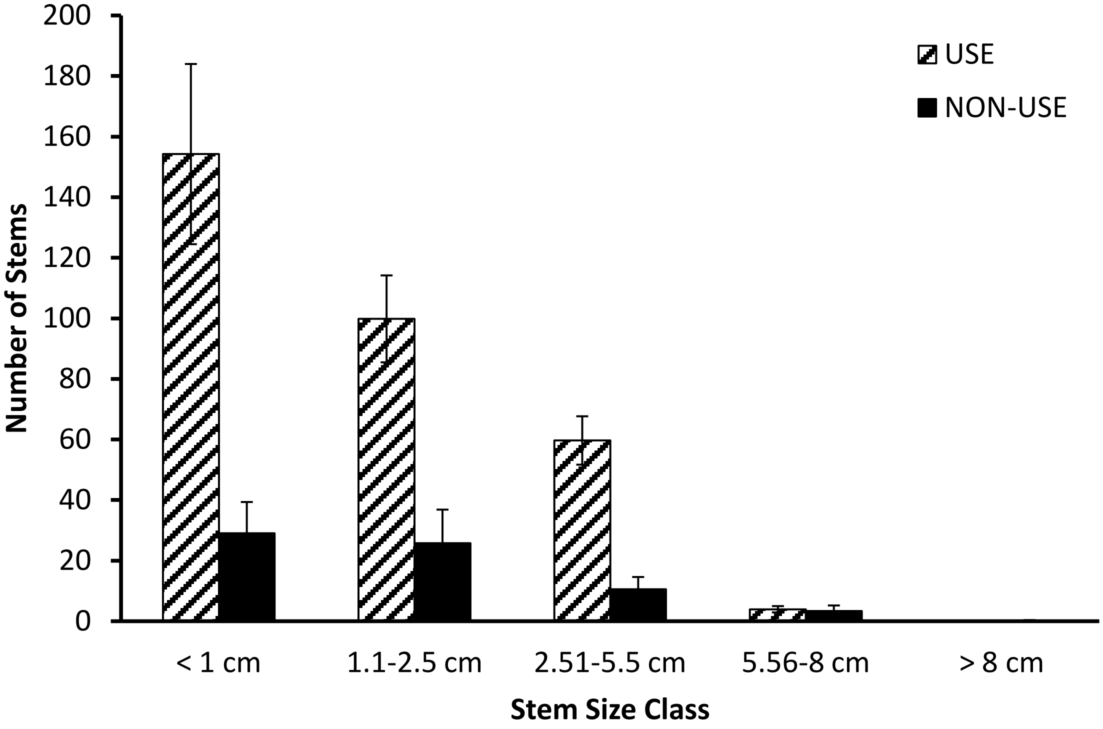

Figure 4.4. Number of willow stems distributed by size class (cm) between Southwestern Willow Flycatcher use and non-use sites.

CHAPTER 5
NEST SITE CHARACTERISTICS AND NEST SUCCESS

INTRODUCTION

Habitat characteristics of nest sites have been demonstrated to influence reproductive success in numerous bird species (Martin and Roper 1988, Holway 1991, Martin 1998). Often, attributes of the nest and surrounding habitat can impact resource acquisition (Holway 1991, Sedgwick and Knopf 1992, Burke and Nol 1998), microclimate suitability (Walsberg 1981, Wiebe 2001), vulnerability to predators (Martin and Roper 1988, Martin 1993, Forstmeier and Weiss 2004) and rates of brood parasitism (Burhans 1997, Burhans and Thompson 1999, Sharp and Kus 2006). As such, individuals should select nest sites based on habitat characteristics at and immediately surrounding the nest that increase the probability of nesting success. Indeed, several studies using multiple bird species have shown greater nesting success is associated with specific habitat preferences (Martin and Roper 1988, Burhans and Thompson 1999, Misenhelter and Rotenberry 2000). However, other researchers have found no such relationship (Holway 1991, Kilgo et al. 1996, Howlett and Stutchbury 1996, Hoover and Brittingham 1998, Wilson and Cooper 1998, Braden 1999, Siepielski et al. 2001).

