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Demographic Analysis for Willow Flycatcher Monitoring in the Central Sierra Nevada, 1997–2010: Final Report

In partial fulfillment of Cost Share Agreement

06-CR-11052007-160

Between

Texas A&M University

And

U.S.D.A. Forest Service, Region 5

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15 May 2011

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Executive Summary

Once common through out the western United States, the Willow Flycatcher (*Empidonax traillii*) has been extirpated from much of its range. In central California, this Neotropical migrant is limited to breeding in montane meadows. Surveys indicating a declining population trend led to the listing of the Willow Flycatcher as a California state endangered species, which prompted the initiation of a distribution and demographic study in 1997. Our research program includes over 30 study sites (meadows) grouped into 3 regions: South Lake Tahoe (south of Lake Tahoe), Truckee (north Lake Tahoe, Truckee meadows and vicinity), and Warner Valley (south of Lassen Volcanic National Park). Our primary objectives are to (1) determine the distribution of breeding Willow Flycatchers; (2) quantify reproductive success, recruitment, dispersal and survival of Willow Flycatchers in selected meadows; (3) examine factors influencing demographic patterns through associated graduate research projects; and (4) use the results to make management and restoration recommendations.

In 2010, we completed our 14th year of research. Long-term monitoring began in the south and central regions with 4 sites in 1997 and increased to 15 sites in 1998. In 2003, we added 10 more sites, including 4 sites in the north, and 2005, we added 2 more sites in the central region. Each year thereafter varied in regards to which sites were monitored due to available funding. All territories and nesting activity were monitored every 5-7 days. We banded all nestlings using the cohort method (i.e., bands designate year and natal site of hatching) until 2007 when we begun banding nestlings with unique combinations. In 2005, we began target-netting adults and banding them with unique combinations. We conducted presence/absence surveys in additional meadows throughout the central Sierra Nevada and obtained color band resights when birds were detected. Resighting of color-banded birds occurred in all monitoring sites and at neighboring meadows.

The Willow Flycatcher population in the central Sierra Nevada declined during the course of our 14-year monitoring study. We observed an apparent contraction of their range from south to north, in that populations in the South Lake Tahoe region all but disappeared during the course of our 14-year study, likely resulting from initial small population size, stochastic weather events, and low reproduction that influenced dispersal dynamics. The population of flycatchers in the Truckee regions exhibited annual fluctuations around stability but with an overall declining trend. The persistence of flycatchers in the Truckee region likely was facilitated by the proximity of large (>100 ha) meadows with suitable breeding habitat interspersed with smaller meadows.

The flycatcher population in Warner Valley was stable during our monitoring period from 2005 to 2008. Using population growth models and comparative analysis with a reference site, we determined that fecundity was limiting flycatcher populations and that reproductive success has cascading effects on local dispersal patterns.

Our population growth models suggested that populations in the South Lake Tahoe and Truckee region would approach stable ($\lambda = 1$) with increased reproductive success (i.e., fecundity). Nest predation was the primary cause of nest failure at our study sites. Nest success rates at our south and central region were lower than for Willow Flycatchers breeding in other states. Parasitism during our study was limited to a few sites in our study regions; however, these sites supported some of the highest abundance of flycatcher territories in the region (i.e., Perazzo meadows, Little Truckee sites).

During the course of this study, several graduate students researched various factors that limited flycatcher occupancy, survival, and reproductive success. We provide a synthesis of results from these projects and elaborate on the conclusions for management and future research. First, relative to populations of Willow Flycatchers in lower elevation and nonmoutainous regions, flycatchers in the South Lake Tahoe and Truckee regions are constrained by the amount of time available to nest within a season. The nestling period and early fledgling period, and thus the month of July and early August, is a critical period determining reproductive success for an individual flycatcher. Riparian shrub density at the territory scale and extent of meadow inundation by water are the most influential habitat components.

We recommend a meadow restoration initiative throughout several meadows of the Sierra Nevada within the current range of the flycatcher and at adjacent sites that supported flycatchers in the recent past. Habitat restoration would likely enhance nest success and it is one action that we can take on the nesting grounds that has some potential to increase juvenile recruitment and adult survival. Second, Willow Flycatchers are still actively breeding through the end of August, thus we recommend moving grazing out of meadows with breeding flycatchers until the end of August. Current management practices allow for grazing starting in mid-July but this is a sensitive period for flycatchers in determining nesting survival, renesting possibilities, and post-fledgling survival. Brown-headed cowbird control would be beneficial in the short-term at some of the meadows that support currently breeding flycatchers but that for long-term sustainability meadow restoration will buffer the negative effects of parasitism. Last, these populations required continued monitoring to determine the effectiveness of meadow restoration practices and other management protections.

INTRODUCTION

The Willow Flycatcher (*Empidonax traillii*) is a Neotropical migrant that breeds across the northern and southwestern United States and into Canada. Whereas populations in the east and northwest appear to be increasing, populations in the southwest and California have declined in the past three decades. Variations in the ecology and life-history strategies of subspecies and differences in land-use practices likely accounts for different population trajectories of the species (Whitfield et al. 2003). Across the range, flycatchers rely on riparian or early-successional shrub vegetation for breeding, often associated with regenerating clearcuts in the east and northwest (Altman et al. 2003). In the southwest and California, flycatchers are dependent upon dense riparian vegetation for breeding.

The three subspecies of the Willow Flycatcher that occur in California (Aldrich 1951, Unitt 1987) are listed as state endangered because of considerable population declines detected in the late 1980s (Serena 1982, Harris et al. 1987). The southwestern subspecies, *E. t. extimus*, has received considerable attention in response to its federal status as an endangered species and concern over habitat loss and destruction. However, information is lacking on the population status and breeding ecology of the two subspecies, *E. t. brewsteri* and *E. t. adastus*, that occur north of *E. t. extimus* (Green et al. 2003). These subspecies are divided along the Sierra Nevada and Cascades mountain ranges but there is likely intergradation between the subspecies (Paxton 2008).

Historically, flycatchers were common across California wherever dense riparian vegetation, primarily willow (Salix spp.), occurred (Grinnell and Miller 1944). In the past three decades, flycatchers have undergone substantial population declines in California; for example, E. t. brewsteri no longer occurs in the Central Valley (Green et al. 2003) where more than 90% of native riparian vegetation is converted or degraded (Katibah et al. 1984). As recently as the 1940s, Willow Flycatchers were locally common in the patchily distributed montane meadows in the Sierra Nevada; however, surveys conducted in the 1980s and 1990s documented a dramatic population decline, with population estimates of only 300 to 400 individuals (Serena 1982, Harris et al. 1987, Bombay 1999). These surveys documented that the majority of flycatchers detected were located in only a few large meadow systems with several smaller sites supporting only a few (i.e., 1-3) flycatchers. A 2007 study in Yosemite National Park in the central Sierra Nevada concluded that the park no longer supports Willow Flycatchers (Siegel et al. 2008). With the exception of a small population of *E. t. extimus* in Inyo National Forest, California (McCreedy and Heath 2004), there exists a large gap in flycatcher sightings since the 1980s between the extimus subspecies and current known populations of brewsteri and adastus (Harris et al. 1987, Bombay 1999).

Riparian ecosystems in the Sierra Nevada have had a long history of human-induced disturbances to natural ecological processes as a result of urbanization, grazing, water diversion, timber harvesting, mining, and recreational use (Schlesinger et al. 2008, Raumann and Cablk 2008). Timber harvesting in the late 1850s to early 1920s, and grazing practices in the early 1900s considerably degraded conditions in riparian systems throughout the Sierra Nevada, especially in the Lake Tahoe Basin. Lower elevation meadows served as transportation corridors to support the logging industry and higher elevation meadows provided grounds for heavy grazing by sheep. These practices initiated a cascading effect of erosion and gullying with subsequent sedimentation down stream (McKelvey and Johnston 1992). North of Lake Tahoe, water control structures constructed in the early 1900s at the outlet of the lake resulted in water availability problems in the Truckee River valley. In the South Lake Tahoe

region, wetland systems experienced the largest loss of area during peak urbanization after the 1940s. Although livestock grazing in the Sierra Nevada has decreased considerably in the later half of the 1900s, lasting effects from intense grazing pressure persist through out the region, and are compounded by other human activities. Roads that bisect meadows or that are located upslope hinder sheet flow and construction of culverts under roads create single-source, high-flows that contribute to gullying, soil erosion and sedimentation.

Possibly the primary altered process is to the hydrology of these meadows, which influences the holding capacity of the meadow flood plain, recruitment of riparian vegetation, diversity and abundance of aquatic insects, and the multitude of aquatic and terrestrial vertebrates that rely on riparian systems. Meadows in the Sierra Nevada are ground-water dependent systems that rely on winter snowpack and spring temperatures that determine the timing of snowmelt (Allen-Diaz 1991, Hagberg 1995, Loheide II et al. 2009). During the summer, these meadows shift from mesic conditions to xeric conditions, and in extremely dry years xeric conditions may experience earlier vegetation senescence. Woody upland vegetation will encroach into meadows as conditions become more favorable and competition with riparian species is relaxed (Vale 1981, Berlow et al. 2003, Bilyue et al. 2008). Loss and degradation of individual riparian patches could have profound impacts on population dynamics of riparian birds by increasing isolation of suitable patches (Villard et al. 1995) or by eliminating high-quality habitat (Pulliam 1988). Further loss and degradation of riparian habitat is expected through the synergistic effects of climate change and human-induced disturbances. Climate studies have shown that over the last several decades spring snowmelt has occurred earlier in the year (Stewart et al. 2005) thus changing vegetation and insect phenology and potentially altering availability of resources later in the summer caused by declines in groundwater level.

Project objectives

In response to increasing concerns over population declines, we studied Willow Flycatchers from 1997 to 2010 in montane meadows in the Sierra Nevada, California. This report contains the results of surveys and demographic monitoring conducted from 1997 to 2010 under U.S. Forest Service agreement 06-CR-11052007-160. We report results from site occupancy surveys, territory and nest monitoring, and band and resight efforts. We used this information to evaluate population change of the Willow Flycatcher. As the duration of this project progressed, supplemental projects were added over the years to examine the different factors influencing Willow Flycatcher and the threats to the population on the breeding grounds. In 2005 we began investigating the demographics of a subpopulation of flycatchers located to the north of our long-term monitoring sites to provide a reference location in which to compare our results.

Objectives:

- 1. Determine annual and long-term demographics (productivity, recruitment and survival) of Willow Flycatchers
- 2. Determine annual and long-term juvenile and adult dispersal patterns
- 3. Determine factors affecting demographic and land use patterns (through associated graduate research projects)

4. Given this information determine the types of sites, as well as specific locations where meadow restoration/management would contribute to result in future colonization and successful reproduction.

STUDY AREA

The study area includes sites (i.e., montane meadows) located in Lassen, Plumas, Sierra, Nevada, Placer, El Dorado, and Alpine counties in California. When we initiated the project, we conducted occupancy surveys in 1997 and 1998 in montane meadows based on three criteria: (1) current or historical records of occupancy, (2) appropriate hydrological and vegetative components, and (3) randomly selected sites adjacent to other study sites with minimum habitat requirements. We surveyed 104 sites at which we detected Willow Flycatchers at 19% (n = 104) of the survey sites. We selected 15 of these sites for a long-term demographic study (hereafter original study sites). In addition to monitoring sites, we routinely visited sites in the region to confirm occupancy or breeding status, to search for banded birds, or to conduct supplemental research projects. The number of study sites differed among years because of differences in annual funding, accessibility of properties, and reoccupation by flycatchers of meadows adjacent to our study sites (Appendix A). See Appendix B for more information on location of monitoring sites.

We grouped study sites into 2 regions (South Lake Tahoe and Truckee) based on latitude. Although meadows in the Sierra Nevada are unique because of heterogeneity in abiotic characteristics (Loheide II et al. 2009), vegetative characteristics and land-management practices, study sites in the Truckee region were similar. Study sites in this region were patchily distributed across the landscape and ranged in size from 5 to 162 ha and in elevation from 1,700 to 2,400 m. The USDA Forest Service (USFS), California Department of Fish and Game (CDFG), or private landowners managed these study sites. Study sites in the South Lake Tahoe

region ranged in size from 6 to 98 ha at elevations of 1,900 to 2,400 m. These sites were approximately 40 km south of study sites in the Truckee region. All study sites in the Truckee region ranged in size from 10 to 162 ha and in elevation from 1,730 to 2,120 m.

Study sites were montane meadows classified as shrub meadows that rely on periodic flooding to maintain their transitional state (Fites-Kaufman et al. 2007). Meadows were located along streams and rivers, adjacent to lakes, or entirely springfed. Most precipitation falls in the form of snow between November and March, and these groundwater-dependent meadows rely on snowmelt, streams, rivers, and springs to maintain a shallow water table during the dry months of the summer (Loheide, II et al. 2009). There is a north-south gradient in climate with sites farther north receiving higher precipitation (Fites-Kaufman et al. 2007). Riparian deciduous shrubs typically paralleled active and abandoned stream and river channels, and along lake edges but also were scattered in large clumps across the meadows, or were concentrated in spring-fed areas. The riparian shrub community was predominantly comprised of Geyer's willow (*Salix geyeriana*) and Lemmon's willow (*S. lemmonii*) in the South Lake Tahoe

and Truckee regions. Sedges (primarily *Carex utriculata* and *C. nebrascensis*), grasses, rushes (*Juncus* spp.), and forbs dominated the herbaceous community. Sagebrush (*Artemisia* spp.) was intermittently located in upper portions of the meadows, surrounded by a mixed coniferous forest dominated by lodgepole pine (*Pinus contorta*), with stands of quaking aspen (*populus tremuloides*)interspersed (Weixelman et al. 1999).

In 2003, we established an additional study region in Warner Valley, Lassen National Forest, located 125 m north of the Truckee region, where previous surveys had recorded dense populations of Willow Flycatchers (Green et al. 2003) to provide comparative data on the reproductive success of flycatchers breeding outside of the long-term study regions in the Truckee Sierra Nevada. Based on Green et al. (2003), Warner Valley is one of the five meadows in the northern Sierra Nevada reported to contain a high number of breeding territories. Warner Valley is an extensive meadow of 250 ha, of which we monitored 80 ha divided into four study sites based on natural vegetative and topographic divisions (e.g., where portions of the meadow narrow because of upland conifer forest). We monitored flycatchers in the Warner Valley region from 2003 to 2005 and in 2008. Study sites ranged in size from 15 to 24 ha at elevations of 1,550 to 1,590 m. These sites were all lower in elevation than any site in the South Lake Tahoe

or Truckee Regions. CDFG and private landowners managed these study sites. In Warner Valley, the vegetation community was similar but in many cases the riparian shrub community was predominately mountain alder (*Alnus tenuifolia*) with Lemmon's, and Geyer willow occurring as well. Lodgepole pine and quaking aspen were more predominant within the meadow community, than at sites further south.

We began demographic monitoring of Willow Flycatchers at 4 meadows in the central Sierra Nevada in 1997. In 1998, we added 11 more meadows for a total of 15 demographic monitoring sites. Our goal was to monitor continuously at these sites for at minimum 10 years until 2006. These sites were located south of Lake Tahoe (6 meadows) and in our central region, north of Lake Tahoe (9 meadows). Monitoring ceased after 2006 at Prosser Creek and after 2007 at Webber Lake, both because of changes in property ownership and management.

In 2003, we expanded our monitoring efforts to include more sites in the south and central Sierra Nevada. Milton Reservoir was the first site monitored that is located on the west slope of the Sierra Nevada. Also in 2003, we began monitoring in the north Sierra Nevada in Warner Valley, south of Lassen Volcanic National Park. It is 1 continuous meadow; however, for ease in monitoring we divided the meadow into 5 sites, 4 of which were monitored from 2003 to 2005, 2007, and 2008. In 2004 and 2008 we added sites located adjacent to Lake Tahoe, Blackwood Creek (central region), Tallac, and Taylor (south region).

Study sites are categorized based on the following definitions:

Surveyed To Protocol Sites: these sites were surveyed according to a standardized protocol developed for Willow Flycatchers in the Sierra Nevada (Bombay et al. 2003*a*).

Surveyed: sites were partially surveyed or were visited early or late in the season.

- **Band Resight Sites**: the objective for site visits was to obtain as many band resights as possible. Number of visits per site varies. We did not conduct surveys according to the standard protocol; however, play back was used inconsistently in order to determine territory locations. The number of territories provided should not be used for comparitive purposes.
- **Monitoring Sites**: Sites that were visited 2–7 days to acquire territory and reproductive information.
- Adaptive Cluster and Conspecific Attraction: these sites received variable levels of monitoring as part of two concurrent studies (H. A. Mathewson et al. unpubl. data).

FIELD METHODS

Surveys and Band Resighting

We surveyed sites using the standardized occupancy survey protocol for Willow Flycatchers in California (Bombay et al. 2003*a*); however, our protocol potentially required additional site visits to determine territory occupancy. According to the standardized survey protocol it is possible to complete 2 required surveys in June and territories are defined based on these detections. To ensure consistency among our study sites we define territories as those that were occupied after 30 June and at which we detected a male for ≥ 10 days. At our study sites that received more intensive monitoring we visited territories weekly through at least the beginning of August, thus formal surveys were not conducted.

Band resighting occurred at all sites during scheduled visits. For a band combination to be considered confirmed, we required ≥ 3 visits by different people confirming the same color combination unless the band colors were determined by target netting effort (see *Nestling and Adult Banding* below). We visited additional sites adjacent to the study sites to determine dispersal information. We estimate the number of territories at each site we visited for resighting purposes but not all estimates were reliable. These sites were not surveyed according to protocol (Bombay et al. 2003*a*) and we often visited these sites only once because of logistical constraints. However, occupancy estimates at band resight sites visited more than once were comparable to surveyed sites because play back was often used during these visits to elicit responses from the adults in order to locate territories and determine band status.

Territory and Reproductive Monitoring

After we determined the number and general locations of singing Willow Flycatchers during surveys, we made subsequent visits to determine reproductive status of territories and fate of nests. Male Willow Flycatchers that did not acquire females were monitored until they were no longer detected on their territory. We defined an adult male as territorial if we detected it at a location for ≥ 10 days and after 30 June to allow comparisons among survey sites and monitoring sites across the years of our study.

