

University of Nevada, Reno

Population Dynamics of Willow Flycatchers in the Sierra Nevada

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in
Ecology, Evolution, and Conservation Biology

by

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ABSTRACT

In the western United States, Willow Flycatcher (*Empidonax traillii*) populations have declined, and the magnitude of these declines varies across the species range likely because of ecological differences among subspecies and variation in biotic and abiotic factors. Three subspecies of Willow Flycatchers breed in California one is the federally endangered southwestern subspecies and the two subspecies to the north are California state endangered species. Once common throughout central and northern California these populations now breed exclusively in montane meadows in the Sierra Nevada and Cascades. Surveys in the 1980s and 1990s indicated that populations were declining in the south and central Sierra Nevada.

My research focused on how multiple factors influenced reproductive performance of flycatchers and the implications of these estimates on population change. I examined these relationships in a low-density population of Willow Flycatchers breeding in the central Sierra Nevada from 1997–2008. Beginning in 2003 I also monitored two higher density flycatcher populations in the north Sierra Nevada to provide comparative estimates of reproductive performance. I grouped study sites into four regions based on geographic separation; however, I collectively refer to them as the central or north regions based on my comparative approach. The central and north regions differ in topography, vegetative characteristics, and land-use practices.

This research addressed the associations among weather, timing of the breeding season, predation and brood parasitism rates, and meadow and nest-scale characteristics and, in turn, how these affected reproductive investment, fecundity, site fidelity, and

potential for population growth. Flycatchers breeding in the central regions initiated nesting on average a week later than populations in the north and nesting was further delayed in years with late-season storms and low temperatures. Flycatchers in both regions ceased renesting attempts by the third week in July, and this pattern was consistent across all years regardless of nest initiation date. Thus, each day delay in the onset of nesting reduced a female's ability to renest. The effect that renesting probability has on fecundity is directly related to predation rates and females in the central region were not only limited by the length of the season but also by higher predation rates than the northern populations.

Reproductive success has strong implications on immigration and emigration processes in a region. Our results concurred with other studies on Willow Flycatchers that reduced reproductive performance encourages breeding dispersal from an area and also may reduce emigration if flycatchers use social cues to determine territory settlement in subsequent years. Furthermore, high natal philopatry contributed to annual site occupancy and considerably reduced fecundity would disrupt this dynamic. I documented a declining trend in flycatcher numbers in the two central populations over the twelve years of this study. Sensitivity analysis of population change models indicated that population growth in this area depended on increases in mean annual fecundity estimates; maximum survival estimates could not compensate for the consistently low fecundity estimates currently observed in the central Sierra Nevada population.

Results of this study indicated that nest survival rates in the central region were affected by weather patterns and meadow characteristics differently from populations in the north. Within the central study regions spring snowfall and a one-year lag affect of

winter snowfall influenced predation rates on flycatchers likely through top-down effects of predator-prey dynamics. While these fluctuations occur naturally, nest survival rates in the central region may be further suppressed alterations to the riparian habitat that they rely on for breeding. I found a trend towards decreased nest survival with distance from forest edges in large meadows where the majority of breeding flycatchers are in the central regions. Alternatively, edge effects predicted survival in Warner Valley with lower survival close to the forest. Large meadows may act to concentrate nest predators because of the availability of resources. Small mammals are common nest predators in my study sites and they rely on the cover of riparian shrubs for protection from their predators. Thus, the proportion of shrubs available for movement and foraging will increase probabilities of encountering nests within the shrub matrix. In small meadows shrubs were denser and provided increased contiguous cover.

Compared to the population in the north, the results of this study implied that reproductive success of flycatchers in the central Sierra Nevada was limited by length of the breeding season and nest predation, and that these factors were influenced by environmental stochasticity, population dynamics, and interactions between meadow-area effects and riparian shrub density. Improvements to the riparian ecosystem through restoration of natural hydrologic regimes and protection of riparian shrubs will improve habitat conditions for breeding flycatchers. Dense riparian shrubs will reduce predation pressure by influencing foraging strategies of predators and increased annual fecundity can buffer against the effects of unfavorable weather conditions.

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CHAPTER 1. REGIONAL DIFFERENCES AND EFFECTS OF WEATHER ON
REPRODUCTION OF WILLOW FLYCATCHERS IN THE SIERRA NEVADA,
CALIFORNIA

Abstract

The effects of weather on avian populations vary across regions and along elevation gradients. Birds breeding at mid- to high-elevations have evolved life-history strategies to cope with stochasticity in the environment; often these involve a trade-off between reproductive success and future survival. I studied the effects of weather on timing of nesting and nest survival and how these factors influenced reproductive investment (i.e., clutch size and renesting) and fecundity in Willow Flycatchers (*Empidonax traillii*) in the Sierra Nevada, California. This long-term study began in 1997 in two study regions in the central Sierra Nevada and I expanded monitoring in 2003 to two study regions in the north Sierra Nevada. I used logistic-exposure models to examine influences of weather on nest survival and individual-based, generalized linear mixed models to assess factors influencing clutch size, renesting probability, and individual fecundity. In my two northern sites, I observed longer nesting seasons, lower nest parasitism, higher daily survival rates, and higher fecundity. Lengths of the breeding season and nest initiation dates were the common variables driving variation in reproductive investment and success. These limitations were associated with temperatures in June. Additionally, an additive effect of increased spring snow and snow in the previous year predicted higher predation rates. Substantial differences in fecundity estimates indicated that factors limiting breeding investment and reproduction at study sites in the central Sierra Nevada might depress populations. I also identified a critical time period for nesting Willow

Flycatchers at the end of July when the majority of nests were in the nestling stage; nest failure at that time may eliminate the possibility of renesting.

INTRODUCTION

Climate can have profound impacts on avian population dynamics through the effects of local weather on reproduction and survival (Stenseth et al. 2002). Migratory birds that breed in seasonal environments have evolved life-history strategies for coping with stochasticity in the environment (Remes and Martin 2002). The relative impact that weather conditions exert on breeding populations varies spatially with elevation because of changes in abiotic and biotic factors in the system (Bears et al. 2009). These variations may be distinct across a relatively small geographic extent (Stenseth et al. 2002). Within species, populations breeding at different elevations may exhibit variation in life-history characteristics that ultimately involve trade-offs between reproduction and survival (Sandercock et al. 2005a,b; Bears et al. 2009). Thus, an understanding of region-specific demographic rates is critical for determining population status and growth rates. In light of recent concern about the impacts of climate change, understanding how annual variability in weather conditions affects bird populations is critical for conservation of songbirds.

Species breeding along elevation gradients have evolved life-history strategies that respond to constraints imposed by unpredictable environments (Sandercock et al. 2005b, Bears et al. 2009). Increases in elevation are associated with lower temperatures, increased frequencies of storms, and snow cover that persists into the end of spring (Ratliff 1985, Loheide II et al. 2009). In concert, these weather variables reduce the length of the growing season, limit primary production, and contribute to unpredictable or

scarce food availability (Hejl et al. 1988, Park et al. 2003). These limitations influence avian breeding populations through increased costs of reproduction, including higher thermoregulatory demands resulting from lower temperatures, seasonal delays in the onset of breeding (Perrins 1970, DeSante 1990, Hendricks 2003), early termination of breeding because of unfavorable conditions (Bears et al. 2009), and lack of synchrony with peaks in food sources (Thomas et al. 2001). At high elevations breeding birds may reduce reproductive effort in years of unfavorable environmental conditions, presumably as a trade-off for increasing individual survival (Sandercock et al. 2005b, Bears et al. 2009) and thus increasing the likelihood of returning in subsequent years when conditions may be optimal for breeding (Perrins 1970).

Weather also can influence reproductive investment and success through alterations in nest predation rates (Morrison and Bolger 2002). This variation may arise from direct effects of weather on predator communities (Picman et al. 1993) or predator foraging behaviors (Post et al. 1999, Morrison and Bolger 2002). Furthermore, changes in the environment that may arise from variation in weather can limit predator access to prey (Picman et al. 1993, Fletcher and Koford 2004, Hoover 2006). Top-down effects on nest survival also can arise from influences of weather events on predator-prey cycles in which predators respond with a time lag induced by weather-related changes to prey populations (Rotenberry and Wiens 1989, Schmidt and Ostfeld 2003)

Weather is an important influence in montane systems, and understanding how temporal and spatial variations in weather patterns influence reproduction of breeding birds is necessary for understanding population dynamics (Rotenberry and Wiens 1989, Wilson and Arcese 2003). In the Sierra Nevada, Willow Flycatchers (*Empidonax traillii*)

rely on wet montane meadows for breeding. Meadows in the Sierra Nevada are groundwater dependent systems that rely on winter snowpack and spring temperatures that determine the timing of snowmelt. During the summer, these meadows shift from mesic conditions to xeric conditions, and in extremely dry years xeric conditions may experience earlier vegetation senescence. 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 levels. Species reliant upon meadows at mid- to high-elevations may be further constrained by local weather events.

To understand how changes in weather patterns may influence populations of Willow Flycatchers, I examined the influence of weather on breeding populations in four regions along a latitudinal gradient in the Sierra Nevada. My first objective was to examine the effect of weather on timing of nesting and predation rates on nests. Second, I evaluated the relative influences of weather, timing of nesting, and predation rates on reproductive investment and fecundity. Within the context of these objectives, I address annual and regional variation in these measures.

METHODS

Study sites

I studied Willow Flycatchers (hereafter flycatchers) as part of a long-term study from 1997–2008 in in the central and north Sierra Nevada. Bombay (1999) selected study meadows (hereafter study sites) based on historical records, occupancy surveys in 1997 and 1998 and known locations of large breeding populations (Green et al. 2003)(C.

Stermer, unpublished data;). The number of study sites differed among years because of differences in annual funding, accessibility of properties, and re-occupation by flycatchers of meadows adjacent to my study sites (Appendix B). Based on latitude, geographic proximity, and the duration of my monitoring efforts, I grouped study sites into four study regions: South Tahoe, Truckee, Warner Valley, and McCloud.

I monitored five to seven sites annually from 1997–2008 in the South Tahoe region, located south of Lake Tahoe, California. These sites ranged in size from 5–98 ha and were at elevations from 1,900–2,410 m. From 1997–2008, I monitored 7–15 sites in my Truckee study region, which is located north of Lake Tahoe approximately 40–100 km from the South Tahoe region. These study sites ranged in size from 10–162 ha and in elevation from 1,730–2,120 m. From 2003–2006 and in 2008, I monitored flycatchers in Warner Valley, located in Lassen County, California. This extensive 250 ha meadow was 125 km north of the Truckee study region. I divided the meadow into four study sites based on vegetative and topographic divisions. These sites ranged in size from 15–24 ha and were at elevations of 1,560–1,590 m. In 2005 and 2006 I added a fourth study region along the McCloud River in Siskiyou County, located approximately 100 km northwest of Warner Valley. Study sites in McCloud ranged from 13–102 ha and were at elevations of 1,080–1,300 m.

My study sites, montane meadows, are classified as shrub meadows that rely on periodic flooding to maintain their transitional state (Fites-Kaufman et al. 2007). 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). These meadows are located along rivers, adjacent to lakes, or are spring fed and riparian deciduous shrubs parallel streams or are scattered in large clumps across the meadows. There is a north-south gradient in climate with sites farther north receiving higher precipitation (Fites-Kaufman et al. 2007). The riparian shrub community in my study sites was predominantly comprised of Geyer's willow (*Salix geyeriana*) and Lemmon's willow (*S. lemmonii*) in the South Tahoe and Truckee regions. In Warner Valley and McCloud, mountain alder (*Alnus tenuifolia*) and quaking aspen (*Populus tremuloides*) were interspersed with willow shrubs. Sedges (*Carex* spp.), grasses, rushes (*Juncus* spp.), and forbs dominated the herbaceous community. Sagebrush (*Artemisia* spp.) was intermittently located in upper portions of meadows, which were surrounded by a mixed coniferous forest dominated by lodgepole pine (*Pinus contorta*). Further details on numbers and locations of study sites and characteristics can be found in Appendix B.

Field Methods

I located all Willow Flycatcher territories using standard territory mapping techniques and adult behavior (Ralph et al. 1993). I used standard nest searching techniques (Martin and Geupel 1993) to locate and monitor nests during June through August. Because my goal was to determine fecundity of females, I consistently monitored all territorial males and females. I monitored nests every two to six days depending on estimated stage transition dates. I checked nest contents during every nest visit using a mirror or by directly observing contents; rarely were nests too high to obtain accurate observations of their contents. After approximately day 10 of the nestling stage, I did not approach the nest but observed it with binoculars from a distance. Although this method reduced the possibility of force fledging a nest, it sometimes hindered my ability to

acquire accurate counts of nestlings. I revisited all nest locations after the estimated fledgling date to determine if fledglings were in the immediate region.

Definition of variables

For all analyses I included only those nests for which I observed nest contents because I could not distinguish between nests that females abandoned during building or prior to laying from those that failed early in the laying period. I defined a nest with accurate initial nest content (i.e., clutch size) as nests located before day four of incubation to reduce inaccuracies associated with early brood loss.

I defined an adult male as territorial if I 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 my study (Bombay et al. 2000). I assumed that I detected all territorial males in my study sites because when defending territories males vocalized from exposed perches and their calls are distinctive. Detection of females varies with the stage of her nest attempt; activity is at a maximum during courtship and nest construction and then it declines considerably during egg laying, incubation, and early nestling stage (Ettinger and King 1980). After fledging, family groups are conspicuous and will remain in the meadow for approximately two weeks (Vormwald 2010). Thus for females not detected during nesting I was likely to detect only the females that successfully fledged young. To account for females not detected during nesting that did not successfully fledge young, I adjusted the number of females detected each year based on the number of females detected for the first time post-fledging (N_{pf}) and nest survival estimates for each year and region from my analysis (\mathcal{S}). I calculated the adjusted total number of females for each year and region as

$$N_t = (N_{pf} / s) + N_d$$

with N_d representing the number of females detected during nesting.

I obtained historical weather variables from the Western Regional Climate Center (Reno, NV). I selected data from weather stations near study regions that provided historical and consistent data across all years and that were at a similar elevation to the study region. I centered each weather variable by subtracting each annual value from the historical mean calculated from the last 50-years, which equates to a period of climatic change in the western United States marked by increased temperature variability and increased mean temperatures and reduced spring runoff from snowpack (Stewart et al. 2005). I defined winter as November through March, and I estimated spring snowfall from April and May.

For each nest I calculated the Julian date for the date incubation was initiated (last egg laid in nest; hereafter nest initiation). For nests found after incubation began I backdated by using known nest transition dates (i.e., nest hatch) or by estimating the age of nestlings; I calculated nest initiation date using the average length of each nest stage (Appendix D). To examine temporal trends within a season I standardized nest initiation dates by subtracting each nest initiation date from the mean nest initiation date from that year and region. To examine annual and regional trends in nesting onset and season length I determined the distribution of nest initiation dates within each region and year. Then I used the tenth and ninetieth percentiles and the standard deviation as indices for the onset of nesting, the annual termination of nesting, and the length of the breeding season, respectively (Chase et al. 2005). I used these indices to reduce the influence of extreme values in the analysis. I standardized each seasonal variable by subtracting it

from its mean across years within each region. I examined the influence of weather variables on nesting season onset using the tenth percentile of the distribution of nest initiation dates each year within a study region.

To estimate critical stage transitions I estimated three days for laying, 14 days for incubation, and nest fledging date at day 13 of the nestling period (total of 31 days of nesting). I assumed a nest was successful if at least one fledgling was located or if the nest was active until at least day 12. By day 12 of the nestling period the young are capable of force fledging (H. A. Mathewson pers. obs.) and thus at least one young may avoid predation. I assumed a nest failed because of predation if the nest was empty prior to day 12 of the nestling period. Although I attempted to locate fledglings within four days post-fledge; effort in determining the total number of young fledged varied across years. Thus for all analyses involving an estimate of young fledged I used the number of young last seen in the nest, which does not account for predation during the last few days of the nestling period or survival post-fledging.

To determine parasitism rates, I included only those nests that I located within the first four days of incubation. By eliminating nests found during later stages I reduced the chance that I would falsely count a nest as unparasitized when in fact parasitism had occurred but predators had removed the cowbird eggs before I found the nest.

I compared differences in clutch size, egg survival, egg hatchability, and nestling survival in parasitized and unparasitized nests to determine how parasitism could compromise my reproductive measures. I calculated egg survival as the number of nestlings observed in a nest within two days of estimated hatch dates relative to the number of known eggs laid for nests located prior to day four of incubation. To estimate

egg hatchability, I included only nests with known number of hatched and unhatched eggs, excluding nests for which any eggs were unaccounted for after the nest hatched. If eggs had any visible evidence of damage, such as punctures or holes in the shells, I considered the egg predated and included it with egg survival estimates. This is because my measure of unhatched eggs was intended to represent embryo mortality or fertilization failure. I calculated nestling survival as the proportion of the number of nestlings fledged to the total number of nestlings hatched for nests with a known number of eggs laid. I did not include nests in these calculations if I was unable to determine the stage during which an egg or nestling disappeared from the nest.

For clutch size estimates I considered the number of eggs in a nest as the maximum number of eggs laid by the female if I located the nest prior to day four of incubation because I cannot account for partial loss of nest contents in nests found at older ages. Furthermore, for clutch size analyses I removed nests that brown-headed cowbirds (*Molothrus ater*) had parasitized because they commonly remove single or multiple eggs.

Although I attempted to find all nests by monitoring females through out the season, I could not accurately determine which nests were first nest attempts. I found the majority of nests during the nest building or egg-laying period (58.8%, $n = 792$). For nests found after the egg-laying period, I used back-dating techniques (Mayfield 1961) and determined that the average day nests were located was 7.4 days (95% CI = 6.46 – 8.31) from the estimated day the first egg was laid.

Willow flycatchers in the southwest have a strong seasonal decline in clutch size (Paxton et al. 2007), as do many passerines. Thus, I classified nests as presumed first

nest attempts or known renesting attempts following a failed nest attempt. In my study regions, I have identified a standard interval within which the majority of females laid the maximum clutch size. Using this interval, distributions of nest initiation dates, and dates when females were located, I identified a subset of data that represented nest attempts by females that were potentially first nest attempts. In other words, females associated with each presumed first nest attempt had the potential to have laid a full clutch of four eggs. As part of my analysis I addressed some of these assumptions.

For each female I assigned a nest attempt number based on assumptions of presumed first nest attempts and on nest initiation order. My analyses regarding the probability of renesting focused on the following question: given that a female's presumed first nest fails, what influences her decision to renest? I defined the probability of renesting as the probability that a female will renest given that her previous nest failed.

I calculated fecundity as the number of female young produced per female detected within each study region assuming a 50:50 nestling sex ratio (Paxton et al. 2002). I included females for which no nests were located based on the assumption that all females attempted to nest; however, I excluded females from territories that were not continuously monitored during the season. If I located a family group (fledglings and adults) for a female that I had not continuously monitored or for a nest that I had not monitored, I included these data but used the mean number of young fledged per successful nest in that study year and region. I adjusted the number of young in these cases because detection of individual fledglings was low and varied with study year and region although detection of a family group was high (Vormwald 2010). My estimate was a maximum estimate of fecundity because I used the number of young last seen in the

nest prior to fledging; thus, I did not account for survival during the last few days of nesting. I adjusted fecundity estimates using the detection probability calculated for determining the number of females (see above).

Statistical analysis

I examined multicollinearity among my weather variables using a variance inflation factor >2.0 as a criterion for removal (Graham 2003). Additionally, I evaluated relationships among weather variables prior to model fit using multiple regressions. I conducted all analyses in SAS version 9.2 (SAS institute, Cary, North Carolina).

I examined the influence of weather variables on nesting season onset using the tenth percentile of the distribution of nest initiation dates each year within a region. I examined univariate normality plots and determined that region-year combinations with ≤ 10 nests were not representative of the distribution of nesting in that year; therefore, I excluded 1997 in the Truckee study region, 2006 in Warner Valley, and 1997 and all years after 2001 in the South Tahoe study region. I used generalized linear modeling and type II sums of squares to evaluate the contribution of individual variables to total variance in annual nest initiation. I examined residuals and predicted values to determine the influence of any potential outliers, but I did not remove any *ad hoc* because extreme variations in weather events were important to my study.

I examined three sets of nest survival models. First I determined the most predictive temporal model, and then I evaluated the effects of weather and parasitism. For the temporal model I considered models that included regional differences; a categorical year effect; linear effect of elevation; either a linear, quadratic, or cubic effect of nest age; and a linear or quadratic effect of date. By allowing nest age and date to vary, I could

better understand how nest survival changed over time; holding either effect constant or considering only a linear effect could mask important ecological patterns that may reflect site-specific adaptations to predators (Grant et al. 2005). For passerines, a cubic effect of age is reasonable because of changes in cues available to predators with transitions to different nesting stages (Grant et al. 2005). I predicted that survival would decrease linearly across the season because predator abundances and activity may increase and accessibility to nests increases as water evaporates (Picman et al. 1993). Additionally, I considered a quadratic effect of date because nest survival may peak in mid-season when alternative prey availability is high.

The weather effects model included winter snow, spring snow, winter snow with a one-year time lag, and temperatures in June and July. I constructed 42 models that included all main effects, combinations of weather variables, and additive combinations of variables selected from my temporal model and each main effect of weather or combination of weather variables. My weather combination models were based on *a priori* hypotheses concerning additive effects of weather that might work in concert over time to influence nest survival rates. Both main effects of weather variables and my combinations are based on the general hypothesis that decreased meadow wetness will result in increased nest predation rates because of accessibility to nests (Picman et al. 1993, Fletcher and Koford 2004). Within this context, I predicted increased nest survival following years with increased winter snowfall or spring snowfall, or with increased temperatures in June or July. Additionally, I considered the effects that weather may have directly on predator abundances by considering a time lag effect of snowfall in the previous winter. This is because small mammal populations often fluctuate with

resources over a two-year period (Rotenberry and Wiens 1989, Schmidt and Ostfeld 2003).

For my temporal and weather model, I included region and elevation in each model. Differences in topography and elevation could influence weather patterns differently, requiring us to account for variations in weather within region-years. Region was highly correlated with elevation ($r = 0.77$) thus I was unable to distinguish between these effects. For any models in which elevation was a significant influence, I *post hoc* replicated the modeling process within study regions to compare between the effects of different regions or elevations.

Nest survival and brood parasitism

I considered the effect that brood parasitism might have on nest survival as a separate analysis. Brown-headed cowbirds are known to remove nest contents after the female has initiated incubation, presumably to force renesting and increase opportunities to parasitize nests during the laying period of the host (Arcese et al. 1996, Kosciuch and Sandercock 2008). Nests that are parasitized may be located in regions with high abundances of cowbirds, increasing susceptibility to predation (Hannon et al. 2009). Alternatively, parasitism and predation by other nest predators may co-occur as a consequence of a poor nest site location or variation in adult behavior (Uyehara and Narins 1995). Researchers have hypothesized that parasitized nests may attract predators during the nestling stage because of increased food demands by the larger cowbird (Hoover and Reetz 2006); however, my practice of addling cowbird eggs removed the effect of cowbird nestlings in nests.

I applied a hierarchical approach for constructing nest survival models (Stephens et al. 2003). I used a logistic-exposure approach (Shaffer 2004, Shaffer and Thompson 2007) that uses a modified logit-link function with an exponent to account for the probability that a nest surviving an interval between nest checks is dependent upon the length of that interval. I used the Akaike information criterion (AIC; Akaike 1973) to evaluate candidate models and considered models with a $\Delta\text{AIC} < 4$ to be competitive models (Burnham and Anderson 2002). The AIC_w indicates the weight of evidence in favor of the model given the set of candidate models. To account for model selection uncertainty, I calculated model-averaged parameter estimates, unconditional standard errors, and 95% confidence intervals. I used odds ratios and associated 95% confidence intervals to evaluate the direction and strength of each relationship. The odds ratio value indicates the likelihood of an outcome for every one-unit increase in the predictor variable. Predictor variables associated with odds ratio confidence intervals that do not include 1.0 are considered to have an effect on the likelihood of a nest either succeeding or failing. I used a Z-transformation on all variables before fitting any models. I used the model-averaged estimates to predict daily survival rates for differing values of a predictor. To calculate predicted estimates I allowed the value of one predictor variable to vary while holding the remaining predictor variables constant at their mean value. I selected the values for the predictor variables from the range of values observed in the field.

Model-selection results indicate the support for a model relative to the other models, but determining how well the model fits the data requires post hoc analyses (Shaffer and Thompson 2007). Typically, the chi-square goodness-of-fit is used to assess

the fit of generalized linear models; however, for small sample sizes the chi-square does not provide a good approximation of the distribution of the continuous covariates. To acquire the observed predicted daily survival rate for continuous predictor variables I grouped observations into several classes and then I estimated the daily survival rate for each class. Precision of observed estimates were often low due to small sample sizes within each class.

In addition to overall nest survival, I examined the influence of brown-headed cowbird parasitism on different reproductive components. I pooled data from all years and study sites for parasitized and unparasitized nests and compared differences between clutch size, proportion of eggs surviving to hatch, proportion of unhatched eggs, and proportion of nestlings surviving to fledge using *t*-tests with a Satterthwaite adjustment for unequal variances.

Reproductive investment and fecundity

I evaluated my assumptions regarding presumed first nest attempts by determining the consistency of seasonal declines in clutch size using general linear models weighted by the number of nests within each study region and year. Furthermore, I examined descriptive statistics of clutch sizes and renesting attempts. To examine the influences of weather, regional variation, predation, and timing on reproductive investment and fecundity I constructed models that were appropriate for each response variable (clutch size, renesting probability, and individual fecundity). Also included in each model were the predicted daily survival rates determined for each region-year from my best temporal and weather-effects model.

Reproductive investment and fecundity

For evaluating the effects on clutch size of presumed first nest attempts, I included the following variables: elevation, daily survival rate, nest initiation date, spring snow, and temperatures in June. I included daily survival rates to control for years with high predation rates that may have decreased my detection of nests. I did not include temperatures in July in these models because the mean and standard deviation of presumed first nest initiation dates, when clutch size is determined, occurred in June in each of my study years. Because of small sample sizes for nests with less than three eggs, I compared between nests with four eggs and those with three eggs or less.

For my models addressing the probability of females reneating following nest failure, I considered elevation, within season temporal variables, all weather variables, and daily survival rates. Within season temporal variables included length of the breeding season (indexed by the standard deviation of the mean of all nest initiation dates) for each region and year and two measures associated with the first nest that failed (nest initiation date and number of exposure days) to examine temporal constraints on reneating probabilities. Weather variables included winter snow, spring snow, and temperatures in June and July. I included nest survival rates because it influences the number of females available to reneate and females may invest less in reproduction in years when nest predation is high.

For individual fecundity for females, I evaluated the effects of elevation, initiation date of first nest, daily nest survival, spring snowfall, and temperatures in June and July. I included nest survival rates to control for variations among years because fecundity is inherently a function of nest survival.

To address variation in reproductive investment and fecundity I used a generalized linear mixed model approach with nested random effects that allowed for binomial distributions for effects on clutch size and re-nesting and a Poisson distribution for fecundity (Littell et al. 1998, Agresti 2007). I treated study sites within years as random effects. Repeated observations of nests within the same study sites and across multiple years suggested potential violation of statistical independence among observations (Littell et al. 2000, Bolker et al. 2009). My intention was not necessarily to examine the variance explained by my random effects but instead to treat them as nuisance variables (Bolker et al. 2009) that serve to improve inferences about the fixed effects (Gutzwiller and Riffell 2007, Bolker et al. 2009). I used a spatial power law covariance structure that allows for correlations within sites across adjacent years when time periods are unequally spaced (Littell et al. 2006). For example, Willow Flycatchers exhibit high site fidelity (Chapter 2 (Sedgwick and Knopf 1989, Paxton et al. 2007), creating a potential violation of statistical independence resulting from repeated observations of the same individuals within sites over time. I used a Laplace approximation to estimate the likelihood because the traditional penalized quasilikelihood estimations are biased for binary data with nested random effects (Breslow and Clayton 1993, Vonesh 1996, Raudenbush et al. 2000).

I determined the significance of random effects by testing whether Z -values were different from zero for the within-subject variance (σ^2) and the correlation coefficient (ρ) (Littell et al. 2006). For each model I examined the fitted effects correlation matrix for potential multicollinearity problems between variables and considered correlations of $r >$

0.7 as influential (Graham 2003). I evaluated variable significance using Type III estimable functions and considered variables non-significant at $P > 0.05$.

RESULTS

From 1997 to 2008, at four study regions in the central and north Sierra Nevada I detected 981 Willow Flycatcher territories, and found 904 nests. To meet sample size requirements for my mixed model analyses I included three study sites in the South Tahoe region, 10 in the Truckee region, four study sites in the Warner Valley region, and three in the McCloud region.

My study coincided with a period of above 50-year mean winter and spring snowfall until 2000 when the Sierra Nevada and California experienced below mean drought years (Roos 2008) Fig. 1) The winter and spring of 2005 were characterized by increased precipitation, but drought years followed again starting in 2006 (Roos 2008). Snowfall and temperature trends were similar across all regions. Temperatures in June and July were above the 50-year mean for all regions (Fig. 2) with some exceptions in years associated with above average spring snowfall.

Winter snowfall was significantly correlated with temperatures in June ($r^2 = 0.463$, $P = 0.06$, $n = 30$) but was not related to snowfall in spring ($r^2 = 0.000$, $P = 0.922$, $n = 30$). Temperatures in June were not correlated with spring snowfall ($r^2 = 0.463$, $P = 0.06$, $n = 30$) or temperatures in July ($r^2 = 0.026$, $P = 0.397$, $n = 30$). Because of the statistical association between winter snowfall and temperatures in June, I eliminated from my sets of candidate models any predicted combined effects of winter snowfall and June temperatures and for some variable combinations I considered two sets, including winter snowfall in one set replaced by June temperatures in the other.

There was no discernible trend among years in nesting season onset, median date, and synchronicity of nest initiations (Fig. 3). However, mean annual nest initiation in Warner Valley and in McCloud was 5.2 days earlier than in the Truckee region and 3.8 days earlier than in the South Tahoe region (Table 1). The Truckee region was 1.4 days earlier than in the South Tahoe region. Nests fledged earlier in the Warner Valley and McCloud regions. 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 ($n = 11$) days in South Tahoe, 61.8 ($n = 12$) days in Truckee, 67 ($n = 4$) days in Warner Valley, and 68.5 ($n = 2$) in McCloud (Table 1).