The availability of suitable nest sites has been suggested to be one of the most important determinants in habitat selection (Steele 1993, Matsouka et al. 1997). For endangered species, individuals are often limited by the quantity of available habitat, and locating suitable nest sites within this habitat can be problematic. Furthermore, spatial variation in rates of nest predation and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) suggest nest microhabitat features contribute to nest success (Martin 1992, Burhans and Thompson 2001, Brodhead et al. 2007, Stumpf et al. 2011). Therefore understanding what constitutes a suitable nest site and how nest microhabitat affects reproductive success remains important. This knowledge of local breeding populations is particularly informative for managers who must balance protection, enhancement and restoration of habitat for endangered species with feasibility and cost effectiveness of such projects.

Here we evaluate nest site characteristics of Southwestern Willow Flycatchers (*Empidonax traillii extimus*) found along the upper Virgin River in southwestern Utah. The Southwestern Willow Flycatcher (hereafter flycatcher) is a riparian obligate that prefers dense, wooded areas near wetlands or standing water (Sogge and Marshall 2000). The St George study area supports a small breeding population of flycatchers and is located near the northern edge of the subspecies' range (Paxton et al. 2008). Specifically, our goals were to measure nest attributes at the microhabitat level, and to identify differences among these attributes based on nest success, predation and brood parasitism by Brown-headed Cowbirds (hereafter cowbirds). We compared nest microhabitat variables between: (i) nest tree species, (ii) successful and failed nests, (iii) successful and depredated nests, and (iv) parasitized and nonparasitized nests.

METHODS

STUDY AREA

This study was conducted in the riparian habitats along an approximately 11 km reach of the lower Virgin River in the cities of St. George and Washington, Utah (hereafter St George study area). Similar to other streams of the desert southwest, the Virgin River is characterized by relatively low flows punctuated by large spring runoff peaks and late summer/early autumn storm driven flow spikes. Large fluctuations in discharge are also accompanied by considerable variation in sediment load and lead to unstable channel substrates. As a result, large marsh complexes have been created in detached oxbows and depressions. Most marsh areas support a mixture of native and exotic plant species; however, in a few locations native woody species continue to dominant the plant community. Dominant native woody species include Fremont Cottonwood (*Populus fremontii*), Coyote Willow (*Salix exigua*), and Mule's Fat (*Baccharis salicifolia*), with Velvet Ash (*Fraxinus velutina*) important at some sites. The two most prolific woody exotic species are tamarisk (*Tamarix* spp.) and Russian Olive (*Elaeagnus angustifolia*). Vegetative structure within the study area varies depending upon substrate and surface water conditions. Sandy areas susceptible to scouring tend to have little to no woody cover, with available cover being short and sparse, while higher elevation sites (e.g., berms, banks) have more fully developed, stable soils that support denser, taller plants. Saturated soils, inundated areas and some bankside locations also support dense stands of cattail (*Typha* spp.) and Common Reed (*Phragmites australis*). Most habitat patches are less than 10 ha in area (Chapter 2).

FIELD METHODS

We monitored Southwestern Willow Flycatcher nests from May to August 2008-2011. We generally checked nests every 2-4 days and assigned nest fates following Martin et al. (1997; see Chapter 3). In this study we defined a successful nest as one that fledged at least one flycatcher, while an unsuccessful or failed nest was one that fledged zero flycatchers. Depredated nests were confirmed to be lost to predators based on observational evidence and nesting phenology (i.e. nest intact but missing eggs or nestlings; Chapter 3). In order for a nest to be classified as parasitized, it contained one or more cowbird eggs or nestlings.

We measured microhabitat characteristics and vegetation data at flycatcher nests (2008-2011) using modified BBIRD methods (Martin et al. 1997; see Chapter 4). We collected nest site data late in the season after flycatcher breeding activity at the nest, territory and adjacent territories had ceased (August-September). 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. We also recorded the species, number and size class (dbh) of all stems contained within a circular plot with a 5-meter radius that was centered on the nest tree (see Chapter 4).

