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Authors: Mathewson, Heather A., Department of Biology, University of Nevada, Reno, Nevada 89523, USA, Morrison, Michael L., Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843, USA, Loffland, Helen L., California State University, Sacramento, California 95819, USA, and Brussard, Peter F., Department of Biology, University of Nevada, Reno, Nevada 89523, USA

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ECOLOGY OF WILLOW FLYCATCHERS (*EMPIDONAX TRAILLII*) IN THE SIERRA NEVADA, CALIFORNIA: EFFECTS OF MEADOW CHARACTERISTICS AND WEATHER ON DEMOGRAPHICS

Heather A. Mathewson,[1,4] Michael L. Morrison,[2] Helen L. Loffland,[3,5] and Peter F. Brussard[1]

[1]*Department of Biology, University of Nevada, Reno, Nevada 89523, USA;*
[2]*Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843, USA; and*
[3]*California State University, Sacramento, California 95819, USA*

Abstract.—Population declines in songbirds are often attributed to regional habitat loss and fragmentation caused by land-use practices, which might be further aggravated by climate change. These concerns are particularly evident in the Intermountain West, where riparian areas are considered a priority for conservation because of predicted reductions in winter precipitation and increases in spring temperatures. These climatic changes might increase the susceptibility of species reliant on riparian areas to regional extirpation from loss of habitat. The Willow Flycatcher (*Empidonax traillii*) is a California species of concern because of precipitous population declines in the past three decades. In 1997, we established a long-term research program to determine population demographics and the effects of weather events and regional-scale meadow distribution and vegetative structure on nesting success of Willow Flycatchers. We monitored territory establishment and reproductive success of 786 territories and 850 nests in meadows distributed south and north of Lake Tahoe, California, from 1997 to 2008. We documented near extirpation of Willow Flycatchers south of the lake and a declining trend in the number of territories north of the lake. Late-spring storms and low temperatures at the start of the breeding season reduced the length of the breeding season, affecting the ability of Willow Flycatchers to renest. Nest age better predicted nest survival than meadow-scale landscape and weather variables. Although weather parameters were not significant as a direct influence on nest survival analyses, our results suggested a weak negative relationship with increased snowfall. For our nest-scale model evaluation, over-nest vegetation concealment increased nest survival in large meadows but had little effect on nest survival in smaller meadows. Evidence from our dispersal data implied that Willow Flycatchers in our study regions had high natal- and breeding-site fidelity, which suggests that recruitment across these study regions might be limited. Given that we observed a declining population trend in the South Tahoe region, our results suggest that populations in the South Tahoe region may not rebound. Compared with a reference site that we established in 2003, where the population of Willow Flycatchers appeared to be stable, reproductive success was lower at our long-term sites. We suggest that differences in breeding-season length and the quality of habitat in meadows contributed to lower reproductive success and to the observed population declines.

Key words: California, *Empidonax traillii*, population change, reproductive success, Sierra Nevada, weather, Willow Flycatcher.

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[4] Present address: Texas A&M Institution of Renewable Natural Resources, 1500 Research Parkway, Suite 110, College Station, Texas 77845, USA. E-mail: heather.mathewson@agnet.tamu.edu.

[5] Present address: Institute for Bird Populations, P.O. Box 1346, Point Reyes Station, California 94956, USA.

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Ecología de *Empidonax traillii* en la Sierra Nevada, California: Efectos de las Características de las Praderas y del Clima en la Demografía