Temperatures in June explained 58.2% of variation in nesting season start date compared to spring snowfall and temperatures in July ($r^2 = 0.592$, $P < 0.000$, $n = 22$; Fig. 4a). A delay in the onset of the nesting season was associated with a decrease in the mean clutch size of presumed first nests ($r^2 = 0.27$, $P = 0.034$, $n = 17$).

Nest survival and brood parasitism

Predation was the primary cause of complete nest failure in 86% ($n = 371$) of nests, whereas abandonment associated with parasitism, unknown causes, and unhatched clutches accounted for the remaining nest losses. For nests I located before day 4 of incubation (i.e., I assumed accurate clutch size estimates) at all study sites from 1997–2008, I documented partial predation in 111 nests (22.1%; $n = 503$), and the percent of nests partially predated was similar for all regions (South Tahoe: 28%, $n = 50$; Truckee: 22%, $n = 313$; Warner Valley: 20%, $n = 140$). Of those nests for which I assumed I accurately documented partial predation, 55.9% ($n = 111$) subsequently failed.

The temporal model that received 99% of support included an additive effect of a cubic trend in nest age and region. Predicted values and observed values were similar indicating goodness-of-fit of my selected model for each region (Fig. 7). The probability of nest survival was lowest on the first day of nest initiation and it increased until approximately the first few days of the incubation period when it remained relatively steady, declining slightly until approximately day 5-6 of nestling period. Probability of survival increased after about day 7-8 of the nestling period.

In evaluating the effects of weather variables on daily nest survival, I found that the best-fit model, considering effects of region and a cubic trend in nest age, included the effects of spring snow (total $AIC_{\omega} = 0.72$) and snow in year $t-1$ (total $AIC_{\omega} = 0.55$, Table 2). Although model-averaged estimates indicated some variation in the direction of the effect of April snow (odds ratio = 0.91, 95% CL: 0.792–1.021), daily nest survival generally decreased with increased snow in the spring. There was less support for the effect of snow in year $t-1$ (odds ratio = 0.96, 95% CL: 0.88–1.064) but the relationship with daily nest survival also was negative.

The mean annual parasitism rate in the South Tahoe region was 18.4% ($n = 11$ years), 11% ($n = 12$) in the Truckee region, and 8.4% ($n = 5$) in the Warner Valley region. I only found one parasitized nest in the McCloud region ($n = 52$ nests). Parasitized nests had a 27.1% smaller clutch size equivalent to one egg ($t = 6.8$, $P < 0.001$), 32.3% higher proportion of unhatched eggs ($t = 3.5$, $P = 0.002$), and 69.1% lower egg survival ($t = 4.9$, $P = 0.0003$) compared to unparasitized nests. There was no difference in nestling survival ($t = 1.24$, $P = 0.2$). Nest survival rate for parasitized nests was 22.2% compared to non-parasitized nests with nest survival rate of 54.7%.

Reproductive investment and fecundity

Within each region clutch size declined significantly with date of nest initiation (South Tahoe: $r^2 = 0.116$, $P = 0.018$, $n = 48$; Truckee: $r^2 = 0.267$, $P < 0.001$, $n = 306$; Warner Valley: $r^2 = 0.147$, $P < 0.001$, $n = 133$; McCloud: $r^2 = 0.266$, $P = 0.002$, $n = 34$). For females with known renesting attempts, 15% ($n = 104$) laid four 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. Based on my classification of presumed nests, I determined that across all nests and years the odds of a female laying a full clutch (four eggs) in a presumed first nest attempt was 79.5% greater than the odds of a small clutch size ($n = 341$). Sample sizes were small in the South Tahoe region for estimating annual clutch sizes (Fig 5a). There was no discernable annual trend in clutch sizes in the Truckee region (Fig. 5b); however, in the Warner Valley region clutch sizes of presumed first nest attempts appeared to decline from 2003–2005 (Fig. 5c).

For my models addressing the effects on clutch size in the South Tahoe and Truckee regions combined, variance within study sites was not significant ($\sigma^2 = 0.36$, $SE = 0.327$, Z -test = 1.09, $P = 0.14$) but there was significant correlation among study years within study sites ($\rho = 0.68$, $SE = 0.304$, $Z = 2.25$, $P = 0.02$). In South Tahoe and Truckee the probability of a female laying a full clutch of four eggs increased with increasing elevation, increased in years with higher snowfall, and decreased with later dates of nest initiation (Table 3). In Warner Valley there were no significant random effects and the probability of a female laying a full clutch of four eggs increased in years with higher temperatures in June (Table 4).

The proportion of females that renested following a failed nesting attempt fluctuated among years within study regions (Fig. 6). Nest initiation date for renests occurred no later than 4 Aug in South Tahoe, 3 Aug in Truckee, and 7 Aug in Warner Valley and McCloud. In all regions combined for females whose first nest attempts failed, the estimated mean nest initiation date for females that renested was 6.0 days earlier than females that did not renest ($t = 8.5$, $P < 0.001$). Similarly, mean nest failure dates of first nest attempts for females that renested were 15.4 days earlier than for females that did not attempt to renest ($t = 13.8$, $P < 0.001$).

In South Tahoe and Truckee, there were no significant random effects on the probability of renesting ($\rho = 0.47$, $SE = 0.816$, Z -test = 0.58, $P = 0.3$; $\sigma^2 = 0.62$, $SE = 0.425$, Z -test = 1.47, $P = 0.1$). The probability of renesting following a failed nest increased (1) in years with longer breeding seasons, (2) following a previous nest attempt that was initiated earlier in the season, (3) following a failed nest attempt that failed earlier in the nesting cycle, (4) in years with reduced spring snowfall, and (5) in years with higher July temperatures (Table 5). In Warner Valley the random effects were not significant. The probability of renesting increased (1) in years with longer breeding seasons, (2) following a previous nest attempt that was initiated earlier in the season, and (3) following a failed nest attempt that failed earlier in the nesting cycle (Table 6)

Minimum fecundity estimates declined in the South Tahoe from 1997-2004 (Fig. 10) after which no more than three females each year were detected. Fecundity estimates in the Truckee region fluctuated annually showing no discernable trend. Mean annual fecundity estimates were 23% higher in Warner Valley (mean = 1.76, $SD = 0.243$, $n = 4$) and McCloud (mean = 1.76, $SD = 0.247$, $n = 2$) than in Truckee (mean = 1.43, $SD =$

0.413, $n = 11$) and 40% higher than South Tahoe (mean = 1.26, SD = 0.645, $n = 10$). In South Tahoe and Truckee there were no significant random effects. Fecundity increased for females that nested earlier in the season and in years with higher nest survival (Table 7). In Warner Valley individual fecundity was not predicted by any of the variables used in this analysis (Table 8).

DISCUSSION

For Willow Flycatchers nesting in the two north Sierra Nevada study regions I observed longer nesting seasons, lower nest parasitism, higher daily nest survival, and higher fecundity compared to estimates in the Truckee and South Tahoe regions. Temperatures in June emerged as an important weather variable influencing the timing of nest initiation by delaying initiation in years with low temperatures. Furthermore, nesting delay was consistently a significant factor influencing reproductive investment and fecundity. Late season storms and low temperatures at the start of the breeding season appear to influence reproduction of flycatchers in the two regions in the central Sierra Nevada more so than the northern populations. However, higher temperatures in June positively influenced investment in clutch size in the north. The strongest influence on populations in the South Tahoe and Truckee regions might be limitations imposed by factors that delay nesting at the start of the breeding season, thus reducing the likelihood of renesting. Because flycatchers nest earlier in the northern populations, temporal constraints may be relatively relaxed compared to the southern regions. Furthermore, reduced nest survival rates in the north regions compounded with reduced temporal constraints may substantially improve reproductive rates in the north. The interactive effect of nest predation rates and as little as five days difference in nest initiation has been

shown to alter fecundity estimates by 0.25 young per female (Marshall et al. 2002). My results highlight the importance of successful, early season nests for improving fecundity of Willow Flycatchers because fecundity is a function of clutch size and re-nesting attempts, both of which are limited as the breeding season progresses.

Nest survival

Nest predation was the primary cause of nest failure at my study sites but I observed considerable annual variation in nest survival, a trend observed in many passerines (Silllett et al. 2000, Knutson et al. 2007). However, model-predicted estimates indicated considerably higher nest survival in the Warner Valley and McCloud regions compared to those in the South Tahoe and Truckee regions. Regional variation in daily nest survival rates in my study may be influenced by a multitude of abiotic and biotic factors such as size and distribution of meadows, elevation, topography, hydrology, or vegetative communities. Furthermore, Willow Flycatcher territory densities in the northern regions are twice as high as those in the Truckee region and almost four times the density in the South Tahoe region (Appendix C), suggesting potential influences of density-dependent factors. Differences in vegetation structure can influence predators by altering their ability to locate nests using auditory, visual, or olfactory cues (Martin 1992) or by physically impeding predator movement through the shrub matrix (Martin 1993, Chalfoun and Martin 2009). The influence of the vegetative community on predator behavior may depend upon the primary nest predators in the region and variation in the abundance (Zimmerman 1984, Andren 1992, Rodewald and Yahner 2001) or the diversity of nest predators (Davidson and Knight 2001, Bakermans and Rodewald 2006). Higher quality of the habitat surrounding nest-site locations can offset negative effects of

increased parental behavior (Weidinger 2002) during the vulnerable early-nestling stage of Willow Flycatchers.

The strongest predictor of nest survival of Willow Flycatchers in all study regions was nest age. Nest survival was lowest during egg laying when nest attendance by adults is low (Soroka and Morrison 2005) and nest predators quickly locate nests placed in poor locations (Martin et al. 2000). Nest survival was high once incubation was initiated but steadily declined until approximately day six of the nestling period. This generated concern that my practice of banding nestlings may have caused reduced survival during that period; however, I *post hoc* ruled out researcher effects because I banded young on day 7-9 and only 7.3% ($n = 588$) of the nests in my study failed after banding of nestlings. Increases in predation from hatch until approximately half-way through the nestling period is common for many passerines Grant et al. 2005 (Purcell 2006) and is commonly attributed to increasing demands in feeding activity at the nest once eggs hatch (Grant et al. 2005). McCabe (1991) described a substantial decline in the time a female Willow Flycatcher spends on the nest with a concomitant peak in feeding activity on approximately day seven during the nestling stage. The impact of adult activity patterns at the nest on predation may depend upon cues used by the primary predators to locate nests or on foraging strategies. Increased survival in the latter half of the nesting period may be because nestlings are too large for some species of nest predators (Montgomerie and Weatherhead 1988, Grant et al. 2005) and because older nestlings may escape predation by force fledging from the nest prematurely (Pietz and Granfors 2000).

Daily nest survival was inversely related to spring snowfall in year t (the nesting season) and winter snowfall in the previous year (1-year lag) indicating an additive effect

between events occurring across a two-year period. Mammals are likely the primary nest predators in my 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.). 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. My model results predicted that increased spring snow fall resulted in increased abundances of nest predators, particularly if winter snowfall in the previous year also was high. Other studies in the Sierra Nevada have detected increased abundances of small mammals in summers following a one-year lag in winter snowfall (Wilson et al. 2008, Cocimano 2009). This pattern of a time lag in weather effects is common in systems reliant upon pulsed resources (McShea 2000, Clotfelter et al. 2007, Wilson et al. 2008).

Small mammals rely on masting events in the fall for over-winter survival (Clotfelter et al. 2007, Kuhn and Vander Wall 2008, Wilson et al. 2008). Masting events are spatially heterogeneous and species-specific, and many conifers will forego masting in drought years (Wilson et al. 2008). Because summers in the Sierra Nevada are dry and drought conditions are determined by precipitation events during the winter and spring months (Loheide II et al. 2009), winter snowfall may determine cone crops in the following autumn (Wilson et al. 2008). Increased food resources result in higher overwinter survival, possibly because density-dependent competition for food may be relaxed (Merritt et al. 2001, Kalcounis-Rueppel et al. 2002).

There is some debate about the direct influences of winter snow on small mammal survival because of interactions with density-dependent processes (Lewellen and Vessey 1998, Kalcounis-Rueppel et al. 2002). Generally it is assumed that snowpack provides benefits through its insulation properties and protection from generalist predators (Merritt et al. 2001, Hansson 2002, Clotfelter et al. 2007). In the spring, reduced snowfall and warm temperatures may increase the rate and timing of snowmelt, resulting in increased mortality of small mammals through increased water in subnivean tunnels (Aars and Ims 2002, Korslund and Steen 2005). Alternatively, earlier snowmelt may provide an opportunity for mammals to reproduce earlier (Wilson et al. 2008).

Generalist (i.e., raptors) and specialist (i.e., mustelids) predators respond to abundances of small mammals, often with a time-lagged numerical response (McShea 2000, Ostfeld and Keesing 2000, Clotfelter et al. 2007). Weather and prey abundance contribute to considerable variation in annual reproduction of predators (Franklin et al. 2000). For example, reproductive success of goshawks increases in the spring following a high mast-year because of increased prey populations (Keane et al. 2006). However, reproduction and territory occupancy of goshawks is reduced in the spring if weather patterns delay emergence of hibernating prey species (Fairhurst and Bechard 2005). Specialist predators, such as weasels, hunt for rodents in subnivean tunnels during the winter (Fitzgerald 1977) and have been shown to reduce populations of rodents in regions with high snowpack (Hansson 1987). Short-tailed weasels specialize on voles and may respond to reduced prey availability by moving out of the region (Fitzgerald 1977); however, long-tailed weasels have diverse diets and may switch to alternative prey items (Fitzgerald 1977, Merritt et al. 2001).

Interpreting my model results is challenging because of the multitude of relationships among abiotic factors (i.e., weather) and community-level processes (Schmidt and Ostfeld 2003). Weather patterns may influence pulsed resources, such as masting events, in my system, which in turn, may produce both bottom-up and top-down effects on the community (Pace et al. 1999).

Overall, daily nest survival was weakly influenced by weather patterns compared to the effects of nest age and brown-headed cowbird parasitism. Parasitized nests had lower daily survival rates, reduced clutch sizes, reduced egg survival, and increased hatching failure, 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). However, because I added cowbird eggs I effectively removed this as a potential mechanism. Another mechanism for increased predation is that parasitized nests may be in suboptimal nest locations facilitating discovery by cowbirds and other nest predators (Arcese et al. 1996, Hannon et al. 2009). Although the effect of parasitism on reproductive output is substantial, parasitism rates were high in the South Tahoe region compared to other species at high elevations (Purcell and Verner 1999, Smith et al. 2005). For a population of flycatchers in southern California parasitism rates would need to be less than 10% for the population to experience growth and estimates from our central study regions exceeded this (Uyehara and Narins 1995, Whitfield et al. 1999). Lower rates in my other study regions should not be dismissed because brood parasitism can act as an additive effect on other limiting factors (Rothstein et al. 2003).

Reproductive investment

The timing of nesting emerged as a primary factor influencing clutch size, probability of renesting, and individual fecundity. Clutch size decreased in presumed first nest attempts with later nest initiation dates. Because these nests are within an interval of time when other females laid full clutch sizes, I assume this response indicates reduced investment in clutch size. In years when nesting was delayed for all females, mean clutch size was lower than other years. Cold weather in June delayed the initiation of the breeding season, likely because of reduced food availability (Hejl et al. 1988) and increased physiological demands during a period of high energetic demands (Ettinger and King 1980). Willow flycatchers are long-distance migratory birds and are predominately insectivorous (Wiesenborn and Heydon 2007). Migratory birds must obtain the necessary nutrients to initiate nesting after their arrival on the breeding grounds. Daily energy expenditure is highest for female flycatchers during courtship, nest selection, and nest construction because of increased activity and because ovogenesis begins during this period (Ettinger and King 1980, Carey 1996). If food acquisition is constrained, females are forced either to delay nesting until acquiring optimal nutrition status or to reduce investment in nesting (Drent and Daan 1980). Low temperatures or late-season storms likely limit the availability of insects because insects are unable to fly below certain temperatures (Finn and Poff 2008) or their emergence is delayed (Harper and Peckarsky 2006, Finn and Poff 2008). Females that arrive in poor condition may be forced to initiate nesting before acquiring optimal nutritional status, and clutch size reduction may compensate. This trade-off between reproduction and survival is common for birds nesting in seasonal environments (Bears et al. 2009).

Another explanation for clutch size reduction in unfavorable years is the potential for a mismatch between the breeding cycle and resource abundances (van Noordwijk et al. 1995). Willow flycatchers arrive later at my study sites than other passerines, resulting in a relatively short breeding season. There is potentially a trade-off between earlier arrival and breeding season length, suggesting that Willow Flycatchers may be timing their nesting cycles to peak resources. If a mismatch in timing results in food shortages, it is advantageous for female Willow Flycatchers to reduce clutch size and, thereby reduce demands for food during the nestling or post-fledging stage. Conditions on the breeding grounds during the pre-breeding stage may provide proximate cues for predicting food availability later in the season. However, Willow Flycatchers are considered generalists in their diet (Wiesenborn and Heydon 2007), and most studies supporting mismatches in peak resources are on species that are more reliant on specific insects, such as Lepidoptera. Results from other studies on the influences of food limitation on clutch size are contradictory and many were associated with food supplementation (Arcese and Smith 1988, Marshall et al. 2002).

I found that clutch size of presumed first nests increased with elevation. Elevation is an important factor in life history trait evolution (Cody 1966, Badyaev 1997), and variation in reproduction and survival is detectable at elevation differences of 1,000 m (Bears et al. 2009), similar to the range of elevations in this study. A long-standing hypothesis is that high-elevation species have higher productivity due to unpredictability of the environment, reduced duration of the breeding season, limited food, and low population densities (Cody 1966). Recent studies contradict this pattern and instead suggest reduced productivity at high elevations (Badyaev 1997, Bears et al. 2009),

particularly if this coincides with the upper end of the breeding distribution (Purcell 2006). My results correspond with the original assumption, in that my study sites at higher elevations (2,000 m) had low population densities and shorter breeding seasons compared to my lower elevation sites (~1000-1500 m). It may be that birds breeding at my high-elevation sites invest more in clutch size because of their limited capacity for renesting should the first nest fail. Alternatively, birds breeding in low-elevation sites may reduce their clutch size because they are able to invest more in renesting efforts. Dark-eyed juncos increase their clutch size in years with reduced time to reneest because of delayed breeding seasons; however, this is a trade-off between years in which they are able to double-brood (Smith and Andersen 1985).

Delaying nesting may not be an option in years limited by temperatures in June because my results indicated that the primary limitations on renesting opportunities are associated with timing of initiation and failure of the initial nest attempt. At my study sites, breeding season length was shortened in years with lower temperatures in June. The timing of spring migration of Willow Flycatchers in my regions already reduces the breeding season length relative to other species because migratory birds are limited in breeding season length by necessary preparation for fall migration. This constraint has been shown for other single-brooded species with relatively short breeding seasons (Marshall et al. 2002, Murphy 2004). Nesting delays reduced the likelihood of being able to reneest if the previous nest fails for flycatchers in all my study regions. My data indicated that mid-July might be the maximum date for a failed nest attempt after which females do not attempt renesting. In *post hoc* examination of my data I found that for all study regions only three ($n = 158$) females reneested 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 Tahoe regions. This suggests that seasonal delays in the onset of the nesting season may have stronger implications in the central Sierra Nevada where the length of the breeding season was shorter than the regions in the north. This is likely due to elevation differences among study regions; breeding seasons in the lower elevation northern sites started earlier and lasted longer. Marshall et al. (2005) demonstrated that a difference of five days in nest initiation might interact with high predation or parasitism rates and cause a reduction in fecundity by 0.25 young per female. My nest survival analyses indicated higher predation in the South Tahoe and Truckee regions, further supporting the significance of the difference in breeding season length on reproductive success among my study regions. My observation of two cases of double-brood attempts by marked females in the Warner Valley study sites also supports the impact of a longer nesting season.

Fecundity

Daily survival rate was the strongest predictor of fecundity for individual females in my study regions. Fecundity also was influenced by the date for which females initiated their first nests of the season. These factors actually work in concert to determine the ability of a female to renest. If nest survival is high, renesting may have less of an impact because fewer females need to renest. When nest predation is high, delays in the onset of the nesting season, caused by low temperatures in June and delays in individual nest initiation effectively shorten the breeding season and can have measurable effects on fecundity estimates. For example, Marshall et al. (2002) found that for red-eyed vireos a delay in nesting of 5 days when predation was high resulted in a

decrease in seasonal fecundity of 0.25 fledglings per female. Thus, my results indicate that females should initiate nesting as early in the season as possible to maximize the potential to reneest.

Management implications

Improving nest survival rates of Willow Flycatchers in the central Sierra Nevada may offset the limitations imposed by shortened breeding seasons and buffer against natural stochasticity in the environment. Reducing disturbances to nesting birds through the end of July will positively influence reproductive success. For some grazing regimes in meadows in the Sierra Nevada livestock are moved in around mid-July, a time period presumably allowing flycatchers to breed undisturbed. However, these results suggest that the end of July remains a critical time period because of effects on reneesting and increased failure rates of nestlings. Improvements to riparian habitat will always positively affect breeding flycatchers through increases in food resources or reduction in predation rates. The results from this study might suggest that climate change patterns towards increased temperatures and fewer storms could benefit flycatchers in the Sierra Nevada. However, this is misleading because ultimately reproductive success is dependent upon high quality breeding habitat.

In the Sierra Nevada, Willow Flycatchers nest exclusively in wet montane meadows that are maintained by high water tables during the summer months (Hagberg 1995, Loheide II et al. 2009). Increased temperatures in the spring and reduced snowpack will result in early onset of xeric conditions in these meadows, which in turn negatively affects riparian shrub recruitment and the herbaceous plant community. 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). Land managers in the Sierra Nevada are thus challenged with the need to improve current conditions in montane meadows to improve nest survival rates and to manage and conserve riparian regions to buffer against potential climate change in the future.

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Table 1. Willow Flycatcher nest initiation, hatch, and fledging dates for the South Tahoe and Truckee regions from 1997 to 2008, the Warner Valley region from 2003 to 2005 and 2008, and in McCloud in 2005 and 2006. Study regions were located in the central and north Sierra Nevada, CA.

Nest Stage Initiation						
Region	<i>n</i>	Min.	Max	Median	Mean	SD
Incubation						
South 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
McCloud	53	5 Jun	19 Jul	23 Jun	26 Jun	12.45
Hatch						
South Tahoe	71	1 Jul	16 Aug	14 Jul	15 Jul	10.37
Truckee	420	27 Jun	15 Aug	15 Jul	16 Jul	10.71
Warner Valley	182	18 Jun	18 Aug	9 Jul	11 Jul	11.67
McCloud	50	21 Jun	3 Aug	9 Jul	11 Jul	12.28
Fledge						
South 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
McCloud	41	5 Jul	20 Aug	22 Jul	25 Jul	12.71

Table. 2. Model-selection results for logistic-exposure models of the effect of age (age3, cubic trend), region, spring snowfall (spring), winter snowfall in year t-1 (snow1), temperatures in June and temperatures in July on daily survival rate of Willow Flycatcher nests in the South Tahoe, Truckee, Warner Valley, and McCloud study regions. The number of observed intervals was 3,228 and the effective sample size was 13, 276. Only models with $AIC_{\omega} > 1$ included.

Model	k	AICc	$\Delta AICc$	AIC_{ω}	Log(L)
age3+snow1+spring+region	9	2090.632	0.000	0.403	-1036.31
age3+spring+region	8	2091.790	1.158	0.226	-1037.89
age3+spring+june+region	9	2093.499	2.867	0.096	-1037.74
age3+snow1+region	8	2093.597	2.965	0.092	-1038.79
age3+snow+snow+region	9	2094.587	3.956	0.056	-1038.29
age3+july+region	8	2095.131	4.499	0.043	-1039.56
age3+region	7	2096.278	5.646	0.024	-1041.13
age3+snow+region	8	2096.408	5.776	0.022	-1040.20
age3+june+july+region	9	2096.588	5.957	0.021	-1039.29
age3+june+region	8	2097.758	7.126	0.011	-1040.87
age3+snow1+spring	6	2099.768	9.136	0.004	-1043.88
age3+spring	5	2102.634	12.003	0.001	-1046.31

Table 3. Generalized linear mixed models of the fixed effects of elevation, nest initiation date, daily nest survival rates (dsr), spring snowfall, and temperatures in June on clutch size of presumed first nest attempts of Willow Flycatchers breeding in South Tahoe and Truckee in the central Sierra Nevada, CA from 1998–2008.

Effect	β	SE	95% CI		ndf	ddf	<i>F</i> -value	<i>P</i>
			Lower	Upper				
Intercept	-0.160	0.949	-2.249	1.929				
Elevation	0.004	0.002	0.001	0.008	1	222	6.866	0.009
Nest date	-0.139	0.031	-0.199	-0.079	1	222	20.736	0.000
dsr	3.486	1.931	-0.321	7.292	1	222	3.257	0.072
Spring snow	0.010	0.004	0.001	0.018	1	222	5.399	0.021
June temp	0.144	0.124	-0.100	0.388	1	222	1.357	0.245

Table 4. Generalized linear mixed models of the fixed effects of elevation, nest initiation date, daily nest survival rates (dsr), spring snowfall, and temperatures in June on clutch size of presumed first nest attempts of Willow Flycatchers breeding in Warner Valley in the north Sierra Nevada, CA from 2003–2005 and 2008.

Effect	β	SE	95% CI		ndf	ddf	<i>F</i> -value	<i>P</i>
			Lower	Upper				
Intercept	12.548	5.677	-5.521	30.616				
Elevation	0.033	0.018	-0.024	0.090	1	3	3.365	0.164
Nest date	-0.041	0.042	-0.126	0.043	1	81	0.949	0.333
dsr	-4.276	3.158	-10.559	2.007	1	81	1.834	0.179
Spring snow	0.003	0.008	-0.014	0.020	1	81	0.128	0.722
June temp	0.806	0.333	0.144	1.468	1	81	5.875	0.018

Table 5. Generalized linear mixed models of the fixed effects of length of breeding season, date of first nest attempt, nest age at failure of first nest attempt (exposure), elevation, spring snowfall, temperatures in June, and temperatures in July on the probability of renesting for Willow Flycatchers breeding in South Tahoe and Truckee in the central Sierra Nevada, CA from 1998–2008.

Effect	β	SE	95% CI		nddf	ddf	<i>F</i> -value	<i>P</i>
			Lower	Upper				
Intercept	0.362	0.449	-0.625	1.349				
Season length	1.381	0.412	0.568	2.194	1	156	11.249	0.001
First nest date	-2.557	0.562	-3.667	-1.447	1	156	20.706	0.000
Exposure	-2.065	0.448	-2.950	-1.179	1	156	21.219	0.000
Elevation	0.151	0.495	-0.826	1.129	1	156	0.094	0.760
Spr snow	-0.904	0.331	-1.559	-0.249	1	156	7.442	0.007
June temp	-0.411	0.343	-1.089	0.266	1	156	1.438	0.232
July temp	1.486	0.697	0.110	2.863	1	156	4.551	0.034

Table 6. Generalized linear mixed models of the fixed effects of length of breeding season, date of first nest attempt, nest age at failure of first nest attempt (exposure), elevation, spring snowfall, temperatures in June, and temperatures in July on the probability of renesting for Willow Flycatchers breeding in Warner Valley in the north Sierra Nevada, CA from 2003–2005 and 2008.

Effect	β	SE	95% CI		nddf	ddf	<i>F</i> -value	<i>P</i>
			Lower	Upper				
Intercept	-4.022	4.723	-17.135	9.090				
Season length	3.633	1.699	0.211	7.056	1	45	4.571	0.038
First nest	-1.800	0.697	-3.204	-0.397	1	45	6.672	0.013
Exposure	-1.954	0.629	-3.220	-0.688	1	45	9.662	0.003
Spr snow	-3.596	3.066	-9.772	2.579	1	45	1.376	0.247
June temp	1.981	2.115	-2.278	6.240	1	45	0.878	0.354

Table 7. Generalized linear mixed models of the fixed effects of elevation, date of first nest attempt, daily nest survival rate (dsr), spring snowfall, temperatures in June, and temperatures in July on individual female fecundity of Willow Flycatchers breeding in South Tahoe and Truckee in the central Sierra Nevada, CA from 1998–2008.

Effect	B	SE	95% CI		ndf	ddf	<i>F</i> -value	<i>P</i>
			Lower	Upper				
Intercept	0.568	0.122	0.300	0.836				
Elevation	-0.031	0.119	-0.266	0.204	1	274	0.067	0.796
Nest date	-0.156	0.055	-0.264	-0.049	1	274	8.180	0.005
dsr	0.170	0.076	0.021	0.319	1	274	5.022	0.026
June temp	0.092	0.083	-0.072	0.256	1	274	1.219	0.271
Spring snow	0.015	0.070	-0.124	0.154	1	274	0.045	0.832
July temp	-0.100	0.179	-0.453	0.253	1	274	0.310	0.578

Table 8. Generalized linear mixed models of the fixed effects of elevation, date of first nest attempt, daily nest survival rate (dsr), spring snowfall, temperatures in June, and temperatures in July on individual female fecundity of Willow Flycatchers breeding in Warner Valley in the north Sierra Nevada, CA from 2003–2005 and 2008.

Effect	B	SE	95% CI		nddf	ddf	<i>F</i> -value	<i>P</i>
			Lower	Upper				
Intercept	41.469	35.076	-70.158	153.096				
Elevation	1.127	1.366	-3.222	5.475	1	3	0.680	0.470
Nest date	-0.140	0.080	-0.298	0.018	1	99	3.086	0.082
dsr	-15.524	13.694	-42.696	11.648	1	99	1.285	0.260
June temp	-29.882	26.305	-82.077	22.313	1	99	1.290	0.259
Spring snow	9.925	8.611	-7.162	27.011	1	99	1.328	0.252
July temp	-5.034	4.369	-13.704	3.636	1	99	1.327	0.252

FIGURE LEGEND

Figure 1. Differences in winter (Nov-Mar) and spring (Apr-May) from the 50-year mean for the (A) South Tahoe, (B) Truckee, (C) Warner Valley, and (D) McCloud study regions in the Sierra Nevada, CA. Data from the Western Regional Climate Center, Reno, NV.

Figure 2 Differences in June and July temperatures from the 50-year mean for the (A) South Tahoe, (B) Truckee, (C) Warner Valley, and (D) McCloud study regions in the Sierra Nevada, CA. Data from the Western Regional Climate Center, Reno, NV.