STATISTICAL ANALYSES

Prior to analysis we opted to split the data file into two sections based on year, 2008-2009 and 2010-2011. Previous separate analyses indicated a significant year effect that was associated with two important biological events: release of Tamarisk Leaf Beetles (*Diorhabda carinulata*) and a shift in habitat use by flycatchers (Chapter 4). 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.

For each dataset, all data were tested for violations of normality, and when data did not meet normality assumptions after transformation, we used non-parametric analyses. 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, using a series of three chi-square analyses 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 (Chapter 3). 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. In 2008-2009 the one nest placed in Russian Olive was an outlier, and therefore was excluded from subsequent analyses. We tested for differences in microhabitat variables using either independent sample *t*-tests or Mann-Whitney *U*-tests.

Last, we conducted a series of tests to measure 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. We used independent sample *t*-tests or Mann-Whitney *U*-tests when data were not normally distributed. All data analyses were conducted using program R (R Development Core Team 2010) and reported values are given as mean ± SE.

RESULTS

NEST TREES

We found a total of 62 Southwestern Willow Flycatcher nests that were distributed among three nest tree species. The majority of nests were located in tamarisk trees, followed by Coyote Willow; one nest was built in Russian Olive (Table 5.1). During 2008-2009, flycatchers nested in areas where tamarisk was the dominant live plant species, and utilized nest tree substrates proportionally ($\chi^2_2 = 4.5$, $P = 0.11$). However, after 2009, nest trees were not selected in proportion to availability ($\chi^2_1 = 37.9$, $P < 0.0001$; Table 5.1). Beginning in 2010, 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 5.1). Nests built in tamarisk were depredated less often than those placed in Coyote Willow. Regardless of these differences, there was no relationship between nest tree species and nests parasitized by Brown-headed Cowbirds in either dataset (2008-2009: $\chi^2_2 = 4.43$, $P = 0.11$; 2010-2011: $\chi^2_1 = 0.08$, $P = 0.77$; Figure 5.2).

The mean height of all nests in 2008-2009 was 2.9 ± 1.2 m, and 2.6 ± 0.1 m in 2010-2011 (Table 5.1), and average relative height of flycatcher nests within nest trees was 0.60 ± 0.03 in 2008-2009 and 0.62 ± 0.03 in 2010-2011. Nest height was variable among the nest tree species (Table 5.1), and was significantly different in 2008-2009 ($t_{3.41} = -3.22$, $P = 0.04$), although not in 2010-2011 ($t_{28.9} = -1.13$, $P = 0.27$). Of the remaining variables, only nest substrate diameter in 2008-2009 differed between the nest tree species (Tables 5.2 and 5.3). In this case, nests located in tamarisk had a larger diameter compared with nests located in Coyote Willow. Despite these among nest substrate differences the remaining variables, were similar among all nest tree species.

NEST SITE CHARACTERISTICS

We found that the majority of nest site characteristics did not differ with nest outcome (Table 5.4). 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 one exception was relative nest height during 2008-2009. Nests that failed were located significantly higher than successful nests (Table 5.4). In spite of this difference, nests that failed as a direct result of predation had similar microhabitat characteristics as those that were successful (Table 5.5).

Nests parasitized by Brown-headed Cowbirds differed from nonparasitized nests in only a few nest attributes (Table 5.6). These results were year dependent such that in 2008-2009 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 5.6). However, in 2010-2011 these differences were absent, although canopy cover surrounding the nest was significantly higher in parasitized nests (Table 5.6).

DISCUSSION

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 exotic tamarisk trees as preferred nest substrates. This is compelling because initially flycatchers' occupied tamarisk-dominated habitat patches, and relocated to willow-dominated habitat patches after 2009 (Chapter 2). During 2010-2011, 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.

In our study area, Southwestern Willow Flycatchers utilized exotic tamarisk as the primary nest substrate plant species, in spite of the extensive 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 exotic vegetation (Sogge and Marshall 2000, Owen and Sogge 2002, Allison et al. 2003, Paradzick 2005, Sogge et al. 2008). However, 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 can be categorized into one of three types: exotic tamarisk dominated, mixed native-exotic, and native dominated areas (Chapter 2). 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 exotic 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).