We mapped Willow Flycatcher territories at the monitoring sites using standard territory mapping techniques (Ralph et al. 1993). Our intention was not to provide an exact measure of territory size but rather to provide a basis for nest searching activities. Additionally, area searching helped to quickly determine whether birds were double-counted or missed during the initial survey efforts. Once approximate territory boundaries were established, we monitored the area to determine reproductive status. We observed each territory for a minimum of 30 min (if Willow Flycatchers were not located) to a maximum of 2 hours (if Willow Flycatchers were located but the nest not found) every 5 to 7 days. If a territory contained only a single male, we continued to monitor the territory through out the season until we concluded the male had left. During each territory visit we observed Willow Flycatchers to determine pairing status and to detect signs of nest building, incubation, or food delivery.

We used behavioral cues of adult female Willow Flycatchers to locate potential nest site locations and to assess the possible nest stage. If we determined the female was building, we did not approach nests to reduce the possibility of nest desertion. After the female initiated incubation we waited until the female was away from the nest before approaching. We observed birds and nests either from a distance using binoculars or by directly checking the nest contents depending on the certainty of the stage of the nest. We spaced nest check intervals to ensure a visit during or immediately after the expected time of hatching or at a minimum interval of 2 days. After we banded nestlings in a nest we observed parental activity from a distance with binoculars and did not directly check the nest until after the expected time of fledging to reduce premature fledging. We assumed a nest was successful if we saw fledglings within the territory or if adults were seen repeatedly carrying food to a location other than the nest. We visited the nest and territory at least 3 times to determine whether nests successfully fledged and to determine how long fledglings remained within the territory.

Nestling and Adult Banding

We originally used the cohort method of color banding rather than unique color combinations, to increase our ability to accurately discern color combinations in future years. To designate natal year, we banded nestlings with uniquely numbered USGS metal bands anodized a specific color (Appendix C). In 1997 and 1998 nestlings received only a single color band to indicate year. From 1999 to 2006 we used a second color band to indicate natal site (Appendix C). Beginning in 2007, we banded nestlings with a unique color band on their left leg (Koronkiewicz et al. 2005). In 2008 we relied on the cohort method for nests in the north region after we used our unique color bands. In 2010 we reduced banding efforts. We banded nestlings when they were between days 6 through 9. Only the crew leaders, with experience in banding, directly handled the nestlings and an assistant accompanied to expedite the process. In 2005, we began using standard target-netting methods (Sogge et al. 2001) to capture adult Willow Flycatchers periodically during the season and band them with unique color combinations. We attempted to resight all birds at our study sites throughout the season as well as any Willow Flycatchers detected at surrounding locations.

ANALYSIS

Number of territories and females

We defined an adult male as territorial if we detected it at a location for ≥ 10 days and after 30 June to allow comparisons among survey sites and monitoring sites across the years of our study. We assumed that we detected all territorial males in our study sites because males vocalized from exposed perches and their calls are distinctive. Detection of females varied with the stage of her nest attempt; activity is at a maximum during courtship and nest construction (Ettinger and King 1980) thus increasing the likelihood of missing females once nest incubation begins. For this reason, we assumed that the likelihood of detecting females was similar across years to allow us to compare trends in numbers and densities of females. We did not adjust the counts of males or females for detection probability because we monitored sites every 2 to 7 days throughout the season and thus, we assume detection probability was near 1. Additionally, without including a detection adjustment we know that our estimates of number of adults are biased low and conservative.

Because study sites varied across the years, we examined annual changes in the abundance of Willow Flycatcher territories and females by calculating the rate of change from year t to year t + 1. We considered all sites monitored in year t and compared this with the same sites monitored in the subsequent year thus excluding any sites not monitored in both years. We included only those territories that met our definition of harboring a territorial male (see *Territory*). We used the same calculation to estimate rate of change in the number of females detected breeding at study sites each year.

Breeding Status

We classified males as unmated if we did not detect a female within their defended territory during the course of the breeding season. We classified males that defended more than one female within their territory as polygynous. The proportion of polygynous territories within years is relative to the total number of territories that attracted a female. We provide descriptive statistics for comparing differences in male mating status because monitoring effort differed among study years; we are unable to compare directly trends in unmated or polygynous males across the years of this study (Mathewson 2010). We estimated territory success (the number of territories that produced ≥ 1 fledgling) for single and polygynous territories.

We defined active nests as those nests in which we observed eggs or nestlings in the nest. To allow for comparisons with other studies we report both the observed nest success and we used the Mayfield method of calculating nest success (Mayfield 1961, 1975). This method takes into account the reality that nests often fail prior to being found by observers, which can result in artificially inflated observed success values. We calculated nest survival estimates based on the number of days exposed to predation risk for the egg laying, incubation, and nestling stages. We estimated the length of each nest stage using data from nests that we had accurate incubation onset dates, hatching dates, or fledging dates. We defined a first nest attempt as the first active nest found for a female early in the season and renests as any subsequent nest attempts. Some nests classified as first nest attempts may actually be renests but we were unable to account for potential errors in data collection and therefore limit our interpretations for first nest attempts.

We considered our knowledge of nest contents accurate if we located the nest prior to day 4 of incubation because we cannot account for partial loss of nest contents in nests found at older ages. We defined unhatched eggs as eggs that had not hatched by the time we banded nestlings from the same nest or eggs that were incubated by females for at least 22 days (almost twice the average length of the incubation period). For our analyses on unhatched eggs we only included nests that we had accurate nest content information at the initiation of incubation and for which we could account for the fate of each egg. In other words, we did not include nests if any of the nest contents disappeared before we could determine if the entire clutch hatched or not.

We considered 2 estimates of brown-headed cowbird parasitism rates that account for biases resulting from finding older nests. We considered all observations of cowbird eggs or nestlings in a nest as positive events regardless of when we found the nest because removal of any events would bias results due to small sample sizes. We calculated maximum parasitism rates by eliminating non-parasitized nests found after day 4 of incubation to reduce falsely counting nests as non-parasitized when in fact the cowbird egg or nestling was no longer present when we located the nest. Maximum parasitism estimates minimized errors associated with misclassification (i.e., false negatives) but estimates were biased high because the definition allowed for removal of non-parasitized nests while retaining parasitized nests. To compare our maximum estimate rate with an estimate that reduced the bias towards high parasitism rates we assumed false negatives in our population were minimal and we calculated a minimum parasitism rate by including all active nests regardless of when we located the nest. Therefore, we derived maximum (BHCO_{MAX}) and minimum (BHCO_{MIN}) parasitism rates as

 $BHCO_{MAX} = N_{BHCO} / N_{BHCO} + N_{ACC}$

 $BHCO_{MIN} = N_{BHCO} / N_{BHCO} + N_{ALL}$

where N_{BHCO} was the total number of parasitized nests, N_{ACC} was the total number of active non-parasitized nests that were found prior to day 4 of incubation, and N_{ALL} was the total number of active non-parasitized nests regardless of nest age when found.

We also examined the data from 1997 to 2008 to see what role partial predation of nest contents might play in the demography study population. We included nests for which we could confirm that at least 1 egg or nestling disappeared during the course of nest monitoring, but at least egg or nestling remained under the care of the adults. We assumed that all eggs or nestlings that disappeared were depredated because other reasons for clutch loss (i.e., removal by adult) were rare enough to be negligible.

Fecundity

We calculated 2 estimates of fecundity (number of young fledged/female) because efforts to locate fledglings varied among study years and sites. We calculated maximum fecundity estimates based on the known total number of nestlings last seen in a nest before fledging. Maximum fecundity estimates were biased high because they did not account for survival of the nestlings during the remaining days in the nest; therefore, we calculated minimum fecundity estimates based on the total number of fledglings detected within 5 days of fledging.

Our maximum fecundity estimates were more consistent than minimum estimates because they were based on known counts of nestlings. Furthermore, minimum fecundity estimates were less precise than maximum fecundity estimates because of the added variability associated with probabilities of detecting fledglings. We used maximum fecundity estimates in our population growth analyses because the consistency of the data allows for comparisons among years and sites but we emphasize the bias associated with this calculation.

Dispersal

Natal dispersal is the distance between the site (meadow) where an individual flycatcher hatched (hatch year; HY) and the site (meadow) where the individual returns in the subsequent year (second-year; SY) to breed (i.e., establishes a territory). In these analyses we included all resignted, territorial SY birds for which we could assign natal locations. We did not include individuals who did not establish a territory at our study sites because we could not account for whether they established a territory elsewhere. We used ArcGIS 9.0 to delineate all study sites based on natural boundaries (e.g., forest edge, lake edge, narrowing of riparian corridor) and to determine a centroid point for each meadow. We assigned each bird to their natal site and first-year breeding location and calculated the distance between the points.

Natal site fidelity is the proportion of SY individuals that returned to their natal site relative to all SY individuals. We did not include in this estimate individuals that were detected as ASY because we intended for this estimate to evaluate the return to a location for an individual's first breeding season.

We calculated juvenile recruitment as the proportion of SY individuals returning from each cohort based on the number of young banded in the previous year with an adjustment for estimated emigration rates (calculated as the proportion of second-year birds resignted outside our core study area to the total number of second-year birds resigned for all years combined). Dispersal distances for second-year birds is commonly extensive for most passerines (Greenwood and Harvey 1982); therefore, we calculated an adjusted juvenile survival estimate

 $j_{t+1} = ([e * N_t] + r_{t+1}) / N_t$

where *e* was the constant rate of emigration, N_t was the number of young available to return in year t + 1 (equal to the number of young banded from successful nests in year t), and and r_{t+1} was the number of SY birds resigned in core study areas. This method assumed that dispersal events outside of our core study areas represented emigration to sites at which we did not monitor consistently over the 14 years of this study, thus likely missing dispersing individuals. We used sites in the Truckee region because of the consistency and quantity of data from that region and because of the extensive surveying conducted in the area for suitable breeding sites.

Breeding dispersal is the distance between the site (meadow) that an individual establishes a breeding territory or nest in 1 year and the site (meadow) that the individual establishes a breeding territory or nest at in the subsequent year (t + 1). Site fidelity is the propensity for individuals to return to the same breeding locations every year (Greenwood and Harvey 1982). In 2005 we began capturing and individually banding adult flycatchers and we estimated breeding site fidelity as the proportion of known adults present in year *t* to those present in the subsequent year (t + 1) at the same site. We estimated adult apparent survival by return rates of breeding flycatchers after their first-year breeding attempt (cohorts pooled to increase sample size). We defined apparent survival as the proportion of banded birds detected in year *t* to the number of banded birds detected in the following year (t + 1).

Population growth

We calculated λ , the rate of population change, for each study region using survival estimates from the Truckee region because of the quantity and consistency of the data. We assumed adult survival and juvenile recruitment was constant across years; therefore, our population models vary among regions and years based on variations in region-specific and annual fecundity estimates. We calculated the annual rate of population change as

$$\lambda = s + (f * j)$$

where *S* was the mean annual estimate for apparent adult survival from banded individuals in the south and central regions. For juvenile survival (*j*), we used the mean annual juvenile survival estimates derived in the central region for each region because sample sizes in the south and north were small. We calculated the maximum fecundity (*f*) estimate pooling across study sites within regions and years. We conducted sensitivity analysis of our population growth models by determining the increase required in each demographic parameter for population stability ($\lambda = 1$).

RESULTS

From 1997 to 2010, at three regions in the Sierra Nevada we detected over 85 Willow Flycatcher territories, found >1,000 nests, banded 1155 nestlings, and banded 56 adults. Male flycatchers typically arrived around the end of May and females arrived shortly thereafter. We rarely detected birds after the end of August. We found the majority of nests during building or egg-laying period (58.8%, n = 792). For nests found after the egg-laying period, the mean nest age was 7.38 (95% CI: 6.46 – 8.31) days.

Territories and Male Breeding Status

The number of territories at a given site fluctuated across study years and ranged from 0 to 14 territories (Table 1). In the South region for all study sites from 1997 to 2010, the mean rate of territory change was -0.11 (SD = 0.263; Fig. 1). In the Truckee region for all study sites from 1997 to 2010, mean rate of territory change was -0.06 (SD = 0.105; Fig 1). In Perazzo meadows the mean rate of territory change was -0.03 (SD = 0.187; Fig). There was no overall change in the number of territories in Warner Valley.

Breeding Status.—The number of female Willow Flycatchers declined in the South Lake Tahoe region until we detected no breeding pairs in 2007 (Table 3, Table 4), thus there was an increasing trend in the number of unmated territorial males detected in the South Lake Tahoe region ($r^2 = 0.403$, P = 0.03, n = 14). Pairing success ranged from 50.9% in 2007 to 76.9% in 1999 in the Truckee region (Table 3). Each year the number of polygynous territories ranged from 1 to 7 (2006; Table 3). In 2007 we observed a male with 3 females in Martis Valley, in the Truckee region.

Reproductive Success

Nest Initiation and Length of Season.—However, mean annual nest initiation in Warner Valley was 5.2 days earlier than in the Truckee region and 3.8 days earlier than in the South Lake Tahoe region (Table 1). The Truckee region was 1.4 days earlier than in the South Lake Tahoe region. The mean annual length of Willow Flycatcher breeding seasons, based on the difference between the earliest nest initiation and the latest fledge date for each study year, was 41 (n = 13 years) days in South Lake Tahoe, 61.8 (n = 14) days in Truckee, and 67 (n = 4) days in Warner Valley (Table 5).

Clutch Size and Renesting.—Maximum clutch size for Willow Flycatchers at all study sites was 4 eggs. The mean annual clutch sizes for nests at all study sites were similar in each study region: South Lake Tahoe = 3.6, SE = 0.31, n = 13 years; Truckee = 3.5, SE = 0.13, n = 14 years; Warner Valley = 3.6, SE = 0.25, n = 5 years. For females with known renesting attempts, 85% (n = 104) laid <4 eggs in a known renest, and 81% (n = 16) of these renest attempts followed a previous nest attempt that failed during the egg-laying stage. Nest initiation date for renests occurred no later than 4 Aug in South Lake Tahoe, 3 Aug in Truckee, and 7 Aug in Warner Valley. For all study regions only three (n = 158) females renested that had a nest fail after 19 July. The difference between this date and the mean annual date when 10% of females in all years initiated nesting is only 30 days in the Truckee and South Lake Tahoe regions. We documented only 2 cases of double-brooding (second nest attempt following a successful nesting) by uniquely marked females, both occurred in Warner Valley.

Nest Failure and Predation.—Predation was the primary cause of nest failure in 86% (n = 371) of nests while abandonment associated with parasitism, unknown abandonment, and unhatched clutches composed the remaining nest losses. Mean annual Mayfield nest success was 22.3% higher in Warner Valley than in the South Lake Tahoe and Truckee regions (Table 6). For nests that we located prior to day 4 of incubation (i.e., we assumed accurate clutch size estimates) at all study sites from 1997 to 2010, we documented partial predation in 111 nests (22.1%; n = 503). The percent of nests partially predated was similar for all regions (south: 28%, n = 50; central: 22%, n = 313; north: 20%, n = 140). Of those nests for which we

assumed we accurately documented partial predation, 55.9% (n = 111) of the nests subsequently failed.

Brown-headed Cowbird Parasitism.—For the following results, we report first a minimum and then a maximum rate of parasitism by brown-headed cowbirds based on assumptions concerning when we found nests (see Methods). Mean annual parasitism rates (minium and maximum) were 15.0% (SD = 11.8, n = 11 years) and 18.4% (SD = 14.8, n = 11) in the South Lake Tahoe region, 7.9% (SD = 5.1, n = 12) and 11.0% (SD = 6.7, n = 12) in the central region, and 6.8% (SD = 6.7, n = 6) and 8.8% (SD = 7.9, n = 6) in the north (Table 7). Within regions, parasitism events occurred at relatively few sites, which influenced the annual variation in parasitism rates. In the South Lake Tahoe region 84.6% (n = 13) of the parasitism events occurred at Uppermost Upper Truckee (Table 8). In the Truckee region, 50.0% (n = 34) of the events were concentrated in Perazzo meadows and 17.7% (n = 34) occurred in Martis Valley. In Warner Valley from 2003 through 2005 and 2008, 58.8% (n = 17) occurred at the southernmost site (South Bog) and 23.5% (n = 17) occurred at East Corral. Nest survival rate for parasitized nests was 22.2% compared to non-parasitized nests with nest survival rate of 54.7%.

Fecundity

Mean annual maximum fecundity in the Truckee region was 1.62 fledglings/female (n = 398 females; Table 4). Mean annual maximum fecundity in the South Lake Tahoe region was 1.65 fledglings/female (n = 64 females). For the years we monitored nests in Warner Valley, mean annual fecundity was higher were 20% higher with 2.07 fledglings/female (n = 167 females) than in the Truckee region.

Return Rates

Juvenile Return Rates.—From 1997 through 2010, 15% (n = 644) of nestlings banded at our south and central study sites returned to breed in the following year (Table 9). We estimated mean annual juvenile survival of 29.4% (SD = 0.09, n = 12) assuming a constant annual emigration rate of 14.5%. We derived the immigration rate from the recruitment of young hatched in our 10 original study sites in the central region but resighted during their first breeding season at a site other than these 10 study sites (Mathewson 2010). We adjusted the juvenile return rate from each study year by 14.5% to estimate juvenile survival, which we then used in the population growth models for the central region.

Adult Survival and Breeding Site Fidelity.—We captured 38 individual adults and marked them with unique combinations. We resigned 73.7% of uniquely marked adults in year t + 1 (n = 38) and only 10.7% of the individuals changed breeding sites (n = 28). Mean annual adult survival was 72.8% (SD = 0.64, n = 155) using the cohort method and pooling return rates across years and sites in the south and central regions.