Figure 3. Tenth quartile, median, and ninetieth quartiles of dates of presumed first nesting attempts for (A) South Tahoe, (B) Truckee, and (C) Warner Valley regions. The tenth quartile (negative error bars) represent seasonal nesting onset and the length of both error bars represent the synchronicity of nest initiations.

Figure 4. Relationship between seasonal onset of nesting and June temperatures for 1997-2001 in the South Tahoe region, 1997-2008 in the Truckee region, and 2003-2008 in the Warner Valley regions in the Sierra Nevada, CA.

Figure. 5. Mean clutch size for presumed first nest attempts of Willow Flycatchers in (A) South Tahoe, (B) Truckee, (C) Warner Valley, and (D) McCloud regions. Error bars are standard deviations.

Fig. 6. Proportion of female Willow Flycatchers that renested following a failed nesting attempt in the South Tahoe, Truckee, and Warner Valley study regions in the Sierra Nevada, CA.

Figure 7. Observed values and 95% confidence intervals of the effect of nest age on daily nest survival rate of Willow Flycatchers in the (A) South Tahoe region from 1997 to 2006, (B) Truckee region from 1997 to 2007, (C) Warner Valley region from 2003 to 2006, and (D) McCloud from 2005 and 2006 in the Sierra Nevada, CA. Values were estimated using the logistic-exposure model based on grouping the data into age intervals and provide a goodness-of-fit evaluation for the model-selected effect of a cubic trend in nest age.

Figure 8. Predicted annual nest survival and 95% confidence intervals for Willow Flycatcher nests in (A) South Tahoe, (B) Truckee, (C) Warner Valley, and (D) McCloud study regions of the Sierra Nevada, CA. Values were estimated using the logistic-exposure model for annual variation.

Figure 9. Fecundity (number of female young/female) estimates for Willow Flycatchers breeding in four study regions in the Sierra Nevada, California.

Figure 1.

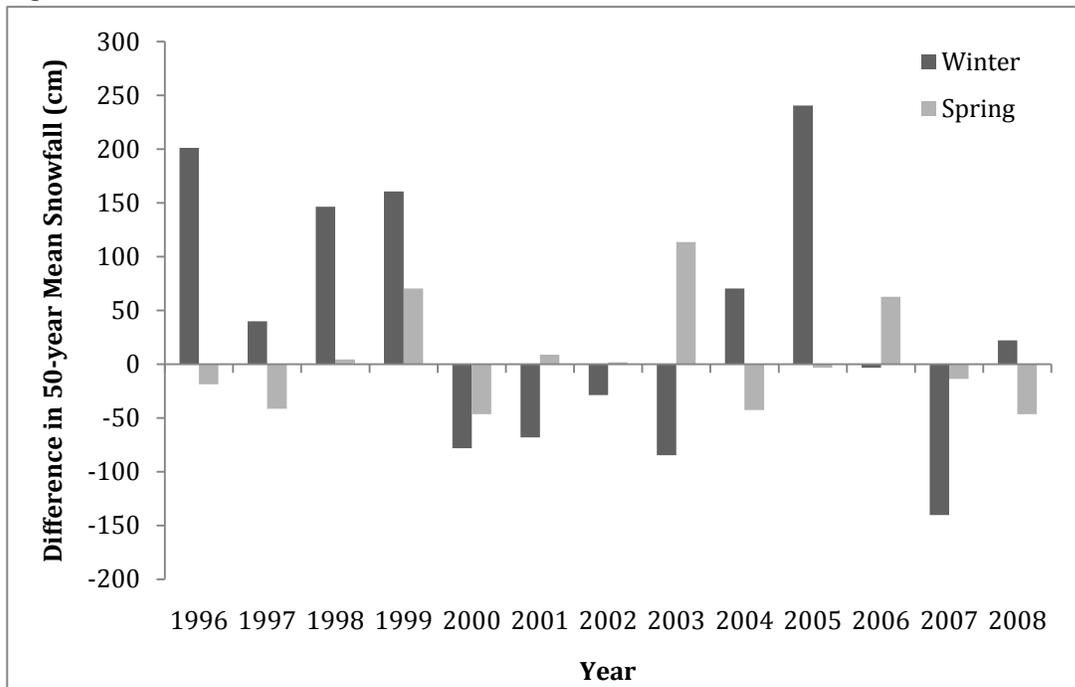


Fig. 1B

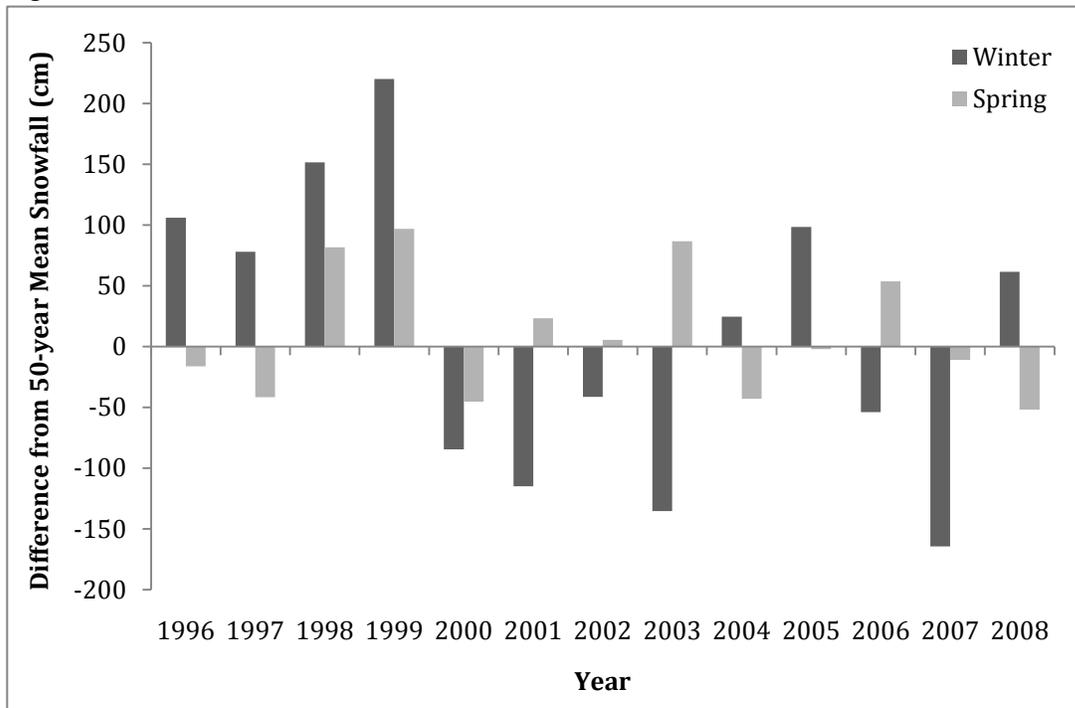


Fig. 1C

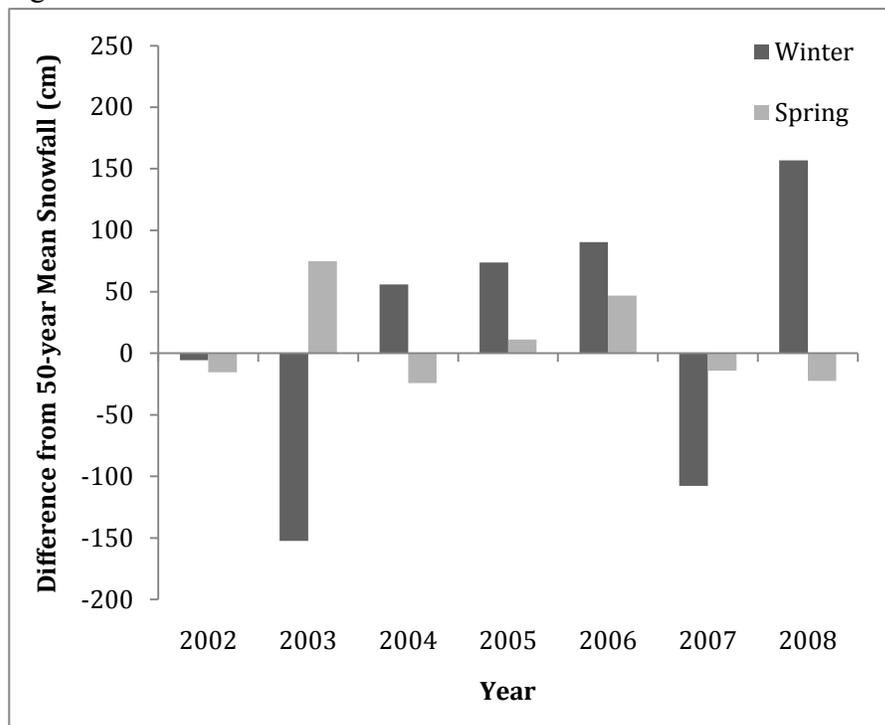


Fig. 1D

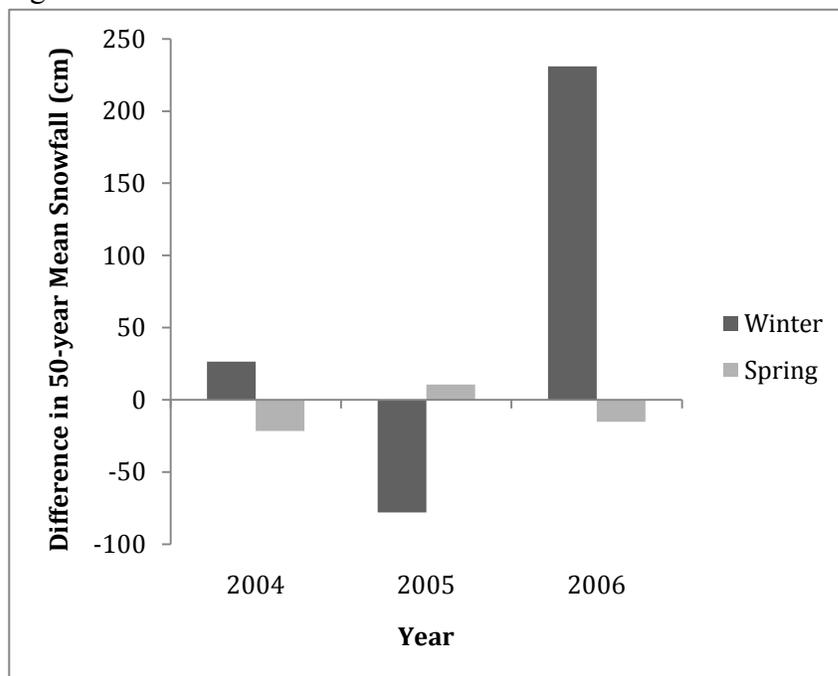


Fig. 2A

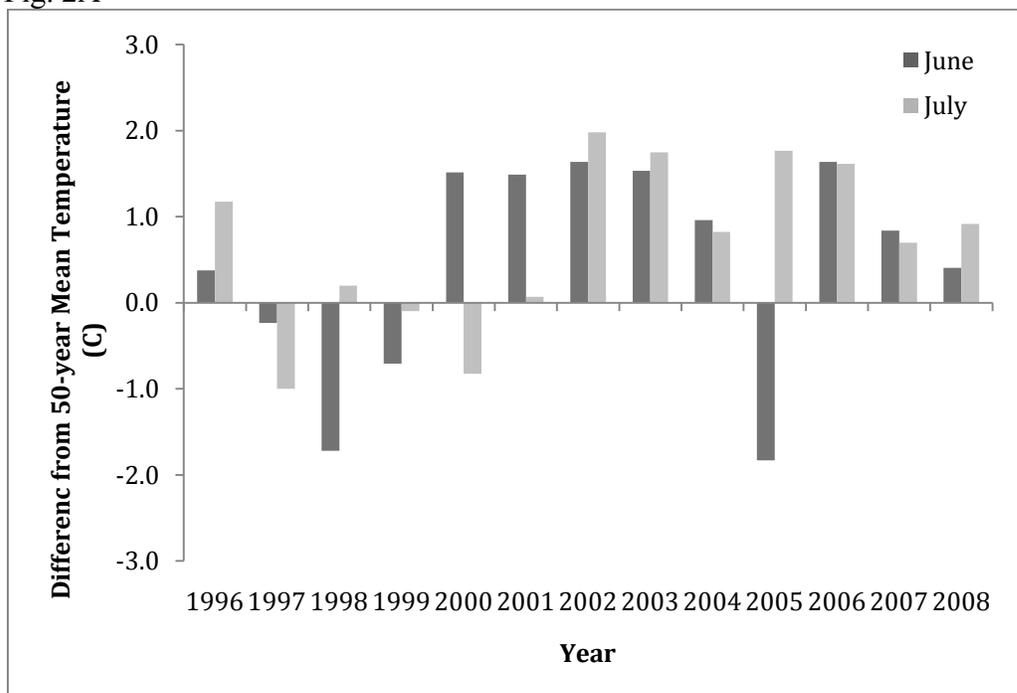


Fig. 2B

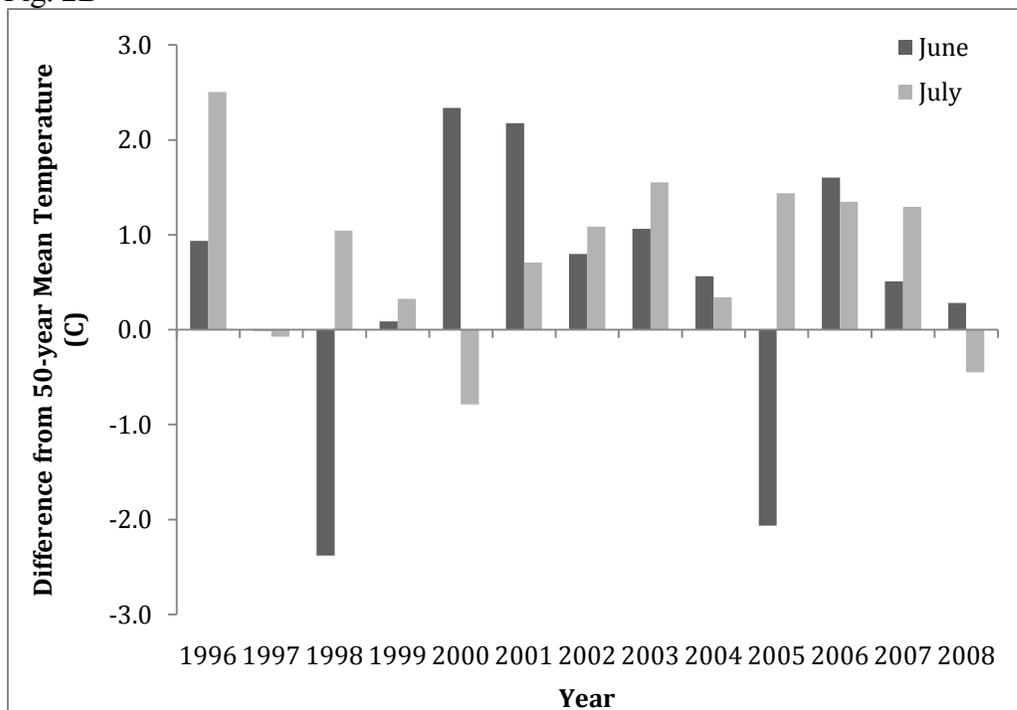


Fig. 2C

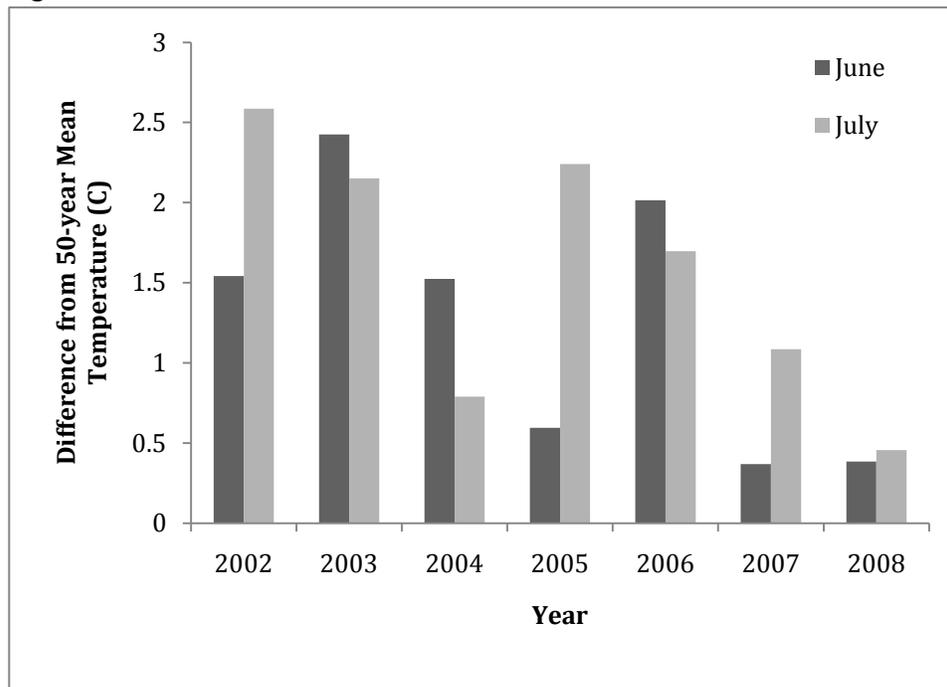


Fig. 2D

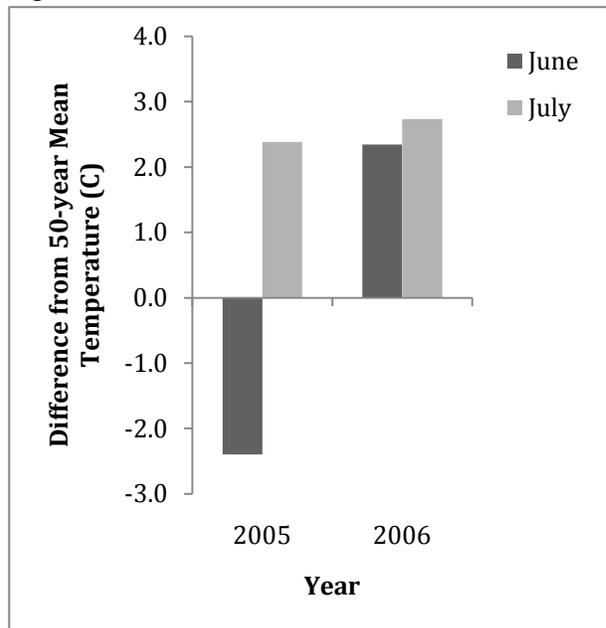


Fig. 3A

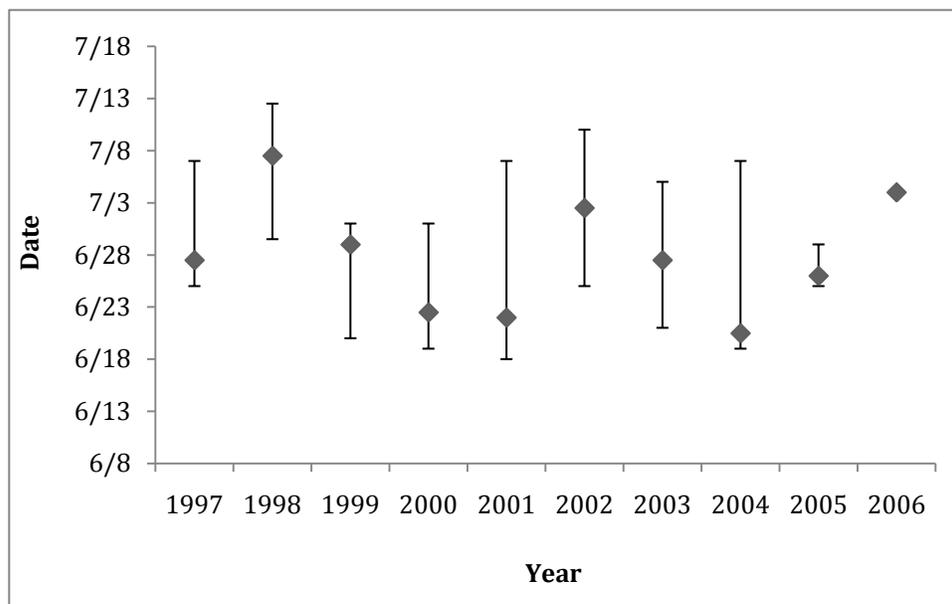


Fig. 3B

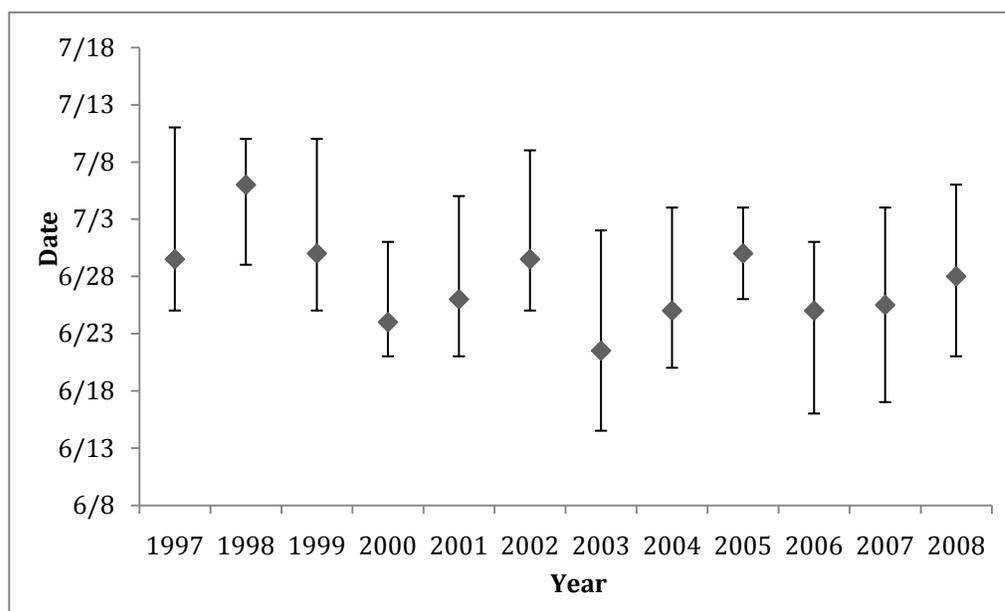


Fig. 3C

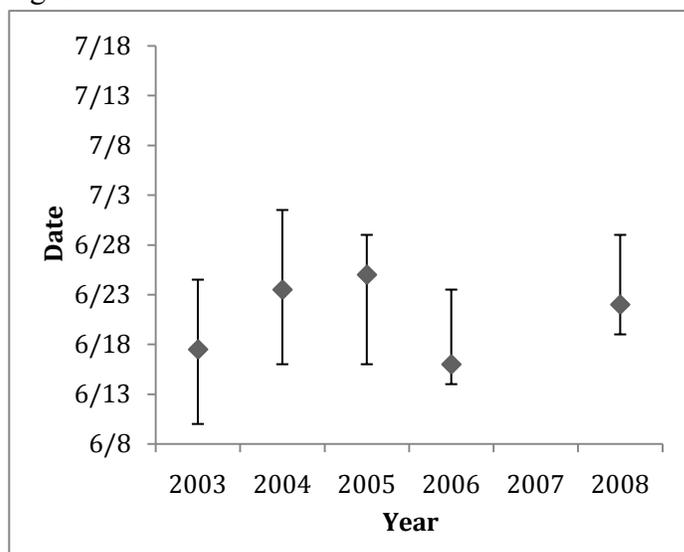


Fig. 4.

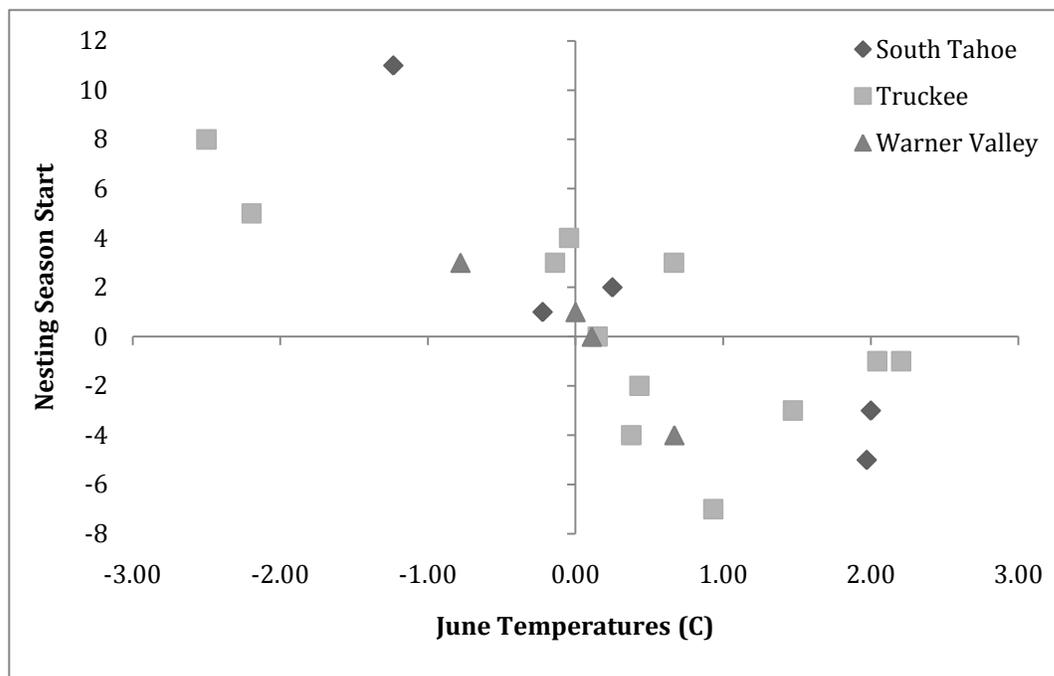


Fig. 5A.

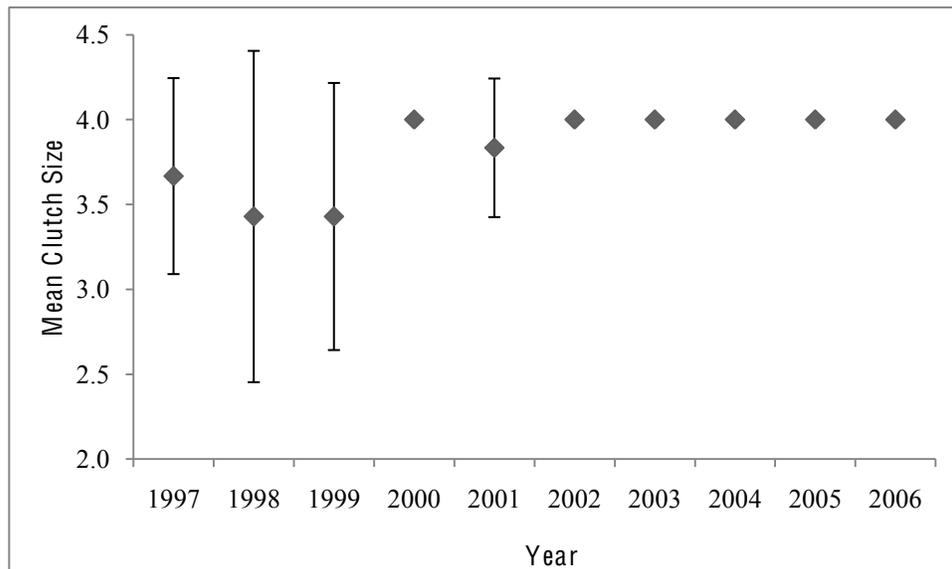


Fig. 5B

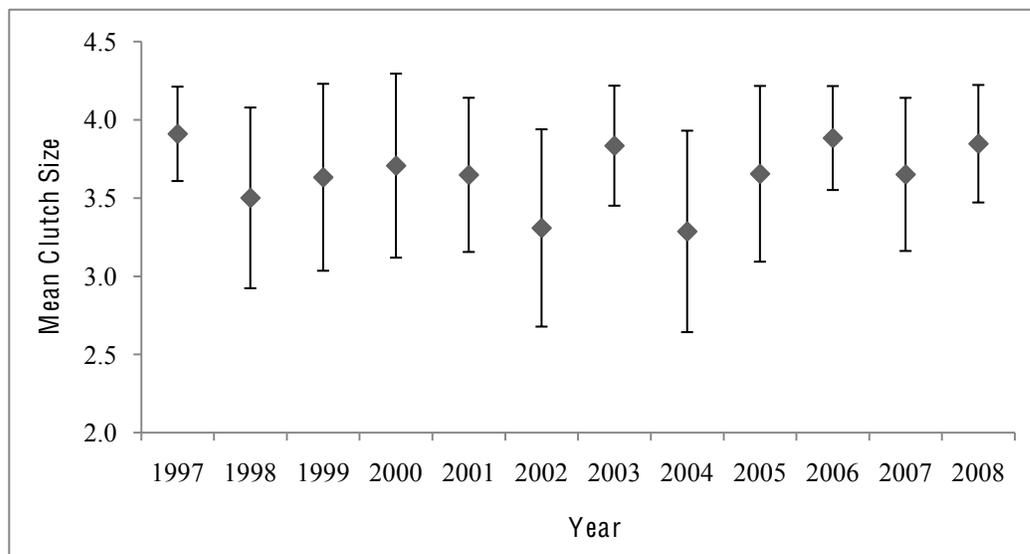


Fig. 5C.

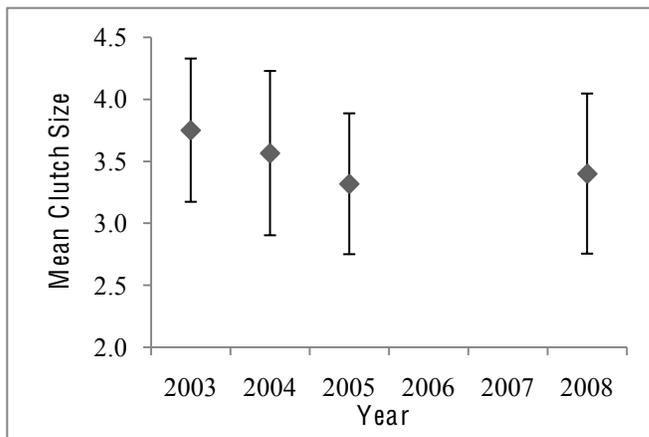


Fig. 5D.