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 (Chapter 3). 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, Chapter 4). Our study measured a number of nest scale microhabitat characteristics and found none of the variables differed between successful and depredated nests; however, 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, Chapter 3). 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 in New Mexico most flycatchers nest in Boxelder (*Acer negundo*), a tree with a substantially higher canopy, (e.g. parasitized and nonparasitized 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 (Chapter 4). Moreover, among nest sites, understory vegetation at native dominated sites is more open and the branching structural complexity is lower relative to mixed and exotic 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. 2001, Durst 2004, Durst et al. 2008). Studies indicate that insect abundance and flycatcher diet vary among habitat patch type (DeLoach et al. 2000, Drost et al. 2001, but see Durst 2004, Durst et al. 2008), although this variation does not lead to differences in the 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 Northern Tamarisk Leaf Beetles (*Diorhabda carinulata*). 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 collection of additional data related to microhabitat characteristics, including nest concealment and identification of the major nest predators.

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Table 5.1. Southwestern Willow Flycatcher nests, total number of available stems and percent occurrence of each species within nest sites and nest height shown for each plant species.

	2008-2009				2010-2011			
			Nest Height				Nest Height	
Plant Species	Number (%) nests	Number (%) stems use sites	Mean ± SE (m)	Range	Number (%) nests	Number (%) stems use sites	Mean ± SE (m)	Range
Tamarisk	21 (84%)	1556 (23%)	3.0 ± 0.2	2.1 - 4.8	22 (59%)	2068 (15%)	2.7 ± 0.2	1.7 - 4.2
Coyote willow	3 (12%)	1238 (18%)	2.0 ± 0.3	1.5 - 2.5	15 (41%)	8765 (64%)	2.4 ± 0.1	1.7 - 3.1
Russian Olive	1 (4%)	65 (< 1%)	2.9	---	---	28 (< 1%)	---	---
Mule’s Fat	---	86 (1%)	---	---	---	272 (2%)	---	---
Velvet Ash	---	112 (1%)	---	---	---	28 (< 1%)	---	---
Snag	---	3825 (55%)	---	---	---	2531 (18%)	---	---
Sweetscent (*Pluchea odorata*)	---	12 (< 1%)	---	---	---	---	---	---
Ash (*Fraxinus spp.*)	---	---	---	---	---	22 (< 1%)	---	---
Total	25 (100%)	6894 (100%)	2.9 ± 1.2	1.5 - 4.8	37 (100%)	13688 (100%)	2.6 ± 0.1	1.7 - 4.2

Table 5.2. Southwestern Willow Flycatcher nest site microhabitat characteristics listed by nest substrate species for 2008-2009. Bold values indicate significant differences among groups.

2008-2009	Tamarisk (*n* =21)		Coyote Willow (*n* =3)		Russian Olive (*n* = 1)	All Species		
Variable	Mean ± SE	Range	Mean ± SE	Range	Mean	Mean ± SE		*P*-value
Nest substrate height (m)	5.5 ± 0.4	3.0 - 8.5	3.5 ± 1.0	2.1 - 5.5	8.5	5.4 ± 0.4	$t_{2.53} = -1.85$	0.18
Nest substrate dbh (cm)	6.8 ± 0.9[b]	2.5 - 14.5	2.2 ± 0.9	1 - 4	25	7.0 ± 1.2	$t_{7.37} = -3.53$	**0.009**
Nest canopy height (m)	6.1 ± 0.2	3.8 - 7.5	5.8 ± 0.3	5.5 - 6.5	8.5	6.2 ± 0.2	$U = 20.5$	0.35
Relative nest height (m)	0.50 ± 0.03	0.32 - 0.66	0.34 ± 0.06	0.27 - 0.45	0.34	0.48 ± 0.02	$t_{2.87} = -2.69$	0.08
Nest canopy cover (%)	96.4 ± 1.1[c]	78.5 - 100	99.2 ± 0.3	98.5 - 99.5	99	96.8 ± 0.9	$U = 46$	0.16

[a] Test statistics exclude Russian Olive

[b] Sample size for this group differs; Tamarisk *n* = 18

[c] Sample size for this group differs; Tamarisk *n* = 20

Table 5.3. Southwestern Willow Flycatcher nest site microhabitat characteristics listed by nest substrate species for 2010-2011.