Population Growth Rate Model

Our estimates of population change indicate that the flycatcher population in the South Lake Tahoe region has declined by 14.1% since 1997 ($\lambda = 0.859$). In the Truckee region, the population has declined by 8.8% ($\lambda = 0.912$) since 1997. In Warner Valley, the mean annual population change from 2003 to 2008 ranged from a mean annual increase of 0.04% to a mean annual decrease of 3.3% ($\lambda = 1.004$ to 0.967). In the Truckee region, to bring population

growth rate up to stability, adult survival would need to increase by 11.5%, or juvenile survival or fecundity would need to increase by 35.6%. Our population estimates predicted a stable population in Warner Valley as long as adult survival does not decrease by more than 1.1% and juvenile survival or fecundity by 2.6%.

DISCUSSION

The Willow Flycatcher population in the central Sierra Nevada declined during the course of our 14-year monitoring study. We observed an apparent contraction of their range from south to north, in that populations in the South Lake Tahoe region all but disappeared during the course of our 14-year study, likely resulting from initial small population size, stochastic weather events, and low reproduction that influenced dispersal dynamics. The population of flycatchers in the Truckee regions exhibited annual fluctuations around stability but with an overall declining trend. Using population growth models and comparative analysis with a reference site, we determined that fecundity is limiting flycatcher populations and that reproductive success has cascading effects on local dispersal patterns. Here we discuss:

- 1. Results of our population monitoring and population growth models
 - a. Local extirpation in South Lake Tahoe
 - b. Declining population in Truckee, although considerable annual fluctuations
 - c. Stable population in reference site in Warner Valley
- 2. Dispersal probably reason why South is dead, isolation of meadows in the regions
- 3. Reproductive success/fecundity low relative to Warner Valley and some other places
- 4. Parasitism was localized and high at same study sites
- 5. Factors contributing to population changes and productivity from research studies and implications for management and conservation

Population Changes

South Lake Tahoe

Flycatcher abundances in the South Lake Tahoe area were low at the beginning of our study and were thus susceptible to stochastic effects that might have reduced the population to sizes too low for recovery. Record high snow in first 4 years of study when the detected number of territories was highest but reproductive success fluctuated reaching a considerable low in 1999. These years were followed by drought conditions starting in 2000 and a reduction in reproductive success in 2001. Subsequently, the number of male and female adults in the following year, 2002, was reduced to only a few individuals. The population of flycatchers in the south has not recovered from these factors and by 2007 we no longer detected females at higher elevation study sites (>7,000 ft). Although surveys conducted by ourselves using an adaptive cluster analysis and the USDA Forest Service and CDFG have detected individuals in adjacent meadows, these sites might not be consistently occupied each year - the number of territories within these sites rarely exceeds 2 territorial males and we did not detect any breeding activity (Appendix A). There also has been a decline and loss of breeding pairs at Blackwood Creek, located in the Lake Tahoe Basin; this site is the southernmost site that we included in with the Truckee region because of its latitude; however, it's adjacency to residential areas is more similar to sites in the South Lake Tahoe region. We discuss possible explanations for the near extirpation of flycatchers from the South Lake Tahoe region below.

Truckee

In the Truckee region, abundances of flycatchers declined across the years of our study but there were considerable temporal and spatial fluctuations. This region included several larger meadows compared to those in the South Lake Tahoe region and 2 of the meadows were once considered to support the highest number of flycatcher territories in the Sierra Nevada (Sanders and Flett 1989, Green et al. 2003).

Uncertainty remains about the persistence of flycatchers in the Truckee region because the number of territories within meadows in this region was small (<14) and a several sites supported few territories (Appendix A). At many sites the number of territorial males remained stable during the study, fluctuating between 1 and ~3 individuals, such as Independence Lake, Stampede Reservoir, and Martis Creek. A consistent decline in the number of territorial males is evident at Webber Lake, Little Truckee 3, Cottonwood Creek. Some of our larger sites, such as Perazzo meadows, experienced a strong reduction in the number of breeding pairs during the drought years from 2000 to 2004 but numbers rebounded following the wet year in 2005; however, these numbers are on the low end of the range derived from surveys in Perazzo meadows from 1982 to 1986 (range: 8 to 17; Harris et al. 1987).

Population Growth: Fecundity and Survival

Population growth models estimated a declining trend in population change of Willow Flycatchers in South Lake Tahoe and, to a lesser extent in the Truckee regions, since the initiation of this study in 1997. In comparison, population growth models using survival estimate from Truckee but fecundity estimates from Warner Valley indicated the population was stable. Sensitivity analysis of population growth models and comparison of vital rates (i.e., fecundity, juvenile survival, and adult survival) with other populations of Willow Flycatchers, indicate that fecundity is the vital factor limiting population growth of flycatchers in the Lake Tahoe area.

Our estimates of return rates for juvenile and adult flycatchers are similar to survival estimates from flycatcher populations in Oregon (13%; Sedgwick 2004) but our estimates were lower than the return rate in Arizona (25%; Paxton et al. 2007) and southern California (34%; M. J. Whitfield pers. comm. in Paxton et al. 2007). Adult return rates were within the range of annual maximum likelihood estimates for southwestern Willow Flycatchers (53%-73%; Paxton et al. 2007). Mean annual survival of long-distance migrants is generally estimated between 50-70% (Ricklefs 1992, Sherry and Holmes 1992, Donovan and Thompson III 2001).

Our fecundity estimates were at or below the reported fecundity values for Willow Flycatchers elsewhere and our fecundity estimates are likely biased high because we used the maximum number of potential fledglings from a nest, defined as the last number of nestlings observed in a nest just prior to fledging. We used this high estimate to standardize our calculations because we attempted to check nests prior to fledging but we were unable to derive an accurate number of fledglings because of low detection rates. Fecundity estimates from other regions are 0.99 to 2.0 in Arizona (Davidson and Allison 2003, Paxton et al. 2007), 1.44 at Kern River, California (Whitfield, unpublished data in Stoleson et al. 2000), and 1.45 to 2.13 in Oregon (Altman et al. 2003). In a 10-year study on Willow Flycatchers in Arizona, Paxton et al. (2007) estimated mean annual fecundity at two large study sites of 1.6 and 2.0

fledglings/adult female, estimates comparable to our minimum and maximum estimates in the Warner Valley region.

Dispersal and the distribution of meadows

The persistence of flycatchers in the Truckee region likely is facilitated by the proximity of large (>100 ha) meadows with suitable breeding habitat interspersed with smaller meadows. Because flycatcher habitat is susceptible to local disturbances within sites, a scattering of meadows across the landscape provides a buffer so that in certain years if local conditions in a meadow are unsuitable, flycatchers can move to adjacent sites to breed (Kus et al. 2003, Sogge et al. 2003). It has been suggested that this pattern of small and large habitat distribution might contribute to the persistence of flycatchers in southern California (Kus et al. 2003) and Arizona (Sogge et al. 2003). In the South Lake Tahoe region, residential and commercial development in the South Lake Tahoe area removed or altered many large meadows known to support any Willow Flycatchers in the past (Ray 1903; 1913). If still intact, these systems likely could have served as source habitat to the current population. The large meadows that still exist in the region (e.g., Upper Truckee and Trout Creek Watersheds, Grass Lake, Hope Valley, Charity Valley) have lowered water tables, and degraded conditions. What remains are smaller meadows that support only a few (e.g., 1 to 3) territories per site that were unable to sustain a population likely because of stochastic events, such as late storms in the late 1990s, coupled with high predation rates, resulting from adjacency to densely populated residential or recreation areas. The likelihood of re-population of the South Lake Tahoe region is reliant upon long distance dispersal of individuals from other population centers but we observed little movement of individuals between the South Lake Tahoe and Truckee regions, indicating that the distance between larger meadows in the Truckee region (e.g., Perazzo meadows) were unable to supply enough dispersing individuals to sustain a population of flycatchers in South Lake Tahoe.

Limited long-distance dispersal may result from high site fidelity and high return rates of adults in our population. Our estimate of natal philopatry at the site-scale (i.e., meadow) was higher than estimates reported for Willow Flycatchers in Oregon (7.8%; Sedgwick 2004) and in Arizona (25%; Paxton et al. 2007). Breeding (adult) site fidelity was higher than that reported for other studies (57%, Paxton et al. 2007; 52%, Sedgwick 2004). Furthermore, return rates for adult flycatchers was higher than that reported for Willow Flycatchers in Oregon (45%, Sedgwick and Klus 1997), southwestern Willow Flycatchers in Arizona (55%, Paxton et al. 2007, in California (M. J. Whitfield unpubl. data in Paxton et al. 2007), and Michigan (Walkinshaw 1966). When site fidelity and regional return rates are high, low reproductive success across a region will interrupt these dispersal dynamics and result in local population reductions. Breeding adult flycatchers might use information from previous breeding seasons to determine whether to disperse to different sites in subsequent breeding seasons (Mathewson 2010), which is a common pattern observed in Willow Flycatchers in Oregon (Sedgwick 2004) and Arizona (Paxton et al. 2007) and has been shown in other species (Hoover 2003, Part and Doligez 2003). Loss and degradation of riparian habitat in the Sierra Nevada may limit natal and breeding dispersal options for Willow Flycatchers, especially if individuals rely upon prospecting behavior in their natal year (Paxton et al. 2007).

Although our overall estimates indicated only slight differences in dispersal patterns between males and females, the proportion of unmated males increased in the South Lake Tahoe region as females failed to return in subsequent years even though site persistence was maintained by a few returning males. Although variable among years, the proportion of unmated males in the Truckee region also increased. In several small meadows in the Truckee region we observed declines in site occupancy by females while a single territorial male consistently returned for several years. This suggests that females are more likely to disperse from areas with low reproductive success, which is a common patterns exhibited in passerines. Populations with estimates of >30% of unmated males is considered to be at a higher risk of extinction (Dale 2001), and estimates from the South Lake Tahoe region and several meadows in Truckee exceeded this proportion.

Reproductive success

Our population growth models suggested that populations in the South Lake Tahoe and Truckee region would approach stable ($\lambda = 1$) with increased reproductive success (i.e., fecundity). Nest predation was the primary cause of nest failure at our study sites. Nest success rates at our south and central region were lower than for Willow Flycatchers elsewhere (54 to 56%; Paxton et al. 2007) and were lower than estimates for other nesting passerines in our study sites (yellow warbler: Cain et al. 2003, dusky flycatcher: Cain and Morrison 2003). Observed nest success for southwestern Willow Flycatchers ranged from close to 30% to almost 70% depending on study site, for example: Kern River, California. (1989-1997) 36.4%, n = 324 nests (Whitfield unpublished data in Stoleson et al. 2000); San Luis Rey River, California. 66.0%, n = 70 nests (Haas pers. comm. in Stoleson et al. 2000); statewide average, Arizona 42.9%, n = 163 (Sferra et al. 1997); southwest New Mexico 43.3%, n = 298 nests (Stoleson and Finch pers. comm. in Sedgwick 2000). This information suggests that Sierra Nevada Willow Flycatchers have nest success rates slightly below those usually observed for the endangered southwestern subspecies and other shrub-nesting passerines.

Nest Predation

Nest predation was the primary cause of nest failure we observed considerable annual variation in nest survival, a trend observed in many passerines. Mammals are likely the primary nest predators in our study regions, including deer mice (*Peromyscus maniculatus*), short-tailed weasels (*Mustela erminea*), long-tailed weasels (*Mustela frenata*), Douglas's squirrels (*Tamiasciururs douglasii*), and chipmunks (*Tamias* spp.) (Cain 2001). Other regularly detected nest predators in my study regions include accipiters (*Accipiter* spp.), Stellar's Jays (*Cyanositta stelleri*), and garter snakes (*Thamnophis* spp.) (Cain et al. 2003). Brown-headed cowbirds also are common and can be considered a nest predator because they are known to remove eggs or nestlings from other species' nests to induce females to renest. Model-predicted estimates indicated considerably higher nest survival in Warner Valley compared to those in the South Lake Tahoe and Truckee regions.

Brown-headed Cowbird parasitism

Parasitism during our study was limited to a few sites in our study regions; however, these sites supported some of the highest abundance of flycatcher territories in the region (i.e., Perazzo meadows; Green et al. 2003). For a population of Willow Flycatchers in southern California parasitism rates would need to be less than 10% for the population to experience growth (Uyehara and Narins 1995, Whitfield et al. 1999). Parasitism rates were high in the South Lake Tahoe region compared to other species at high elevations (Purcell and Verner 1999, Smith et al. 2005) but were localized primarily at Uppermost upper Truckee, which is

embedded within a residential area and its primary use is for recreational purposes. Increased abundance of cowbirds and parasitism rates are positively associated with livestock grazing (Goguen and Mathews 2001) and proximity to residential areas (Borgmann and Morrison 2010). Livestock grazing and other brown-headed cowbird associated activities were both spatially and temporally varied during our study. In the South Lake Tahoe region grazing had ceased at most study sites and other nearby meadows shortly before our research began (with the exception of some private lands where grazing still occurs). Although livestock use was greatly reduced during our study other cowbird associated activities remained within the South Lake Tahoe region. One pack station operates near study sites bordering Lake Tahoe, but possibly more significant in scale has been the continued residential and recreational expansion throughout the area.

In the Truckee study region livestock grazing existed at all but one of our study sites when research began in 1997, but season of use was varied across sites. Over the course of our study livestock use was eliminated, deferred to later in the season, or occurred only a rotational basis. But several of the sites along the Truckee River are adjacent to grazing allotments and within the range of cowbirds foraging at these sites. Recreation in or near meadows is reduced relative to the South Lake Tahoe region, but a human presence is apparent at most sites, and campground or dispersed camping areas occur in relatively close proximity to all sites. Like the South Lake Tahoe Region all sites are within a short distance of a somewhat urban setting, with a major interstate, and the associated development that attracts brown-headed cowbirds.

The Warner Valley study region, while close to residential and recreational areas, does not have the same intensity of human use or livestock grazing relative to our study sites in the South Lake Tahoe and Truckee regions. Grazing still occurs along the shores of Lake Almanor, and development there also has increased.

In many years of our study parasitism rates exceeded the suggested maximum of 10% for population growth (Uyehara and Narins 1995, Whitfield et al. 1999) but even in years when parasitism rates were low they should not be dismissed because brood parasitism can act as an additive effect with other limiting factors such as predation (Rothstein et al. 2003). Parasitized nests had lower daily survival rates, reduced clutch sizes, reduced egg survival, and increased hatching failure (Mathewson 2010), results which concur with other studies on flycatcher populations (Sedgwick and Iko 1999). Increased predation of parasitized nests often is attributed to increased activity or begging associated with cowbird nestlings (Parker et al. 2002, Hoover and Reetz 2006). Because we addled cowbird eggs we effectively removed this as a potential mechanism, yet parasitized nests still experienced higher predation rates. Parasitized nests might experience greater predation risk because nests might be in suboptimal nest locations facilitating discovery by cowbirds and other nest predators (Arcese et al. 1996, Hannon et al. 2009).

Factors contributing to population change and productivity

During the course of this study, several graduate students researched various factors that limited flycatcher occupancy, survival, and reproductive success. These studies focused on the influences of habitat characteristics, predator movement and activity, post-fledgling movement and survival, weather, insect abundance, and a comparative analysis with a reference site, Warner Valley, concerning differences in factors influencing reproductive success. The following conclusions based on these studies increase our understanding of factors that limit Willow Flycatcher populations and have direct implications on conservation

and management decisions in this region of the Sierra Nevada. We elaborate on each conclusion below.

1. Relative to populations of Willow Flycatchers in lower elevation and nonmoutainous regions, flycatchers in the South Lake Tahoe and Truckee regions are constrained by the amount of time available to nest within a season.

2. The nestling period and early fledgling period, and thus the month of July and early August, is a critical period determining reproductive success for an individual flycatcher.

3. Riparian shrub density at the territory scale and extent of meadow inundation by water are the most influential habitat components.

Seasonal and constraints

Willow Flycatchers in the Sierra Nevada, CA are late-spring migrants and they initiate fall migration earlier than other species (Sanders and Flett 1989, Yong and Finch 1997). The breeding season in the Tahoe region was consistently shorter than the length of the season in Warner Valley. It has been shown that even a difference of 5 days in nesting onset can have profound implications on seasonal fecundity of a single-brooded, monogamous passerine (Marshall et al. 2002). Willow Flycatchers arrive on the breeding grounds at the end of May, later than other passerines that nest in the meadows, and in some years the difference compared to Dusky flycatchers, a congener, can be as much as 3 weeks. The reason for this late arrival is unknown but may be associated with an evolved avoidance of late season spring storms, which often occur in the Sierra Nevada at the end of May. Late spring storms are associated with delayed onset of nesting for late arriving species, reduced food availability, and mortality of eggs or nestlings (H. A. Mathewson, personal observation). Elevation of a location determines the magnitude and timing of late season storms and several of the sites in the South Lake Tahoe and Truckee regions were at higher elevation than the sites in Warner Valley.

Late spring and early summer storms directly constrain nest initiation because of physiological demands of the flycatcher but also through delayed onset of leaf eruption in willow and other riparian shrubs necessary for concealing nests. Mathewson (2010) found a relationship between cold temperatures in June and delayed initiation of the breeding season and reduced opportunities for renesting, indirectly these influences effected predation rates. In *post hoc* examination of data we found that for all study regions only three (n = 158) females renested that had a previous nest fail after 19 July. In other words, as the season progresses, a pair is less likely to attempt to renest following a nest failure and if a nest fails after 19 July, the pair likely will not attempt to renest (Mathewson 2010). Simulation models for passerines indicate that limiting nesting attempts to one reduces a population to below replacement levels even if nest success is high (Donovan and Thompson III 2001).

Willow Flycatchers are further constrained by both cold fronts from the north and monsoonal thunder storms from the south at the end of the breeding season. On several occasions, we found nestlings dead in a nest following cold fronts in early August. Vormwald et al. (2011) found that nest success and post-fledging survival was reduced in 2009 following a cold front in early August in the Tahoe region. Results from a study on relative insect abundances at our study sites detected significant decreases in insects at the beginning of

August, and the trend was consistent across three study years (H. A. Mathewson unpubl. data). Flycatchers in lower elevation sites likely do not experience storms this early at the end of the summer, nor are they impacted as often by monsoonal thunderstorms that concentrate at higher elevations. Likewise, when early cold fronts enter the region, temperatures at low elevation sites are not so cold that they adversely affect insect populations.