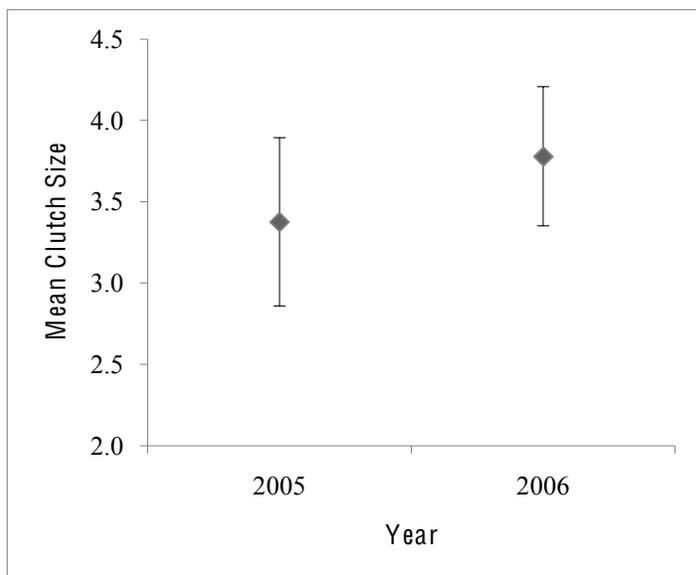


Fig. 6.

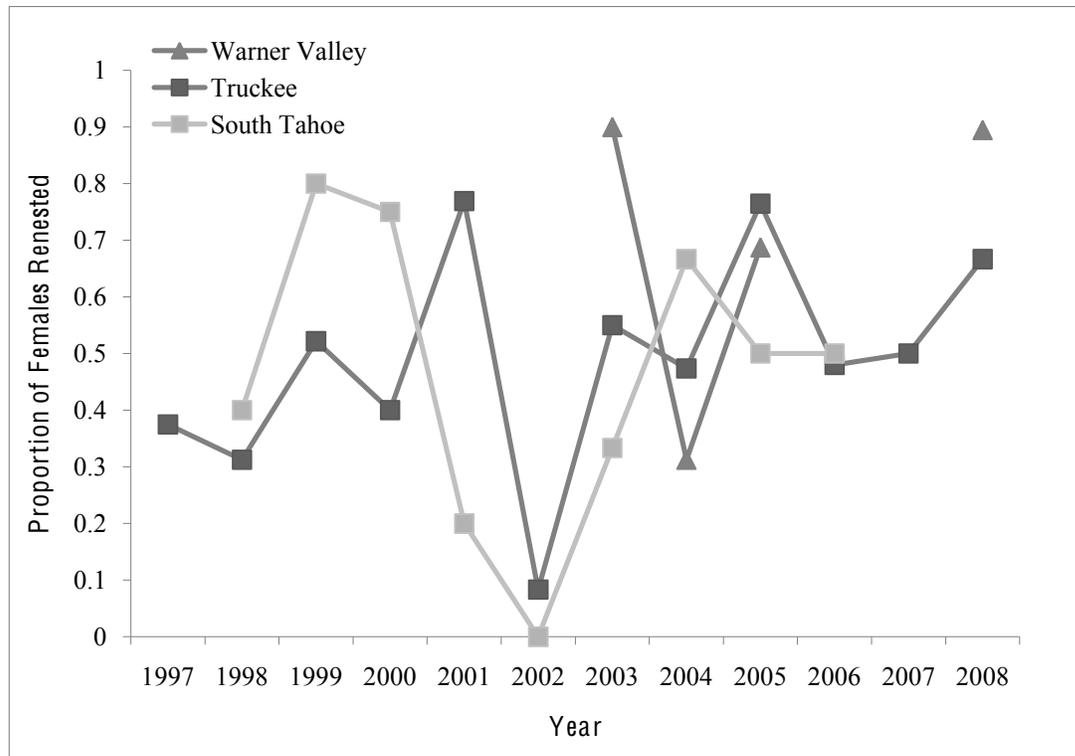


Fig. 7A

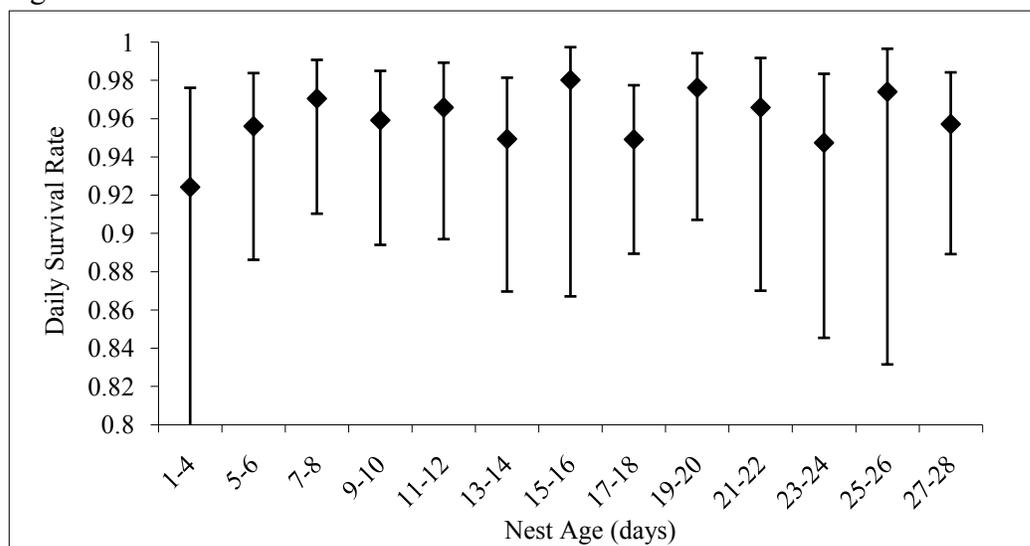


Fig. 7B

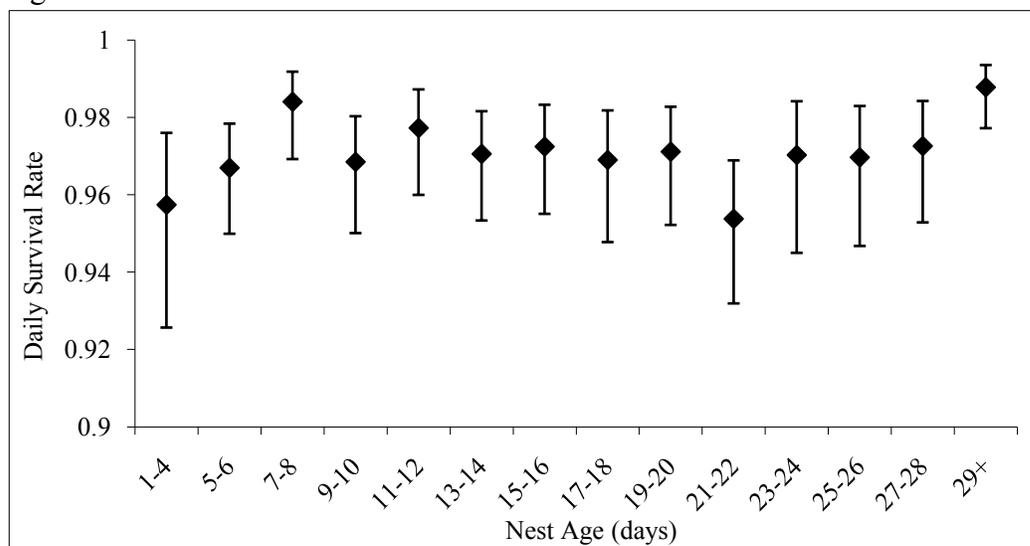


Fig. 7C

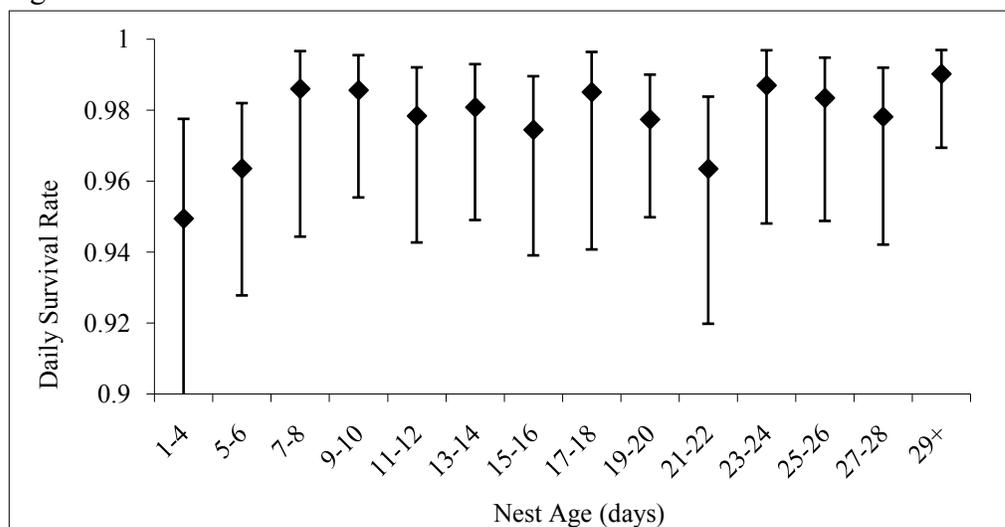


Fig. 7D

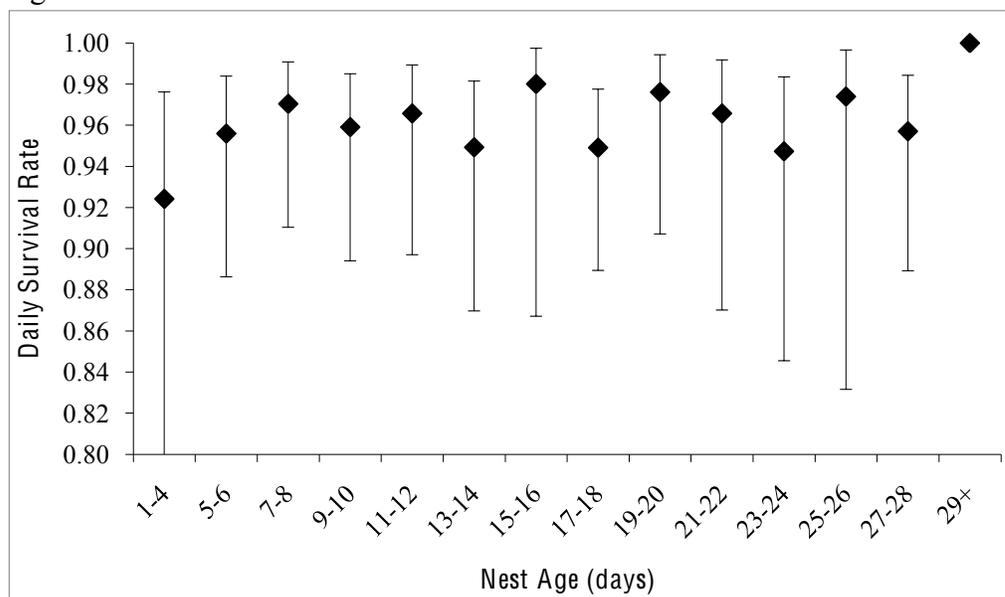


Fig. 8A

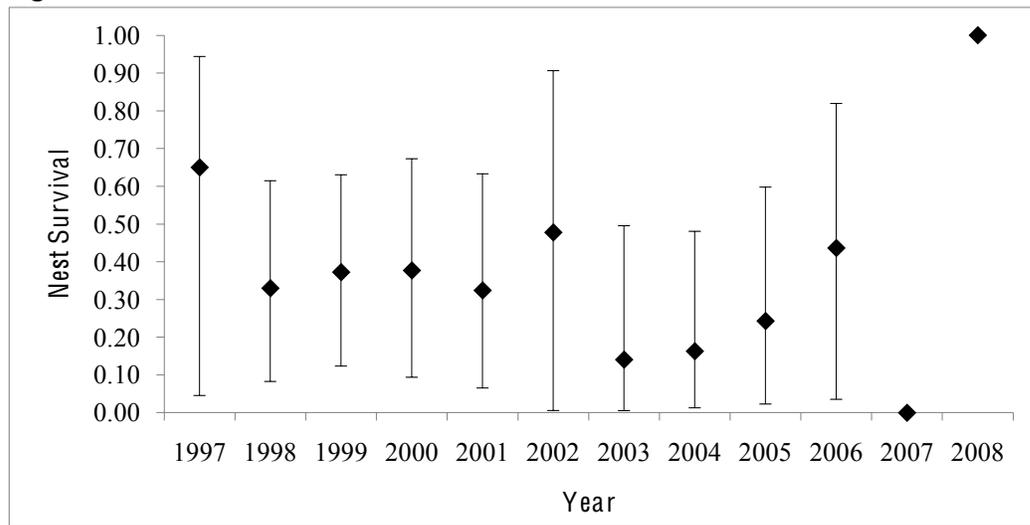


Fig. 8B

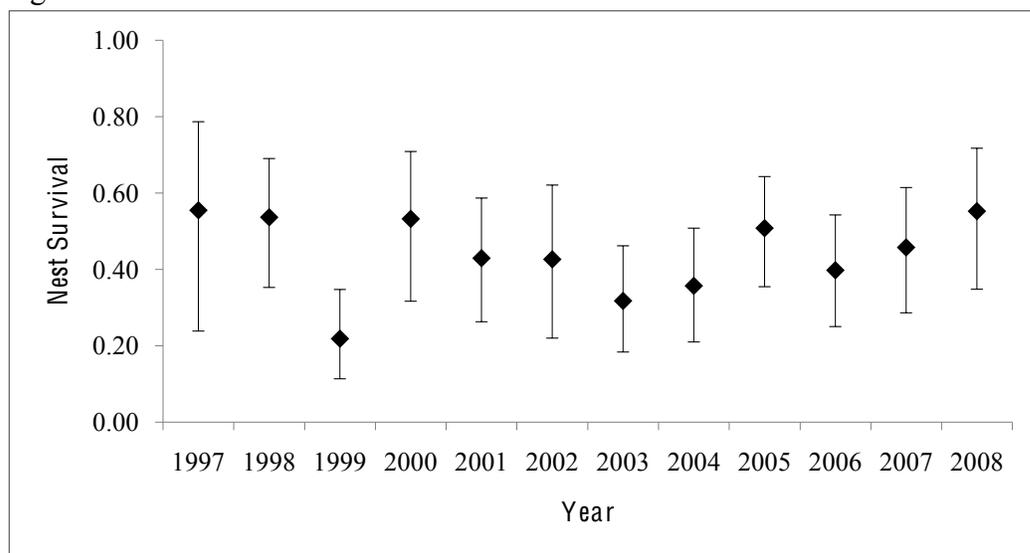


Fig. 8C

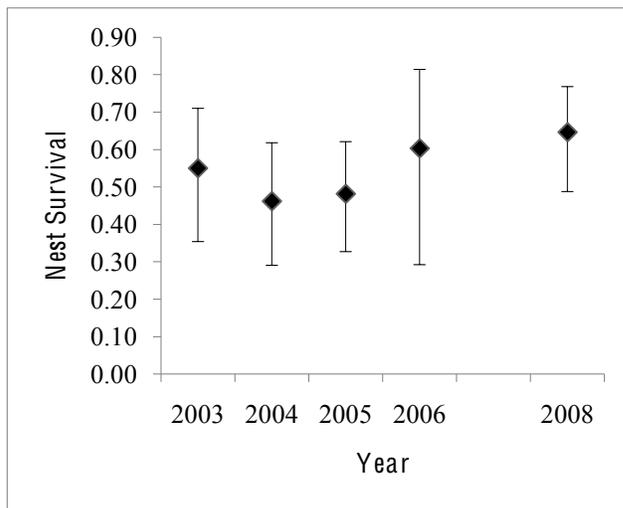


Fig. 8D

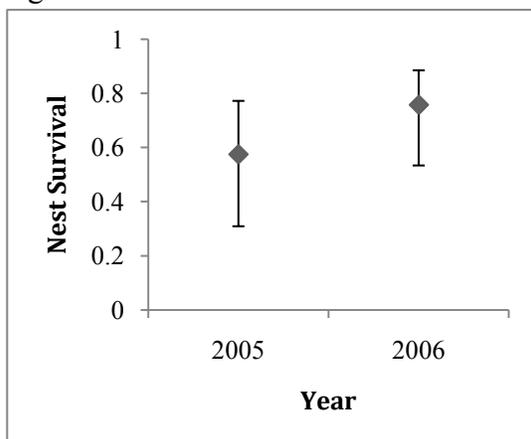
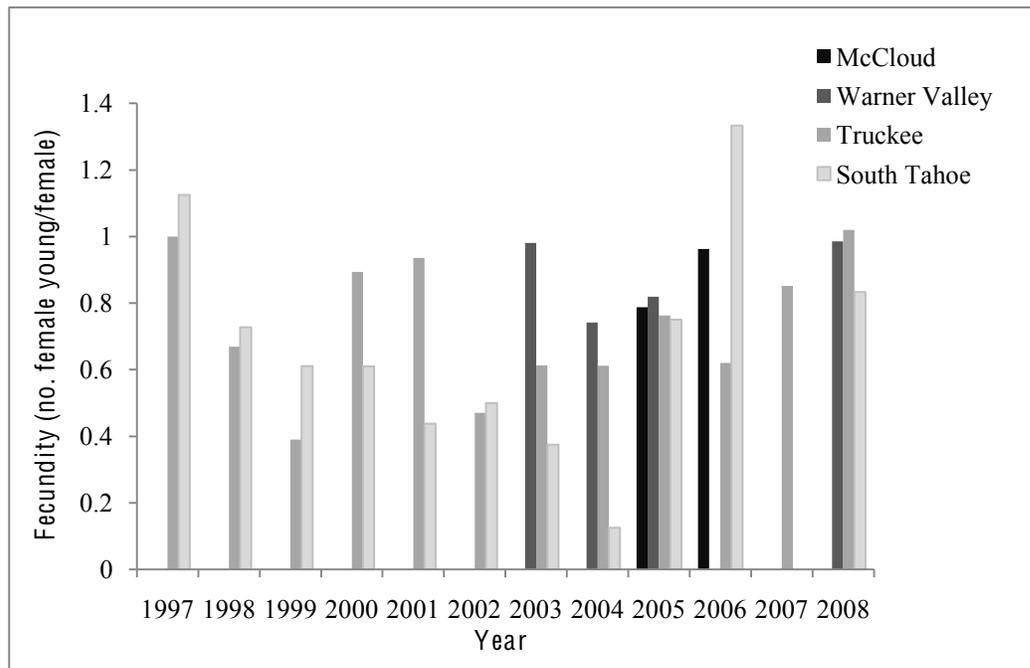


Fig. 9



CHAPTER 2. DEMOGRAPHY OF WILLOW FLYCATCHERS IN THE SIERRA NEVADA, CALIFORNIA

Abstract

Population dynamics of migratory songbirds are driven by survival and fecundity, and obtaining accurate estimates of these parameters is challenging. In the western United States, Willow Flycatchers (*Empidonax traillii*) have been experiencing population declines that likely vary across the species range due to variations in the ecology of subspecies and land-use practices. In 1997, I initiated a long-term research program on Willow Flycatchers breeding in two study regions the central Sierra Nevada, California. In 2003 and 2005 I added two study regions in the north Sierra Nevada. My objectives for the central study regions were to examine annual fluctuations in population trends and to estimate return rates and site fidelity of adults and juveniles. I also examined how factors in the previous breeding seasons contributed to these estimates. I used sensitivity analysis of deterministic population models to compare variation in fecundity of flycatchers in the central Sierra Nevada study regions against those of the two northern populations of flycatchers. Populations in the central regions declined during the course of my study. In one of the two central regions, low fecundity may have promoted female dispersal from the region. Additionally, fecundity estimates were lower compared to the two northern regions and sensitivity analysis indicates that population stability cannot be attained without considerable increases in fecundity of these flycatcher populations. I found no support for the hypothesis that the timing of nesting in the breeding season contributed to return rates for juveniles or adults. Reproductive success did not predict return rates of juveniles, but adults may be more likely to return to the

area following years with increased survival of nestlings. Reproductive success may encourage site fidelity among this population and may explain persistence of breeding populations in an area.

INTRODUCTION

Many species of migratory land birds in North America have declined in recent decades (Sauer et al. 2008). For some species, population declines are ubiquitous, but for other species population trajectories may vary across regions (Sauer et al. 2008, Buehler et al. 2009). Numerical changes observed in the abundance or density of populations are consequences of changes in demographic parameters (Lampila et al. 2005): fecundity, survival, immigration, and emigration. Population changes can be assessed using census data or by estimating demographic rates and associated variation (Sibly and Hone 2002). Demographic analysis may have increased statistical power compared to censuses to detect changes in low-density populations (Taylor and Gerrodette 1993) and evaluating variation in demographic parameters across spatial and temporal scales provides information on the processes contributing to population changes (Anders and Marshall 2005). However, the challenges of obtaining accurate estimates of vital rates, separating process from sampling variation, and accounting for unknown future environmental stochasticity can result in unrealistic estimates of population growth rates. This is particularly true for endangered or threatened species for which little information on basic population ecology may exist and reporting biased vital rate estimates or population projections can lead to mismanagement for these species. Thus, deterministic models, which require fewer parameter estimates, are often used to synthesize data and to gain an

understanding of the relative influence of individual vital rates on population change estimates.

Intensive and long-term field studies are required to gain the empirical data necessary for estimating demographic parameters. Survival estimates are particularly challenging because they are confounded by detection probabilities (Nichols 1992). High site fidelity by adults and natal philopatry of second-year birds can improve on apparent survival estimates, yet without demonstrating that emigration does not occur, apparent survival estimates always will underestimate survival (Marshall et al. 2004). Accurate estimates of juvenile survival are the most difficult to obtain even in species with high natal philopatry because dispersal may follow a leptokuric distribution, in that more individuals return at either short or long distances than expected by chance (Hanski 2002). Statistical methods exist for estimating survival but these require at least three years of data to estimate survival and detection for one year (Beissinger et al. 2006). In the absence of empirical data on juvenile or adult survival, researchers can use return rates to examine factors that may influence survival, immigration, and emigration.

Population declines in Neotropical migratory birds are likely the result of multiple mechanisms operating during and between stages of the annual cycle (Sillett and Holmes 2002). Mortality is high during migration, as has been demonstrated for Willow Flycatchers (*Empidonax traillii extimus*, Paxton et al. 2007) and other migratory passerines (Sillett and Holmes 2002). Survival during fall migration may be influenced by factors occurring on the breeding grounds, such as nest predation rates or food availability (Stokke et al. 2005). Adults and young may benefit from early-season nest success because of increased time on the breeding grounds to prepare for fall migration

(Morton 1992, Sedgwick and Iko 1999). High predation rates increase the probability of having to renest, which decreases post-fledging time before migration. Although renesting increases individual fecundity, the energetic stress of renesting (Haas 1998, Hoover 2003), combined with reduced preparation time, may result in reduced survival during migration.

Fledglings from early-season nests may experience higher survival during migration and winter because of increased developmental and resource acquisition time on the breeding grounds (Krementz et al. 1989). If migration is delayed for adults and late-fledging young they may experience increased costs of territory establishment on the winter grounds (Marra and Holmes 2001, Koronkiewicz et al. 2006).

Independent from survival probabilities, factors occurring during the breeding season may influence return rates in the following breeding season if birds use decision rules to determine future breeding locations (Hoover 2003). Decision rules may be based on an individual's own breeding experience along with that of its neighbors (Part and Doligez 2003). Following a breeding season in which several pairs of flycatchers experienced reduced breeding success, adults may avoid areas of high predation in subsequent breeding seasons (Sedgwick 2004). Flycatchers breeding in their first season are less likely to return when brood parasitism rates are high (Sedgwick and Iko 1999). Juveniles may use information acquired during their post-fledging stage to determine whether or not to return to the area, which contributes to high natal philopatry (Dale et al. 2006).

In demographic models it is important to include consideration of sex ratios because they may be an indication of population status. Skewed sex-ratios may arise from

sex-biased dispersal patterns or sex-biased mortality, and ratios favoring males may lead to higher extinction risk (Donald 2007). Site-fidelity is linked to habitat quality and the consistent presence of unmated males over time may indicate areas of low-quality habitat (Schmidt 2004) or skewed sex-ratios in young produced or dispersal patterns (Donald 2007). This phenomenon may be more exaggerated in species with flexible mating systems. The polygyny threshold model predicts that if the cost of selecting a male in low-quality habitat is higher than the cost of forming a polygynous pair bond in high-quality habitat, females should choose polygyny (Verner and Willson 1966, Orians 1969, Hansson et al. 2000). While considering the proportions of unmated males and polygynous territories in a population is important in population demographic studies, skewed sex-ratios become increasingly stochastic as populations decline and may be difficult to detect (Donald 2007). Long-term and spatially extensive studies are needed to address ecological patterns associated with population changes (Collins 2001). Here I examine associations between reproduction and population changes of a threatened species over a 12-year period and across a large geographical scale.

In the western United States, Willow Flycatcher (*Empidonax traillii*) populations have declined, and the magnitude of these declines likely vary across the species range due to variations in the ecology of subspecies and land-use practices (Whitfield et al. 2003). The three subspecies of 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). Populations of the southwestern subspecies (*E. t. extimus*) are well studied but information on population status and breeding ecology of the remaining two subspecies, *E. t. brewsteri* and *E. t.*

adastus, is lacking (Green et al. 2003). In response to increasing concerns over population declines, I studied Willow Flycatchers as part of a long-term research program in the central and northern Sierra Nevada. Prior to my study, surveys for site occupancy were conducted across the region (Harris et al. 1987) but little information existed on population demography of Willow Flycatchers in this area (but see Flett and Sanders 1987).

I studied the demography of Willow Flycatchers breeding in montane meadows in the central Sierra Nevada from 1997–2008 and I added study regions in the north Sierra Nevada in 2003 and 2005. At the initiation of this long-term research program, surveys indicated that populations of flycatchers in the central regions were declining and that occupied sites were clustered and separated from areas with larger populations (Bombay 1999, Green et al. 2003).

My first objective was to report annual fluctuations in observed population trends, mating status, and fecundity estimates from my long-term data set and to calculate site fidelity and natal philopatry from adult and juvenile return rates. Additionally, I addressed hypotheses concerning the effects of reproductive success and timing of breeding from the previous year on return rates. For juveniles, I predicted that reproductive success and timing of nesting in the previous year (i.e., natal year) would positively affect return rates of juveniles. For adults, I predicted that several measures of reproductive success and timing of nesting in the previous breeding season would increase return rates. Additionally, I predicted that adults would be less likely to return in years when the breeding season was delayed.

My second objective was to assess whether fecundity estimates from study sites in my long-term study regions were sufficient to support persistence of these populations. To do so, I compared reproductive success of flycatchers from the long-term study regions with that of two larger populations of flycatchers also breeding in the Sierra Nevada but under different abiotic and biotic conditions (King and King 2003)(C. Stermer unpubl. data). Using estimates from these regions as a baseline (i.e., assuming population stability), I used sensitivity analyses from population growth models to compare relative differences in fecundity estimates among the study regions and to determine the magnitude of change needed to obtain population stability in the long-term study regions. My intention was not to project population growth trends but instead to use sensitivity analyses to evaluate different biologically feasible scenarios of changes in vital rates (Beissinger and Westphal 1998).

METHODS

Study Sites

Based on historical records and habitat characteristics described for Willow Flycatcher breeding sites in the central Sierra Nevada, Bombay (1999) conducted occupancy surveys in 1997 and 1998 at 104 meadows within 1.2 million ha at which she detected Willow Flycatchers at 19% ($n = 104$) of the survey sites (Appendix B). Of the 20 occupied sites, 14 supported three or fewer breeding territories (Bombay 1999), but the remaining sites included three of the four meadows supporting the largest number of breeding territories of flycatchers (*E. t. brewsteri* and *E. t. adastus*) within the Sierra Nevada north of the geographic range of the southwestern subspecies (Serena 1982,

Harris et al. 1987, Green et al. 2003). Fifteen of the 20 occupied sites were selected for long-term demographic monitoring (Bombay 1999). Study sites in these two regions (South Tahoe and Truckee) were within approximately 20 km of each other. Due to changes in annual funding and accessibility of properties, some of the study sites changed across the years. I added study sites in both the South Lake and Truckee regions for monitoring in 2003, 2005, and 2008 (Appendix B).

In 2003 and 2005, I established two additional study regions in the north Sierra Nevada where previous surveys had recorded dense populations of Willow Flycatchers (Green et al. 2003, Humple and Burnett 2004; C. Stermer, unpublished data) to provide comparative data on the reproductive success of flycatchers breeding outside of the long-term study regions in the central Sierra Nevada. In 2003 I began demographic monitoring in Warner Valley, Lassen County, California. Based on Green et al. (2003) it was the fourth meadow reported to contain a high number of breeding territories. Warner Valley (hereafter Warner Valley region) is an extensive meadow of 250 ha, of which I monitored 80 ha divided into four study sites based on natural vegetative and topographic divisions. I monitored flycatchers in the Warner Valley region from 2003–2005 and in 2008. From 2005–2006 I monitored in a fourth study region along the McCloud River in Siskiyou County, California.

The four study regions were located along a latitudinal gradient with decreasing elevation. Study sites in the South Lake region ranged in size from 6–98 ha at elevations of 1,900–2,400 m. These sites were approximately 40–100 km south of study sites in the Truckee region. All study sites in the Truckee region ranged in size from 10–162 ha and in elevation from 1,730–2,120 m. The Warner Valley region was located 125 m north of

the Truckee region, and its study sites ranged in size from 15-24 ha at elevations of 1,560-1,590 m. Located approximately 100 km northwest of the Warner Valley region, study sites in McCloud ranged from 13.6–103 ha at elevations of 1,080-1,300 m.

Within all regions, study sites were montane meadows classified as shrub meadows that rely on periodic flooding to maintain their transitional state (Fites-Kaufman et al. 2007). 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 streams, rivers, and lake edges but also were scattered in large clumps across the meadows. The riparian shrub community was predominantly comprised of Geyer's willow (*Salix geyeri*) and Lemmon's willow (*S. lemmonii*) in the South Lake and Truckee regions. In the Warner Valley and McCloud regions, mountain alder (*Alnus tenuifolia*) and quaking aspen (*Populus tremuloides*) were interspersed with the willow. Sedges (*Carex* spp.), grasses, rushes (*Juncus* spp.), and forbs dominated the herbaceous community. Sagebrush (*Artemisia* spp.) was intermittently located in upper portions of the meadows, which were surrounded by a mixed coniferous forest dominated by lodgepole pine (*Pinus contorta*).