2010-2011	Tamarisk (*n* =19)		Coyote Willow (*n* =12)		All Species		
Variable	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Test Statistic	*P*-value
Nest substrate height (m)	4.2 ± 0.3	2.7 - 6.8	4.6 ± 0.4	2.6 - 6.2	4.3 ± 0.2	$t_{22.3} = 0.82$	0.42
Nest substrate dbh (cm)	3.7 ± 0.8	1.1 - 12.8	2.5 ± 0.3	1.1 - 3.7	3.2 ± 0.5	$U = 107$	0.79
Nest canopy height (m)	6.1 ± 0.2	4.6 - 7.8	5.7 ± 0.4	3.1 - 7.2	5.9 ± 0.2	$t_{17.8} = -1.13$	0.27
Relative nest height (m)	0.44 ± 0.03	0.26 - 0.77	0.44 ± 0.03	0.29 - 0.66	0.44 ± 0.02	$U = 123$	0.73
Nest canopy cover (%)	94.7 ± 0.6	87 - 96	95.4 ± 0.3	93.3 - 96	94.9 ± 0.4	$U = 106.5$	0.28

Table 5.4. Southwestern Willow Flycatcher nest site microhabitat characteristics for successful and unsuccessful nests. Values are given as mean ± SE.

	2008-2009				2010-2011			
Variable	Successful ($n = 9$)	Unsuccessful[a] ($n = 16$)	Test Statistic	P-value	Successful ($n = 12$)	Unsuccessful[a] ($n = 19$)	Test Statistic	P-value
Nest height (m)	2.8 ± 0.2	2.9 ± 0.2	$t_{21.9} = 0.74$	0.47	2.7 ± 0.2	2.5 ± 0.1	$t_{21.9} =-0.74$	0.46
Nest substrate height (m)	5.8 ± 0.6	5.2 ± 0.5	$t_{16.9} = -1.2$	0.25	4.1 ± 0.4	4.4 ± 0.3	$t_{22.5} = 0.71$	0.49
Nest substrate dbh (cm)	5.0 ± 1.1[b]	8.2 ± 1.7[b]	$t_{18.6} = 1.11$	0.28	3.6 ± 1.0	3.0 ± 0.5	$U = 124$	0.69
Nest canopy height (m)	6.6 ± 0.2	5.9 ± 0.3	$U = 38.5$	0.08	5.9 ± 0.2	5.9 ± 0.3	$t_{28.5} = 0.32$	0.75
Relative nest height (m)	0.42 ± 0.03	0.51 ± 0.03	$t_{21.8} = 2.08$	**0.05**	0.46 ± 0.04	0.43 ± 0.03	$U = 98$	0.53
Nest canopy cover (%)	97.0 ± 0.8	96.8 ± 1.4[c]	$U = 75$	0.47	94.5 ± 0.7	95.2 ± 0.3	$U = 103.5$	0.51

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

[b] Sample sizes for these groups differ; Successful $n = 8$, Unsuccessful $n = 14$

[c] Sample size for this group differs; Unsuccessful $n = 15$

Table 5.5. Southwestern Willow Flycatcher nest site microhabitat characteristics for successful and depredated nests. Values are given as mean ± SE and bold values indicate significant differences between groups.