Nestling and Fledgling period – July and August are still important

During the breeding season, nest survival is the vital rate limiting population growth and nest predation is the primary cause of nest failure. Nest survival analyses indicated that most flycatcher nests failed during the nestling period (Mathewson 2010). The nesting stage is associated with higher activity of both the male and the female to meet the increased demands of feeding nestlings (Soroka and Morrison 2005). High shrub and herbaceous cover resulting in concealment of not only the nest but parental movements in the area surrounding the nest site locations can offset negative effects of increased parental behavior (Weidinger 2002). In large meadows in our system, over-nest concealment was a strong predictor of nest survival (Mathewson 2010). Overall territory success is predicted by high shrub cover at the territory scale, perhaps because vegetative complexity across the entire territory provided concealment of parental behavior resulting in better nest outcomes (Bombay et al 2003a). The nestling period coincides with the hottest periods of the summer when water is no longer present to impede access to riparian shrubs by mammalian predators (Cain et al. 2003, Cocimano et al. 2011), the primary nest predators in our system (Cain 2001). Most mammals hunt opportunistically and if riparian habitat is degraded, adult flycatchers may have to spend more time away from the nest foraging for themselves and their young, reducing the time the adult is available to defend the nest (Soroka and Morrison 2005).

Predation during the nestling stage also impacts adult return rates (Mathewson 2010). Adult return rates to the Truckee study region correlated with the proportion of young in nests that survived to fledge in the previous year but with no other component of reproductive success indicating that evaluation of breeding success depends on their ability to fledge their entire brood successfully and not on overall nesting success. In other words, partial predation or nest failure during the nestling period may have considerable influences on site fidelity decisions. Additionally, unsuccessful individuals may use the success of neighbors within the meadow or in adjacent meadows through prospecting behavior to determine site locations in the following year (Doligez et al. 1999, Hoover 2003, Doligez et al. 2004).

The end of July and early August are important time periods for fledling Willow Flycatchers. Vormwald et al. (2011) found that survival is lowest during the first week after fledgling, which coicides with the end of July and early August. During this time fledglings are more susceptible to predators because of reduced flight capabilities and defense behaviors. Family groups of flycatchers remained in the meadows and used home ranges of 1.8 ± 1.4 ha that consisted primarily of riparian habitat; although the fledglings and parents often forage in the forest they use and return to the riparian areas for the majority of their time until migrating out of the study sites.

Importance of riparian shrubs and water

Bombay (1999) determined that the proportion of shrub cover at the meadow, territory, and nest scale predicted habitat selection decisions of flycatchers and that shrub cover also was predictive of reproductive success at the meadow and territory scale. Similarly, when over-

nest vegetation was low daily nest survival in large meadows was significantly lower compared to nests in small meadows; however, survival rates converged for the two meadow sizes with increased over-nest concealment (Mathewson 2010). The significance of shrub cover in large meadows likely is due to differences in local predator abundances and activity patterns relative to the distribution of water and riparian shrubs across the meadow.

Large meadows have expanses of large, open areas of grassland oftentimes with water sources and shrubs concentrated towards the center of the meadow or along one side. In these meadows, riparian shrubs provide cover for mammalian predators that avoid open grassland areas. In smaller meadows riparian shrubs cover the majority of the meadow and often abut the forest edge. Short-tailed and long-tailed (*Mustela frenata*) weasels and garter snakes (*Thamnophis* spp.) were significantly more active in the larger meadows. Both weasel species may concentrate activity within the riparian deciduous shrubs and avoid open areas because of their foraging and predator-avoidance behavior (Fitzgerald 1977). Snakes may concentrate at grassland and shrub interfaces (Davison and Bollinger 2000), which may explain their association with larger meadows (Cain 2001) because riparian shrubs are interspersed within expanses of open grassland. Large meadows also experience a greater portion of the day in the sun when compared to small meadows that have higher relative shading from the adjacent forest. In higher elevation sites with cool morning temperatures, adequate basking sites may be important for garter snakes.

Habitat selection also was associated with vegetation indicative of meadows with elevated water tables and low disturbance levels (Bombay 1999). Shallow water tables and surface water maintain mesic conditions needed for riparian vegetation growth and establishment (Auble et al. 1994, Stromberg et al. 1996, Stromberg 2001). Riparian obligate herbs are sensitive to even small declines in the groundwater (Stromberg et al. 1996), and reduction of herbaceous cover facilitates encroachment of sagebrush (Berlow et al. 2003). Riparian shrubs respond positively to natural disturbance regimes (Shafroth et al. 2002), but recovery from disturbances depends upon groundwater levels (Bilyeu et al. 2008). Changes in natural and human-induced disturbance regimes as well as climate changes towards reduced precipitation contribute to reduced riparian shrub cover and encroachment by woody upland vegetation, such as lodgepole pine and red and white fir in our region (Vale 1981, Allen-Diaz 1991, Royce and Barbour 2001). Standing water in the meadows was important in predicting flycatcher reproductive success and associations with mammal predators. Chipmunks and squirrels were the primary nest predators in the Sierra Nevada (Cain 2001) yet they were significantly active in meadows with less water cover (Cain 2001, Cocimano et al. 2011) and are generally associated with drier, forested habitats.

MANAGEMENT RECOMMENDATIONS

Based on our research and incorporated with that of other researchers on flycatchers, degradation and alteration of Willow Flycatcher habitat has been identified as the primary factor contributing to population declines (Green et al. 2003). Some examples of factors resulting from meadow degradation include (1) alterations to the hydrological patterns leading to drying of the meadows, (2) destruction of shrub vegetation resulting in loss of nesting sites and cover for predator avoidance, (3) increased predator access to meadow interiors, (4) loss of foraging substrate and decreased insect abundance, and (5) potentially increased contact with brown-headed cowbirds.

Livestock grazing

1. No grazing early in season. Grazing reduces foliage and creates openings into the willow and flycatchers need foliage for nest concealment. Cattle use willow for shade when in open meadows and can create large openings into willow clumps. Wet soils are also more susceptible to compaction and shearing of stream banks which exacerbates water table decline.

2. Move late season grazing to the end of August. In mid-July the majority of the birds are still nesting and likely in the nestling stage or incubation stage for renests or for birds in higher elevation meadows. The nestling stage is a critical period for the young because nest survival analyses (Mathewson 2010) found that nest age is the most predictive variable determining nest survival. Late season grazing should be closely monitored to prevent browsing on seedling stage willow (which occurs when protein levels in graminoids decline with cool temperatures). Seedling and sapling stage willow are extremely important for maintaining and increasing riparian shrub cover within meadows.

3. Grazing is associated with brown-headed cowbirds. Although we did not examine this, several studies have found that cowbirds will forage in and around livestock grazing and then they will travel up to 20 km to reach areas to reproduce. Several of the study areas that support \geq 3 territories of flycatchers are within this distance of grazing areas.

Meadow restoration

We suggest 2 types of restoration that need to occur. First, meadows that are currently occupied by breeding Willow Flycatchers need improvements through habitat restoration. Second, meadows within 5 miles (8 km) of occupied sites are needed for providing habitat for dispersing flycatchers. The primary objective for restoration efforts should focus on increasing nesting success early in the season (first nest attempts) and fledgling survival (improving recruitment). Large-scale restoration efforts needed in many of the larger meadows. Restoration is underway or completed in Upper Truckee, Trout Creek, Cold Stream, and a grant was just received to begin planning restoration for Hope Valley.

Habitat restoration would likely enhance nest success and it is one action that we can take on the nesting grounds that has some potential to increase juvenile recruitment and adult survival. Extensive willow cover is imperative for the survival of Willow Flycatchers in that it provides optimal thermal conditions for roosting or nesting, plentiful forage substrate and it promotes healthy insect populations. Bombay et al. (2003*b*) reported that within our study area, riparian shrub cover was consistently the best predictor of Willow Flycatcher use and success at the meadow, territory and nest spatial scales. For example, Willow Flycatcher territories were 50% more likely to produce successful nests with each 10% increase in riparian shrub cover. The meadows in the Sierra Nevada are historically characterized as "montane wetland shrub habitat" (Sawyer and Keeler-Wolf 1995) based on their high saturation of water. Therefore, the current desiccation of the meadows may be the most important focus for restoration, as it will automatically encourage vegetation growth and health.

Restoration of the vegetation and water levels may reduce predation rates on nests, fledglings and adults. Corroborating our estimates, Cain et al. (2003) concluded that predators are the primary cause of nest failure in our study areas. They suggested that enhancing meadow wetness could reduce the access of some predators (e.g., weasels, chipmunks) to nests. Predation pressure can be reduced by habitat improvement. Water levels are typically higher early in the season and by encouraging meadow wetness, first nesting attempts could be alleviated of intense predation pressure. Habitat improvements will also impact juvenile recruitment by proving ample shrub cover for fledglings, which are subject to relatively high mortality rates. For these same reasons, adults will benefit from increased opportunities to avoid predator detection. Although it is well known that predation is the leading cause of breeding failure in songbirds, minimizing the influence of this factor on nest success is needed to manage the declining population of Willow Flycatchers in the Sierra Nevada.

Habitat restoration efforts would be most effective at currently occupied meadows and at those adjacent to and within the average dispersal distance to these meadows (> 5 miles [8 km]). The meadows along the Little Truckee (Perazzo, Little Perazzo, Little Truckee 1, 2, and 3) once supported more Willow Flycatcher territories than they currently hold. Examination of aerial photographs suggest that Little Truckee 2 is not supporting the same amount of willow as similar oxbow and spring locations further upstream on the Little Truckee river. Perazzo is a large meadow that once supported as many as 12 territories. Furthermore, there are other meadows within dispersal distance from these central meadows that could receive dispersed juveniles. For example, Saddle Meadow, located down stream and within dispersal distance from Little Truckee 2, last supported 1 Willow Flycatcher territory in 1998. Efforts to improve the water table and protect willow seedlings could increase habitat at these sites. Furthermore, increasing the extent of water and willow cover will increase nesting success, provide fledglings with cover to avoid predators and allow for the meadow to support more territories.

Meadows in El Dorado and Alpine County, south of Lake Tahoe, once supported more Willow Flycatcher territories. Currently, ≤ 3 pairs a season establish territories at these sites. Restoration at these sites would increase habitat for Willow Flycatchers. Hope Valley, along the west Carson River, has potential to support large Willow Flycatcher populations. Willow has increased since land was purchased by the state in the 1990s and soon shrubs may be extensive enough to support breeding flycatchers. Water table issues need to be addressed at this site as well as at Faith Valley, a historic site that is now publicly owned. Restoration to this valley, as well as other historically occupied sites in the area potentially will positively influence Willow Flycatcher demographics.

What may be a more important disturbance is the impact of roads on the surface and subsurface hydrology of the meadows. Roads may impede or alter the natural flow of water runoff reducing the flow of water into the meadows. Oftentimes, roads may create collected flows that contribute to soil erosion and sedimentation. Of special concern are roads that bisect meadows or use associated drainage structures that redirect runoff. Prohibiting the construction of new roads in areas that influence Willow Flycatcher habitat (e.g., roads built up slope from meadows) will prevent further alterations to the hydrology. Restoration efforts should include measures to redesign roads currently adjacent to the meadows (Green et al. 2003).

Brown-headed cowbird control

Direct control of cowbirds is often suggested as a means of increasing nesting success. Although cowbird parasitism rates at our sites are below those thought to substantially impact songbird populations (i.e., ~25-30%), our data clearly indicate that steps must be taken to increase fecundity. For any species of concern, any factor that limits their population should be considered in management regimes (Rothstein et al. 2003) and removing the effects of cowbird parasitism could contribute to the goal of increasing nest success. Thus, some form of

cowbird control appears to be warranted, especially given the continued decline of the Willow Flycatcher in much of our study area. Parasitism events are predictable at several of our meadows so initial efforts to control cowbirds should focus on those specific sites (e.g., Uppermost Upper Truckee, Little Perazzo), including in the area south of Lake Tahoe where only a few breeding territories exist and where parasitism rates are highest. Cowbird parasitism rates are high (>30%) in many songbird species being monitored currently in the Lake Tahoe Basin (Borgmann and Morrison 2010).

Monitoring for population changes

A trend in population change was not observed until after several years of monitoring, thus short-term windows could create misinterpretations of true population trends.
It is important to survey several sites in the region, using Perazzo, or other large meadows as indicators of population trend is misleading. Although population trends in Perazzo reflected population changes, the magnitude of change was lessened because smaller meadows are probably the last sites settled so monitoring only large sites won't show declines until too late.
Surveys for only the male are misleading because males might stay in an area that is reproductively unsuitable longer than females. In the South Lake Tahoe sites, it took a few years after the females left before the males stopped returning

4. Surveys every 3-4 years at a site is probably insufficient because territory numbers in most of the meadows is low and they fluctuate annually. To determine a trend \geq 3 data points should be considered but a survey rotation scheduled every 4 years would result in an 8 years time period before obtaining 3 data points, which is too long for land managers to respond to a declining population. As demonstrated in the South Lake Tahoe region, it only took a couple of years for the small population to reach levels that were unsustainable.

Our long-term demography study has created a baseline data set in which future restoration efforts can then be compared to. In order to fully assess the effectiveness of any management activity on populations it is necessary to have an ample number of reference sites over several years. If restoration efforts are implemented soon, the Willow Flycatcher population in the central Sierra Nevada has the potential to return to a stable population level.

Future Research Needs

Effectiveness and impact of meadow restoration. Focus restoration on meadows within optimal dispersal distances. Adults return to same meadows but young disperse ~10km; thus, younger birds are more likely to settle in nearby meadows. Additionally, the effectiveness of restoration techniques needs to be evaluated through monitoring of flycatchers. Ideally this would be accomplished through comparing monitoring at meadows before restoration with post-restoration conditions. Monitoring should not focus only on detecting males because their presence does not necessarily indicate breeding, as seen in our study. Instead, monitoring should be designed to assess productivity within meadows post-restoration.

<u>Monitor cowbird parasitism</u> and initiate control to determine effectiveness (i.e., does it help or are nests just lost to predation, etc.).

<u>Conspecific attraction.</u> This refers to the phenomenon when a species uses the presence of conspecifics to determine where to settle territories. We conducted a small study examining the possibility that playing vocalizations of flycatchers could attract flycatchers to a specific area. Although our study lacked the sample size for any significant results, the breeding flycatchers that re-established in Taylor Creek did so following an experimental year in which we played flycatcher vocalizations at the site. We recommend future research on this behavioral component to habitat selection in flycatchers.

ACKNOWLEDGMENTS

The USDA Forest Service, Region 5, supported this project and we especially thank P. Krueger, J. Robinson, and T. Mark. Additionally we thank C. Stermer and R. Schlorff at California Department of Fish & Game and V. Lyons, S. Zanetti, and M. Hurt at USDA Lake Tahoe Basin Management Unit for continued support of this research. We are grateful to Department of Biology and the Ecology, Evolution and Conservation Biology program at the University of Nevada, Reno and the Department of Wildlife and Fisheries Sciences at Texas A&M University for logistical support. We thank the following researchers for contributions to data: J. Steele, R. Burnett, K. Borgmann, M. Easton, T. Koronkiewicz, M. Whitfield, J. Sedgwick, E. Paxton, R. Netter. Graduate student work completed during the course of this study included: D. Soroka (California State University, Sacramento, CA), J. Cain (California State University, Sacramento, CA), A. Tegeler-Amones (Humboldt State University, Humboldt, California), C. Cocimano, and L. Vormwald (Texas A&M University, College Station, Texas). We are especially grateful for the hard work and dedication from dozens of field assistants, in particular we acknowledge C. Nishida, G. Martinez, M. Wickens, L. Vormwald, K. Comolli, A. Merritt, A. Johnson, A. Tegeler, and S. Copeland. We thank C. Loffland for GIS assistance. Owners and managers at private lands associated with Webber Lake Ranch, Carpenter Valley, and Warner Valley provided generous access to their property and enthusiastic support of our research.

Literature Cited

- Aldrich, J. W. 1951. A review of the races of the Traill's Flycatcher. Wilson Bulletin 63:192– 197.
- Allen-Diaz, B. 1991. Water table and plant species relationships in Sierra Nevada meadows. American Midland Naturalist 126:30-43.
- Altman, B., M. Boulay, S. Dowlan, D. Crannell, K. Russell, K. Beal, and J. Dillon. 2003. Willow Flycatcher nesting ecology and habitat relationships in the Willamette Basin, Oregon. Studies in Avian Biology 26:73–80.
- Arcese, P., J. N. M. Smith, and M. I. Hatch. 1996. Nest predation by cowbirds and its consequences for passerine demography. Proceedings of the National Academy of Sciences 93:4608-4611.
- Auble, G. T., J. M. Friedman, and M. L. Scott. 1994. Relating riparian vegetation to present and future streamflows. Ecological Applications 4:544–554.
- Berlow, E. L., C. M. D'Antonio, and H. Swartz. 2003. Response of herbs to shrub removal across natural and experimental variation in soil moisture. Ecological Applications 13:1375-1387.
- Bilyeu, D. M., D. J. Cooper, and N. T. Hobbs. 2008. Water tables constrain height and recovery of willow on Yellowstone's northern range. Ecological Applications 18:80-92.
- Bombay, H. L. 1999. Scale perspectives in habitat selection and reproductive success for Willow Flycatchers (*Empidonax traillii*) in the central Sierra Nevada, California. Thesis, California State University, Sacramento, California, USA.
- Bombay, H. L., M. L. Morrison, and L. S. Hall. 2003b. Scale perspectives in habitat selection and reproductive success for Willow Flycatchers (*Empidonax traillii*) in the central Sierra Nevada, California. In M. K. Sogge, B. E. Kus, M. J. Whitfield, and S. J. Sferra, editors. Ecology and conservation of the Willow Flycatcher. Studies in Avian Biology 26:60-72.
- Bombay, H. L., T. M. Benson, B. E. Valentine, and R. A. Stefani. 2003*a*. A Willow Flycatcher protocol for California. USDA Forest Service, Region 5. Vallejo, California, USA.
- Borgmann, K. L., and M. L. Morrison. 2010. Factors influencing the frequency of nest parasitism by Brown-headed Cowbirds in the northern Sierra Nevada. Western North American Naturalist 70:137–143.
- Cain, J. W. 2001. Nest success of Yellow Warblers (*Dendroica petechia*) and Willow Flycatchers (*Empidonax traillii*) in relation to predator activity in montane meadows of the central Sierra Nevada, California. M.S. Thesis, California State University, Sacramento, California.
- Cain, J. W., and M. L. Morrison. 2003. Reproductive ecology of dusky flycatchers in montane meadows of the central Sierra Nevada. Western North American Naturalist 63:507-512.
- Cain, J. W., M. L. Morrison, and H. L. Bombay. 2003. Predator activity and nest success of Willow Flycatchers and yellow warblers. Journal of Wildlife Management 67:600-610.
- Cocimano, M. C., M. L. Morrison, H. A. Mathewson, L. M. Vormwald. 2011. The influence of meadow moisture levels on activity of small mammal nest predators in the Sierra Nevada, California. Northwestern Naturalist 92:50–56.