In addition to the monitoring sites, I conducted protocol surveys to determine site occupancy or I visited other meadows to acquire band resight information but these sites were not visited on a consistent basis (Appendix B). In 2003 and 2004 I collaborated with the California Department of Fish and Game to survey meadows across the central and

north Sierra Nevada (C. Stermer, unpubl. data). In 2005 I implemented an adaptive cluster technique for locating flycatchers adjacent to my study sites. I surveyed 26 meadows and located flycatchers at two of these sites. Because of my extensive surveys in meadows (Appendix B) and because I collaborated with the USFWS as part of their Sierra Nevada Forest Initiative Plan, with California Department of Fish and Game (C. Stermer, unpublished data), and with Point Reyes Bird Observatory in Lassen County, my study likely includes the majority of the habitat available to breeding flycatchers in this region, although I can not account for private lands (Green et al. 2003).

Field Methods

I used a standardized protocol that incorporated use of playback to determine occupancy and abundance of Willow Flycatchers in study site meadows (Bombay et al. 2000). At sites not receiving demographic monitoring, if both survey visits as required by the survey protocol occurred prior to 1 July, I required at least one additional visit in July to meet my criterion for defining territorial males. Band resighting occurred at all sites during scheduled visits.

I located all Willow Flycatcher territories using standard territory mapping techniques and adult behavior (Ralph et al. 1993). I used standard nest searching techniques (Martin and Geupel 1993) to locate and monitor nests during June through August in 2006 and 2007. I monitored nests every two to six days depending on estimated stage transition dates. I checked nest contents during every nest visit using a mirror or direct observation. After approximately day 10 I did not approach the nest but observed it with binoculars from a distance. Although this method reduced the possibility of force fledging a nest, it hindered my ability to acquire accurate counts of nestlings in

the nests. To estimate critical stage transitions I estimated three days for laying, 14 days for incubation of the eggs, and nest fledging date anytime after day 13 of the nestling period (total of 31 days of nesting; Appendix F). I assumed a nest was successful if at least one fledgling was located or if the nest was active at least until day 12. By day 12 of the nestling period, the young are capable of force fledging (H. A. Mathewson pers. obs.), and thus at least one young may avoid predation. I assumed a nest failed due to predation if the nest was empty prior to day 12 of the nestling period. I attributed the loss of ≥ 1 egg or nestling during nest monitoring to partial predation. I revisited all nest locations after the estimated fledgling date to determine if fledglings were in the immediate area. Across the years of this study I increased the emphasis on resighting fledglings. Initially, the goal was to locate the family group once to determine if the nest had fledged or failed and to record the estimated number of young detected. In 2005, I increased my focus on acquiring multiple observations of the family group.

Since 1997, I have banded all nestlings at my study sites once nestlings were approximately seven to nine days old. I used a cohort banding method until 2007 when I began banding nestlings with individually unique band combination. In 1997 and 1998, nestlings received a single color band to designate natal year and a numbered USGS band. From 1999-2006, nestlings received an anodized (colored) USGS numbered band on the right leg to designate natal year and a single colored band on the left leg to designate site. In 2007, I began individually banding nestlings with pinstriped bands (Koronkiewicz et al. 2005).

During the 12 years of this study, I implemented various techniques for banding adults in collaboration with other local researchers. J. Steele (pers. comm.) conducted

periodic passive mist netting in two of the large study sites beginning in 1992. In 2005, I 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 using pinstriped bands. If I captured an adult with cohort bands, I changed the unnumbered band to a pinstripe band to create a unique combination and left the numbered USGS band in place.

I resighted birds using binoculars and spotting scopes. To consider a resight confirmed I required agreement by at least three observers on more than one visit to the territory. I attempted to resight all birds at my study sites throughout the season as well as any Willow Flycatchers detected at surrounding locations. Additionally, I visited locations with known breeding territories to document banded birds (Appendix B).

Population Trends and Ratio of Males to Females

I defined an adult male as territorial if I detected it at a location for ≥ 10 days and after 30 June to allow comparisons among survey and monitoring sites across the years of my study. I assumed that I detected all territorial males in my study sites because when defending territories males vocalized from exposed perches and their calls are distinctive.

Females are less conspicuous than males with a reduced likelihood of detection; thus, I adjusted the number of females detected each year using a probability detection based on whether I detected a female the first time while she was nesting or after successfully fledging a nest. Family groups with fledglings have a high detection probability (H. A. Mathewson pers. obs.), thus increasing the likelihood of detecting previously undetected females if their nest fledged. My adjusted total number of females was the number of females not detected until successfully fledging a nest divided by my

maximum likelihood estimates for nest survival for each region and year and added to the total number of females detected while nesting.

Once males were detected on territories, I monitored territories continuously during the season to determine if males acquired a female. Even after the first female was located I monitored the area within the territory for second females. To determine the proportion of unmated males I considered only males defined as territory holders.

Even in the presence of unmated males, some female Willow Flycatchers nest in polygynous territories, potentially due to reduced selection for any particular mating strategy (Sedgwick and Knopf 1989, Davidson and Allison 2003). For the proportion of polygynous territories I used data collected after 2003 because I increased my efforts in locating polygynous females. I considered only those territories occupied by females (i.e., excluded territories with unmated males). I examined the proportion of unmated males and polygynous males and females relative to age using a subset of known-aged birds from my banding and resighting efforts

Because study sites varied across the years (Appendix B), I examined annual changes in the number of Willow Flycatcher territories by calculating the rate of change from year t to year $t+1$. I 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. I included only those territories that met my definition of a territorial male. I used the same calculation to estimate rate of change in the number of females detected breeding at study sites each year.

Demographic parameters and statistical analysis

I provide descriptive statistics for comparing differences in reproductive parameters among years and study regions. I examined annual trends within regions in the number of territories at consistently monitored sites, proportion of unmated males, and proportion of polygynous territories using generalized linear models (GLM) weighted by the total number of territories each year.

I calculated fecundity as the number of female young fledged per female within each study year and region assuming a 50:50 nestling sex ratio (Paxton et al. 2002). My estimate is a maximum estimate of fecundity because I used the number of young last seen in the nest prior to fledging; thus, I did not account for survival during the last few days of nesting. I used the number of females adjusted for detection probability (see above), and I assumed that all females bred in their first breeding season (Buehler et al. 2009).

I calculated juvenile return rates as the proportion of second-year individuals returning from each cohort to the number of young banded in the previous year. Dispersal distances for second-year birds is commonly extensive for most passerines (Greenwood and Harvey 1982); therefore, I 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 calculated as the proportion of second-year birds resighted outside my core study area to the total number of second-year birds resighted for all years combined. This method assumed that dispersal events outside of my core study areas represented emigration. The number of young available to return in year $t + 1$ (N_t) was equal to the number of young banded from successful nests in year t ,

and r_{t+1} was the number of second-year birds resighted in my core study areas. I 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.

I constructed capture histories for uniquely identified individuals to provide known-age information that the cohort method cannot address (i.e., individual-based reproductive information), to refine my survival estimates, and to examine breeding site fidelity. To estimate breeding site fidelity, I considered captures only after the bird received unique band combinations regardless of known age information acquired from the USGS band number when I recaptured the bird. The probability of detection for these adults varied with changes in my methodology. For example, I captured several adults previously banded as nestlings using the cohort method or adults that were captured using passive mist netting techniques and banded with single numbered bands. I acquired information about natal location and year or when I first banded the adults but I cannot account for the location of the bird during the interval between initial banding and the recapture event; this interval ranged from one to six years. Therefore, I assumed equal survival and detection probability for all years and individuals and did not consider breeding status, individual age, or detection $> t + 1$. I examined changes in breeding site locations beginning with the year the adults received individual band combinations. I was unable to consider the age of the bird due to small samples sizes and differences in methodology. I examined the probability of breeding at the same site in year t and year $t + 1$.

I calculated adult survival using two data sets: the data that included cohort banding and the capture histories. I based adult apparent survival on return rates of breeding flycatchers after their first-year breeding attempt. I defined apparent survival as the proportion of banded birds detected in year t to the number of banded birds detected in the following year ($t+1$). Using the capture history data set, I assumed equal probability among years and individuals because of small sample sizes; thus, I pooled years and individuals for this analysis. I calculated adult survival as

$$s = (r_{t+1} / p_{t+1}) / M_t$$

where the number of individuals resighted in year $t+1$ (r_{t+1}) was associated with a detection probability (p_{t+1}) relative to the sum of the individuals that were banded and present in year t (M_t) (Williams et al. 2002). I determined detection probability based on the number of individually banded adults resighted in a year relative to the total number of adults available to resight (i.e., individuals available but not detected were birds not seen in one year but detected in later years), assuming that birds not detected in subsequent years did not survive.

For each study region, I calculated the annual rate of population change as

$$\lambda = s_{t+1} + (j_{t+1} * f_t)$$

where s was the overall estimate of adult return rates adjusted for detection (i.e., constant) because apparent survival estimates for adults are unreliable due to changes in study sites, methods, and samples sizes each year and because I was unable to account for variation in survival by age due to small sample sizes. For juvenile survival (j), I used a constant estimate calculated as the mean annual adjusted juvenile survival estimate from the Truckee study region. I used the maximum fecundity (f) estimate from each study year

and region in my calculations, which allowed me to examine annual differences within each region based on variation in fecundity.

I conducted sensitivity analysis of vital rates using a manual perturbation approach that involves adjusting vital rates by amounts that are biologically relevant (Mills and Lindberg 2002). Willow flycatchers in my study area have limited fecundity compared to other passerines because they raise only one brood per year (see chapter 1). There is a decline in clutch size with renesting attempts so that the mean number of young fledged per successful nest typically ranges from two to three young (Appendix C). Species with limited fecundity may have higher survival estimates than those reported for more fecund species (Martin 1995, Buehler et al. 2009). Because my intent was to examine the magnitude of change needed in fecundity estimates to attain a stationary population, I considered different adult and juvenile survival estimates obtained from estimates in this study and from other studies on Willow Flycatchers (Koronkiewicz et al. 2006, Paxton et al. 2007). I also used maximum estimates from the literature on passerines (Donovan and Thompson III 2001), assuming that the range of these estimates represent realistic possibilities of survivorship of flycatchers.

I used general linear modeling to examine how measures of reproductive success and timing influenced return rates of juveniles and adults. I weighted each model by sample sizes within years for each of the predictor variables. I used only data from the Truckee region because of the length of the study in that region and because effort was relatively consistent across years. I examined how annual juvenile return rates were affected by factors from their natal year: fecundity, daily survival rate, clutch size of successful nests, onset of nesting season, and mean date of successful nests. For adults, I

evaluated the probability of adults returning to the study region in subsequent years based on estimates of fecundity, daily nest survival rate, and three measures of brood loss: egg survival, nestling survival, and total proportion fledged. I defined egg survival as the probability of an egg surviving to hatch, nestling survival as the probability that a hatch-day nestling will survive to fledge, and total proportion fledged as survival from egg-laying to fledging. Additionally, I examined how adult return rates were influenced by the timing of nesting in the previous year, measured by onset of the nesting season and mean date of nest initiation for successful nests, and by whether the nesting season was delayed in the returning year.

RESULTS

From 1997 to 2008, I detected 981 Willow Flycatcher territories, found 904 nests, banded 1,167 nestlings, resighted 348 adults, and banded 56 adults.

Population trends

The numbers of territories at my long-term study sites in the South Lake and Truckee regions ranged from 0-14 and there was considerable annual variation within sites (Fig. 1). In the southern region I detected no flycatchers at five of the six consistently monitored sites after 2004 (Fig. 1a) and no females in any study sites after 2006 (Fig 2a). The mean annual rate of change in number of territories was a decline of 17.9% (SD = 0.212, Fig. 2a), and the mean annual rate of change in the number of females was an 8.3% decline (SD = 0.5). At 13 study sites in the Truckee region monitored consistently across study years the number of territories declined during this study. Trends in number of females were similar to that of males (Fig. 1b). The declining trend was less obvious in the Truckee region because of annual fluctuations at study sites,

but the mean annual rate of change in number of territories was a decline of 6.1% (SD = 0.087). Females declined at a mean rate of 6.4% (SD = 0.14, Fig. 2b). In Warner Valley territory numbers have fluctuated between 32-40 and females reflect a similar trend (Fig. 1c). In this region there was a mean rate of decline of territories in 2004, 2005, and 2008 of 1.9% (SD = 0.26). I have only two years of data to determine the change in number of females and these show a 31.3% increase from 2003-2004 and a decline of 9.5% from 2004-2005 (Fig. 2c). I did not monitor females in the Warner Valley region in 2007, but using estimates of females from 2005 there was a 23.7% decrease in their number in 2008 (Appendix D). In the McCloud region there was a 10% increase from 2005 in the number of territories detected in 2006.

There was an increasing trend in the number of unmated territorial males detected in the South Lake region ($r^2 = 0.403$, $P = 0.03$, $n = 12$; Fig. 3) and in the Truckee region ($r^2 = 0.555$, $P = 0.005$, $n = 12$) across all study years. From 2003-2008 the proportion of unmated males in Warner Valley increased from 8-9% in 2003-2005 to 14.6% in 2008 ($r^2 = 0.939$, $P = 0.03$, $n = 4$). Compared to the South Lake and Truckee regions from 2003-2008, the mean annual proportion of unmated males in Warner Valley was 78.1% and 83.8% less, respectively (South Lake: mean = 0.383, SD = 0.337, $n = 6$; Truckee: mean = 0.283, SD = 0.075, $n = 6$; Warner Valley: mean = 0.062, SD = 0.053, $n = 4$). I was unable to estimate proportions of unmated males in the McCloud region because I did not monitor all territories continuously during the season.

From 2003 to 2008, the proportion of polygynous territories in three regions did not change significantly (South Lake: $r^2 = 0.344$, $P = 0.2$, $n = 6$; Truckee: $r^2 = 0.271$, $P = 0.3$, $n = 6$; Warner Valley: $r^2 = 0.110$, $P = 0.7$, $n = 4$), although there was a slight

increasing trend in the Truckee region (Fig. 4). In 2007 I found a male with three females in the Truckee region and in 2004 I documented double-brooding of a banded female in Warner Valley. I detected two polygynous territories in the McCloud region in 2006. For known-aged territorial males, 60.6% of first-year males were unmated ($n = 33$) and 20.5% ($n = 39$) of second-year males were unmated. I detected only one first-year breeding male with a polygynous territory. The majority of males with polygynous territories were second-year birds (44%, $n = 9$). For known-aged first-year females, 25.8% ($n = 31$) were in polygynous territories compared to 13.3% ($n = 60$) of known-aged females older than their first breeding year.

Population demographics

Natal site fidelity was 34.3% ($n = 70$) in the Truckee region and 31.3% ($n = 16$) in the Warner Valley region. In the South Lake region, all birds resighted that I could assign to a natal location returned to their natal sites ($n = 7$). Of those individuals that returned to their natal locations, males comprised 47.8% ($n = 23$) in the Truckee region and 44.4% ($n = 9$) in the Warner Valley region. In the Truckee region, 14.5% ($n = 72$) of the resighted second-year breeding birds dispersed outside of my 10 original study sites. There was one long-distance natal dispersal event of 134 km documented for a female from Warner Valley breeding in the Truckee region.

From 1997 through 2008, 15.5% ($n = 578$) of nestlings banded at the South Lake and Truckee study sites returned to breed in the following year (Table 1). The annual proportion of juveniles recruited into the breeding population at my study sites varied across the years ranging from 6.1% from the 2001 cohort to 25.4% from the 2005 cohort

(mean = 0.15, SD = 0.07, $n = 11$; Fig. 5). I estimated mean annual juvenile recruitment of 29.9% (SD = 0.08, $n = 11$) assuming a constant annual immigration rate of 14.5%.

I captured 38 individual adults and marked them with unique combinations. I resighted 73.7% of these uniquely marked adults in year $t + 1$ ($n = 38$) and only 10.7% of the individuals changed breeding meadows ($n = 28$). Mean annual adult return rate was 70.0% (SD = 0.497, $n = 151$) using the cohort method and pooling return rates across years and sites in the South Lake and Truckee regions. For a subset of 38 individually marked birds I combined all years and individuals and calculated a return rate of 68.7% ($n = 70$) adjusted with a detection probability of 95.7% ($n = 46$).

Fecundity estimates declined in study sites in the South Lake region from 1997–2004 and in 2007 no females were detected in the region (Table 2). Fecundity estimates in the Truckee region fluctuated annually showing no discernable trend. Mean annual maximum fecundity estimates were 23% higher in both the Warner Valley and McCloud regions than in the Truckee region and 40% higher than the South Lake region. The lowest annual fecundity estimate in the Warner Valley or McCloud region was 0.74 female young per adult female, which was higher than 50% of the annual fecundity estimates in the Truckee region and 67% of the estimates in the South Lake region.

Using constant juvenile (30%) and adult survival rates (70%) obtained from my adjusted return rate estimates, fecundity would need to equal one female young per adult female for population stability ($\lambda = 1$). Based on my annual fecundity estimates few of my study years exceeded fecundity estimates > 1.0 (Table 2). However, an increase of only 3% in each vital rate would result in population stability in the Warner Valley and McCloud study regions. Based on sensitivity analysis, if my adult and juvenile survival

estimates (70% and 30%, respectively) were accurate then fecundity would need to increase by 52% in the South Lake region and by 35% in the Truckee region. Using estimates from a long-term study on southwestern Willow Flycatchers that used a maximum likelihood approach and estimated adult survival of 64% and juvenile survival of 34%, fecundity would need to increase by 61% in the South Lake and 43% in the Truckee region. Only if I assumed that survivorship in this population of flycatchers was similar to maximum estimates of adult survival rates for migratory passerines (80%; Greenberg 1980) and that juvenile survival is half that of adult survival (Temple and Carey 1988, Buehler et al. 2009), is population stability achieved in the South Lake region with no changes to the current fecundity estimate. In the Truckee region, fecundity estimates could decline by 40% to 0.44 for population stability under current conditions.

Breeding season influences on return rates

Return rates of juveniles to their natal region were not affected by fecundity, daily survival rate of nests, clutch size of successful nests, date of nest initiation of successful nests, and timing of nest initiation during their natal year (Table 3). However, juvenile return rates were negatively influenced by adult return rates ($\beta = -0.55$, $SE = 0.22$, $F_{1,9} = 6.2$, $P = 0.03$). Adult return rates were positively influenced by the number of nestlings fledged per nest in the previous year ($\beta = 0.43$, $SE = 0.18$, $F_{1,9} = 6.0$, $P = 0.03$). No other measures of reproductive success or seasonal timing from the previous breeding season influenced return rates in the following breeding season. Similarly, there was no influence of timing of nest initiation in the return year on adult return rates.

DISCUSSION

I detected a decline in the population of Willow Flycatchers in the South Lake and Truckee regions since the initiation of this study in 1997. The decline was strongest in the South Lake region where five of six study sites monitored since 2003 no longer support flycatcher territories, and females were no longer detected at these sites after 2006. The population decline was less severe but still indicated a declining trend in the Truckee region. Sensitivity analysis of population growth models indicated that populations in the Warner Valley and McCloud regions were likely stable, and it suggested that low fecundity estimates in the South Lake and Truckee regions contributed to the declining populations in these regions.

I found no support for the hypothesis that timing of nesting in previous breeding seasons influenced juvenile or adult return rates. Juvenile return rates were associated with adult return rates in their returning year. Adult return rates were influenced by nestling survival in the previous breeding season but not by other factors associated with breeding success. Reproductive success influences emigration and immigration processes and may explain persistence of breeding pairs in a location.

Juvenile return rates

Annual juvenile return rates were not associated with factors that occurred during their natal breeding season but were related to adult return rates and seasonal nest initiation in their return year (i.e., second-year). The negative association with adult return rates suggests that in years with high breeding site fidelity competition for territories or mates might encourage second-year breeding birds to disperse or not to settle in a breeding territory that year. Second-year birds may be at a competitive

disadvantage compared to older, experienced birds because arrival times for second-year birds were later than older birds, a common pattern exhibited by many passerines (Murphy 2004, Sedgwick 2004). Increased competition with experienced adults may encourage second-year birds to disperse to smaller meadows outside of my study areas. Increased breeding success is positively associated with adult site fidelity in Willow Flycatchers in Oregon (Sedgwick 2004) and in Arizona (Paxton et al. 2007).

My second hypothesis predicted that juvenile recruitment would increase following years in which successful nests were earlier in the season compared to other years. Clutch size, which reflects success of earlier nests, seasonal nest initiation, and mean nest initiation were not related to juvenile return rates. Studies on Willow Flycatchers in Oregon (Sedgwick and Iko 1999) and Arizona (Paxton et al. 2007) determined that fledge date is an important factor predicting juvenile recruitment in Willow Flycatchers. Other studies have found a similar pattern for populations of wood thrush (Brown and Roth 2002), and white-crowned sparrows (Morton 1992). One explanation for a lack of a seasonal effect is that food is not limiting at the end of the season (Lack 1966); however, results from a study on relative insect abundances at my 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). Increased survival from early-season nests is also explained by the increased amount of time the young have on the breeding grounds to prepare for migration (Brown and Roth 2002). Increased time on the breeding grounds may not influence the physical condition of the young because during migration they may increase their stopover time to build up necessary fat reserves (Otahal 1998); however, this may delay their arrival on the

wintering grounds. Juveniles in better physical condition or that fledged from early-season nests may arrive on the wintering grounds earlier and can settle in higher quality territories. On the wintering grounds Willow Flycatchers exhibit high site fidelity and aggressive territory defense and detections of non-territorial birds suggests habitat may be limiting (Lynn et al. 2003, Koronkiewicz et al. 2006). I may have been unable to detect any effects because I used population-level data instead of an individual-based approach. Current research on flycatchers in this population will address these issues.

My mean annual juvenile return rate, prior to adjustments for detection, at my Truckee study region was similar to estimates for Willow Flycatchers in Oregon (13%; (Sedgwick 2004) but 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). My adjusted juvenile recruitment estimate across all years of 30% was lower than maximum likelihood estimates for southwestern Willow Flycatchers in Arizona (34%; Paxton et al. 2007) and 34.8% lower than in those in southern California (46%; Whitfield pers com in Paxton et al. 2007).

My hypotheses concerning juvenile return rates were dependent upon high natal philopatry to the study area to detect differences among study years. My 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). Natal philopatry is typically low for most migratory passerines (Gauthreaux 1982, Weatherhead and Forbes 1994), but in my study system there may be a selective advantage to returning to natal grounds. Juveniles may assess the area during their post-fledging period for future territory settlement decisions (Morton 1992, Dale et al. 2006).

This scenario is likely given that little time exists at the start of breeding seasons for males to prospect for breeding locations, which also may contribute to high breeding site fidelity in my population.

I detected a negative relationship between return rates of adults and juveniles, which might arise from competition for territories in high-density populations; however, densities at my study sites in the South Lake and Truckee regions were lower than densities in the two study regions to the north (Appendix C). Low densities and high natal philopatry suggests that competition for territory space may be relaxed at some of my study sites in the central Sierra Nevada regions. However, Willow Flycatchers exhibit a facultative polygynous mating system and second-year males may experience competition with older males not over space but for mate acquisition. Unmated males may be less likely to remain in an area, thus reducing detection probabilities (Paxton et al. 2007). In this study, second-year females were paired with polygynous males more often than older females. Female productivity in southwestern Willow Flycatchers is not affected by settlement in polygynous or monogamous territories (Pearson 2002, Davidson and Allison 2003, Pearson et al. 2006) potentially because male parental care is minimal. *Post hoc* examination of my data suggest that detections of polygynous females may be lower than monogamous females, although studies have described increased aggressive behavior between females in polygynous territories (Prescott 1986; but see Sedgwick 2004). I detected a slight bias towards higher philopatry in females than in males, but the significance of this and the mechanism underlying any trends is unknown. Pronounced philopatry in my study population agrees with other studies on patchily-distributed and isolated breeding populations (Hansson et al. 2002). Loss and degradation of riparian

habitat in the intermountain west may limit natal dispersal options for Willow Flycatchers, especially if juveniles rely upon prospecting behavior in their natal year (Paxton et al. 2007).

Adult return rates

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. Daily nest survival rates were not a strong predictor of return rates; thus, Willow Flycatchers may evaluate breeding success based on their ability to fledge their entire brood successfully and not on overall nesting success (Part and Doligez 2003). In other words, partial predation or nest failure during the nestling period may have considerable influences on site fidelity decisions. In addition to site fidelity, a neighborhood effect may have contributed to this region-wide pattern. 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 number of young fledged predicted site fidelity 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).

I found no relationship between adult return rates and measures of early-season nesting success. A positive relationship may indicate that completing the breeding cycle earlier would increase survival over the nonbreeding season by allowing for more time to prepare for migration (Sedgwick and Iko 1999). Survival of adults is inversely related to fecundity in some birds because increased nesting attempts require more energy

expenditure (Martin 1995). However, Hoover (2003) found no support for the hypothesis that increased renesting reduces survival of Prothonotary Warblers.

Observed breeding site fidelity in my Truckee region was higher than that reported for other studies (57%, Paxton et al. 2007; 52%, Sedgwick 2003). My return rate for adult Willow Flycatchers was higher than that reported for Willow Flycatchers in Oregon (45%, Sedgwick and Klus), southwestern Willow Flycatchers in Arizona (55%, Paxton (2007), in California (M. J. Whitfield unpubl. data in Paxton et al. 2007), and Michigan (Walkinshaw 1966). Koronkiewicz et al. (2006) reported a return rate of 65% on the wintering grounds. My adult return rate was higher than those reported for other passerines species (Brown and Roth 2002, Gardali et al. 2003). Although I did not estimate a survival rate using maximum likelihood, my adjusted adult survival estimate was 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).

Population trends

The proportion of unmated males increased in the South Lake 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 I have observed declines in site occupancy by females while a single territorial male consistently returned for several years (Appendix C). As populations became increasingly male-skewed I observed a slight but non-significant increase in the proportion of polygynous

territories. In monogamous or polygynous mating systems, a disproportionate sex ratio that favors males has a higher risk of extinction (Dale 2001). Estimates of >30% of unmated males is considered a high proportion (Dale 2001), and estimates from several of my study years exceeded this proportion.

In my system, males and females are constrained by the length of the breeding season (Chapter 1); therefore, it is advantageous to reduce time spent acquiring territories at the initiation of the breeding season. Because male territory defense increases costs of dispersal to new locations (Nolan 1978), it may be advantageous to return to a location regardless of breeding success or mate acquisition in the previous year, a pattern exhibited by Willow Flycatchers in Oregon (Sedgwick 2004). Even if sites are not settled in subsequent years by the same individual male, new males may continue to settle in some meadows if they evaluate the quality of habitat differently from females (Sedgwick and Knopf 1992, Schmidt 2004) and thus are unable to predict the probability of female occurrence. Conversely, female Willow Flycatchers are more discriminate about habitat than males (Sedgwick and Knopf 1992) and they may be more likely to use decision rules, such as previous years' breeding success, to determine settlement patterns (Sedgwick 2004). Reduced costs of dispersal associated with territory selection for females may be facilitated by a flexible mating strategy in which females experience few or no costs from polygyny (Sedgwick and Knopf 1989, Pearson 2002, Davidson and Allison 2003). The polygyny threshold model states that if the costs of breeding in low quality habitat exceed the benefits of a monogamous pair bond (i.e., male parental care), then females will select polygyny in high quality territories (Verner and Willson 1966, Orians 1969, Hansson et al. 2000). In addition to increased female immigration from a

region, female mortality while nesting may be higher in low-quality sites, contributing to a male-biased sex ratio. Changes in habitat quality or other factors influencing reproductive success in flycatchers in my study regions may thus make a site unsuitable for breeding even though territorial males may continue to return. Failing to incorporate sex ratios in demographic modeling will result in underestimating extinction probabilities (Brook et al. 2000).

Population sensitivity analysis

The population of flycatchers in the South Lake region has been steadily declining, and although surveys conducted by ourselves and the USDA Forest Service have detected individuals in adjacent small meadows, the total number of flycatchers detected in the South Lake region in recent years never exceeds five males. In the Truckee region, territory estimates at two of the largest meadows have fluctuated during this study but generally have declined compared to estimates from the first few years and from surveys conducted in the 1980s (Serena 1982, Harris et al. 1987). Based on survey data, populations of Willow Flycatchers may be stable or increasing in Warner Valley (King and King 2003, Humple and Burnett 2004). Surveys conducted in Warner Valley from 1998-2001 estimated between 30-35 territorial males (King and King 2003) and surveys conducted by my research group in 2003 estimated 32 territorial males (Appendix B). The CDFG conducted surveys for Willow Flycatchers in the McCloud region in 1997 and 1998 (C. Stermer unpubl. data) but no other research on Willow Flycatchers has been done in this region on.

Using deterministic population growth models and sensitivity analysis relative to estimates of fecundity from the two northern regions, I determined that population

stability in the South Lake and Truckee regions depended on increases in fecundity estimates because increases necessary in survival rates would exceed realistic mean annual estimates (Donovan and Thompson III 2001, Paxton et al. 2007). Using current mean annual fecundity estimates in the South Lake and Truckee region I was unable to obtain population stability until I used the maximum adult survival rates of 80% reported in the literature and assumed that juvenile survival was half that of adult survival. This is unrealistic because I considered these estimates constant across years, and demographic stochasticity requires that constants represent mean values. My estimates of survival and those derived from a long-term study on southwestern Willow Flycatchers are likely more realistic. Using these values in sensitivity analysis indicated that to attain population stability in the South Lake and Truckee regions would require increases in fecundity estimates of 52–61% and 35–43%, respectively.