Resumen.—Las disminuciones en las poblaciones de aves canoras frecuentemente se atribuyen a la pérdida de hábitat a nivel regional y a la fragmentación causada por algunas prácticas del uso de la tierra, lo que podría verse agravado por el cambio climático. Estas preocupaciones se hacen particularmente evidentes en el occidente intermontano de Norte América, donde las áreas ribereñas son consideradas una prioridad para la conservación debido a las reducciones previstas en la precipitación de invierno y a los aumentos esperados en las temperaturas de primavera. Estos cambios climáticos podrían incrementar la susceptibilidad de las especies que dependen de las áreas ribereñas ante la pérdida regional del hábitat. *Empidonax traillii* es una especie californiana de importancia debido a disminuciones poblacionales precipitadas en las tres últimas décadas. En 1997, establecimos un programa de investigación a largo plazo para determinar la demografía de la población y para evaluar los efectos de eventos climáticos y de la distribución regional y estructura vegetativa de las praderas sobre el éxito de anidación de *E. traillii*. Monitoreamos el establecimiento de los territorios y el éxito reproductivo de 786 territorios y 850 nidos en praderas distribuidas al sur y al norte del lago Tahoe, California, entre 1997 y 2008. Documentamos la virtual desaparición de *E. traillii* al sur del lago y una tendencia a la disminución en el número de territorios al norte del lago. Las tormentas del final de la primavera y las bajas temperaturas al inicio de la temporada reproductiva redujeron la duración de la misma, afectando la habilidad de *E. traillii* para volver a anidar. La edad de los nidos fue un mejor predictor de su supervivencia que las variables a escala del paisaje de las praderas o las variables climáticas. Aunque los parámetros climáticos no presentaron una influencia directa significativa sobre la supervivencia de los nidos, nuestros resultados sugieren una débil relación negativa de ésta con el incremento de las nevadas. En cuanto a la evaluación de modelos a la escala de los nidos, el ocultamiento de los nidos desde arriba por vegetación incrementó su supervivencia en praderas grandes, pero tuvo poco efecto en praderas pequeñas. Nuestros datos de dispersión implican que los individuos de nuestra región de estudio presentaron alta fidelidad tanto al sitio de nacimiento como al sitio de reproducción, lo que sugiere que el reclutamiento podría ser limitado a través de las regiones de estudio. Dado que observamos una tendencia poblacional negativa en la región del sur de Tahoe, nuestros resultados sugieren que esas poblaciones podrían no recuperarse. En comparación con un sitio de referencia que establecimos en 2003, donde la población de *E. traillii* parece ser estable, el éxito reproductivo fue menor en nuestros sitios de monitoreo a largo plazo. Sugerimos que las diferencias en la duración de la temporada reproductiva y la calidad del hábitat en la praderas contribuyen a un menor éxito reproductivo y a las disminuciones poblacionales observadas.

Introduction

Population declines in Neotropical migratory birds are often attributed to human-induced habitat loss and fragmentation on the breeding grounds, processes that are further aggravated by climate change (Travis 2003, Opdam and Wascher 2004). This synergistic relationship is particularly evident in riparian systems in western North America, where ecological processes are driven by hydrological cycles that are sensitive to annual weather patterns and human-induced alterations (Fites-Kaufman et al. 2007). Although rare in distribution, comprising <1% of the region's vegetation (Knopf et al. 1988), riparian ecosystems provide breeding habitat for >60% of passerine species in the western United States (Saab 1999). These systems have undergone considerable loss and degradation over the past several decades (Dettinger and Cayan 1995, Scott et al. 2003, Barnett et al. 2008) and, thus, are considered a priority for conservation (Donovan et al. 2002). Recent climate studies have shown that over the past 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 because of declines in groundwater level. Synergistic effects of climate change and human-induced disturbances will cause further loss and degradation of riparian habitat (Opdam and Wascher 2004, Ewers and Didham 2006).

Riparian systems in the West range across elevation gradients from the central valleys and coastlines to higher-elevation montane meadows. Many species of Neotropical migrants that rely on these riparian systems were historically distributed across these elevation gradients. However, loss of much of the lower-elevation riparian habitat over the past several decades has limited distributions of migrants to higher-elevation, mountainous regions (Grinnell and Miller 1944, Rood et al. 2003). These regions experience greater annual fluctuations in weather patterns, with higher magnitude and frequency of storms, and shorter breeding seasons, compared with lower-elevation regions (Fites-Kaufman et al. 2007). These impacts must be accounted for in conservation planning for these species, requiring long-term studies that capture the stochastic nature of weather events such as these (Collins 2001, Porzig et al. 2011). The first step in conservation planning is acquiring basic ecological information through multiyear comparative studies (Donovan et al. 2002, Faaborg et al. 2010a).