	2008-2009				2010-2011			
Variable	Successful ($n = 9$)	Depredated ($n = 9$)	Test Statistic	P-value	Successful ($n = 12$)	Depredated ($n = 16$)	Test Statistic	P-value
Nest height (m)	2.8 ± 0.2	2.8 ± 0.3	$t_{12.7} = 0.22$	0.83	2.7 ± 0.2	2.5 ± 0.2	$t_{23.8} = -0.69$	0.49
Nest substrate height (m)	5.8 ± 0.6	5.5 ± 0.7	$t_{15.1} = -0.35$	0.73	4.1 ± 0.4	4.5 ± 0.3	$t_{23.4} = 0.72$	0.48
Nest substrate dbh (cm)	5.0 ± 1.1[a]	9.5 ± 2.8[a]	$U = 43$	0.27	3.6 ± 1.0	3.0 ± 0.6	$U = 103$	0.76
Nest canopy height (m)	6.6 ± 0.2	6.2 ± 0.4	$t_{10.9} = -0.81$	0.44	5.9 ± 0.2	5.8 ± 0.3	$t_{25.9} = -0.14$	0.89
Relative nest height (m)	0.42 ± 0.03	0.47 ± 0.05	$t_{13.1} = 0.79$	0.44	0.46 ± 0.04	0.44 ± 0.03	$t_{25} = -0.33$	0.74
Nest canopy cover (%)	97.0 ± 0.8	98.0 ± 1.0[b]	$U = 46.5$	0.33	94.5 ± 0.7	95.1 ± 0.4[d]	$U = 76.5$	0.81

[a] Sample sizes for these groups differ; Successful $n = 8$, Depredated $n = 8$

[b] Sample sizes for this group differs; Depredated $n = 9$

[c] Sample sizes for these groups differ; Depredated $n = 12$

Table 5.6. Southwestern Willow Flycatcher nest site microhabitat characteristics for parasitized and nonparasitized nests. Values are given as mean ± SE and bold values indicate significant differences between groups.

	2008-2009				2010-2011			
Variable	Parasitized (n = 8)	Nonparasitized (n = 17)	Test Statistic	P-value	Parasitized (n = 12)	Nonparasitized (n = 19)	Test Statistic	P-value
Nest height (m)	2.5 ± 0.1	3.1 ± 0.2	$t_{11.5} = 1.81$	0.10	2.6 ± 0.2	2.6 ± 0.2	$t_{24.4} = -0.07$	0.95
Nest substrate height (m)	4.3 ± 0.7	5.9 ± 0.4	$t_{19.6} = 4.23$	**<0.001**	4.6 ± 0.3	4.2 ± 0.3	$t_{26.2} = -0.93$	0.36
Nest substrate dbh (cm)	6.5 ± 2.9	7.3 ± 1.1[a]	$t_{14.3} = 2.04$	0.06	3.5 ± 0.8	3.0 ± 0.7	$U = 80$	0.17
Nest canopy height (m)	6.6 ± 0.3	6.0 ± 0.3	$U = 55$	0.79	6.0 ± 0.2	5.9 ± 0.3	$t_{27.5} = -0.46$	0.65
Relative nest height (m)	0.39 ± 0.04	0.52 ± 0.03	$t_{9.4} = 2.19$	**0.05**	0.43 ± 0.04	0.45 ± 0.03	$U = 125$	0.67
Nest canopy cover (%)	98.3 ± 0.8	96.2 ± 1.3[b]	$U = 35.5$	0.18	95.8 ± 0.1[c]	94.4 ± 0.6[c]	$U = 41.5$	**0.03**

[a] Sample sizes for this group differs; Nonparasitized n = 14

[b] Sample sizes for this group differs; Nonparasitized n = 16

[c] Sample sizes for these groups differ; Parasitized n = 10, Unsuccessful n = 17