- Davidson, R. F., and L. J. Allison. 2003. Effects of monogamy and polygyny of reproductive success in southwestern Willow Flycatchers (*Empidonax traillii extimus*) in Arizona. Studies in Avian Biology 26:118–124.
- Davison, W. B., and E. Bollinger. 2000. Predation rates on real and artificial nests of grassland birds. Auk 117:147–153.
- Doligez, B., E. Danchin, J. Clober, and L. Gustafsson. 1999. The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. Journal of Animal Ecology 68.
- Doligez, B., T. Part, and E. Danchin. 2004. Prospecting in the collared flycatcher: gathering public information for future breeding habitat selection? Animal Behaviour 67:457-466.
- Donovan, T. M., and F. R. Thompson, III. 2001. Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. Ecological Applications 11:871–882.
- Ettinger, A. O., and J. R. King. 1980. Time and energy budgets of the Willow Flycatcher (*Empidonax traillii*) during the breeding season. Auk 97:533–546.
- Fites-Kaufman, J., P. Rundel, N. Stephenson, and D. A. Weixelman. 2007. Montane and subalpine vegetation of the Sierra Nevada and Cascade ranges. Pages 456–501 in Terrestrial Vegetation of California (M. G. Barbour, T. Keeler-Wolf, and A. A. Schoenherr, Eds.). University of California Press, Berkeley, California.
- Fitzgerald, B. M. 1977. Weasel predation on a cyclic population of the montane vole (*Microtus montanus*) in California. Journal of Animal Ecology 46:367–397.
- Fletcher, J. R. J., and R. R. Koford. 2004. Consequences of rainfall variation for breeding wetland blackbirds. Canadian Journal of Zoology 82:1316-1325.
- Goguen, C. B., and N. E. Mathews. 2001. Brown-headed Cowbird behavior and movements in relation to livestock grazing. Ecological Applications 11:1533–1544.
- Green, G. A., H. L. Bombay, and M. L. Morrison. 2003. Conservation Assessment of the Willow Flycatcher in the Sierra Nevada. USDA Forest Service, Region 5, Vallejo, California, USA.
- Grinnell, J. A., and A. H. Miller. 1944. The distribution of the birds of California. Cooper Ornithological Club, Berkeley, California.
- Hagberg, T. D. 1995. Relationships between hydrology, vegetation and gullies in montane meadows of the Sierra Nevada. Thesis, Humboldt State University, Arcata, California, USA.
- Hannon, S. J., S. Wilson, and C. A. McCallum. 2009. Does cowbird parasitism increase predation risk to American Redstart nests? Oikos 118:1035–1043.
- Harris, J. H., S. D. Sanders, M. A. Flett. 1987. Willow Flycatcher surveys in the Sierra Nevada. Western Birds 18:27-36
- Hoover, J. P. 2003. Decision rules for site fidelity in a migratory bird, the prothonotary warbler. Ecology 84:416–430.
- Hoover, J. P., and M. J. Reetz. 2006. Brood parasitism increases provisioning rate, and reduces offspring recruitment and adult return rates in a cowbird host. Oecologia 149:165–173.
- Katibah, E. F., N. E. Nedeff, and K. J. Dummer. 1984. Summary of riparian vegetation areal and linear extent measurements from the central valley riparian mapping project. *In* California Riparian Systems: Ecology, Conservation, and Productive Management (R. E. Warner and K. M. Hendrix, Eds.). University of California Press, Berkeley, California.

- Koronkiewicz, T.J., E.H. Paxton, and M.K. Sogge. 2005. A technique for aluminum colorbands for avian research. Journal of Field Ornithology 76:94-97.
- Kus, B. E., P. P. Beck, and J. M. Wells. 2003. Southwestern Willow Flycatcher populations in California: distribution, abundance, and potential for conservation. Studies in Avian Biology 26:12–21.
- Lampila, P., M. Monkkonen, and A. Desrochers. 2005. Demographic responses by birds to forest fragmentation. Conservation Biology 19:1537-1146.
- Loheide II, S. P., R. S. Deitchman, D. J. Cooper, E. C. Wolf, C. T. Hammersmark, and J. D. Lundquist. 2009. A framework for understanding the hydroecology of impacted wet meadows in the Sierra Nevada and Cascade Ranges, California, USA. Hydrogeology Journal 17:229–246.
- Marshall, M. R., R. J. Cooper, J. A. DeCecco, J. Strazanac, and L. Butler. 2002. Effcts of experimentally reduced prey abundance on the breeding ecology of the Red-eyed Vireo Ecological Applications 12:261–280.
- Mathewson, H. A. 2010. Population dynamics of Willow Flycatchers in the Sierra Nevada. Dissertation, University of Nevada, Reno, NV.
- Mayfield, H. F. 1961. Nesting success calculated from exposure. Wilson Bulletin. 73:255-261.
- Mayfield, H. 1975. Suggestions for calculating nesting success. Wilson Bulletin 87:456–466.
- McCreedy, C., and S. K. Heath. 2004. Atypical Willow Flycatcher nesting sites in a recovering riparian corridor at Mono Lake, California. Western Birds 35:197–209.
- McKelvey, K.S. and J. D. Johnston. 1992. Historical perspectives on forests of the Sierra Nevada and the transverse ranges of southern California; forest conditions at the turn of the century. Pages 225-246 *in* The California Spotted Owl: A Technical Assessment of its Current Status. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station; Gen. Tech. Rep. PSW-GTR-133
- Parker, G. A., N. J. Royle, and I. R. Hartley. 2002. Begging scrambles with unequal chicks: interactions between need and competitive ability. Ecology Letters 5:206-215.
- Part, T., and B. Doligez. 2003. Gathering public information for habitat selection: prospecting birds cue on parental activity. Proceedings of the Royal Society B: Biological Sciences 270:1809–1813.
- Paxton, E. H. 2008. Geographic variation and migratory connectivity of Willow Flycatcher subspecies. Dissertation, Northern Arizona University, Flagstaff, Arizona.
- Paxton, E. H., M. K. Sogge, S. L. Durst, T. C. Theimer, and J. R. Hatten. 2007. The ecology of the southwestern Willow Flycatcher in central Arizona: a 10-year synthesis report. U.S. Geological Survey Open File Report 2007–1381. Flagstaff, Arizona, USA.
- Pulliam, R. H. 1988. Sources, sinks, and population regulation. American Naturalist 132: 652 661.
- Purcell, K. L., and J. Verner. 1999. Abundance and rates of brood parasitism by Brown-headed Cowbirds over an elevational gradient in the southern Sierra Nevada. Studies in Avian Biology 18:97–103.
- Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. De Sante, 1993. Handbook of field methods for monitoring landbirds. Gen. Tech. Rep. PSW-GTR-144. Albany, CA: Pacific Southwest Research Station, USDA Forest Service, Albany, California, USA.
- Raumann, C. G. and M. E. Cablk. 2008. Change in the forested and developed landscape of the Lake Tahoe basin, California and Nevada, USA, 1940–2002. Forest Ecology and

Management 255:3424-3439.Ray, S. M. 1903. Land birds of Lake Valley, CA. Auk 20:185.

- Ray, S.M. 1913. Some further notes on Sierran Fieldwork. Condor 15:198-203.
- Ricklefs, R. E. 1992. The megapopulation: a model of demographic coupling between migrant and resident landbird populations. Pages 537-548 *in* J. M. Hagan III and D. W. Johnston, editors. Ecology and conservation of Neotropical migratory birds. Smithsonian Institution Press, Washington DC.
- Rothstein, S. I., B. E. Kus, M. J. Whitfield, and S. J. Sferra. 2003. Recommendations for cowbird management in recovery efforts for the southwestern Willow Flycatcher. In M. K. Sogge, B. E. Kus, S. J. Sferra, and M. J. Whitfield, editors. Ecology and conservation of the Willow Flycatcher. Studies in Avian Biology 26:157-167.
- Sanders, S. D., and M. A. Flett. 1989. Ecology of a Sierra Nevada population of Willow flycatchers (*Empidonax traillii*), 1986–1987. California Department of Fish and Game, Sacramento, California, USA.
- Sawyer, J. O., and T. Keeler-Wolf. 1995. A manual of California vegetation. California Native Plant Society, Sacramento, California, USA.
- Schlesinger, M. D., P. N. Manley, and M. Holyoak. 2008. Distinguishing stressors acting on land bird communities in an urbanizing environment. Ecology 89:2302–2314.
- Sedgwick, J. A. 2000. Willow Flycatcher *in* The Birds of North America, Number 533. The Natural Academy of Sciences, Philadelphia, Pennsylvania, USA.
- Sedgwick, J. A. 2004. Site fidelity, territory fidelity, and natal philopatry in Willow Flycatchers (*Empidonax traillii*). Auk 121:1103-1121.
- Sedgwick, J. A. and R. J. Klus. 1997. Injury due to leg bands in Willow Flycatchers. Journal of Field Ornithology 68: 622-629.
- Sedgwick, J.A. and W.M. Iko. 1999. Costs of brown-headed cowbird parasitism to Willow Flycatchers. *In* M.L. Morrison, L.S. Hall, S.K. Robinson, S.I. Rothstein, D.C. Hahn, and T.D. Rich, editors. Research and management of the brown-headed cowbird in western landscapes. Studies in Avian Biology 18:167-181.
- Serena, M. 1982. The status and distribution of the Willow Flycatcher (*Empidonax traillii*) in selected portions of the Sierra Nevada, 1982. California Department of Fish and Game, Sacramento, California, USA.
- Sferra, S.J., T.E. Corman, C.E. Paradzick, J.W. Rourke, J.A. Spencer and M.W. Sumner. 1997. Arizona Partners in Flight southwestern willow flycatcher survey: 1993-1996 summary report. Technical Report 113. Arizona Game and Fish Department, Nongame and Endangered Wildlife Program. Phoenix, Arizona. 46 pp.
- Shafroth, P. B., J. C. Stromberg, and D. T. Patten. 2002. Riparian vegetation response to altered distrubance and stress regimes. Ecological Applications 12:107–123.
- Sherry, T. W., and R. T. Holmes. 1992. Population fluctuation in a long-distance Neotropical migrant: demographic evidence for the importance of breeding season events in the American redstarts. Pages 431-442 *in* J. M. Hagan III and D. W. Johnston, editors. Ecology and conservation of Neotropical migratory birds. Smithsonian Institution Press, Washington D. C.
- Siegel, R. B., R. L. Wilkerson, and D. F. DeSante. 2008. Extirpation of the Willow Flycatcher from Yosemite National Park. Western Birds 39:8–21.

- Smith, J. I., M. D. Reynolds, and G. LeBuhn. 2005. Warbling vireo reproductive success and nest-site characteristics in the northern Sierra Nevada, California. Journal of Field Ornithology 76:383-389.
- Sogge, M.K., J.C. Owen, E.H. Paxton, S.M. Langridge and T.J. Koronkiewicz. 2001. A targeted mist net capture technique for the Willow Flycatcher. Western Birds 32:167-172.
- Soroka, D.E., and M.L. Morrison. 2005. Behavioral activities and breeding success of Willow Flycatchers in the Sierra Nevada. Western North American Naturalist 65:441-450.
- Stewart, I. T., D. R. Cayan, and M. D. Dettinger. 2005. Changes toward earlier streamflow timing across western North America. Journal of Climate 18:1136–1156.
- Stoleson, S. H., M. J. Whitfield, and M. K. Sogge. 2000. Demographic characteristics and population modeling. Pages 83 – 94 *in* D. M. Finch, and S. H. Stoleson, editors. Status, ecology, and conservation of the Southwestern Willow Flycatcher. Gen. Tech. Rep. RMRS-GTR-60. USDA, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Stromberg, J. C. 2001. Restoration of riparian vegetation in the southwestern United States: importance of flow regimes and fluvial dynamism. Journal of Arid Environments 49:17–34.
- Stromberg, J. C., R. Tiller, and B. Richter. 1996. Effects of groundwater decline on riparian vegetation of semiarid regions: the San Pedro, Arizona. Ecological Applications 6:113– 131.
- Unitt, P. 1987. Empidonax traillii extimus: an endangered species. Western Birds 18:137–162.
- Uyehara, J. C., and P. M. Narins. 1995. Nest defense by Willow Flycatchers to brood parasitic intruders. Condor 97:361–368.
- Vale, T. R. 1981. Tree invasion of montane meadows in Oregon. American Midland Naturalist 105:61–69.
- Villard, M.-A., G. Merriam, and B. A. Maurer. 1995. Dynamics in subdivided populations of Neotropical migratory birds in a fragmented temperate forest. Ecology 76:27-40.Vormwald, L. M., M. L. Morrison, H. A. Mathewson, M. C. Cocimano, and B. A. Collier. 2011. Survival and movements of fledgling Willow and Dusky Flycatchers. Condor 113:834–842.
- Weidinger, K. 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. Journal of Animal Ecology 71:424–437.
- Weixelman, D. A., D.C. Zamudio, and K. A. Zamudio. 1999. Eastern Sierra Nevada riparian field guide. R-4-ECOL-99-01. USDA Forest Service, Intermountain Region. Sparks, Nevada.
- Whitfield, M. J., K. M. Enos, and S. P. Rowe. 1999. Is Brown-headed Cowbird trapping effective for managing populations of the endangered Southwestern Willow Flycatcher? Studies in Avian Biology 18:260-266.
- Whitfield, M. J., M. K. Sogge, S. J. Sferra, and B. E. Kus. 2003. Ecology and behavior -Introduction. Studies in Avian Biology 26:53–55.
- Yong, W. and D. M. Finch. 1997. Migration of the Willow Flycatcher along the Middle Rio Grande. Wilson Bulletin. 109:253–268.

Monitoring Site Group																
Region																
Study Site	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	x	SE
Original Demography Sites																
South Lake Tahoe																
Red Lake I	3	3	1	1	2	1	1	1	0	0	0	0	0	1	1.0	0.3
Red Lake II	2	2	3	3	4	1	1	1	0	0	0	0	0	0	1.2	0.4
Maxwell Creek		1	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.1
Grass Lake		3	1	1	1	0	0	0	0	0	0	0	0	0	0.5	0.3
Upermost Upper Truckee		2	3	3	2	2	2	1	1	1	1	1	1	1	1.6	0.2
Washoe State Park		1	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.1
Total $(n = 6)$	5	12	8	8	9	4	4	3	1	1	1	1	1	2	4.3	1.0
Truckee																
Independence Lake		3	2	3	1	3	2	2	2	3	2	2			2.3	0.2
Saddle Meadow		1	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.1
Little Truckee 3		4	6	4	5	4	3	3	3	4	3	1	2	2	3.4	0.4
Little Truckee 2		6	5	4	4	5	5	5	8	6	5	3	5	3	4.9	0.4
Little Truckee 1	5	7	7	5	4	5	5	3	3	3	3	3	3	3	4.2	0.4
Little Perazzo		1	1	0	1	1	2	2	2	1	1	1	1	1	1.2	0.2
Perazzo	12	9	7	5	3	2	5	4	4	11	8	8	8	8	6.7	0.8
Total $(n = 7)$	17	31	28	21	18	20	22	19	22	28	22	18	19	17	21.6	1.2
Webber Lake		12	14	12	12	7	8	9	5	5	6	3	4		8.1	1.1
Prosser Creek		7	5	4	6	6	5	6	8	5					5.8	0.4
Total $(n = 9)$	17	50	47	37	36	33	35	34	35	38	28	21	23	17	32.2	2.8
All Original Sites $(n = 12)$	22	62	55	45	45	37	39	37	36	39	29	22	24	19	36.5	3.5
Perazzo Meadow Complex ^a $(n = 5)$	17	27	26	18	17	17	20	17	20	25	20	16	19	17	19.7	1.0

Table 1. Number of territories detected in study sites in the central and north Sierra Nevada. Data was collected in collaboration with USDA Forest Service, Lake Tahoe Basin Management Unit (USFS), and California Fish and Game.

^a Perazzo Meadow Complex includes the Little Truckee sites, Perazzo and Little Perazzo meadows.