I used return rates as indices of survival rates in my sensitivity analysis, which likely underestimated actual survival rates. My juvenile survival rate of 30% was slightly lower than maximum likelihood estimates for southwestern Willow Flycatchers of 34% (Paxton et al. 2007) but was within the range of estimates reported for other species (Donovan and Thompson III 2001). My estimate of adult survival of 70% was higher than the 64% (95% CI: 62–66%) reported for southwestern Willow Flycatchers from a long-term demography study that used maximum likelihood methods to account for detection probabilities (Paxton et al. 2007). Furthermore, demographic studies on other passerines rarely report adult survival estimates above 65% (Martin et al. 1995). My high estimate of adult survival may be contributed to high site fidelity in my Truckee region, which increases detection probabilities of returning adults although some bias may still

exist (Martin et al. 1995). Increasing the spatial extent of a study area often improves detection probability and survival estimates, especially for populations with a patchy distribution (Hansson et al. 2002); yet accurate estimates for open populations are unavoidably limited because of dispersal outside of finite study areas (Marshall et al. 2004). Paxton et al. (2007) demonstrated that survival estimates converged at their full study area extent, which represented approximately 444 ha of occupied habitat plus additional adjacent locations. My original 10 study areas in the Truckee region encompass over 500 ha of suitable habitat, and an additional 200 ha of occupied meadows were added to my study in 2003. Regardless of my attempts to survey at a large spatial extent, my estimates of juvenile survival are likely underestimated. My fecundity estimates were overestimated because I used the maximum number of young last seen in the nest. Additionally, my practice of hindering cowbird eggs from hatching further overestimates fecundity because most Willow Flycatcher nestlings in parasitized nests do not survive to fledge (Sogge et al. 1997).

Management implications

My study suggested that declining populations of Willow Flycatchers breeding in meadows in the central Sierra Nevada, California, might be a result of factors limiting fecundity, which in turn can influence site persistence. Low productivity at local scale is compensated by immigration and may be reoccupied by flycatchers after the limitation on reproduction has been removed. However, extirpation of flycatchers across a broader region may disrupt metapopulation dynamics because distances between breeding populations may exceed dispersal distances. Additionally, conspecific attraction may be an important mechanism in flycatcher territory establishment (H. A. Mathewson et al.

unpubl. data). Willow Flycatchers exhibit high natal philopatry and site fidelity (Sedgwick 2004) reducing the frequency of long-distance dispersal events. Since surveys conducted over two decades ago detected a gap between flycatchers breeding in the southern and central Sierra Nevada (Serena 1982, Harris et al. 1987). Recent surveys in Yosemite National Park identified extensive suitable habitat yet the area remained unoccupied (Siegel et al. 2008).

As evidenced by this study and those in other flycatcher population ranges conservation and restoration of breeding habitat should occur in and adjacent to currently occupied breeding areas. Often it isn't until a population is declining that actions to enhance riparian habitat are enacted. By comparing estimates against high-density populations of flycatchers, this long-term study indicates that measures to improve fecundity estimates are imperative for meadows in the central Sierra Nevada to continue to support breeding populations of Willow Flycatchers. Because population stability in fecundity-limited species relies on high estimates of survival during the migratory and wintering periods, it is imperative that conservation efforts for Willow Flycatchers occur at locations outside of just their breeding range. Although Willow Flycatchers no longer breed outside of the Sierra Nevada and Cascades in California, riparian areas along the coast, in Truckee California, and historical locations in the southern Sierra Nevada remain important stopover locations during migration (Otahal 1998). On the wintering grounds habitat may be limiting (Lynn et al. 2003, Koronkiewicz et al. 2006) and survival is likely to be affected by loss or degradation of riparian areas in Central America.

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Table 2. Number of female Willow Flycatchers detected, maximum number of fledglings detected in nest before fledging, and annual fecundity estimates for four study regions in the Sierra Nevada, CA.

Region	Year	No. of Females Detected	Maximum No. of Fledglings	Fecundity (No. female young/adult female)
South Tahoe				
	1997	4	9	1.13
	1998	11	16	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
	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
	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)			0.88(0.12)
McCloud				
	2005	22	37	0.79
	2006	35	68	0.96
	Mean (SD)			0.88 (0.12)

FIGURE LEGEND

Figure 1. Number of Willow Flycatcher territories monitored each year at study sites in the (A) South Lake, (B) Truckee, and (C) Warner Valley study regions in the central and north Sierra Nevada, CA. Original sites were six sites in the South Lake region and nine sites in the Truckee region that were monitored each year during the long-term study from 1998–2008.

Figure 2. Willow flycatcher rate of population change for (A) males and (B) females detected in the South Lake, Truckee, and Warner Valley study regions.

Figure 3. Proportion of unmated territorial Willow Flycatcher males relative to total territorial males in the South Lake, Truckee, and Warner Valley study areas.

Figure 4. Proportion of Willow Flycatcher polygynous territories in the South Lake, Truckee, and Warner Valley study regions in the Sierra Nevada, California.

Figure 5. Comparison between adjusted juvenile return rates (assuming 14.5% annual emigration rate) and adult return rates for Willow Flycatchers banded in the Truckee study region.

Fig. 1A

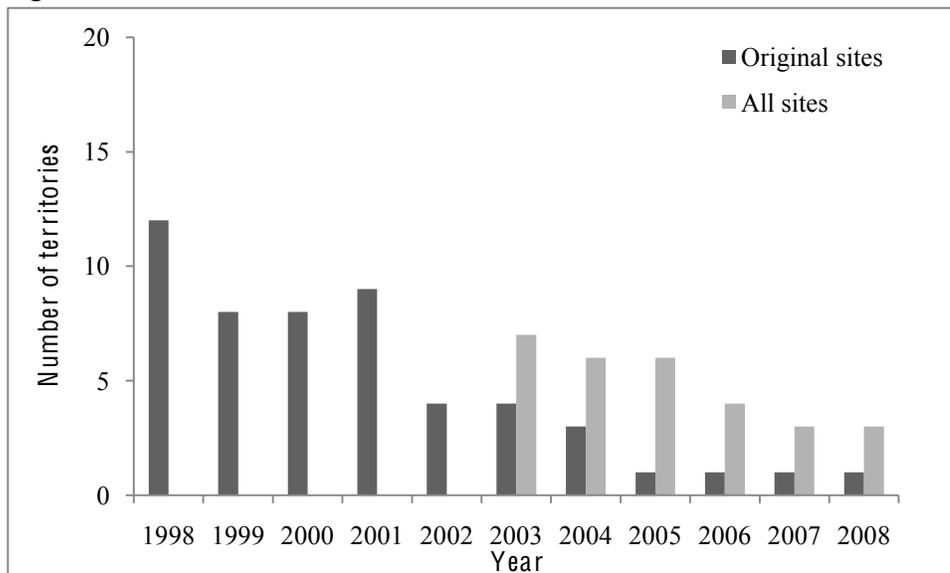


Fig. 1B

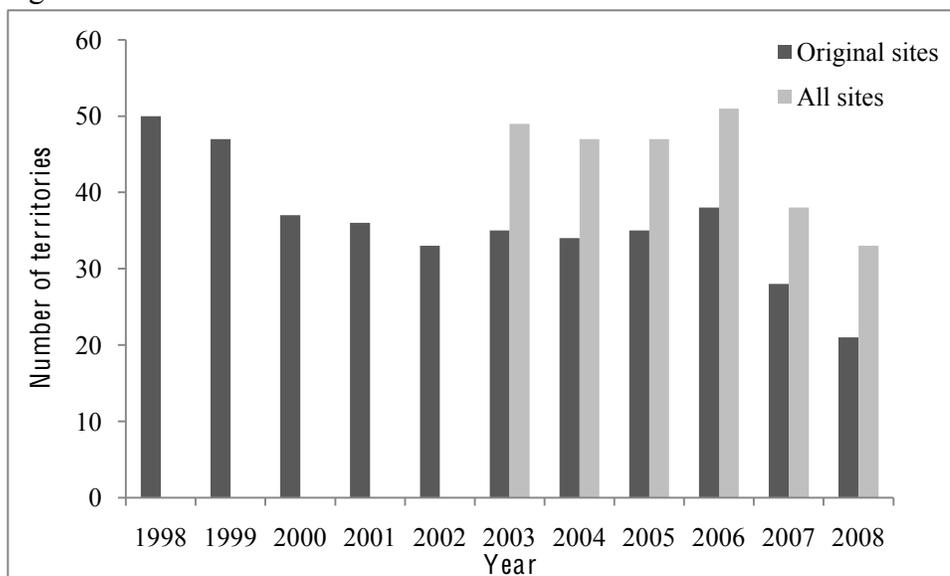


Fig. 1C

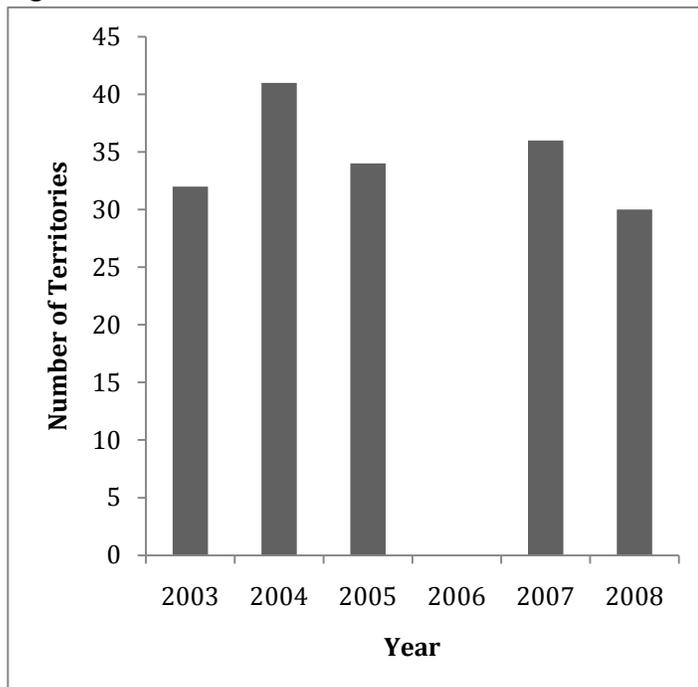


Fig. 2A

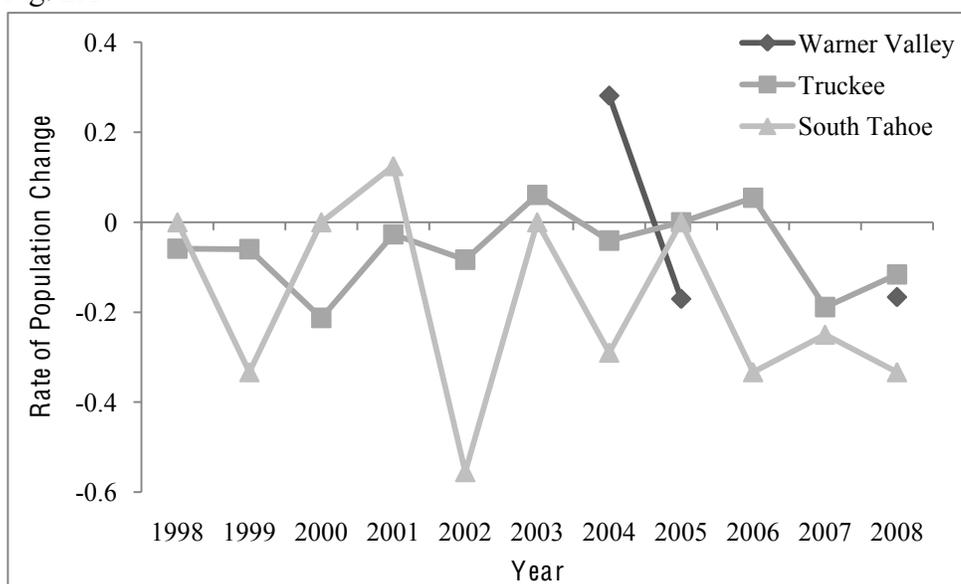


Fig. 2B

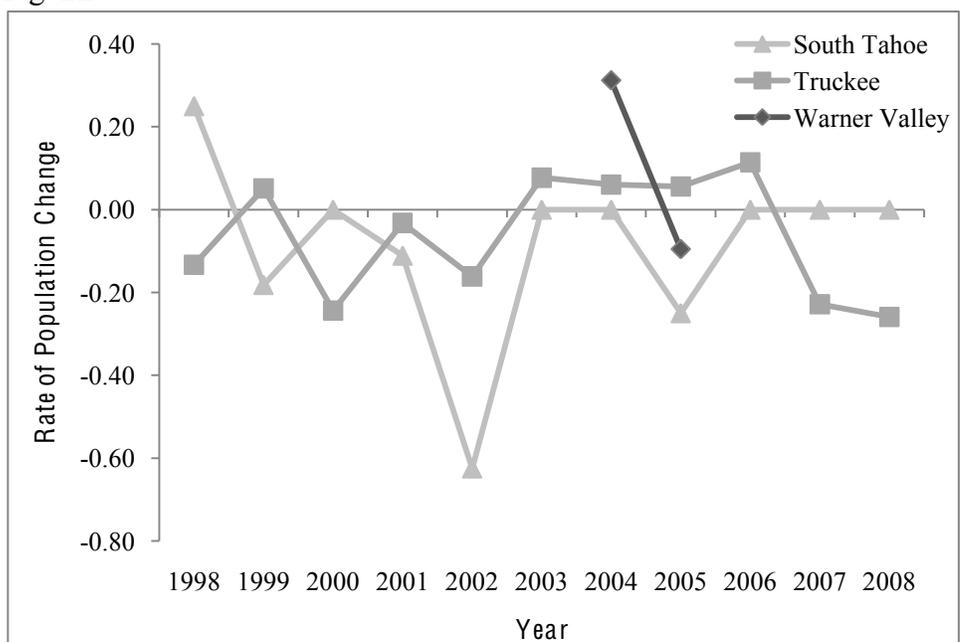


Fig. 3.

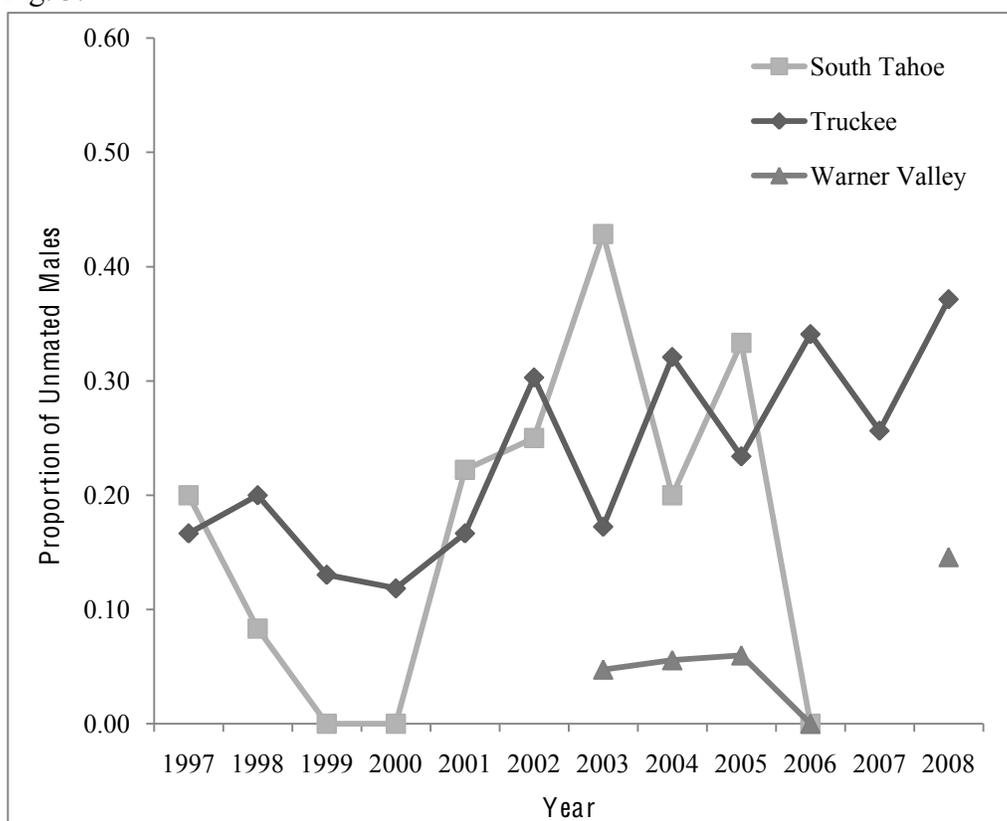
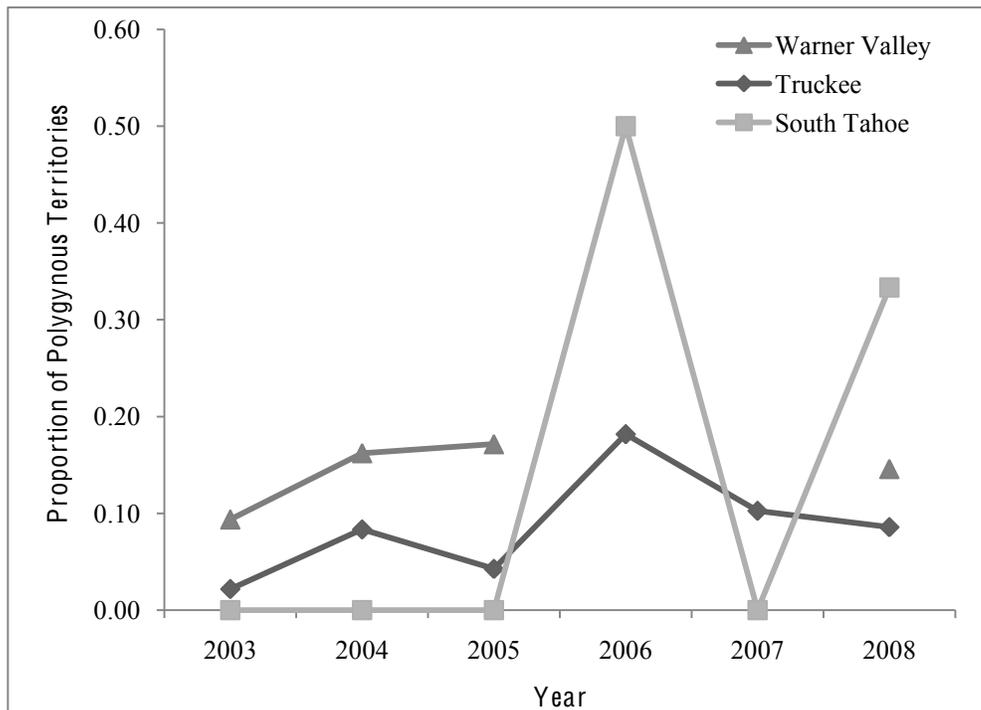
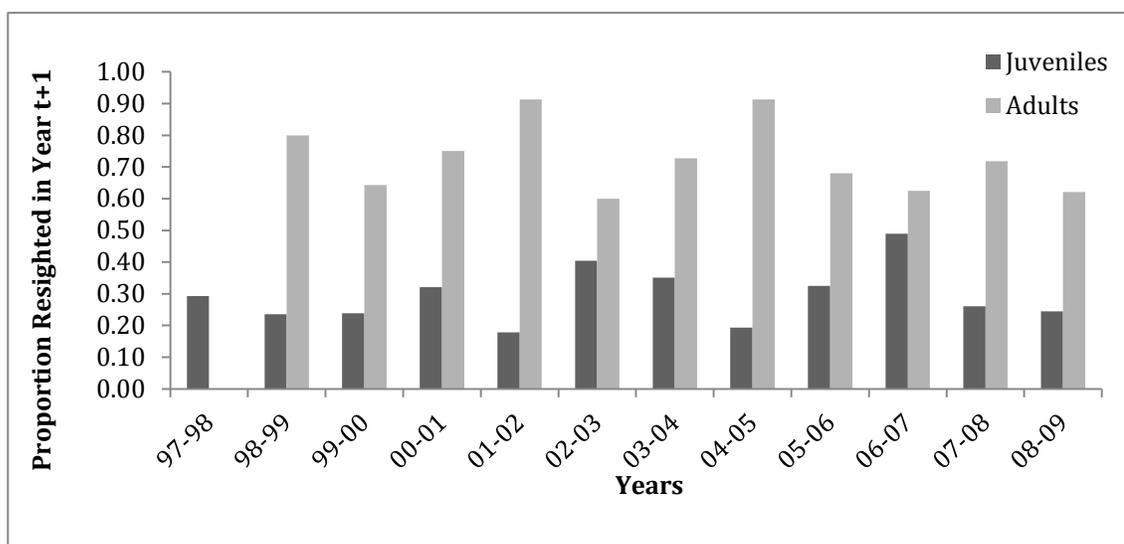


Fig. 4





CHAPTER 3. AREA AND EDGE EFFECTS INFLUENCE WILLOW FLYCATCHER NEST SURVIVAL

Abstract

Loss and degradation of riparian habitat could have profound impacts on population dynamics of riparian birds breeding in the western United States through increased isolation of riparian patches or by eliminating high-quality habitat. Factors within landscapes such as those associated with patch size, edge effects, and habitat structure at the nest-scale may separately or in combination explain observed variation in nest survival. I examined how meadow area, edge, and nest-scale variables influenced nest survival of Willow Flycatchers (*Empidonax traillii*), a riparian-obligate, Neotropical migrant restricted to breeding in montane meadows in the Sierra Nevada. This study uses data acquired from a long-term monitoring program initiated in 1997 in the central Sierra Nevada and expanded in 2003 to a study region in the north Sierra Nevada. I monitored nests and recorded habitat measures once nests were inactive from 2003–2006. I acquired spatial data for meadow-scale and edge effects analyses using color orthoquad maps. Meadows in the central region were combined by sizes into small and large groups to compare meadow-area effects. For nest survival analysis I used the logistic-exposure method. I used an hierarchical approach by selecting the best model from a set of temporal variables. Then I added variables from each set of spatial models in sequence: meadow-area, edge, and nest-scale effects. In large (79–162 ha) meadows in the central regions, nest survival increased with over-nest cover. In small (5–37 ha) meadows, the relative magnitudes of these effects were lower indicating that spatial variation did not influence nest survival. In the north region, nest survival increased with distance from

edge and was not associated with nest-scale variables. Although I did not detect edge effects in the central region, observed estimates of survival suggested that in both study regions survival increased with distance from edge within the first 40 m but declined as distance increased. These results indicate that nest predators may concentrate within large meadows and that riparian shrub cover influenced survival. In smaller meadows, edge effects may be important influences on nest survival.

INTRODUCTION

Factors that limit survival and productivity of a species determine population dynamics, community composition, and the evolution of life-history traits. For passerines, nest predation is the primary factor limiting reproductive success (Martin 1992) and is therefore a strong selective agent shaping habitat selection decisions and avian behavior (Montgomerie and Weatherhead 1988, Weidinger 2002, Fontaine and Martin 2006, Chalfoun and Martin 2007). Nest predation rates are influenced by complex interactions among predator and prey population dynamics (Schmidt et al. 2001, Schmidt and Ostfeld 2003). Increased susceptibility to predation may result from alterations to habitat quality and quantity, and depressed nest survival rates may manifest at different spatial or temporal scales (Gates and Gysel 1978, Chalfoun et al. 2002b, Bombay et al. 2003). Effective conservation of avian species requires identification of multiple factors influencing reproductive success in addition to understanding the magnitude of the effect of these factors and their long-term repercussions on population persistence (Caughley 1994, Peery et al. 2004).

In the western US, riparian ecosystems are the primary breeding locations for >60% of passerine species (Saab 1999), yet they comprise <1% of the vegetation types in

the western United States (Knopf et al. 1988). Loss and degradation of riparian ecosystems are of increasing concern because of climate changes (Dettinger and Cayan 1995, Barnett et al. 2008), altered hydro-geomorphic processes (Shafroth et al. 2002), and other human induced disturbances (Miller et al. 2003, Scott et al. 2003). Loss and degradation of individual riparian patches could have profound impacts on population dynamics of riparian birds by increasing isolation of suitable patches or by eliminating high-quality habitat (Pulliam 1988). Changes at the landscape scale may constrain or facilitate factors at finer scales (Thompson III et al. 2002). Predator populations differ among landscapes and may best explain variation in nest survival in certain systems (Chalfoun et al. 2002b, Thompson III et al. 2002, Stephens et al. 2003). Factors within landscapes such as those associated with patch size, edge effects, and habitat structure at the nest-scale may separately or in combination explain observed variation in nest survival (Gates and Gysel 1978, Chalfoun et al. 2002b, Fletcher et al. 2007). Most research relating multiple spatial scales and variation in nest survival is predominately focused on the effects of habitat fragmentation in forested areas (Sisk and Battin 2002). Research is rare in riparian habitats (Lahti 2001, Batary and Baldi 2004), particularly for habitats that occur naturally in patchy and isolated distributions (Sisk and Battin 2002).

Within a region differences in patch size and shape may explain variation in nest survival (Zanette and Jenkins 2000, Albrecht 2004). Patch-size effects directly and indirectly can influence population size, density, and species richness of both nest predators and avian species (Helzer and Jelinski 1999, Fahrig 2003). The resource concentration hypothesis (Root 1973) predicts that population size and density are lower in small patch sizes because of the reduction in the amount and diversity of resources

(Ries et al. 2004), including availability of space for territories. However, increased predation pressure in large meadows due to increased density of predator and prey may be mitigated by a dilution effect, which predicts that an increase in the density of prey will decrease the probability that an individual nest is encountered and predated (MacArthur et al. 1972). Patch-area and edge effects significantly covary; as patch size increases there is a concomitant decrease in patch edge length (Sisk and Battin 2002, Fletcher et al. 2007). Fletcher et al. (2007) differentiated between patch-size effects and patch-area effects in that the former is a change in an ecological response arising from patch area that is independent from other causes, such as edge effects, whereas patch-area effects may include several potential causes. The relative amount of edge around the patch (i.e., patch-area effect; Fletcher et al. 2007) is dependent upon the area of a patch, the shape of the patch, and non-linearity of the patch edge (Helzer and Jelinski 1999).

Edge effects are ecological changes that occur with increasing distance from a boundary between two distinct patches (Ries et al. 2004). The size of a meadow constrains the distance at which a bird can place its nest from the forest edge; therefore, edge effects may be more important in small patches because all habitat is close to the forest edge. Edge effects may increase the probability of predation on nests located closer to forest edges because of increased predator abundance along edges (Gates and Gysel 1978, see review in Lahti 2001). Commonly proposed mechanisms for increased predator activity along edges include reliance on edges for travel or foraging (Fritzell 1978) and response to concentrations of food resources (Gates and Gysel 1978). For example, edges may influence movement patterns of snakes (Carfagno et al. 2006), which may rely on forest edges for thermoregulation. Furthermore, edges provide access to spatially

segregated resources (i.e., Brown-headed Cowbirds *Molothrus ater*; Morrison and Hahn 2002, Ries et al. 2004), and prey densities may be greater along habitat edges (Ries et al. 2004, Ries and Sisk 2004).

At the nest-scale, nest-placement decisions are nonrandom and oftentimes adaptive (Martin 1993a); birds place nests in locations that reduce the probability that a predator will detect a nest (Martin and Roper 1988, Martin 1992, Martin and Li 1992, Weidinger 2002). Additionally, nest-placement decisions involve consideration of parental behavior such as nest defense strategies (Montgomerie and Weatherhead 1988, Martin 1992), thermoregulatory demands (Conway and Martin 2000), and densities of other nesting passerines (Liebezeit and George 2002). Furthermore, birds respond in an hierarchical manner when making decisions (Kristan 2006); therefore, the selection of fine-scale nest location may depend upon coarse-grained habitat characteristics. For example, if aerial predation is significant along habitat edges (Chalfoun et al. 2002a), then birds may place nests in locations with increased over-nest cover relative to the distance from the habitat edge (Donovan et al. 1997).

I examined how meadow area, edge, and nest-scale variables influenced nest survival of Willow Flycatchers (*Empidonax traillii*), a riparian-obligate Neotropical migrant restricted to breeding in montane meadows in the Sierra Nevada. Willow flycatchers in California rely almost exclusively on riparian ecosystems in the Sierra Nevada for breeding habitat, and there is increasing concern for riparian ecosystems resulting from historical and current disturbances to natural ecological processes (Manley et al. 2000). Population declines since the 1940s were attributed to loss of habitat and an increase in nest predation rates (Green et al. 2003).

In 1997, I initiated a long-term study on two subspecies of Willow Flycatchers (*E. t. adastus* and *E. t. brewsteri*) in two study regions in the central and north Sierra Nevada. Nest predation was the primary factor associated with estimates of fecundity in both regions (Chapter 1). The primary objective of this study was to examine spatial variation in nest survival within regions. I employed a hierarchical modeling approach to determine the general factors influencing probability of nest survival by examining the relative strength of predictor variables associated with meadow area, edge, or nest-scale effects within regions compared to a temporal model. Long-term research programs such as this are necessary for understanding the effects of multiple temporal and spatial factors on nest survival.

I predicted that large-scale effects, such as temporal and meadow area effects, would emerge as strong predictors of nest survival. For the meadow area and edge effects models, I examined the hypothesis that patch-area effects and edge effects interact (Andren 1992, Albrecht 2004) so that nests located in small meadows would experience increased risk of predation because of the influence of edge proximity relative to large meadows. I predicted that the probability of nest survival would decrease with decreasing patch size and decreasing distance from forest edge but that the strength of these relationships depends on the size of the patch. For the last three years of the study, I examined the effects of nest-scale factors on nest survival rates. I examined the hypothesis that increased concealment around the nest would minimize predation risk. I predicted that survival would increase with increased nest height, over-nest cover, and distance from willow shrub edge. Furthermore, assuming the risk of predation is greater in small meadows, as predicted by the previously discussed relationship between meadow

size and edge effects, I predicted that the effect of concealment would be more pronounced in small meadows.

METHODS

Study sites and field methods

I completed this research in conjunction with a long-term research study on Willow Flycatchers (hereafter flycatchers) breeding in wet montane meadows in the central and north Sierra Nevada, California (Appendix A). Study sites were meadows grouped into study regions based on geographic distance and differences in topography, vegetative characteristics, and differences in land-use practices. For this study I grouped two of the study regions (South Tahoe and Truckee) because of small sample sizes in South Tahoe and I referred to them as the central region. Study sites in this region were located in the central Sierra Nevada, south and north of Lake Tahoe, California. These sites were part of a long-term study on flycatcher demography initiated in 1997 (Bombay 1999). The number of study sites monitored each year in this region fluctuated because of differences in annual funding and accessibility of properties (Appendix B). In 2003 I added study sites in Warner Valley, a large meadow in the north Sierra Nevada just south of Lassen Volcanic National Park, California.

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 central region were similar. Study sites in this region were patchily distributed across the landscape and ranged in size from 5–162 ha and in elevation from 1,700–2,400 m. The USDA Forest Service, California Fish & Game, or private landowners managed these study sites.