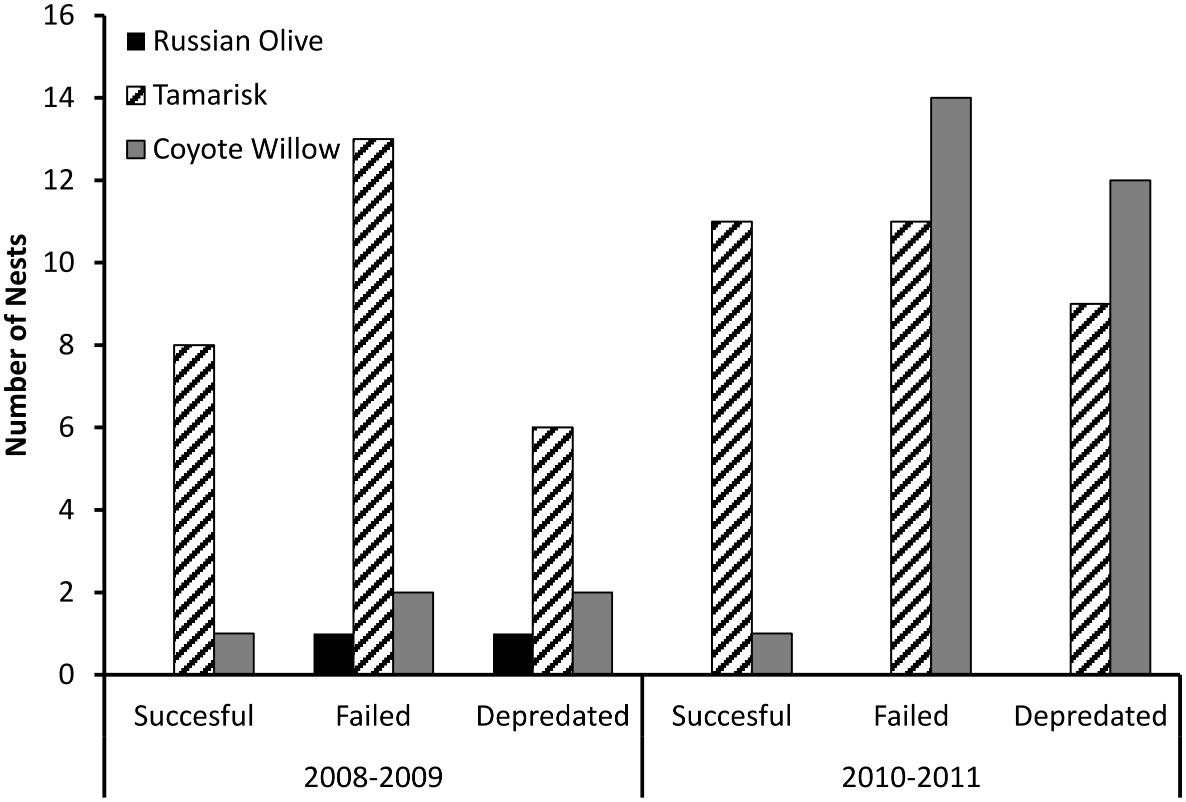

Figure 5.1. Fate of Southwestern Willow Flycatcher nests by substrate tree. Failed nests in this case include multiple causes of nest failure, including: depredation, parasitism, failure to hatch and abandonment. Depredation was the leading cause of failed nests.