Table 1 continued																
Monitoring Site Group																
Region																
Study Site	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	x	SE
Additional Sites																
South Lake Tahoe																
Red Lake Peak							3	2	2	1	1	0	0	0	1.1	0.4
Tallac								1	3	2	1	1	1	2	1.6	0.3
Taylor												1	2	1	1.3	0.3
Total $(n = 3)$							3	3	5	3	2	2	3	3	3.0	0.3
Truckee																
Martis							2	3	3	1	3	3	3	2	2.5	0.3
Stampede Reservoir					1	1	2	1	0	1	0	1	1	1	0.9	0.2
Cottonwood Creek							2	2	2	5	3	2	2	1	2.4	0.4
Milton Reservoir					4	3	5	5	6	6	4	4	4	2	4.3	0.4
Total $(n = 4)$					5	4	11	11	11	13	10	10	10	6	9.1	0.9
Mabie							3	2	1		0	2	0		1.3	0.5
Blackwood Creek									3	2	1	1	1	0	1.3	0.4
Salmon Creek					3		6		6	5	4	4	4	4	4.5	0.4
Donner Camp										0		1	0	0	0.3	0.3
Total $(n = 4)$					3		9	2	10	7	5	8	5	4	5.9	0.9
Total $(n = 8)$					8		20	13	21	20	15	18	15	10	15.6	1.5
Warner Valley																
North Meadow							8	10	8		9	10	8	8	8.7	0.4
East Corral							6	8	9		10	7	6	7	7.6	0.6
West Corral							7	11	7		9	5	5	4	6.9	0.9
South Bog							11	12	10		8	8	8	9	9.4	0.6
Total $(n = 4)$							32	41	34		36	30	27	28	32.6	1.8
Swamp												18	17	12	15.7	1.9

Willow Flycatchers in the Sierra Nevada, CA from 1997 to 2010: Final Report

Region		
Year	Num. of Territories	Percent Success
South Lake Tahoe		
1997	5	60.0
1998	13	53.8
1999	8	62.5
2000	8	87.5
2001	9	22.2
2002	5	20.0
2003	7	14.3
2004	5	20.0
2005	6	33.3
2006	3	33.3
2007	0	N/A
2008	3	66.7
2009	4	75.0
2010	4^{a}	N/A
Total	76	46.1
Truckee		
1997	20	50.0
1998	56	42.9
1999	50	22.0
2000	36	52.8
2001	42	50.0
2002	40	30.0
2003	48	41.7
2004	49	36.7
2005	62	38.7
2006	45	37.8
2007	29	62.1
2008	58	56.9
2009	34	29.4
2010	27	40.7
Total	596	41.6

Table 2. Territory success (number of territories that fledged ≥ 1 nestling from ≥ 1 nest) of Willow Flycatchers in the Sierra Nevada, CA from 1997 to 2010.

^a In 2010, all nests were found after fledging so estimate was not included in totals.

Table 3. Pairing success (proportion of territories with females; %) and percent of willow
flycatcer territories that were polygynous (>1 female) from 1997 to 2010 in the Sierra Nevada,
CA.

Region				
	Year	Num of Territories	Pairing Success	Polygyny
South Lake	Tahoe			
	1997	5	80.0	0.0
	1998	13	84.6	0.0
	1999	8	100.0	12.5
	2000	8	100.0	12.5
	2001	9	77.8	11.1
	2002	5	60.0	0.0
	2003	7	57.1	0.0
	2004	5	80.0	0.0
	2005	6	66.7	0.0
	2006	4	50.0	25.0
	2007	6	0.0	0.0
	2008	3	66.7	33.3
	2009	4	75.0	0.0
	2010	6	66.7	16.7
Truckee				
	1997	20	75.0	10.00
	1998	56	73.2	1.8
	1999	52	76.9	1.9
	2000	43	69.8	2.3
	2001	42	71.4	2.4
	2002	40	57.5	7.5
	2003	52	67.3	1.9
	2004	52	59.6	7.7
	2005	63	57.1	3.2
	2006	51	54.9	13.7
	2007	57	50.9	7.0
	2008	65	64.6	9.2
	2009	44	68.2	4.6
	2010	29	69.0	13.8

Kegion	Num. of Females	Maximum No.	Fecundity
	Delected	of Fledgings	
South Lake Tanoe	4	0	1 12
1997	4	9	1.13
1998	11	10	0.73
1999	9	11	0.61
2000	9	13	0.61
2001	8	7	0.44
2002	3	3	0.50
2003	4	3	0.38
2004	4	1	0.13
2005	4	6	0.75
2006	3	8	1.33
2007	0	0	0.00
2008	3	5	0.83
2009	3	7	2.33
2010	4	11	2.75
Mean (SD)			0.57 (0.36)
Truckee			
1997	17	34	1.00
1998	41	56	0.67
1999	41	32	0.39
2000	31	57	0.89
2001	31	58	0.94
2002	26	27	0.47
2003	36	52	0.61
2004	35	45	0.61
2005	38	58	0.76
2006	38	49	0.62
2007	27	46	0.85
2008	25	51	1.02
2009	27	28	1.00
2010	21	35	1.67
Mean (SD)			0.71(0.21)
Warner Valley			
2003	32	66	0.98
2004	42	64	0.74
2005	38	64	0.82
2006	15	30	1 00
2008	43	88	0.99
Mean (SD)	15	00	0.88 (0.12)

Table 4. Number of female Willow Flycatchers detected, maximum number of fledglings detected in nest before fledging, and annual fecundity estimates for 3 study regions in the Sierra Nevada, CA. Fecundity is the number of young fledged per female.

Nest Stage Initiation						
Region	n	Min.	Max	Median	Mean	SD
Incubation						
South Lake						
Tahoe	73	15 Jun	2 Aug	30 Jun	30 Jun	10.86
Truckee	432	11 Jun	31 Jul	29 Jun	1 Jul	10.94
Warner Valley	195	2 Jun	3 Aug	24 Jun	26 Jun	11.97
Hatch						
South Lake						
Tahoe	71	1 Iul	16 Aug	14 Iul	15 Jul	10.37
Truckee	420	27 Jun	15 Aug	15 Jul	16 Jul	10.37
Warner Valley	182	18 Jun	18 Aug	9 Jul	11 Jul	11.67
Fledge						
South Lake						
Tahoe	34	16 Jul	23 Aug	27 Jul	28 Jul	8.94
Truckee	220	11 Jul	27 Aug	29 Jul	31 Jul	10.41
Warner Valley	113	6 Jul	23 Aug	23 Jul	24 Jul	9.92

Table 5. Willow Flycatcher nest initiation, hatch, and fledging dates for the South Lake Tahoe and Truckee regions from 1997 to 2010, the Warner Valley region from 2003 to 2005. and 2008. Study regions were located in the central and north Sierra Nevada, CA.

Table 6. Mayfield nest survival estimates of Willow Flycatchers breeding in the Sierra Nevada, CA from 1997 to 2010.

Region		
Year	No. of nests	Percent Success
South Lake Tahoe		
1997	4	74.5
1998	12	27.2
1999	12	31.5
2000	10	45.9
2001	8	23.8
2002	2	53.9
2003	5	16.7
2004	6	12.3
2005	5	36.1
2006	3	62.1
2008	2	100.0
2009	4	70.5
All years	73	40.1
Truckee		
1997	19	34.6
1998	42	40.2
1999	48	19.0
2000	29	53.9
2001	39	43.6
2002	26	35.5
2003	40	37.5
2004	39	41.6
2005	48	50.6
2006	44	36.0
2007	30	42.5
2008	30	58.7
2009	44	34.5
2010	22	45.3
All years	434	40.5
Warner Valley		
2003	38	46.7
2004	42	43.9
2005	48	50.0
2006	15	64.4
2008	55	57.4
All years	198	51.5
All years and		
regions	702	42.8

Region	No. parasitized	Maximum Estimate ^a		Minimum	n Estimate ^a
Year	nests	п	%	п	%
South					
1997	0	2	0.0	4	0.0
1998	2	9	22.2	12	16.7
1999	2	10	20.0	13	15.4
2000	4	9	44.4	12	33.3
2001	1	8	12.5	8	12.5
2002	0	1	0.0	2	0.0
2003	1	5	20.0	5	20.0
2004	1	6	16.7	6	16.7
2005	1	3	33.3	6	16.7
2006	1	3	33.3	3	33.3
2007 ^b					
2008	0	1	0.0	3	0.0
2009	0				
Total	13	57	22.8	74	17.6
Mean (SD)	1.2 (1.17)	5.2 (3.40)	18.4 (14.80)	6.7 (4.00)	15.0 (11.80)
Central					
1997	2	14	14.3	19	10.5
1998	0	32	0.0	44	0.0
1999	0	36	0.0	44	0.0
2000	2	24	8.3	29	6.9
2001	4	29	13.8	35	11.4
2002	1	13	7.7	24	4.2
2003	5	31	16.1	41	12.2
2004	4	26	15.4	37	10.8
2005	2	29	6.9	48	4.2
2006	8	36	22.2	47	17.0
2007	3	27	11.1	39	7.7
2008	3	19	15.8	31	9.7
2009	3	20	15.0	30	10.0
2010	1				
Total	34	316	10.8	438	7.8
Mean (SD)	2.8 (2.25)	26.3 (7.66)	11.0 (6.67)	36.5 (9.21)	7.9 (5.10)

Table 7. Number of parasitized nests, maximum and minimum parasitism rates for Willow Flycatcher nests in the Sierra Nevada, CA from 1997 to 2010.

^a Minimum estimate ^b No nests located in 2007 and 2010 (fledglings found only after fledge in 2010)

Region	No. parasitized	Maximun	n Estimate ^a	Minimum Estimate ^a		
Year	nests	п	%	п	%	
North						
2003	1	27	3.7	37	2.7	
2004	4	29	13.8	37	10.8	
2005	2	30	6.7	52	3.8	
2006	0	8	0.0	17	0.0	
2008	10	51	19.6	61	16.4	
Total	17	145	11.7	204	8.3	
		29.0		40.8	6.8	
Mean (SD)	3.4 (3.97)	(15.25)	838 (7.90)	(16.80)	(6.71)	
All Regions						
Total	64	518	12.4	716	8.9	
		18.5	13.5	25.6	10.5	
Mean (SD)	2.3 (2.40)	(13.51)	(11.21)	(18.00)	(9.08)	

Table	7.	continued
		• • • • • • • •

Region	No.	Movimum	Estimato ^a	Minimum	Fetimete ^a
Site	parasitizeu			Minimum	
South	nests	n	70	n	70
South Weaker SD	2	2	100.0	2	100.0
washoe SP	2	2	100.0	2	100.0
Uppermost Upper Truckee	11	20	55.0	25	44.0
Grass Lake	0	4	0.0	5	0.0
Maxwell Creek	0	1	0.0	1	0.0
Red Lake I	0	7	0.0	11	0.0
Red Lake II	0	15	0.0	19	0.0
Red Lake Peak	0	7	0.0	7	0.0
Tallac	0	1	0.0	2	0.0
Taylor	0			2	0.0
Total	13	57		74	
Mean (SD)	1.4 (3.64)	7.1 (6.96)	19.4 (37.84)	8.2 (8.56)	16.0 (34.70)
Central					
Webber Lake	2	53	3.8	76	2.6
Perazzo	5	43	11.6	61	8.2
Little Perazzo	5	10	50.0	12	41.7
Little Truckee I	1	40	2.5	54	1.9
Little Truckee II	6	52	11.5	68	8.8
Little Truckee III	1	34	2.9	39	2.6
Independence	0	10	0.0	16	0.0
Prosser Creek	3	29	10.3	45	6.7
Martis	6	14	42.9	17	35.3
Stampede Res.	1	3	33.3	3	33.3
Cottonwood	3	7	42.9	10	30.0
Milton Res.	0	15	0.0	25	0.0
Mabie	1	3	33.3	5	20.0
Blackwood	0	2	0.0	2	0.0
Salmon Creek	0	- 1	0.0	4	0.0
Donner Camp	0	-		1	0.0
Total	34	316		438	0.0
Mean (SD)	2.1 (2.25)	21 1 (18 89)	163(1851)	27 4 (25 90)	119(1487)
North	2.1 (2.25)	2111 (10.07)	10.0 (10.01)	27.1 (25.50)	11.5 (11.07)
South Bog	10	44	22.7	55	18.2
West Corral	4	38	10.5	48	83
Fast Corral	-	15	67	4 0 30	3.3
Last Collar North Mandow	1	22	0.7	18	5.5 2.1
Swamp	1	55 15	5.0	40 22	2.1 1 2
Swamp Total	1 17	13 145	0.7	20 204	4.3
10tal	$\frac{1}{2}$	145	0.0(7.22)	204	72(CEA)
Mean (SD)	3.4 (3.91)	29 (13.36)	9.9 (7.63)	40.8 (13.39)	1.3 (6.54)
Total	64	518		716	
Mean (SD)	2.1(2.97)	18.5 (16.92)	16.1 (23.83)	23.9 (22.91)	12.4 (21.47)

Table 8. Site-specific number of brown-headed cowbird parasitism events and maximum and minimum rate of parasitism in Willow Flycatcher nests in the Sierra Nevada,CA from 1997-2010.

Table 9. Annual juvenile and adult Willow Flycatcher recruitment and return in the South Lake Tahoe and Truckee study regions from
1998 to 2009. Cohort is the natal year during which a bird was first banded. The number and proportion of returning is given for each
cohort year and return year.

Cohort	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
1997	5	4	3	1	1	0	0	0	0	0	0	0	0
(n = 33)	0.152	0.800	0.750	0.333	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
1998		10	6	5	3	2	1	2	1	0	0	0	0
(<i>n</i> = 71)		0.141	0.600	0.833	0.600	0.667	0.500	1.000	0.500	0.000	0.000	0.000	0.000
1999			3	3	3	0	0	1	0	0	0	0	0
(<i>n</i> = 43)			0.070	1.000	1.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000
2000				14	14	11	6	5	3	2	2	2	2
(<i>n</i> = 70)				0.200	1.000	0.786	0.545	0.833	0.600	0.667	1.000	1.000	1.00
2001					4	2	2	4	0	1	1	0	0
(<i>n</i> = 66)					0.061	0.500	1.000	1.000	0.000	1.000	1.000	0.000	0.00
2002						7	7	2	2	0	0	0	0
(<i>n</i> = 30)						0.233	1.000	0.286	1.000	0.000	0.000	0.000	0.000
2003							7	7	4	1	2	1	0
(n = 52)							0.135	1.000	0.571	0.250	1.000	0.500	0.000
2004								4	3	3	3	2	0
(n = 50)								0.080	0.750	1.000	1.000	0.667	0.000
2005									15	13	12	7	2
(<i>n</i> = 59)									0.254	0.867	0.923	0.583	0.29
2006										12	3	3	0
(n = 50)										0.240	0.250	1.000	0.000
2007											6	3	0
(<i>n</i> = 54)											0.111	0.500	0.000
2008												6	2
(<i>n</i> = 66)												0.091	0.33
2009													2
(<i>n</i> = 54)													0.04



Figure 1. Rate change in the number of Willow Flycatcher territories in (A) the South Lake Tahoe region and (B) the Truckee region and, within this region, in the Perazzo Meadows system in the Sierra Nevada, CA from 1997 to 2010.



Figure 2. Percent nest success using Mayfield analysis for Willow Flycatchers in the South Lake Tahoe, Truckee, and Warver Valley (WV) study regions from 1997 to 2010.

Appendix A

Study sites and reasons for visits from 1997-2010 (see also Bombay 1999) for Willow Flycatcher research in the Sierra Nevada, CA
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Site	Year	No. WIFL	Reason for visit	County	Region
Austin Mdw	1997	0	surveyed to protocol	Sierra	central
Barker Mdw	1997	0	surveyed to protocol	Placer	central
Bear Valley	1997	0	surveyed to protocol	Sierra	central
Bear Valley East Sec	1997	0	surveyed to protocol	Alpine	south
Bear Valley South	1997	0	surveyed to protocol	Sierra	central
Beartrap Basin	1997	0	surveyed to protocol	Calaveras	
Big Meadow Creek- NE	1997	0	surveyed to protocol	El Dorado	south
Blackwood Creek	1997	0	surveyed to protocol	Placer	central
Bloomfield Mdw	1997	0	surveyed to protocol	Alpine	south
Butcher Ranch	1997	0	surveyed to protocol	Sierra	central
Caltrans Spring	1997	0	surveyed to protocol	Amador	
Caples Creek Mdw	1997	0	surveyed to protocol	Alpine	south
Church Mdw	1997	0	surveyed to protocol	Sierra	central
Donner Camp	1997	0	surveyed to protocol	Nevada	central
Faith Valley	1997	0	surveyed to protocol	Alpine	south
Forni Bog	1997	0	surveyed to protocol	El Dorado	south
Forni Mdw North	1997	0	surveyed to protocol	El Dorado	south
Forni Mdw South	1997	0	surveyed to protocol	El Dorado	south
Foster Mdw	1997	0	surveyed to protocol	Amador	
Freeman Mdw	1997	0	surveyed to protocol	Sierra	central
Gold Valley	1997	1	surveyed to protocol	Sierra	central
Graegle Lodge	1997	1	surveyed to protocol	Yuba	central
Grass Lake	1997	1	surveyed to protocol	Yuba	central
Haypress Bridge	1997	0	surveyed to protocol	Sierra	central
Haypress Valley -E	1997	0	surveyed to protocol	Sierra	central
Haypress Valley -W	1997	0	surveyed to protocol	Sierra	central
Hermit Valley	1997	0	surveyed to protocol	Alpine	south
Hope Valley	1997	0	surveyed to protocol	Alpine	south
Jelmini Basin	1997	0	surveyed to protocol	Calaveras	
Kirkwood Mdw	1997	0	surveyed to protocol	Alpine	south

Appendix A. continued

	1007	0	1		
Landstrip I	1997	0	surveyed to protocol	El Dorado	south
Landstrip II	1997	0	surveyed to protocol	El Dorado	south
Little Truckee I	1997	7	surveyed to protocol	Sierra	central
Loney Mdw	1997	0	surveyed to protocol	Nevada	central
Long Valley	1997	0	surveyed to protocol	Amador	
Long Valley I	1997	0	surveyed to protocol	Sierra	central
Long Valley II	1997	0	surveyed to protocol	Sierra	central
Lower Castle	1997	0	surveyed to protocol	Nevada	central
Magonigal	1997	0	surveyed to protocol	Nevada	central
Mattley Mdw	1997	0	surveyed to protocol	Calaveras	
Mckrae Mdw	1997	1	surveyed to protocol	Yuba	
Miller Lake	1997	0	surveyed to protocol	El Dorado	south
Miller Mdw East	1997	0	surveyed to protocol	El Dorado	south
Miller Mdw West	1997	0	surveyed to protocol	El Dorado	south
Mountain Mdw	1997	0	surveyed to protocol	Placer	central
Page Mdw	1997	0	surveyed to protocol	Placer	central
Perazzo Meadow	1997	11	surveyed to protocol	Sierra	central
Prosser Dam Mdw	1997	0	surveyed to protocol	Nevada	central
Ramelli Ranch	1997	0	surveyed to protocol	Yuba	
Rattlesnake I	1997	0	surveyed to protocol	Nevada	central
Rattlesnake II	1997	0	surveyed to protocol	Nevada	central
Rd350/Little Truckee	1997	0	surveyed to protocol	Sierra	central
Red Lake I	1997	3	surveyed to protocol	Alpine	south
Red Lake II	1997	2	surveyed to protocol	Alpine	south
Red Lake III	1997	0	surveyed to protocol	Alpine	south
Sagehen E	1997	0	surveyed to protocol	Nevada	central
Sagehen W	1997	0	surveyed to protocol	Nevada	central
Solari Mdw	1997	1	surveyed to protocol	Yuba	
Stanislaus Mdw	1997	0	surveyed to protocol	Alpine	south
Tallac/Baldwin Mdw	1997	0	surveyed to protocol	El Dorado	south
Tryon Mdw	1997	0	surveyed to protocol	Alpine	south
Upper Castle	1997	0	surveyed to protocol	Nevada	central
Upper Charity Valley	1997	0	surveyed to protocol	Alpine	south
Upper Pleasant Mdw	1997	0	surveyed to protocol	El Dorado	South
Ward Creek	1997	0	surveyed to protocol	Placer	central
			-		