Study sites in Warner Valley were part of a 250-ha meadow, of which I monitored 80 ha divided into four study sites. This region was located approximately 125 km to the north of the central study region. Study sites ranged in size from 15–24 ha at elevations of 1,550–1,590 m. California Fish and Game and private landowners managed these study sites.

Within both study regions, 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 rivers or adjacent to lakes and riparian deciduous shrubs paralleled water sources, were scattered in large clumps across the meadows, or were concentrated in spring-fed areas. 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 streams, rivers, and lake edges but also were scattered in large clumps across the meadows. The riparian shrub community was predominantly comprised of Geyer's willow (*Salix geyeriana*) and Lemmon's willow (*S. lemmonii*) in the South Lake and Truckee regions. In Warner Valley, mountain alder (*Alnus tenuifolia*) and quaking aspen (*Populus tremuloides*) were interspersed with the willow. Sedges (*Carex* spp.), grasses, rushes (*Juncus* spp.), and forbs dominated the herbaceous community. Sagebrush (*Artemisia* spp.) was intermittently located in upper portions of the meadows, which were surrounded by a mixed coniferous forest dominated by lodgepole pine (*Pinus contorta*).

Field methods

I located all Willow Flycatcher territories using standard territory mapping and used behavioral cues from adults (Martin and Geupel 1993) to locate and monitor nests during June through August in 1997 through 2007. I monitored nests every two to six days depending on estimated stage transition dates. For length of nesting stages, I used three days for laying, 14 days for incubation, and nest fledging date anytime after day 13 of the nestling period (total of 31 days of nesting; H. L. Loffland et al. unpubl. data). I assumed that nests were successful if at least one fledgling was located or if the nest was active at least until day 12. By day 12 of the nestling period the young were capable of force fledging (H. A. Mathewson, pers. obs.) and thus at least one young may avoid predation. I designated a nest as failed if the nest was empty prior to day 12 of the nestling period. Predation was the primary cause of failure of Willow Flycatcher nests (Chapter 1). For analyses in this study, I removed nests that failed from other causes such as weather or failure of eggs to hatch to avoid overestimating the effect of nest predation.

Nest survival models

I examined nest survival as a function of multiple habitat variables selected for their hypothesized association with differences in predator activity or abundances. I used a hierarchical modeling approach (Stephens et al. 2003, Hood and Dinsmore 2007) in which I determined the most predictive temporal effects model that considered nest age, date, and region, against which I compared the relative strength of predictor variables associated with meadow area, edge, or nest-scale effects. This approach involved a two-step process because data for nest-scale effects were only available for a subset of my study years.

First I examined influences on nest survival at the meadow-scale representing the effect of either meadow area or edge effects. This analysis used nest-monitoring data from 1997–2007 in the South Tahoe and Truckee region and from 2003–2006 in the Warner Valley region. I outlined meadow-scale factors visually using color orthoquad maps and Arc View GIS 3.2. In 2007 I ground-truthed my estimated delineation of trees and shrubs to increase my ability to delineate meadow features accurately using digital orthoquads. I measured the following variables using GIS: meadow area (size), meadow perimeter, total shrub cover, and total perimeter of individual shrub clumps (shrub perimeter). Using these measurements, I calculated three additional covariates used in nest survival models. To represent meadow shape standardized for meadow size I calculated the ratio of the meadow perimeter relative to the perimeter of a circle of the same area as the meadow. The proportion of shrub cover equaled the total shrub cover standardized by meadow area, and it represented cover as well as its inverse, proportion of open space. Shrub perimeter to area ratio represented the amount of within meadow shrub fragmentation. I modeled patch size as a categorical variable because the range of area of my study sites was a bimodal distribution with sites either 2–41 ha or 70–162 ha, thus providing a useful division into small and large meadows. For the Warner Valley region I removed measures of meadow area because of lack of variability. Also using GIS orthoquad maps, I estimated two measures of within-patch forest edge effects: the minimum distance to the continuous forest edge (forest) and the distance to the nearest tree or snag (>2 m tall).

For the second set of models, I selected measures that I hypothesized represented fine-scale effects on the ability of a predator to detect or access a nest. I hypothesized that

the effect of habitat variables may differ with patch size; therefore, I included interactions between patch size and distance from forest, over-nest cover, nest height, and edge.

These models included nest-monitoring data from 2005–2007, when I recorded habitat measurements once nests were inactive. These measures also were recorded at nests in 1997 and 1998 (Bombay 1999) and I compared model-selection results between these two sets of years.

Because data addressing nest-scale variables were available for only a subset of my study years, the data set used for this final stage of the modeling is a subset of that used for previous temporal and meadow-scale analyses; therefore, I performed post hoc model analysis by readjusting the set of candidate models based on the final performance of the temporal and meadow-scale variables. I then compared the same set of candidate models with data collected in 1997 and 1998 when my research group initiated the project (Bombay 1999) to examine the generality of the predictive models. For the Warner Valley model I was unable to include meadow-area variables because of the lack of variability among the variables but I followed the same procedure as in the South Tahoe and Truckee regions. I then compared model results to examine region-specific influences on daily nest survival.

Nest survival analysis

I defined a 31-day nesting period beginning on the day the first egg was laid in the nest. I defined the laying period as nest ages one through three, incubation from ages four through 17, and nestling period beginning on day 18 until the first bird left the nest, approximately day 31 (H. L. Loffland et al. unpubl. data). I standardized dates so that for

each region and year the date the first nest of the season was initiated was assigned day one and each day after until the day the last nest fledged was sequentially numbered.

I conducted all analyses in SAS version 9.2 (SAS institute, Cary, North Carolina). Prior to constructing nest survival models, I examined multicollinearity between the predictor variables. Variables with a variance inflation factor ≥ 2 ($r > 0.7$; Graham 2003) indicate potential problems with parameter estimates and were not included together in any sets of models. After examining correlations between variables within each region, I selected proportion of shrub cover, meadow shape, and distance from forest for use in my analyses. In Warner Valley there was no significant correlation between distance from forest and distance from tree or snag ($r = 0.20$), so I included both variables in models addressing edge effects in Warner Valley. Elimination of collinear variables did not alter my original hypotheses because I assumed that collinearity suggested that variables represent the same or similar influences on nest predator activity and abundance. I standardized all covariates for these analyses.

I used a logistic-exposure approach (Shaffer 2004, Shaffer and Thompson 2007) to evaluate nest survival as a function of my hypothesized variable combinations. This method allows for varying visitation intervals by using a modified logit-link function. The link function contains an exponent ($1/t$) that accounts for the probability that a nest surviving an interval between nest checks is dependent upon the length of that interval. The logistic-exposure method allows for inclusion of continuous, categorical, temporal, and spatial scale predictor variables. Assumptions of the logistic-exposure model are independence of nest fate and constant survival probability for nest-days specified by an

explanatory variable. I used generalized linear modeling procedure to fit candidate models.

I used the Akaike Information Criterion (AIC; Akaike 1973) to evaluate candidate models using an hierarchical modeling process (Stephens et al. 2003, Hood and Dinsmore 2007) for which I added covariates singly to the best approximating temporal model and retained any covariates if the model had a $\Delta AIC < 4$ (Akaike 1973, Burnham and Anderson 2002). If more than one covariate had a $\Delta AIC < 4$, I combined those variables to create additive-effects models. The AIC_{ω} indicates the weight of evidence in favor of the model given the set of candidate models. To account for model selection uncertainty, I calculated model-averaged parameter estimates, unconditional standard errors, and 95% confidence intervals. I employed odds ratio and associated 95% confidence intervals to evaluate the direction and strength of each relationship. The odds ratio indicates the likelihood of an outcome for every one-unit increase in the predictor variable. Predictor variables associated with odds ratio confidence intervals that do not include 1.0 are considered to have an effect on the likelihood of a nest either succeeding or failing. I used a z transformation on all variables before fitting any models; therefore, the estimates of effect sizes were comparable among the parameters but were not directly interpretable as absolute effects. I used the model-averaged estimates to predict daily survival rates for differing values of a predictor. To calculate predicted estimates, I allowed the value of one predictor variable to vary while holding the remaining predictor variables constant. For temporal models I allowed nest age and date to increment together because these variables naturally covary. I selected the values for the predictor variables from the range of values observed in the field.

I examined the fit of my predicted model by constructing plots of the observed daily survival rate for model-predicted influential explanatory variables (Shaffer and Thompson 2007). Model-selection results indicate the support for a model relative to the other models, but determining how well the model fits the data requires post hoc analyses. Typically, the chi-square goodness-of-fit is used to assess model fit of generalized linear models; however, for small sample sizes the chi-square does not provide a good approximation of the distribution of the continuous covariates. To acquire the observed predicted daily survival rate for continuous predictor variables the observations are grouped into several classes and then a daily survival rate (DSR) is estimated for each class. Precision of observed estimates are often low because of small sample sizes within each class; therefore, my goal was not necessarily to compare exact estimates but rather to examine agreement between the overall magnitude and direction of the effects of multiple biological variables.

RESULTS

From 1997–2007 I monitored 465 nests in the central region. The number of nests found in study sites in the southern part of this region steadily declined as the study progressed, and no nests were located in 2007 (Chapter 1). In the Warner Valley study sites I monitored 141 nests from 2003–2006.

Meadow area and edge effects

I examined the effects of nest age, meadow area and edge effects (distance to meadow edge) on daily survival rates of nests in the central region from 1997 to 2008. My analysis included 451 nests from the central region. I classified 14 meadows in this study as small meadows (<40 ha) and the remaining six meadows as large (>70 ha). I

found 165 nests in small meadows and 286 nests in the large meadows. Nests in small meadows were closer to a forest edge (mean = 56.8 m, 95% CI = 55.0-60 m) than those in large meadows (mean = 107.3 m, 95% CI = 101.1-111.1 m).

For nests in the central region I included a cubic effect of age from the best temporal model ($AIC_{\omega} = 0.99$) and I examined single-effects of size of meadow, distance from forest edge, proportion of shrub cover, and meadow shape variables. Distance from forest was the strongest single-effects model ($AIC_{\omega} = 0.805$) followed by proportion of shrub cover and meadow shape. I combined these three variables with nest age into additive models to determine if variables performed better in multiple-effects models (Hood and Dinsmore 2007). The best approximating models ($\Delta AIC < 4$) included additive effects of nest age (cubic trend), distance from forest, proportion shrub cover, meadow shape, and an interaction of size and distance from forest (Table 1). Nest age and the interaction between size and distance from forest edge significantly influenced the likelihood of survival (age: odds ratio = 1.3, 95% CI = 1.1-1.56; size and edge interaction: odds ratio = 0.69, 95% CI = 0.49-0.96). Model-predicted estimates suggested a negative influence of distance from forest on the probability of nest survival in large meadows and relatively no effect in small meadows (Fig. 1). However, observed logistic-exposure estimates based on nests categorized into distance intervals from the forest indicated substantial variability in daily nest survival as a function of distance from the forest edge in large meadows (Fig. 2a). Observed estimates suggested a linear increase in nest survival in large meadows from forest edge within approximately 40 m (Fig. 2a) and a quadratic effect of distance from forest edge in small meadows within approximately 40 m (Fig. 2b).

In the Warner Valley region I was unable to model meadow-area effects because of lack of variability in site measures; however, I considered two measures of edge effects. Nests in the Warner Valley region were located closer to the forest edge (mean = 51.0 m, 95% CI: 45.5-56.6, $n = 139$) than those in the central region (mean = 89.1 m, 95% CI = 81.8-96.4, $n = 453$). Four competing models with $\Delta AIC < 4$ all contained a quadratic date effect and distance from forest (total $AIC_{\omega} = 0.910$; Table 2), and the effect was significant for both terms (date², odds ratio = 0.79, 95% CI = 0.64-0.96; forest, odds ratio = 1.6, 95% CI = 1.1–2.4). Daily nest survival increased with distance from forest edge and was lower for early and late-season nests (Fig. 3). Observed estimates of daily nest survival calculated using logistic-exposure based on distance intervals of nests from the forest edge indicated variability in the effect but also that survival rates increased within approximately 40 m of the forest edge (Fig. 4).

Nest-scale effects

For nest-effects models, I included 54 nests in the central region from 2005–2007, 54 nests in the central region from 1997-1998, and 63 nests in the Warner Valley region from 2005-2006. For the central region (2005–2007) two models received almost all model support (sum $AIC_{\omega} = 0.999$), and these included interactive effects of meadow size with distance to forest edge and size with over-nest vegetation cover (Table 3). The main effect of over-nest cover (odds ratio = 1.96, 95 % CI = 1.17-3.27) and the interaction between over-nest cover and meadow size significantly influenced the likelihood of nest survival (odds ratio = 0.36, 95% CI = 0.2-0.66). Model-predicted estimates indicated that nests in small meadows were more likely to survive with decreasing amounts of over-nest cover, and the opposite was true for large meadows (Fig.

5). Observed estimates of daily nest survival at varying levels of over-nest cover supported the predicted models: the effect of over-nest cover was opposite in small versus large meadows (Fig. 6a,b).

The influences of distance from forest and over-nest cover were weakly supported by comparisons with the 1997 and 1998 data set in the central region. There were eight competitive models with a $\Delta AIC < 4$ (Table 4), and no variable significantly influenced the likelihood of survival. Nonetheless, the competitive models suggested an influence of over-nest cover (sum $AIC_{\omega} = 0.56$), nest height (sum $AIC_{\omega} = 0.44$), and distance from forest edge (sum $AIC_{\omega} = 0.43$) on daily nest survival rates, but there was little support for effects of meadow size, age, proportion of shrub cover, or meadow shape.

In the Warner Valley region there was no evidence of any significant influence of the nest-scale variables on daily nest survival (Table 5). Twelve models were competitive with $\Delta AIC < 4$; the models with the lowest AIC both contained the variable for over-nest cover (sum $AIC_{\omega} = 0.54$).

DISCUSSION

In this study, nest survival was predicted by interactions among meadow size and edge effects and meadow size with over-nest concealment, the influence of which was stronger in large meadows. In small meadows, the relative magnitudes of these effects were lower indicating that spatial variation did not influence nest survival. In large meadows, nest survival decreased with distance from the edge; however, observed survival rates for large meadows indicated increasing survival from edge within the first 40 m after which it declined. Additionally, survival in large meadows increased with over-nest cover. In Warner Valley, nest survival increased with distance from edge and

was not associated with nest-scale variables. These results indicate that nest predators may concentrate within large meadows and that vegetation influences survival within the meadows. Predator densities may be higher due to increased resources in large meadows (Root 1973), and expanses of large, open areas may serve further to concentrate small mammals within the willow matrix to avoid predation.

Meadow size and edge effects

In this study, regional and meadow size influences constrained the direction and magnitude of edge effects. Large meadows in the central region consisted of both riparian deciduous shrubs and open meadow, oftentimes with water sources and shrubs concentrated towards the center of the meadow or along one side. Meadow size was inversely correlated with shrub cover suggesting a detrimental effect of open grassland. Similarly, Bombay (1999) determined that the proportion of shrub cover at the territory-scale positively influenced reproductive success for Willow Flycatchers at these study sites. Functionally, meadows in the Sierra Nevada may represent three separate edge types: forest-riparian shrub, forest-grassland, and riparian shrub-grassland. Additionally, the prevalence of standing water in the meadows adds to the complexity of habitat associations. The interaction of three ecotones and water may have profound implications for predator-specific activity patterns influenced by hydrological conditions of meadows. Riparian systems are highly productive and water sources may attract predators (Root 1973, Pasinelli and Schiegg 2006) or Brown-headed Cowbirds (Broadhead et al. 2007). Diversity and availability of resources increases with patch size, thereby concentrating species in larger meadows (Ries et al. 2004).

Cain (2001) predicted increased small mammal activity in small meadows; however, I propose that the extensive grassland area in larger meadows may allow terrestrial predators increased accessibility to riparian deciduous shrubs. Furthermore, riparian shrubs provide the necessary concealment that many species need from to avoid predation on themselves (Howlett and Stutchbury 1996). In 1999 and 2000 in the central region Cain (2001) examined activity patterns of nest predators and correlated activity with meadow characteristics. In 2007 and 2008 Cocimano (2009) examined activity of nest predators relative to wet and dry areas of the meadows. Cain (2001) used cameras at artificial nests and documented 14 total predation events by short-tailed weasels (*Mustela erminea*; 21.4%), Douglas's squirrels (*Tamiasciurus douglasii*; 28.9%), chipmunks (*Tamias* spp.; 42.9%), and one deer mouse (*Peromyscus maniculatus*; 7%). Activity patterns of these and several other potential nest predators were correlated with increased riparian shrub cover, a variable that typifies large meadows. Specifically, short-tailed and long-tailed (*Mustela frenata*) weasels and garter snakes (*Thamnophis* spp.) were significantly more active in the larger meadows. 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 2009) and are generally associated with drier, forested habitats. 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). Deer mice are generalists and may have no association with specific land cover, instead requiring appropriate cover provided by ground litter, grasses, and shrubs (Wilson et al. 2008). Snakes may concentrate at grassland/shrub interfaces (Davison and Bollinger 2000), which may explain their

association with larger meadows (Cain 2001). Brown-headed cowbirds and several avian predators such as accipiters (*Accipiter* spp.) and corvids are associated with forest and edge vegetation (Chalfoun et al. 2002a, Broadhead et al. 2007), whereas larger raptors would associate with the open grasslands available in larger meadows.

Meadow-size effects on predators and nest survival may overwhelm edge effects so that little or no effects were detected. In small patches edge effects may prevail throughout the patch so that distance to edge would not explain variation in nesting success. Examination of observed daily nest survival estimates from both regions and for small and large meadows suggested that edge effects may dissipate after approximately 30-40 m into a meadow (Figs. 2 and 4), and inclusion of all nests at all distances may have obscured my detection of edge effects (Fletcher et al. 2007). Paton (1994) observed the threshold of edge effects at about 50 m, but other studies have proposed distances from 25 m (reviewed in Batary and Baldi 2004) up to 200 m (Albrecht 2004). Distance to meadow edge was not significant in two previous studies in 1997-1998 and 1999-2000 at some of the same study sites in the central region (Bombay 1999, Cain 2001). In the Warner Valley region nests were placed closer to the forest edge, and densities of territorial Willow Flycatchers were two to three times higher than densities in the central region (Appendix C). Inconsistent support for edge effects may result from variation in nesting density of flycatchers in the study regions. Predators may respond to high nesting densities by increasing search effort within areas of greater prey availability (Davidson and Allison 2003) such as in the Warner Valley region. In the central region reduced nest densities may relax spatial constraints on nest placement decisions, allowing adults to place nests selectively in low-risk areas (Eggers et al. 2006). Edge effects also may vary

in strength due to predator-specific activity patterns in a region (Chalfoun et al. 2002a). Based on evidence from modeling and field studies, researchers generally conclude that the influence of patch-area and edge effects are specific to region, scale of study, landscape and habitat context, and predator and prey taxa (Chalfoun et al. 2002b, Tewksbury et al. 2006). Furthermore, studies examining the influence of patch area and edge effects in riparian systems are relatively rare compared to those in other ecosystems (Picman et al. 1993, Albrecht 2004, Pasinelli and Schiegg 2006).

Nest-scale effects

In the central region, meadow size interacted with the influence of over-nest concealment on daily nest survival so that the probability of nest survival was higher for nests in large meadows placed deeper into the riparian deciduous shrub (i.e., increased over-nest cover). The predicted effect of over-nest cover in small meadows was weaker and the trend was toward reduced survival with increased cover (Fig. 6). Over-nest cover in this study was not correlated with height of nest nor did it associate with any other variables. Nest concealment is important when the primary nest predators use visual cues for foraging, and common nest predators in my study areas that use visual cues include both weasel species, snakes, and raptors (Fitzgerald 1977). Brown-headed Cowbirds also use visual cues for locating host nests and in recent years brood parasitism was higher in larger meadows in this study (Appendix C). Patch area and proximity to water sources are positively correlated with cowbird parasitism in southwestern Willow Flycatchers (Brodhead et al. 2007). A positive association between nest survival and increased over-nest cover has been documented in other shrub nesting passerines (Hannon et al. 2009)

The goal of this study was to describe the relationships among multiple extrinsic factors across spatial and temporal scales. I assumed nest predation was a direct result of predator activity and abundance, although this relationship still warrants rigorous examination (Ryall and Fahrig 2006, Chalfoun and Martin 2007). This study suggested that resources provided in the center of the larger meadows may attract nest predators and that the amount of vegetative cover in these meadows is important for nest survival. Riparian vegetation also provides the necessary cover for small mammals to avoid predation; therefore, reduced cover will concentrate predators in the shrub matrix. Increased density and cover of riparian shrubs in meadows may influence foraging efficiency of nest predators by hindering their ability to locate nests using cues from nesting adults (Martin and Roper 1988, Martin 1993b) or reduce the likelihood of encountering nests (Schmidt 1999, Chalfoun and Martin 2009). Predator responses to landscape, site, and local-scale effects are specific to the primary predator types and their interactions with the environment (Chalfoun et al. 2002, Stephens et al. 2003, Tewksbury et al. 2006). Without a more thorough understanding of the dynamics of the primary predators and how populations fluctuate over time and with spatial variability, my results lack a mechanistic understanding of factors influencing nest predation rates (Ryall and Fahrig 2006). Nonetheless, examining daily nest survival is an effective assessment of the mechanisms affecting the demographics of an avian population (Lampila et al. 2005)

Management implications

This study suggested that managing for dense, continuous riparian habitat in meadows may reduce predation pressure on nesting birds, particularly in large meadows. Collectively, both area and edge effects can be mitigated by restoration activities directed

at improvement of geomorphic and hydrological processes that influence the recruitment and survival of riparian vegetation (Scott et al. 2003). 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 (Vale 1981, Allen-Diaz 1991, Royce and Barbour 2001). Restoration activities that enhance structural diversity of riparian vegetation are associated with increased breeding bird abundance and diversity (Sabo et al. 2005, Gardali et al. 2006) and increased nest success (Ellis et al. 2009).

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Table 1. Model-selection results for logistic-exposure models of the effect of meadow-scale variables on daily survival rate of Willow Flycatcher nests in meadows in the central region of the Sierra Nevada, CA from 1997 to 2007. Factors in the model included a cubic effect of age (age^3), distance to forest edge (for), proportion of shrub cover (shr), and an index of meadow shape (pta). The number observed was 2,753 and the effective sample size was 11,506.

Model	Log(L)	k	AIC	ΔAIC	AIC_{ω}
$age^3+for+shr+pta$	-672.01	7	1358.02	0	0.545
$age^3+for+shr$	-674.08	6	1360.16	2.13	0.188
$age^3+shr+pta+for*size$	-671.49	9	1360.98	2.96	0.124
$age^3+for+pta$	-675.21	6	1362.41	4.39	0.061
$age^3+shr+for*size$	-673.56	8	1363.13	5.11	0.042
age^3+for	-677.33	5	1364.67	6.64	0.020
$age^3+pta+for*size$	-674.64	8	1365.28	7.26	0.014
$age^3+for*size$	-676.64	7	1367.28	9.26	0.005
for+shr	-682.58	3	1371.16	13.13	0.001
for+pta	-684.12	3	1374.24	16.21	0.000
for	-686.11	2	1376.22	18.18	0.000
for+size	-685.95	3	1377.90	19.86	0.000
for*size	-685.53	4	1379.05	21.02	0.000
age^3+shr	-695.72	5	1401.44	43.41	0.000
age^3+pta	-697.19	5	1404.37	46.34	0.000
age^3	-698.88	4	1405.75	47.72	0.000
shr	-705.50	2	1415.00	56.96	0.000
age^2	-705.39	3	1416.79	58.75	0.000

Table 2. Model-selection results for logistic-exposure models of the effect meadow and temporal variables on daily survival rate of Willow Flycatcher nests in the Warner Valley region of the Sierra Nevada, CA from 2003 to 2006. Factors included in this model were nest age (age), a quadratic effect of date (date²), distance to forest edge (for), and distance to nearest tree or snag (tree). The number observed was 652 and the effective sample size was 2,559.

Model	Log(L)	k	AIC	Δ AIC	AIC ω
date ² + for +age	-180.46	5	370.92	0.00	0.258
date ² + for	-181.60	4	371.19	0.27	0.226
date ² +for+age+tree	-179.60	6	371.21	0.30	0.222
date ² +for+ age	-180.69	5	371.38	0.46	0.205
for+ age	-184.78	3	375.55	4.62	0.026
for + age + date ²	-184.08	4	376.16	5.24	0.019
for	-186.20	2	376.40	5.46	0.017
for + age	-185.49	3	376.98	6.05	0.013
age + age + date ²	-184.33	5	378.66	7.74	0.005
age + date ²	-185.77	4	379.54	8.62	0.003
age + date ²	-185.80	4	379.61	8.69	0.003
age	-187.28	3	380.57	9.64	0.002
date ² + age	-188.28	3	382.55	11.62	0.001
age	-189.59	2	383.17	12.24	0.001
age	-189.98	2	383.97	13.03	0.000
null	-191.35	1	384.70	13.76	0.000
date	-191.33	2	386.65	15.72	0.000

Table 3. Model-selection results for logistic-exposure models of the effect of nest-scale variables on daily survival rate of Willow Flycatcher nests in the central region of the Sierra Nevada, CA in 2005 to 2007. Factors included in this model were meadow area (size), proportion of shrub cover (shr), an index of meadow shape (pta), distance to forest edge (for), over-nest cover (cover), distance to edge of willow shrub (edge), and nest height (height). The number observed was 639 and the effective sample size was 2,559. Models with $\Delta AICc > 25$ were removed.

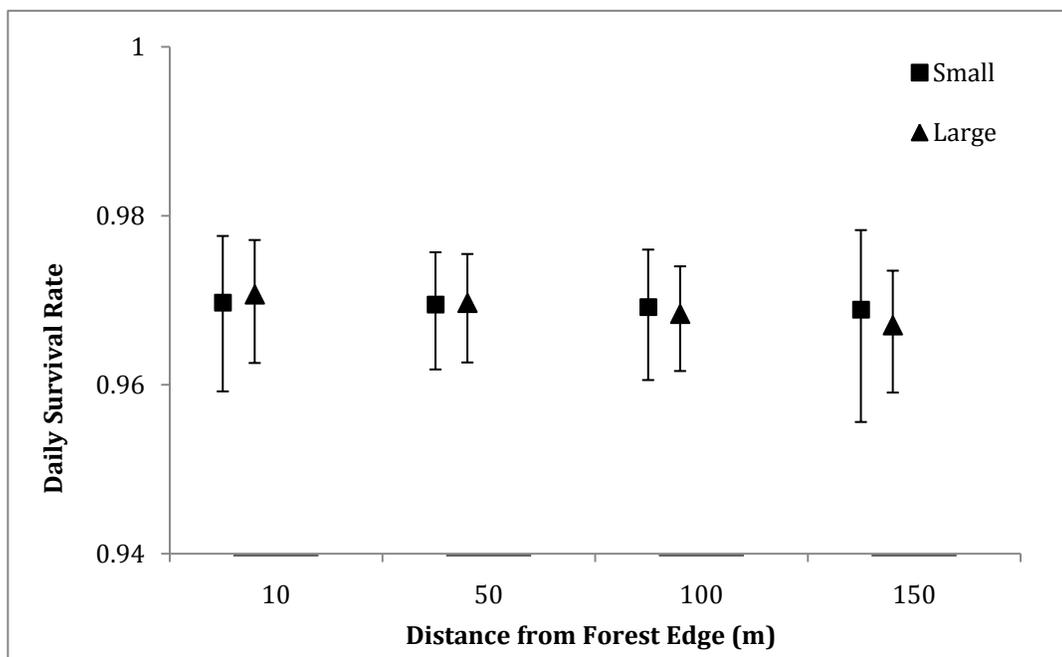
Model	Log(L)	k	AICc	$\Delta AICc$	AIC ω
size*for+size*cover	-193.45	6	398.91	0.00	0.694
for +size*cover	-195.29	5	400.59	1.67	0.301
for +cover	-201.56	3	409.12	10.19	0.004
for +edge	-204.99	3	415.97	17.04	0.000
for + age ³	-205.75	5	421.50	22.58	0.000
age ³ +pta+for*size	-202.75	8	421.51	22.62	0.000
for	-209.14	2	422.29	23.35	0.000
age ³ +shr+pta+for*size	-202.28	9	422.56	23.69	0.000
for +size	-208.37	3	422.75	23.82	0.000
age ³ +for*size	-204.36	7	422.71	23.82	0.000
size*cover	-207.41	4	422.82	23.89	0.000
age ³ +for+pta	-205.43	6	422.85	23.94	0.000
for +height	-208.60	3	423.19	24.26	0.000
age ³ +for+shr	-205.75	6	423.50	24.59	0.000
age ³ +shr+for*size	-203.82	8	423.64	24.75	0.000
for +pta	-208.86	3	423.72	24.79	0.000
size*for	-207.89	4	423.79	24.86	0.000
for +shr	-209.14	3	424.28	25.35	0.000

Table 4. Model-selection results for logistic-exposure models of the effect of nest-scale variables on daily survival rate of Willow Flycatcher nests in the central region of the Sierra Nevada, CA in 1997 and 1998. Factors included in this model were a cubic effect of age (age^3), meadow size (size), proportion of shrub cover (shr), an index of meadow shape (pta), distance to forest edge (forest), over-nest cover (cover), distance to edge of willow shrub (edge), and nest height (height). The number observed was 218 and the effective sample size was 1,165. Models with $\text{AIC}_\omega = 0$ were removed.