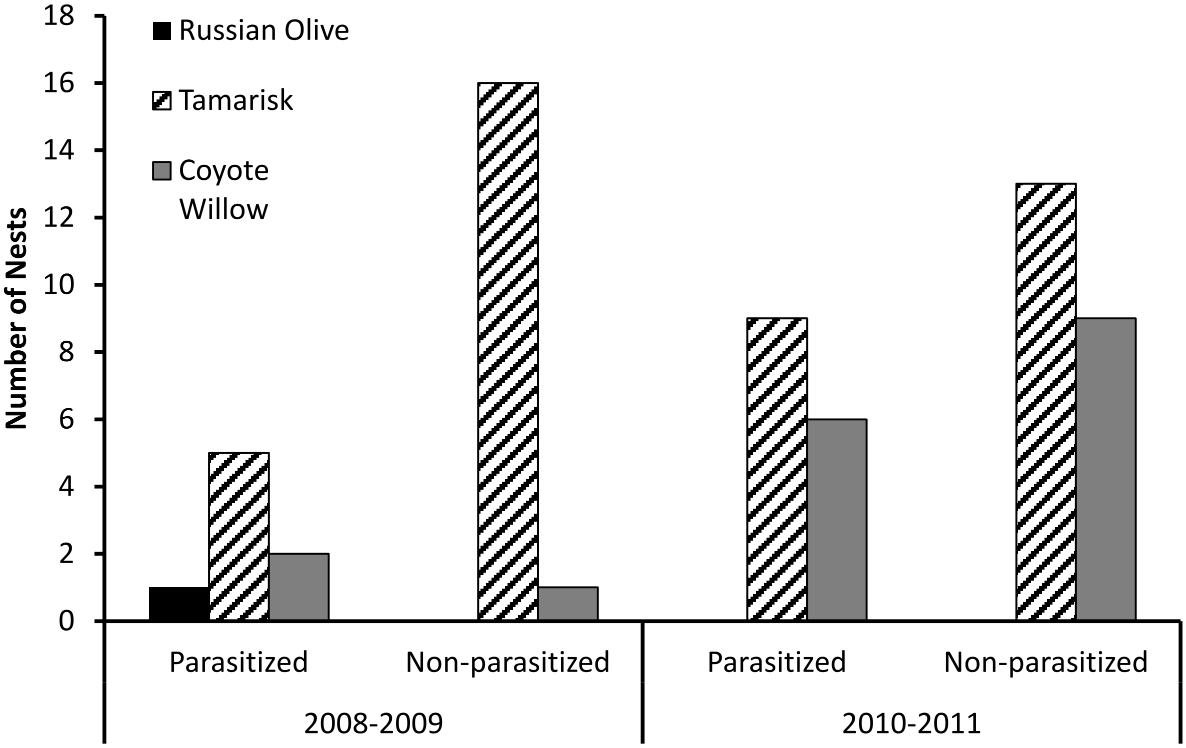

Figure 5.2. Number of Southwestern Willow Flycatcher nests parasitized by Brown-headed Cowbirds by substrate tree.

CHAPTER 6
MANAGEMENT RECOMMENDATIONS

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

   Results of flycatcher nest monitoring during the 2008-2011 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. Beetles have presumably decreased the suitability of tamarisk-dominated habitat indefinitely, and we expect the trend of flycatchers nesting in more native-dominated habitat, where they appear to be more prone to nest predation and brood parasitism, to continue. Additional flycatcher nest monitoring is necessary to identify conservation actions that may minimize or mitigate factors limiting flycatcher productivity under these new 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 2008-2011 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. *Implement efforts to addle Brown-headed Cowbird eggs in parasitized Southwestern Willow Flycatcher nests in the St George study area*.

   Addling or removing cowbird eggs, or removing cowbird nestlings, in/from parasitized nests may minimize effects of brood parasitism on host nest success (Kus 1999, Winter and McKelvey 1999, Siegle and Ahlers 2004). Note, however, that because cowbirds often remove eggs from host nests, addling or removing cowbird eggs and/or nestlings does not eliminate effects of brood parasitism. In addition to, or in the absence of, a cowbird control program, however, addling or removing cowbird eggs may increase the productivity of individual flycatcher nests.

   We recommend addling cowbird eggs and then replacing them back in flycatcher nests, as opposed to removing cowbird eggs permanently from flycatcher nests.

Removing cowbird eggs from host nests permanently may increase host nest abandonment (Siegle and Ahlers 2004). Further, recent research suggests that cowbirds may be more likely to depredate nests in which hosts eject (or, potentially, humans remove) cowbird eggs (Hoover and Robinson 2007).

4. *Implement 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 merit the implementation of cowbird control 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 establishing a cowbird control program involving cowbird traps located at multiple (e.g., 4-5) flycatcher breeding sites in the St George study area. We recommend using a cowbird trap design and following trapping protocols outlined by Siegle and Ahlers (2004). 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 2008-2011 (this report) represent a pre-cowbird control baseline, with which effects of cowbird control efforts may be compared. Pre-cowbird control data on cowbird abundance data will be collected in 2012, during general avian population monitoring in the St George study area (M. Johnson, Colorado Plateau Research Station).

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

   Identification of 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. High rates of nest predation by Brown-headed Cowbirds, for example, may merit the implementation of a cowbird control program. 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 video photography of flycatcher nests during incubation and nestling periods to document nest predators. We recommend employing a video photography setup consisting of a video camera that records continuous footage to an internal hard drive, mounted on a tripod and powered by a rechargeable car battery. Cameras, tripods, and batteries should be covered and/or wrapped in camouflage fabric, and placed as far from nests as possible while achieving high-quality imagery.

6. *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.

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

   All 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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