Appendix A. continued

Washoe State Park	1997	1	surveyed to protocol	El Dorado	south
Willow Creek	1997	0	surveyed to protocol	Plumas	north
Wrights Lake	1997	0	surveyed to protocol	El Dorado	south
Big Meadow	1998	0	surveyed to protocol	ElDorado	south
Carmen/Knuthson Meadow	1998	0	surveyed to protocol	Sierra	central
Celio Ranch Upper Truckee	1998	0	surveyed to protocol	ElDorado	south
Donner Memorial State Park	1998	0	surveyed to protocol	Nevada	central
Grass Lake / Luther Pass	1998	3	surveyed to protocol	ElDorado	south
Hope Valley West End	1998	0	surveyed to protocol	Alpine	south
Hope valley/danberg camp	1998	0	surveyed to protocol	alpine	south
Horsetheif Canyon	1998	0	surveyed to protocol	Alpine	south
Independence Creek	1998	0	surveyed to protocol	Sierra	central
Independence Lake	1998	3	Monitoring site	Nevada	central
Lacey Valley - east of road	1998	7	surveyed to protocol	Sierra	central
Lacey Valley - west of road	1998	5	surveyed to protocol	Sierra	central
Lake Van Norden - Summit Valley	1998	0	surveyed to protocol	Nevada/	
				Placer	central
Little Perazzo	1998	1	Monitoring site	Sierra	central
Little Truckee - upper bridge	1998	0	surveyed to protocol	Sierra	central
Little Truckee I	1998	7	Monitoring site	Sierra	central
Little Truckee II	1998	6	Monitoring site	Sierra	central
Little Truckee III	1998	4	Monitoring site	Sierra	central
Maxwell Creek	1998	1	Monitoring site	Alpine	south
Palisade Fork - R	1998	0	surveyed to protocol	Placer	central
Perazzo Meadow	1998	9	Monitoring site	Sierra	central
Prosser Creek - Carpenter Valley	1998	7	Monitoring site	Nevada	central
Red Lake East	1998	0	surveyed to protocol	Alpine	south
Red Lake I	1998	3	surveyed to protocol	Alpine	south
Red Lake II	1998	2	surveyed to protocol	Alpine	south
Saddle Meadow	1998	1	surveyed to protocol	Sierra	central
Sagehen Creek Below Campus	1998	0	surveyed to protocol	Nevada	central
Sierra House	1998	0	surveyed to protocol	ElDorado	south

Appendix A. continued

Smithneck Creek - Ranch	1008	0	surveyed to protocol	Sierra	control
Sorenson's	1998	0	surveyed to protocol		south
Stampada Reservoir/Sagehen	1008	0	surveyed to protocol	Sierra	control
Stampede Revington Mill R	1008	0	surveyed to protocol	Sierra/	Cellulai
Stampede-Doyington with -K	1990	0	surveyed to protocor	Nevada	control
Taylor Creek	1998	0	surveyed to protocol	FlDorado	south
Trout Creek	1998	0	surveyed to protocol	ElDorado	south
Truckee Marsh (East)	1998	0	surveyed to protocol	ElDorado	south
Upper Forestdale Creek	1998	0	surveyed to protocol	Alpine	south
Upper Silver Lake	1008	0	surveyed to protocol	Amador	south
Upper Truckoa Airport	1998	0	surveyed to protocol	FlDorado	aouth
Upper Truckee Amport	1990	0	surveyed to protocol	ElDorado	south
Upper Huckee Downstream Anport	1990	3	surveyed to protocol	ElDorado	south
Wabbar Laka North L	1998	5	surveyed to protocol	Sierre	south
Webber Lake North II	1990	0	surveyed to protocol	Sierra	central
Foith Volley	1998	0	surveyed to protocol	Almina	central
Grass Labe / Littler Dage	1999	0	Surveyed to protocol	FIDerede	south
Grass Lake/ Luther Pass	1999	1	Monitoring site	ElDorado	south
Hope Valley (downstream of nwy 88, along	1999	0	surveyed to protocol	Alpine	a a 41a
Independence Lake	1000	2	a lan hand nasisht	Navada	south
	1999	2 1	Color band resignt	Nevada	central
Little Translas L	1999	1	Monitoring site	Sierra	central
	1999	/	Monitoring site	Sierra	central
	1999	5	Monitoring site	Sierra	central
	1999	0	Monitoring site	Sierra	central
Maxwell Creek	1999	1	Monitoring site	Alpine	south
Perazzo Meadow	1999	7	Monitoring site	Sierra	central
Prosser Creek - Carpenter Valley	1999	5	Monitoring site	Nevada	central
Red Lake I	1999	1	surveyed to protocol	Alpine	south
Red Lake II	1999	3	surveyed to protocol	Alpine	south
Saddle Meadow	1999	1	surveyed to protocol	Sierra	central
Scotts Lake Meadow	1999	0	surveyed to protocol	Alpine	south
Upper Charity Valley	1999	0	surveyed to protocol	Alpine	south
Uppermost Upper Truckee	1999	3	surveyed to protocol	ElDorado	south
Uppermost Upper Truckee/ Morton st.	1999	0	surveyed to protocol	ElDorado	south
Washoe State Park	1999	1	surveyed to protocol	El Dorado	south
Webber Lake/ Lacey Valley	1999	14	surveyed to protocol	Sierra	central

Appendix A. continued

Grass Lake/ Luther Pass	2000	1	Monitoring site	ElDorado	south
Independence Lake	2000	2	color band resight	Nevada	central
Little Perazzo	2000	1	Monitoring site	Sierra	central
Little Truckee I	2000	7	Monitoring site	Sierra	central
Little Truckee II	2000	5	Monitoring site	Sierra	central
Little Truckee III	2000	6	Monitoring site	Sierra	central
Maxwell Creek	2000	1	Monitoring site	Alpine	south
Perazzo Meadow	2000	7	Monitoring site	Sierra	central
Prosser Creek - Carpenter Valley	2000	5	Monitoring site	Nevada	central
Red Lake I	2000	1	Monitoring site	Alpine	south
Red Lake II	2000	3	Monitoring site	Alpine	south
Saddle Meadow	2000	1	surveyed to protocol	Sierra	central
Uppermost Upper Truckee	2000	3	Monitoring site	ElDorado	south
Uppermost Upper Truckee/ Morton st.	2000	0	Monitoring site	ElDorado	south
Washoe State Park	2000	1	Monitoring site	El Dorado	south
Webber Lake/ Lacey Valley	2000	14	Monitoring site	Sierra	central
Anderson Meadow	2001	0	surveyed to protocol	Sierra	central
Burnside Lake SE meadows	2001	0	surveyed to protocol	Alpine	south
Cold Stream Meadow	2001	0	surveyed to protocol	Sierra	central
Grass Lake/ Luther Pass	2001	1	Monitoring site	ElDorado	south
Hope Valley	2001	0	surveyed to protocol	Alpine	south
Independence Lake	2001	1	Monitoring site	Nevada	central
Little Perazzo	2001	1	Monitoring site	Sierra	central
Little Truckee I	2001	4	Monitoring site	Sierra	central
Little Truckee II	2001	4	Monitoring site	Sierra	central
Little Truckee III	2001	5	Monitoring site	Sierra	central
Maxwell Creek	2001	0	Monitoring site	Alpine	south
Milton Reservoir	2001	4	Surveyed to protocol	Sierra/Nevada	central
Perazzo Meadow	2001	3	Monitoring site	Sierra	central
Prosser Creek - Carpenter Valley	2001	6	Monitoring site	Nevada	central
Prosser Reservoir @ Prosser Creek inflow	2001	0	surveyed to protocol	Nevada	central
Red Lake I	2001	2	Monitoring site	Alpine	south
Red Lake II	2001	4	Monitoring site	Alpine	south
Red Lake III	2001	0	surveyed to protocol	Alpine	south
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Appendix A. continued

Saddle Meadow	2001	0	surveyed to protocol	Sierra	central
Salmon Creek	2001	3	surveyed	Sierra	central
Stampede Reservoir @ Little Truckee inflow	2001	1	surveyed	Sierra	central
Upper Perazzo Canyon	2001	0	surveyed to protocol	Sierra	central
Uppermost Upper Truckee	2001	2	Monitoring site	ElDorado	south
Uppermost Upper Truckee/ Morton st.	2001	0	surveyed to protocol	ElDorado	south
Washoe State Park	2001	0	Monitoring site	El Dorado	south
Webber Lake/ Lacey Valley	2001	12	Monitoring site	Sierra	central
Benwood Meadow	2002	0	color band resight	El Dorado	south
Faith Valley	2002	1	color band resight	Alpine	south
Grass Lake/ Luther Pass	2002	0	Monitoring site	El Dorado	south
Horse Meadow	2002	0	color band resight	El Dorado	south
Independence Lake	2002	4	Monitoring site	Nevada	central
Lily Lake	2002	0	color band resight	El Dorado	south
Little Perazzo	2002	1	Monitoring site	Sierra	central
Little Truckee I	2002	6	Monitoring site	Sierra	central
Little Truckee II	2002	6	Monitoring site	Sierra	central
Little Truckee III	2002	4	Monitoring site	Sierra	central
Lower Charity Valley	2002	0	color band resight	Alpine	south
Maxwell Creek	2002	0	Monitoring site	Alpine	south
Meiss Lake	2002	0	color band resight	El Dorado	south
Milton Reservoir	2002	3	color band resight	Sierra/Nevada	central
Perazzo Meadow	2002	4	Monitoring site	Sierra	central
Prosser Creek - Carpenter Valley	2002	8	Monitoring site	Nevada	central
Prosser Reservoir @ Prosser Creek inflow	2002	0	surveyed to protocol	Nevada	central
Red Lake Creek	2002	0	color band resight	Alpine	south
Red Lake I	2002	1	surveyed to protocol	Alpine	south
Red Lake II	2002	2	surveyed to protocol	Alpine	south
Saddle Meadow	2002	0	surveyed to protocol	Sierra	central
Sagehen Creek (from campground to reservoir)	2002	1	surveyed to protocol	Sierra	central
Stampede Res. to Boca Res.	2002	0	surveyed to protocol	Sierra/Nevada	central
Stampede Reservoir @ Little Truckee inflow	2002	1	color band resight	Sierra	central
Uppermost Upper Truckee	2002	2	surveyed to protocol	El Dorado	south

Appendix A. continued

Uppermost Upper Truckee/ Morton st.	2002	0	surveyed to protocol	El Dorado	south
Washoe State Park	2002	0	surveyed to protocol	El Dorado	south
Webber Lake/ Lacey Valley	2002	7	surveyed to protocol	Sierra	central
Charity Valley	2003	1	color band resights	Alpine	south
Cookhouse Meadow	2003	0	color band resights	El Dorado	south
Cottonwood Creek	2003	2	color band resights	Sierra	central
Delleker	2003	1	color band resights	Plumas	north
Faith Valley	2003	1	color band resights	Alpine	south
Graegle Lodge	2003	2	color band resights	Plumas	north
Grass Lake/ Luther Pass	2003	0	Monitoring site	El Dorado	south
Independence Lake	2003	2	Monitoring site	Nevada	central
Lily Lake	2003	0	color band resights	El Dorado	south
Little Perazzo	2003	3	Monitoring site	Sierra	central
Little Truckee I	2003	6	Monitoring site	Sierra	central
Little Truckee II	2003	5	Monitoring site	Sierra	central
Little Truckee III	2003	3	Monitoring site	Sierra	central
Mabie	2003	6	Monitoring site	Plumas	north
Martis Creek	2003	2	Monitoring site	Placer	central
Maxwell Creek	2003	0	Monitoring site	Alpine	south
McRae Meadow	2003	1	color band resights	Yuba	
Milton Reservoir	2003	5	Monitoring site	Sierra/Nevada	central
Perazzo Meadow	2003	5	Monitoring site	Sierra	central
Prosser Creek - Carpenter Valley	2003	6	Monitoring site	Nevada	central
Ramelli Ranch	2003	0	color band resights	Plumas	north
Red Lake I	2003	1	Monitoring site	Alpine	south
Red Lake II	2003	1	Monitoring site	Alpine	south
Red Lake Peak	2003	3	Monitoring site	Alpine	south
Saddle Meadow	2003	0	surveyed to protocol	Sierra	central
Sagehen Creek (between station and lower gate)	2003	0	color band resights	Sierra	central
Salmon Creek	2003	6	color band resignts	Sierra	central
Smithneck Creek	2003	1	color band resignts	Sierra	central
Stampede Reservoir @ Little Truckee inflow	2003	2	color band resignts	Sierra	central
Tallac/Baldwin Beach	2003	1	color band resignts	El Dorado	south

Appendix A. continued

Uppermost Upper Truckee	2003	2	Monitoring site	El Dorado	south
Uppermost Upper Truckee/ Morton st.	2003	0	Monitoring site	El Dorado	south
Warner Valley – bog thicket	2003	2	color band resights	Plumas	north
Warner Valley – East Corral	2003	8	Monitoring site	Plumas	north
Warner Valley – North Meadow	2003	8	Monitoring site	Plumas	north
Warner Valley – South Bog	2003	11	Monitoring site	Plumas	north
Warner Valley – South River	2003	2	color band resights	Plumas	north
Warner Valley – West Corral	2003	5	Monitoring site	Plumas	north
Warner Valley- North Alder	2003	4	color band resights	Plumas	north
Washoe State Park	2003	0	surveyed to protocol	El Dorado	south
Webber Lake/ Lacey Valley	2003	8	Monitoring site	Sierra	central
Bear Valley	2004	0	adaptive cluster site	Sierra	central
Cold Stream Meadow	2004	0	adaptive cluster site	Sierra	central
Cottonwood Creek	2004	2	monitoring site	Sierra	central
Grass Lake/ Luther Pass	2004	0	Monitoring site	El Dorado	south
Independence Lake	2004	2	Monitoring site	Nevada	central
Little Perazzo	2004	3	Monitoring site	Sierra	central
Little Truckee East	2004	0	adaptive cluster site	Sierra	central
Little Truckee I	2004	4	Monitoring site	Sierra	central
Little Truckee II	2004	5	Monitoring site	Sierra	central
Little Truckee III	2004	3	Monitoring site	Sierra	central
Little Truckee West	2004	0	adaptive cluster site	Sierra	central
Mabie	2004	2	monitoring site	Plumas	north
Martis Creek	2004	3	Monitoring site	Placer	central
Maxwell Creek	2004	0	Monitoring site	Alpine	south
Milton Reservoir	2004	6	Monitoring site	Sierra/Nevada	central
NW (Rice Canyon, SW)	2004	0	adaptive cluster site	Sierra	central
NW 1 of Milton	2004	0	adaptive cluster site	Nevada	central
NW 2 of Milton	2004	0	adaptive cluster site	Nevada	central
NW 3 of Milton	2004	0	adaptive cluster site	Nevada	central
NW of LT 1&2	2004	0	adaptive cluster site	Sierra	central
Perazzo Meadow	2004	5	Monitoring site	Sierra	central
Prosser Creek - Carpenter Valley	2004	6	Monitoring site	Nevada	central
Red Lake I	2004	1	monitoring site	Alpine	south
Red Lake II	2004	1	monitoring site	Alpine	south
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Appendix A. continued

Appendix 71. continued					
Red Lake Peak	2004	2	monitoring site	Alpine	south
Rice Canyon, NE	2004	0	adaptive cluster site	Sierra	central
Round Valley	2004	0	adaptive cluster site	Nevada	central
Saddle Meadow	2004	0	surveyed to protocol	Sierra	central
SE of LT 1&2	2004	0	adaptive cluster site	Sierra	central
SE of Milton	2004	0	adaptive cluster site	Nevada	central
SE of Perazzo	2004	0	adaptive cluster site	Nevada	central
Stampede Reservoir @ Little Truckee inflow ^b	2004	1	monitoring site	Sierra	central
SW 1 of Milton	2004	0	adaptive cluster site	Nevada	central
SW 2 of Milton	2004	0	adaptive cluster site	Nevada	central
SW 3 of Milton	2004	0	adaptive cluster site	Nevada	central
SW of Perazzo	2004	0	adaptive cluster site	Sierra	central
SW of Saddle	2004	0	adaptive cluster site	Sierra	central
Uppermost Upper Truckee	2004	1	monitoring site	El Dorado	south
Warner Valley – East Corral	2004	9	monitoring site	Plumas	north
Warner Valley – North Meadow	2004	11	monitoring site	Plumas	north
Warner Valley – South Bog	2004	13	monitoring site	Plumas	north
Warner Valley – West Corral	2004	12	monitoring site	Plumas	north
Washoe State Park	2004	0	surveyed to protocol	El Dorado	south
Webber Lake/ Lacey Valley	2004	9	monitoring site	Sierra	central
Anderson Meadow	2005	0	adaptive cluster site	Sierra	central
Big Meadow	2005	0	Surveyed to protocol	ElDorado	south
Blackwood Creek	2005	4	Monitoring site	Placer	central
Church Meadow	2005	0	adaptive cluster site	Sierra	central
Cold Stream Meadow	2005	0	adaptive cluster site	Sierra	central
Cookhouse Meadow	2005	0	Surveyed to protocol	El Dorado	south
Coppins Meadow	2005	0	adaptive cluster site		
Cottonwood Creek	2005	3	Monitoring site	Sierra	central
Drakesbad	2005	1	color band resight	Alpine	south
Dry Meadow	2005	0	adaptive cluster site		
English Meadow	2005	0	adaptive cluster site		
Faith Valley	2005	0	Surveyed to protocol	Alpine	south
Fanani Meadow	2005	3	color band resight		
Freeman Meadow	2005	0	adaptive cluster site		