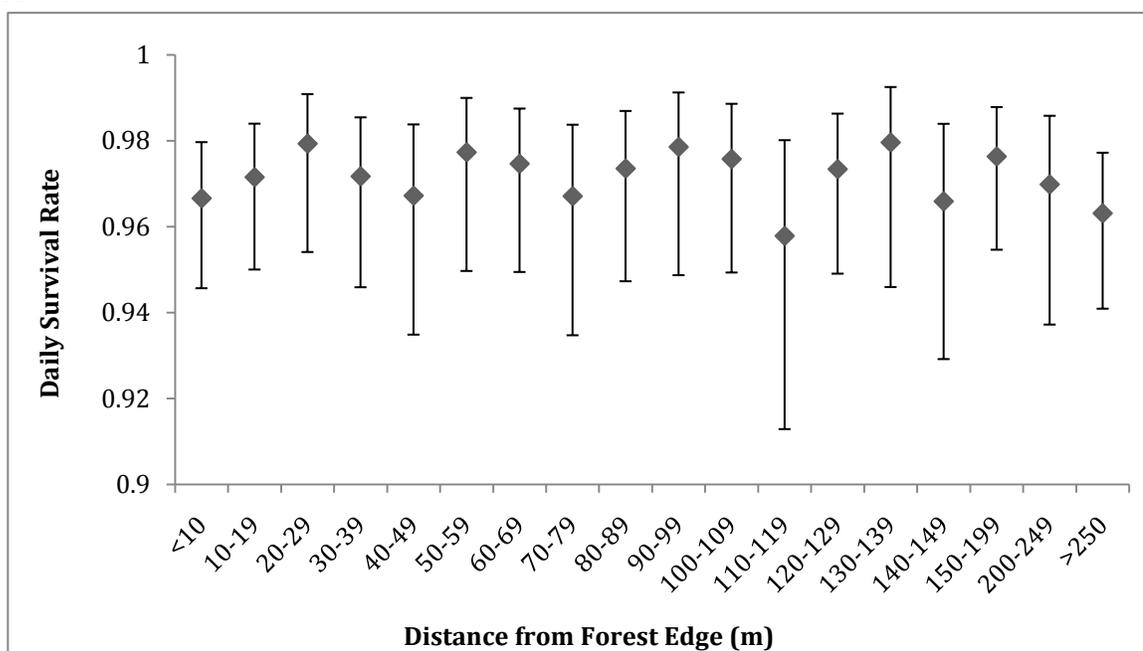
Model	Log(L)	k	AIC	ΔAIC	AIC_ω
cover	-71.15	2	146.30	0	0.240
height	-71.18	2	146.37	0.07	0.231
forest+cover	-70.44	3	146.88	0.59	0.178
forest+height	-70.48	3	146.97	0.68	0.171
size*cover	-70.47	4	148.94	2.66	0.063
forest+size*cover	-69.59	5	149.19	2.93	0.055
size*height	-71.03	4	150.05	3.78	0.036
size*forest+size*cover	-69.47	6	150.94	4.70	0.023

Table 5. Model-selection results for logistic-exposure models of the effect of nest-scale variables on daily survival rate of Willow Flycatcher nests in the Warner Valley region of the Sierra Nevada, CA in 2005 and 2006. Factors included in this model were nest age (age), a quadratic effect of date (date^2), distance to forest edge (for), distance to nearest tree or snag (tree), over-nest cover (cover), distance to edge of willow shrub (edge), and nest height (ht). The number observed was 268 and the effective sample size was 1,198. Models with $\text{AIC}_w = 0.01$ were removed.

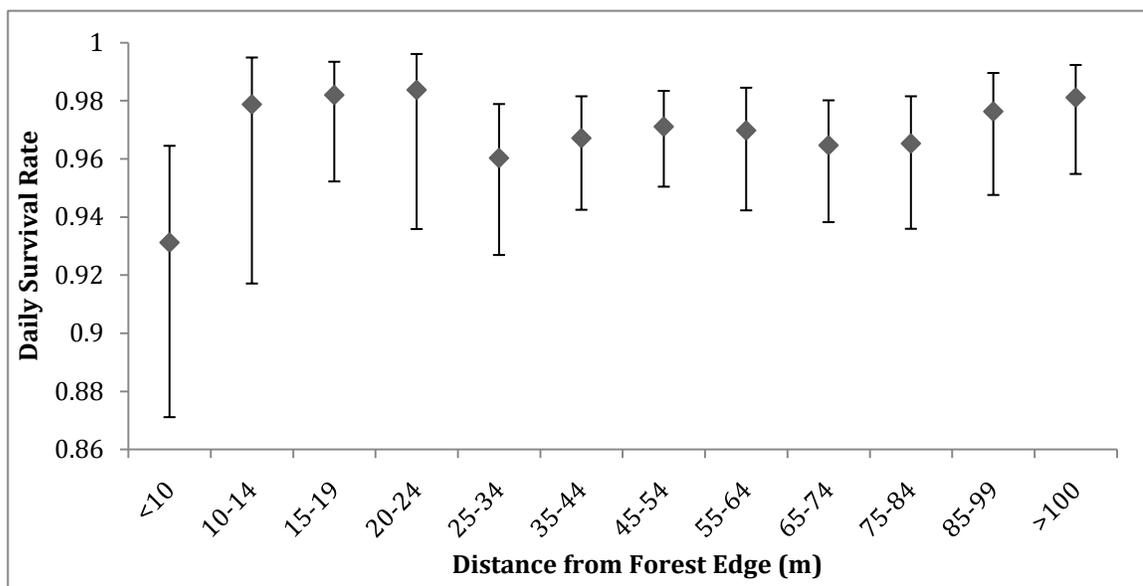
Model	Log(L)	k	AIC	ΔAIC	AIC_w
$\text{date}^2+\text{for}+\text{tree}+\text{age}+\text{cover}$	-73.79	7	161.58	0.00	0.208
$\text{date}^2+\text{for}+\text{tree}+\text{cover}$	-75.23	6	162.46	0.86	0.135
$\text{date}^2+\text{for}+\text{tree}+\text{age}+\text{edge}$	-74.55	7	163.09	1.52	0.097
$\text{date}^2+\text{for}+\text{tree}+\text{age}+\text{ht}$	-74.56	7	163.11	1.54	0.096
$\text{date}^2+\text{for}+\text{tree}+\text{age}+\text{cover}+\text{edge}$	-73.66	8	163.32	1.77	0.086
$\text{date}^2+\text{for}+\text{tree}+\text{age}+\text{cover}+\text{ht}$	-73.79	8	163.58	2.03	0.075
$\text{date}^2+\text{for}+\text{tree}+\text{edge}$	-76.02	6	164.04	2.44	0.061
$\text{date}^2+\text{for}+\text{tree}+\text{ht}$	-76.17	6	164.33	2.73	0.053
$\text{date}^2+\text{for}+\text{tree}+\text{age}+\text{edge}+\text{ht}$	-74.46	8	164.91	3.36	0.039
$\text{date}^2+\text{for}+\text{age}+\text{cover}$	-76.60	6	165.19	3.59	0.035
$\text{date}^2+\text{for}+\text{age}+\text{edge}$	-76.76	6	165.52	3.92	0.029
$\text{date}^2+\text{for}+\text{age}+\text{ht}$	-76.88	6	165.76	4.16	0.026
$\text{date}^2+\text{for}+\text{cover}$	-78.47	5	166.93	5.31	0.015
$\text{date}^2+\text{for}+\text{edge}$	-78.53	5	167.06	5.44	0.014
$\text{date}^2+\text{for}+\text{ht}$	-78.79	5	167.58	5.96	0.011

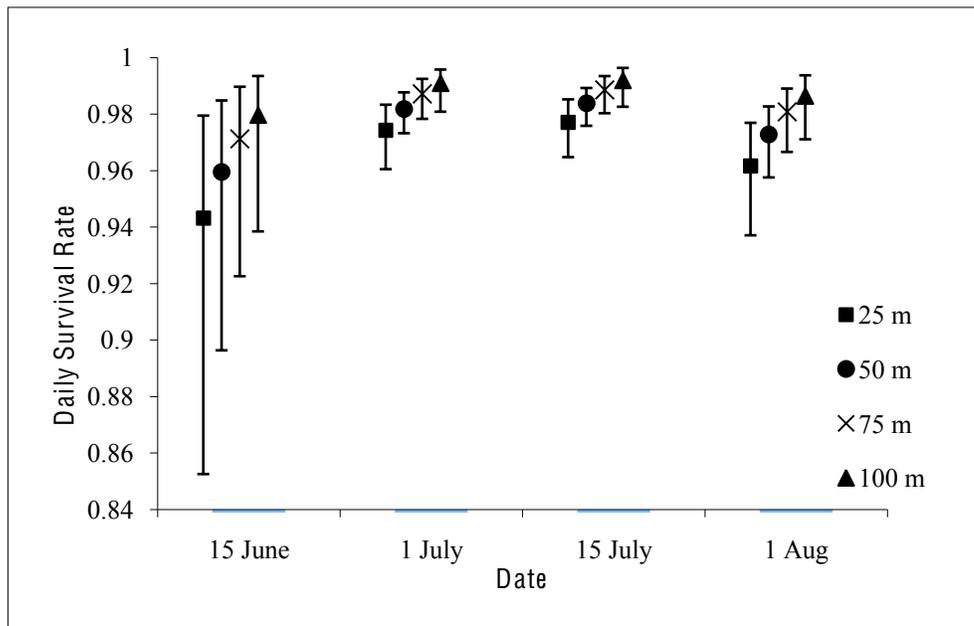


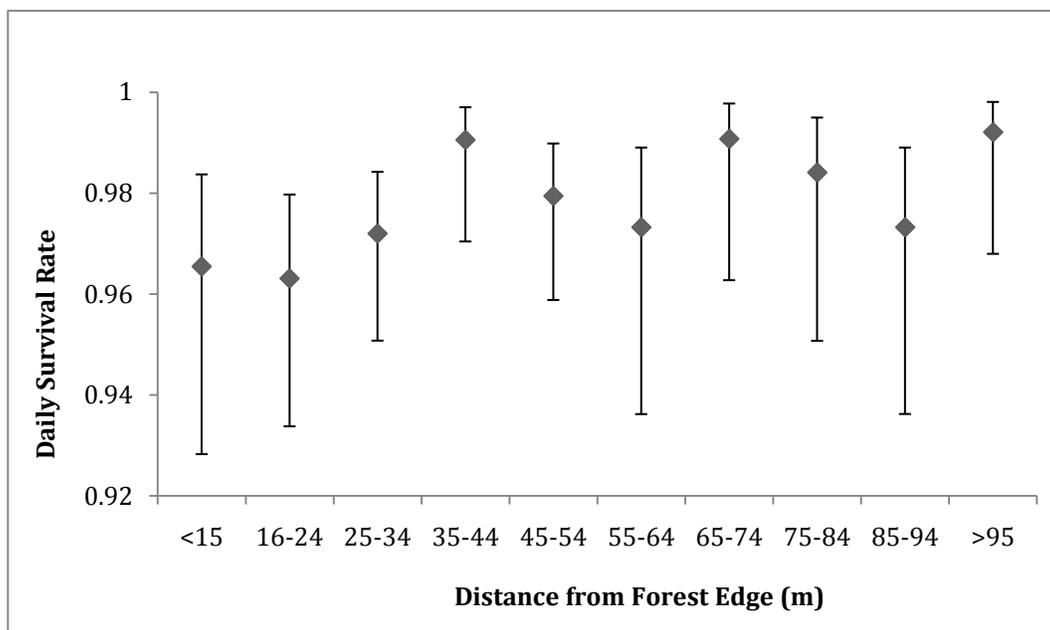
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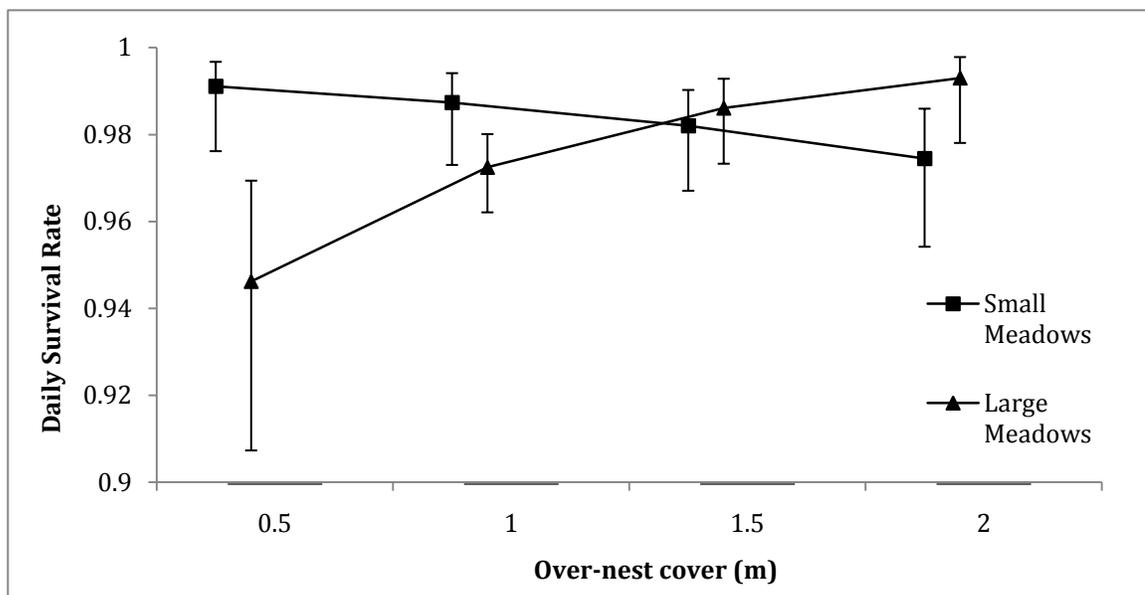


B

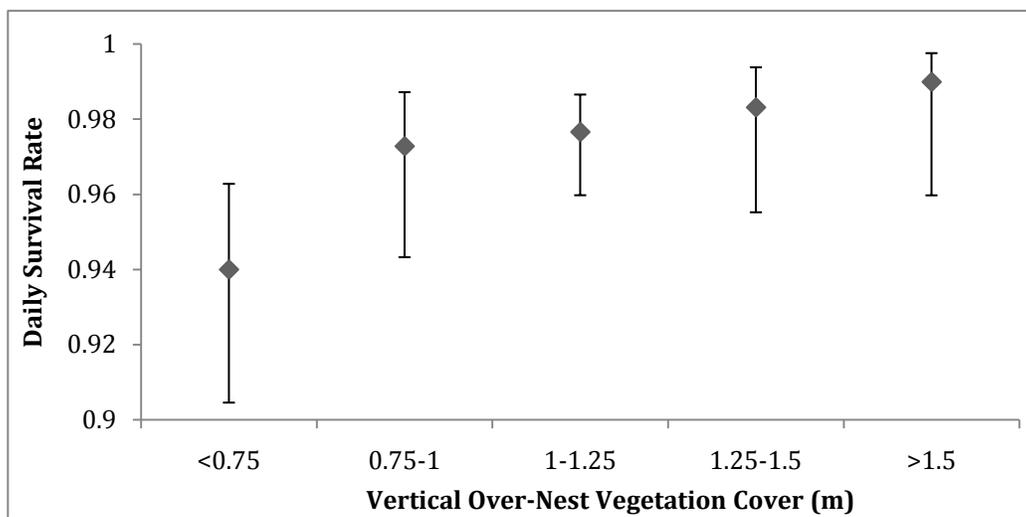




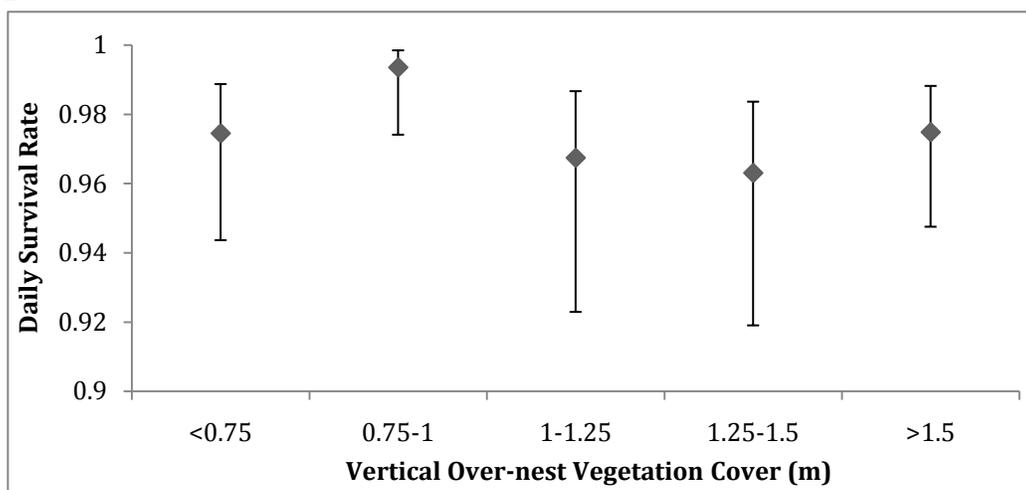




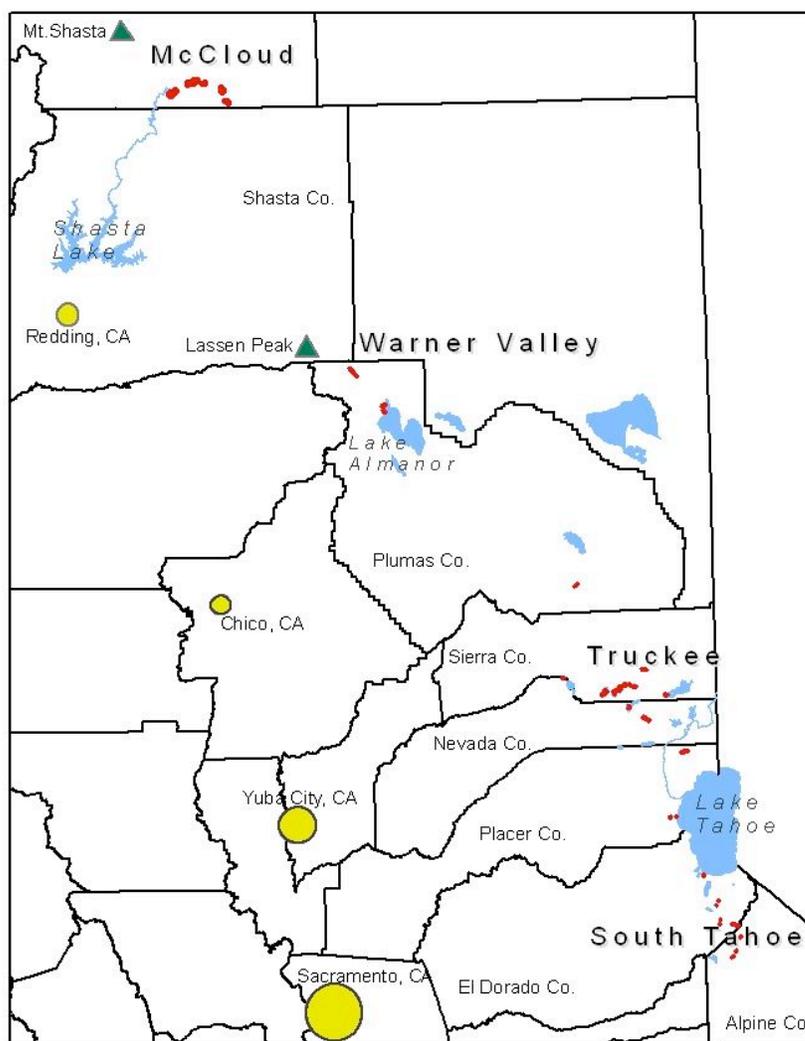
A



B



APPENDIX A. STUDY REGIONS AND SITES (RED) FOR WILLOW FLYCATCHER MONITORING IN THE SIERRA NEVADA, CALIFORNIA.



APPENDIX B. SUPPLEMENTAL INFORMATION

Bombay (1999) 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. She surveyed 104 sites at which she detected willow flycatchers at 19% ($n = 104$) of the survey sites. She selected 15 of these sites for a 10-year demographic study. We also visited other meadows to conduct occupancy surveys and search for dispersed birds banded at our study sites.

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. 2000).

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 comparative 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).

Table 1. Number of sites visited each year for surveys, band resighting, monitoring or conducting other research activities for Willow Flycatchers.

Year	Survey	Monitor	Band resight	Adaptive cluster	Conspecific attraction
1997	68	4	0		
1998	34	15	0		
1999	11	15	1		
2000	1	14	1		
2001	12	14	2		
2002	10	15	9		
2003	2	22	17		
2004	2	23	1	19	
2005	13	28	11	22	
2006	4	17	6		
2007	16	10	15		3
2008	11	20	17		3

Table 2. Locations and ownership of Willow Flycatcher monitoring sites in the Sierra Nevada from 1997–2008.

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

Table 3 continued

Region	Study Site	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
Warner Valley													
	North Meadow							8	10	8		9	10
	East Corral							6	8	9		10	7
	West Corral							7	11	7		9	5
	South Bog							11	12	10		8	8
	Swamp												18
								32	41	34	0	36	30
McCloud													
	Algoma									6			
	Bigelow									18	14		
	McCloud River									27	28		
	Colby									6			
	Curtis									6	14		
										63	56		
Rate of territory change													
	South Tahoe	0.00	-0.33	0.00	0.13	-0.56	0.00	-0.29	0.00	-0.33	-0.25	-0.33	
	Truckee	-0.06	-0.06	-0.21	-0.03	-0.08	0.06	-0.04	0.00	0.05	-0.19	-0.12	
	Warner Valley							0.28	-0.17				-0.17
	McCloud									0.1			

Table 4. Number of females 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.

Region	Study Site	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
South Tahoe													
	Red Lake I	2	3	1	1	1	1	0	1	0	0	0	0
	Red Lake II	2	2	3	4	5	1	1	0	0	0	0	0
	Washoe		1	0	0	0	0	0	0	0	0	0	0
Uppermost													
	U. Truckee		2	4	3	1	1	2	1	1	1	0	0
	Grass Lake		2	1	1	1	0	0	0	0	0	0	0
	Maxwell		1	0	0	0	0	0	0	0	0	0	0
	Red Lake Peak							1	2	2	2	0	0
	Tallac									1	1	0	1
	Taylor												2
Truckee													
	Perazzo Little	9	6	6	4	2	1	4	4	5	6	7	5
	Truckee I	6	7	6	4	4	5	3	2	2	3	2	2
	Webber Little		10	12	12	8	7	5	5	3		6	4
	Perazzo Little		1	1	0	1	1	2	1	1	1	1	1
	Truckee II	2	5	4	3	5	6	4	5	6	7	4	2
	Little Truckee III		4	6	4	4	2	2	3	4	3	3	1
	Independence		2			1	1	2	2	2	1	2	3
	Saddle			0	0	0	0	0	0	0	0	0	0
	Prosser		6	6	4	6	3	6	4	4	4		
	Martis							1	1	2	3	3	3

Table 4. continued

Region	Study Site	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	
	Stampede							1	1	0	0	0	0	
	Cottonwood							1	2	2	3	2	1	
	Milton							2	5	6	7	2	2	
	Mabie							3		0	0	0	0	
	Blackwood								1	1	1	1	0	
	Salmon													
	Creek												4	
	Donner													
	Camp												1	
Warner Valley														
	South Bog							10	12	11			8	
	East Corral							6	8	11			8	
	West Corral							6	9	6			4	
	North													
	Meadow							10	13	10			9	
	South Bog												18	
Rate of change														
	South Tahoe		0.25	-	0.18	0.00	-	0.11	0.63	0.00	0.00	0.25	0.00	0.00
	Truckee		0.13	0.05	0.24	0.03	0.16	0.08	0.06	0.06	0.11	0.23	0.26	
	Warner Valley								0.31	0.10				

Table 5. Mayfield nest survival estimates of Willow Flycatchers breeding in the Sierra Nevada.

Region	Year	No. of days, all stages	No. of nests	Percent success
South Tahoe				
	1997	77	4	74.5
	1998	164	12	27.2
	1999	218	12	31.5
	2000	175	10	45.9
	2001	130	8	23.8
	2002	48	2	53.9
	2003	74	5	16.7
	2004	86	6	12.3
	2005	91	5	36.1
	2006	65	3	62.1
	2008	37	2	100.0
	All years	1165	70	33.8
Truckee				
	1997	267	19	34.6
	1998	709	42	40.2
	1999	704	48	19.0
	2000	535	29	53.9
	2001	667	39	43.6
	2002	468	26	35.5
	2003	677	40	37.5
	2004	723	39	41.6
	2005	1071	48	50.6
	2006	826	44	36.0
	2007	611	30	42.5
	2008	622	30	58.7
	All years	7880	434	40.5
Warner Valley				
	2003	649	38	46.7
	2004	718	42	43.9
	2005	1001	48	50.0
	2006	274	15	64.4
	2008	1190	55	57.4
	All years	3832	198	51.5
	All years and regions	12877	702	42.8

Table 6. Density of Willow Flycatcher territories relative to total shrub cover in each meadow.

Region														
Site	Shrub cover (ha)	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	Mean
South Tahoe														
Red Lake I & II	6.45	0.77	0.77	0.62	0.62	0.93	0.31	0.31	0.31	0.00	0.00	0.00	0.00	0.39
Maxwell Creek	1.18		0.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08
Grass Lake	3.74		0.80	0.27	0.27	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15
Uppermost U. Truckee														
Truckee	1.73		1.16	1.74	1.74	1.16	1.16	1.16	0.58	0.58	0.58	0.58	0.58	1.00
Washoe State Park	1.73		0.58	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
Red Lake Peak	4.32							0.69	0.46	0.46	0.23	0.23	0.00	0.35
Tallac	7.47								0.13	0.40	0.27	0.13	0.13	0.21
Annual Mean			0.83	0.53	0.53	0.47	0.29	0.36	0.21	0.21	0.15	0.13	0.13	0.32
Truckee														
Independence Lake	5.08		0.59	0.39	0.59	0.20	0.59	0.39	0.39	0.39	0.59	0.39	0.39	0.45
Saddle Meadow	2.06		0.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04
Little Truckee I & II	11.23	0.45	1.16	1.07	0.80	0.71	0.89	0.89	0.71	0.98	0.80	0.71	0.53	0.81
Little Truckee III	3.20		1.25	1.87	1.25	1.56	1.25	0.94	0.94	0.94	1.25	0.94	0.31	1.13
Little Perazzo	4.21		0.24	0.24	0.00	0.24	0.24	0.47	0.47	0.47	0.24	0.24	0.24	0.28
Perazzo	12.25	0.98	0.73	0.57	0.41	0.24	0.16	0.41	0.33	0.33	0.90	0.65	0.57	0.52
Prosser Creek	10.88		0.64	0.46	0.37	0.55	0.55	0.46	0.55	0.74	0.46	0.00	0.00	0.53
Webber lake	10.48		1.15	1.34	1.15	1.15	0.67	0.76	0.86	0.48	0.57	0.57	0.48	0.83
Martis	2.64							0.76	1.14	1.14	0.38	1.14	1.14	0.95
Stampede Reservoir	3.86					0.26	0.26	0.52	0.26	0.00	0.26	0.00	0.26	0.23
Cottonwood Creek	2.42							0.83	0.83	0.83	2.07	1.24	0.83	1.10
Milton Reservoir	1.60					2.50	1.87	3.12	3.12	3.74	3.74	2.50	2.50	2.88
Mabie	3.29							0.91	0.61	0.30		0.00	0.91	0.55
Blackwood Creek	2.70								0.37	1.11	0.74	0.37	0.37	0.59
Annual Mean			0.78	0.74	0.57	0.74	0.65	0.80	0.76	0.82	0.92	0.62	0.61	0.77

Table 6. continued

Region														
Site	Shrub cover (ha)	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	Mean
Warner Valley														
North Meadow	6.57							1.22	1.52	1.22		1.37	1.52	1.37
East Corral	3.03							1.98	2.64	2.97		3.30	2.31	2.64
West Corral	8.49							0.82	1.30	0.82		1.06	0.71	0.94
South Bog	6.32							1.74	1.74	1.58		1.26	1.26	1.52
Annual Mean								1.44	1.80	1.65		1.75	1.45	1.62

Table 7. Meadow elevation, size, shape and riparian shrub cover in meadows monitored for Willow Flycatchers.

Site	Meadow size and shape variables				Meadow shrub variables			
	Elevation (m)	Area (ha)	Perimeter (km)	Perimeter : Area*	Shrub Cover (ha)	% Shrub Cover	Perimeter (km)	Perimeter: Area
South								
Grass Lake	7750	98.4	7.7	2.19	3.7	0.038	13.8	0.37
Maxwell Creek	7200	20.8	3.3	2.05	1.2	0.057	7.0	0.59
Red Lake 1 & 2	7900	14.0	3.5	1.92	6.5	0.937	15.1	0.23
Red Lake Peak	7750	20.1	2.8	1.76	4.3	0.215	11.6	0.27
Uppermost	6475	6.2	1.2	1.36	1.7	0.278	6.0	0.35
Washoe SP	6300	5.4	1.4	1.70	1.7	0.204	4.1	0.37
Tallac Creek	6230	36.5	3.5	1.65	7.5	0.205	21.1	0.28
Central								
Webber Lake	6800	162.0	12.8	2.84	10.5	0.065	25.2	0.24
Perazzo	6560	105.2	10.5	2.89	12.3	0.117	41.3	0.34
Little Perazzo	6600	24.5	2.9	1.68	4.2	0.172	18.1	0.43
Little Truckee 1 & 2	6500	97.8	9.2	2.62	11.2	0.115	39.4	0.35
Little Truckee 3	6400	22.7	3.5	2.10	3.2	0.141	13.5	0.42
Saddle	6450	20.2	4.0	2.53	2.1	0.102	8.7	0.42
Independence	6950	19.6	5.3	3.39	5.1	0.259	15.2	0.30
Prosser Creek	6250	85.6	9.0	2.73	10.9	0.127	32.2	0.30
Martis creek	5840	79.5	8.9	2.83	2.6	0.033	13.9	0.53
Stampede Reservoir	5950	32.1	3.3	1.62	3.9	0.120	12.4	0.32
Cottonwood	6235	17.5	5.3	3.57	2.4	0.138	8.5	0.35
Milton Reservoir	5690	14.5	3.6	2.67	1.6	0.111	5.0	0.31
Mabie	4772	16.2	2.5	1.74	3.3	0.203	10.2	0.31
Blackwood Creek	6360	10.7	2.4	2.10	2.7	0.253	6.5	0.24
Mean	6240	50.6	6.0	2.52	5.4	0.140	17.9	0.35

Table 7. continued

Site	Meadow size and shape variables				Meadow shrub variables				
	Elevation (m)	Area (ha)	Perimeter (km)	Perimeter : Area*	Shrub Cover (ha)	% Shrub Cover	Perimeter (km)	Perimeter: Area	
North									
South Bog	5100	18.4	3.3	2.14	6.3		0.344	19.5	0.31
East Corral	5200	15.8	2.2	1.54	3.0		0.192	11.8	0.39
West Corral	5100	23.8	2.9	1.70	8.5		0.357	15.5	0.18
North Meadow	5200	20.3	3.4	2.15	6.6		0.324	15.2	0.23
Mean	5150	19.6	2.9	1.88	6.1		0.304	15.5	0.28