Appendix A. continued

<u>- Appendix 71. continued</u>					
French Meadow	2005	0	adaptive cluster site		
Gold Lake	2005	1	color band resight		
Gold Valley	2005	1	adaptive cluster site	Sierra	central
Grass Lake	2005	0	adaptive cluster site	Yuba	
Grass Lake/ Luther Pass	2005	0	Monitoring site	El Dorado	south
Haypress So. Fork	2005	0	adaptive cluster site		
Haypress Valley	2005	0	adaptive cluster site		
High Meadows	2005	0	Surveyed to protocol	Alpine	south
Hope Valley	2005	0	Surveyed to protocol	Alpine	south
Howard Creek south fork and Haskell Creek	2005	0	adantiva alustan sita		
west	2003	0	adaptive cluster site		
Humbug Valley	2005	9	color band resight	Plumas	north
Independence Lake	2005	2	Monitoring site	Nevada	central
Jones Valley	2005	0	adaptive cluster site		
Lake Almanor NW	2005	9	color band resight	Plumas	north
Lake Almanor SW	2005	5	color band resight	Plumas	north
Lewis Mill	2005	0	adaptive cluster site	Plumas	
Lily Lake	2005	0	Surveyed to protocol	El Dorado	south
Little Perazzo	2005	2	Monitoring site	Sierra	central
Little Truckee I	2005	4	Monitoring site	Sierra	central
Little Truckee II	2005	8	Monitoring site	Sierra	central
Little Truckee III	2005	5	Monitoring site	Sierra	central
Little Truckee West	2005	0	Monitoring site	Sierra	central
Lower Charity Valley	2005	0	Surveyed to protocol	Alpine	south
Mabie	2005	1	surveyed to protocol	Plumas	north
Martis Creek	2005	3	Monitoring site	Placer	central
Maxwell Creek	2005	0	Monitoring site	Alpine	south
Meathouse Meadow	2005	0	adaptive cluster site	Yuba	
Meeks Meadow	2005	0	Surveyed to protocol	Sierra	
Milton Reservoir	2005	6	Monitoring site	Sierra/Nevada	central
Milton SE	2005	0	adaptive cluster site	El Dorado	south
Milton SW	2005	0	adaptive cluster site	El Dorado	south
Perazzo Meadow	2005	6	Monitoring site	Sierra	central
Prosser Creek - Carpenter Valley	2005	11	Monitoring site	Nevada	central

Appendix A. continued

Prosser Reservoir	2005	0	adaptive cluster site	Nevada	central
Red Lake I	2005	0	Monitoring site	Alpine	south
Red Lake II	2005	0	Monitoring site	Alpine	south
Red Lake Peak	2005	2	Monitoring site	Alpine	south
Ruffa Ranch, Butt Creek	2005	3	color band resight	Plumas	north
Saddle Meadow	2005	0	Monitoring site	Sierra	central
Sagehen Creek	2005	0	Monitoring site	Sierra	central
Salmon Creek	2005	6	adaptive cluster site	Sierra	central
Salmon Creek	2005	3	color band resight	Sierra	central
Sand Pond	2005	0	adaptive cluster site	sierra	central
Stampede Reservoir @ Little Truckee inflow	2005	1	Monitoring site	Sierra	central
Tallac Creek	2005	3	Monitoring site	El Dorado	south
Taylor Creek	2005	0	Surveyed to protocol	ElDorado	south
Trout Creek	2005	0	Surveyed to protocol	ElDorado	south
Upper Charity Valley	2005	0	Surveyed to protocol	Alpine	south
Upper Deer creek (6 parts)	2005	0	adaptive cluster site	Sierra	central
Uppermost Upper Truckee	2005	1	Monitoring site	El Dorado	south
Ward Creek	2005	0	Surveyed to protocol	Placer	central
Warner Valley – East Corral	2005	7	Monitoring site	Plumas	north
Warner Valley – North Meadow	2005	8	Monitoring site	Plumas	north
Warner Valley – South Bog	2005	10	Monitoring site	Plumas	north
Warner Valley – West Corral	2005	8	Monitoring site	Plumas	north
Warner Valley Swamp	2005	13	color band resight	Plumas	north
Washoe State Park	2005	0	Monitoring site	El Dorado	south
Watson Lake	2005	0	color band resight	Placer	central
Webber Lake/ Lacey Valley	2005	7	Monitoring site	Sierra	central
Willow Lake	2005	4	color band resight	Alpine	south
Blackwood Creek	2006	2	Monitoring site	Placer	central
Cottonwood Creek	2006	5	Monitoring site	Sierra	central
Forestdale	2006	0	point count study	Alpine	south
Hope Valley	2006	0	Surveyed to protocol	Alpine	south
Independence Lake	2006	3	Monitoring site	Nevada	central
Little Perazzo	2006	1	Monitoring site	Sierra	central
Little Truckee I	2006	3	Monitoring site	Sierra	central

Appendix A. continued

Appendix 71. continued					
Little Truckee II	2006	7	Monitoring site	Sierra	central
Little Truckee III	2006	4	Monitoring site	Sierra	central
Little Truckee West	2006	1	Surveyed to protocol	Sierra	central
Martis creek @ Truckee river	2006	0	Surveyed to protocol	Sierra	Central
Maxwell Creek	2006	0	Monitoring site	Alpine	south
Milton Reservoir	2006	6	Monitoring site	Sierra/Nevada	central
Perazzo Meadow	2006	10	Monitoring site	Sierra	central
Prosser Creek - Carpenter Valley	2006	5	Monitoring site	Nevada	central
Red Lake I	2006	1	Monitoring site	Alpine	south
Red Lake II	2006	0	Monitoring site	Alpine	south
Red Lake Peak	2006	2	Monitoring site	Alpine	south
Saddle Meadow	2006	0	Monitoring site	Sierra	central
Salmon Creek	2006	5	color band resights	Sierra	central
Stampede Reservoir @ Little Truckee inflow	2006	1	color band resights	Sierra	central
Tallac Creek	2006	2	color band resights	El Dorado	south
Uppermost Upper Truckee	2006	1	Monitoring site	El Dorado	south
Uppermost Upper Truckee/ Morton st.	2006	0	Monitoring site	El Dorado	south
Ward Creek	2006	0	surveyed	Placer	central
Webber Lake/ Lacey Valley	2006	6	color band resights	Sierra	central
Woods Lake	2006	1	color band resights	Alpine	south
Bassett Station	2007	0	conspecific attraction	-	
Blackwood Creek	2007	1	Monitoring site	Placer	central
Carmen Valley	2007	1	conspecific attraction	Sierra	central
Cottonwood Creek	2007	3	Monitoring site	Sierra	central
Faith Valley	2007	0	color band resight	Alpine	south
Fanani Meadow	2007	0	color band resight		
Grass Lake/ Luther Pass	2007	0	surveyed to protocol	El Dorado	south
Humbug Valley	2007	2	color band resight	Plumas	north
Independence Lake	2007	2	Monitoring site	Nevada	central
Lake Almanor SW	2007	16	color band resight	Plumas	north
Lake Almanor SW	2007	13	color band resight	Plumas	north
Little Perazzo	2007	1	Monitoring site	Sierra	central
Little Truckee I	2007	3	Monitoring site	Sierra	central
Little Truckee II	2007	5	Monitoring site	Sierra	central
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Appendix A. continued

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Little Truckee III	2007	3	Monitoring site	Sierra	central
Little Truckee west	2007	0	conspecific attraction	Sierra	central
Mabie	2007	0	surveyed to protocol	Plumas	north
Martis Creek	2007	3	Monitoring site	Placer	central
Maxwell Creek	2007	0	surveyed to protocol	Alpine	south
Milton Reservoir	2007	4	Monitoring site	Sierra/Nevada	central
Perazzo Meadow	2007	8	Monitoring site	Sierra	central
Plumas NF-FR-40102	2007	0	surveyed to protocol	Plumas	north
Plumas NF-FR-40105	2007	0	surveyed to protocol	Plumas	north
Plumas NF-MH-40108	2007	0	surveyed to protocol	Plumas	north
Plumas NF-MH-40125	2007	0	surveyed to protocol	Plumas	north
Red Lake I	2007	0	surveyed to protocol	Alpine	south
Red Lake II	2007	0	surveyed to protocol	Alpine	south
Red Lake Peak	2007	1	surveyed to protocol	Alpine	south
Saddle Meadow	2007	0	color band resight	Sierra	central
Sagehen	2007	0	surveyed to protocol	Sierra	central
Salmon Creek	2007	4	surveyed to protocol	Sierra	central
South Lake Tahoe Airport	2007	1	color band resight	ElDorado	south
Stampede Reservoir @ Little Truckee inflow	2007	1	surveyed to protocol	Sierra	central
Tallac	2007	2	surveyed to protocol	El Dorado	south
Uppermost Upper Truckee	2007	1	surveyed to protocol	El Dorado	south
Warner Valley East Corral	2007	9	color band resight	Plumas	north
Warner Valley North Meadow	2007	9	color band resight	Plumas	north
Warner Valley South Bog	2007	8	color band resight	Plumas	north
Warner Valley Swamp	2007	15	color band resight	Plumas	north
Warner Valley West Corral	2007	9	color band resight	Plumas	north
Washoe State Park	2007	0	surveyed to protocol	El Dorado	south
Webber Lake/ Lacey Valley	2007	6	color band resight	Sierra	central
Willow Creek	2007	3	color band resight	Plumas	north
Woods Lake	2007	0	color band resight	Alpine	south
Big Meadow	2008	0	color band resight	ElDorado	south
Blackwood Creek	2008	1	Monitoring site	Placer	central
Carmen Valley	2008	1	conspecific attraction	Sierra	central
Castle Valley	2008	0	color band resight		
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Appendix A. continued

Cookhouse Meadow	2008	0	conspecific attraction	El Dorado	south
Cottonwood Creek	2008	2	Monitoring site	Sierra	central
Donner Camp	2008	1	Monitoring site	Nevada	central
Fanani Meadow	2008	0	color band resight	Ttevada	central
Forestdale	2008	0	color band resight	Alpine	south
Grass Lake / Luther Pass	2008	0	surveyed to protocol	El Dorado	south
Humbug Valley	2008	5	color band resight	Plumas	north
Independence Creek	2008	0	surveyed to protocol	Sierra	central
Independence Lake	2008	2	Monitoring site	Nevada	central
Lake Almanor NW	2008	9	color band resight	Plumas	north
Lake Almanor SW	2008	13	color band resight	Plumas	north
Little Perazzo	2008	1	Monitoring site	Sierra	central
Little Truckee I	2008	3	Monitoring site	Sierra	central
Little Truckee II	2008	3	Monitoring site	Sierra	central
Little Truckee III	2008	1	Monitoring site	Sierra	central
Little Truckee West	2008	0	conspecific attraction	Sierra	central
Mabie	2008	2	surveyed to protocol	Plumas	north
Mackay Creek	2008	0	color band resight		
Martis Creek	2008	3	Monitoring site	Placer	central
Maxwell Creek	2008	0	surveyed to protocol	Alpine	south
Milton Reservoir	2008	4	Monitoring site	Sierra/Nevada	central
Perazzo Meadow	2008	8	Monitoring site	Sierra	central
Red Lake I	2008	0	surveyed to protocol	Alpine	south
Red Lake II	2008	0	surveyed to protocol	Alpine	south
Red Lake Peak	2008	0	surveyed to protocol	Alpine	south
Saddle Meadow	2008	0	color band resight	Sierra	central
Salmon Creek	2008	4	Monitoring site	Sierra	central
South Lake Tahoe Airport	2008	0	surveyed to protocol	ElDorado	south
Stampede @ Sagehen	2008	0	surveyed to protocol	Sierra	central
Stampede Reservoir @ Little Truckee inflow	2008	0	surveyed to protocol	Sierra	central
Tallac	2008	1	Monitoring site	El Dorado	south
Taylor	2008	1	Monitoring site	ElDorado	south
Trout Creek	2008	0	color band resight	ElDorado	south

Appendix A. continued

Appendix 71. continued					
Truckee Marsh @ Pope Beach	2008	0	color band resight	ElDorado	south
Truckee Marsh @ Upper Truckee	2008	0	color band resight	ElDorado	south
Uppermost Upper Truckee	2008	1	Monitoring site	El Dorado	south
Van Norden	2008	0	color band resight	Sierra	Central
Ward Creek	2008	0	color band resight	Placer	central
Warner Valley East Corral	2008	7	Monitoring site	Plumas	north
Warner Valley North Meadow	2008	10	Monitoring site	Plumas	north
Warner Valley South Bog	2008	8	Monitoring site	Plumas	north
Warner Valley Swamp	2008	18	Monitoring site	Plumas	north
Warner Valley West Corral	2008	5	Monitoring site	Plumas	north
Washoe State Park	2008	0	surveyed to protocol	El Dorado	south
Webber Lake/ Lacey Valley	2008		color band resight	Sierra	central
Wet Meadow	2008	1	color band resight		
Willow Creek	2008	5	color band resight	Plumas	north

Region				
Site	County	UTM east	UTM north	Ownership
South				
Grass Lake / Luther Pass	El Dorado	7 63 839	42 97 881	Lake Tahoe Basin MU
Maxwell	Alpine	7 65 369	42 94 105	Toiyabe National Forest
Red Lake 1	Alpine	7 63 230	42 87 896	CA Dept. of Fish & Game
Red Lake 2	Alpine	7 62 699	42 87 334	CA Dept. of Fish & Game
Red Lake Peak	Alpine	2 42 465	42 89 176	Toiyabe National Forest
Tallac	El Dorado	7 53 663	43 14 111	Lake Tahoe Basin MU
Taylor	El Dorado	7 55 200	43 13 700	Lake Tahoe Basin MU
Uppermost Upper Truckee	El Dorado	7 59 000	42 98 900	Lake Tahoe Basin MU
Washoe SP	El Dorado	7 58 100	43 04 900	Lake Tahoe Basin MU
Truckee				
Blackwood Creek	Placer	7 43 500	43 32 500	Lake Tahoe Basin MU
Cottonwood Creek	Sierra	7 35 639	43 79 791	Tahoe National Forest
Donner Camp	Nevada	7 43 200	43 61 800	Tahoe National Forest
Independence Lake	Nevada	7 30 000	43 67 750	Tahoe National Forest
Little Perazzo	Sierra	7 26 750	43 73 200	Tahoe National Forest
Little Truckee I	Sierra	7 27 400	43 74 350	Tahoe National Forest
Little Truckee II	Sierra	7 28 500	43 74 800	Tahoe National Forest
Little Truckee III	Sierra	7 28 300	43 74 800	Tahoe NF & Private
Mabie	Plumas	7 12 575	44 06 604	Plumas National Forest
Martis	Placer	7 47 880	43 53 938	Martis Creek Lake NRA
Milton Reservoir	Sierra	7 08 600	43 77 200	Nevada PUD
Perazzo	Sierra	7 25 250	43 72 700	Tahoe National Forest
Saddle	Sierra	7 31 700	43 74 300	Tahoe National Forest
Salmon Creek	Sierra	7 04 800	43 88 450	Tahoe National Forest
Stampede	Sierra	7 41 800	43 71 700	Tahoe National Forest
Webber Lake	Sierra	7 22 800	43 74 150	Private
Warner Valley				
East Corral	Plumas	6 41 250	44 75 750	Warner Valley State WA
North Meadow	Plumas	6 40 700	44 76 300	Warner Valley State WA
South Bog	Plumas	6 42 700	44 74 000	Warner Valley State WA
Swamp	Plumas	6 41 200	44 75 394	Warner Valley State WA
West Corral	Plumas	6 41 200	44 75 394	Warner Valley State WA

Appendix B. Locations and ownership of Willow Flycatcher monitoring sites in the Sierra Nevada, CA from 1997–2010.

Appendix C. Color bands used during cohort banding from 1997 to 2004 and periodically from 2005 to 2010.

Year	USGS Band Color
1997	white
1998	black
1999	violet
2000	turquoise
2001	dark green
2002	dark blue
2003	electric yellow
2004	bronze
2005	silver
2006	red
2007	purple
2008	blue

Color of anodized USGS metal bands designating natal year.

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Region	Site	Band Color
South	Red Lake I	silver (1997-2004)
	Red Lake II	silver (1997-2004)
	Red Lake Peak	orange plastic (2003-2006), blue/pink plastic (2006)
	Maxwell Creek	NA ^a
	Grass Lake	pink (1998) or violet (1999-2001)
	Uppermost Upper Truckee	orange (1998) or turquoise (1999-2004)
	Washoe State Park	NA ^a
	Tallac	silver (2005)
Truckee	Prosser Creek	light green
	Indepedence Lake	black (1998-2005), silver (2006)
	Saddle Meadow	NA ^a
	Little Truckee 3	red
	Little Truckee 2	gold
	Little Truckee 1	gold
	Little Perazzo	violet (2002) or red/white (2003-2005)
	Perazzo	bronze
	Webber lake	royal blue
	Martis Valley	mauve plastic
	Cottonwood Creek	white plastic (2005)
	Stampede Reservoir	light green plastic
	Milton Reservoir	pink plastic
	Mabie	white plastic (2003)
	Blackwood Creek	purple/white plastic (2005)
Warner Val	ley	
	South Bog	electric yellow ^b
	East Corral	violet (2003-2005) or turquoise (2005, 2006, 2008 ^b)
	West Corral	violet (2003-2005) or turquoise (2005, 2006)
	North Meadow	violet (2003-2005) or turquoise (2005, 2006)

^a Nestlings have not yet been banded at these sites, therefore no colors are assigned.