The merit of long-term ecological studies is well understood in ecology, and although the prevalence of these studies is fortunately increasing, they are still rare (Collins 2001, Porzig et al. 2011, Lindenmayer et al. 2012). Many of these studies are conducted within single public land holdings, such as parks or reserves, or at field stations designated for scientific research (Holmes 2007, 2011; Porzig et al. 2011). Oftentimes, the research focuses on community-level responses or on a few focal species for more intense monitoring (Holmes 2007, 2011). The Breeding Bird Survey (Sauer et al. 2008) and Monitoring Avian Productivity and Survival (DeSante et al. 2001) programs provide nationwide information on trends across a broad extent. However, few studies exist that focus on regional, long-term variation in reproductive success and population dynamics (Chase et al. 2005, Martin 2007).

Here, we provide results from a long-term study conducted across three regions in the Intermountain West that focused on a riparian-obligate species with a nationwide species distribution, the Willow Flycatcher (*Empidonax traillii*; hereafter "flycatcher"). Although much research exists on the subspecies of the flycatcher in the arid Southwest (Davidson and Allison 2003, Kus et al. 2003, Sogge et al. 2003, Brodhead et al. 2007, Paxton et al. 2007, Ellis et al. 2009) and multiple other shorter-term or community-level studies have provided insight in to the breeding ecology of this species (Altman et al. 2003, Kulba and McGillivray 2003, McCreedy and Heath 2004, Sedgwick 2004), ours is the first long-term study of flycatchers breeding across an altitudinal cline in the Intermountain West. This population of flycatchers is particularly important because our study area spans the regions just north of the range of the federally endangered southwestern subspecies.

SIERRA NEVADA MONTANE MEADOWS AND WILLOW FLYCATCHERS

The flycatcher is a Neotropical migrant that breeds across the northern and southwestern United States and into Canada. Populations in the North and Northeast are reportedly stable or increasing, whereas populations in the Southwest and California have declined substantially in the past three decades (Sedgwick 2000). Variation among subspecies in ecology and life-history strategies, as well as differences in land-use practices, likely account for different population trajectories within the species (Whitfield et al. 2003). For example, flycatchers in the East often rely on brushy forest-edge vegetation communities for breeding, and flycatchers in the Pacific Northwest are associated with early-successional shrub communities, including regenerating clearcuts (Chambers et al. 1999, Altman et al. 2003; but see Kulba and McGillivray 2003). Alternatively, in the Southwest and California, flycatchers depend on dense riparian vegetation for breeding (Bombay et al. 2003b, King and King 2003, Sogge et al. 2003).

Three subspecies of flycatcher occur in California (Aldrich 1951, Unitt 1987) and are state-listed as endangered because of considerable population declines detected in the late 1980s (Serena 1982, Harris et al. 1987). The southwestern subspecies, *E. t. extimus*, has received considerable attention in response to its federal status as an endangered species and concern over habitat loss and destruction (U.S. Fish and Wildlife Service 1995, 2002; Whitfield et al. 2003). However, information is lacking on the population status and breeding ecology of the two subspecies, *E. t. brewsteri* and *E. t. adastus*, that occur north of *E. t. extimus* (Green et al. 2003).

Historically, flycatchers were common across California wherever dense riparian vegetation, primarily willow (*Salix* spp.), occurred (Grinnell and Miller 1944). In the past three decades, flycatchers have undergone substantial population declines in California, where >90% of native riparian vegetation has been lost to conversion or degradation (Katibah et al. 1984). Extirpation of

E. t. brewsteri from the Central Valley of California (Green et al. 2003, Riparian Habitat Joint Venture 2004) and *E. t. adastus* from the lower Truckee River in Nevada (Klebenow and Oakleaf 1984, Rood et al. 2003) has restricted breeding habitat to montane meadows of the Sierra Nevada. With the exception of a small flycatcher population of an unknown subspecies in Mono County, California (McCreedy and Heath 2004), there exists a large geographic gap in flycatcher sightings between the *extimus* subspecies to the south and current known populations of *E. t. brewsteri* and *E. t. adastus* (Harris et al. 1987, Bombay 1999, Siegel et al. 2008). As recently as the 1940s, flycatchers were locally common in patchily distributed montane meadows in the Sierra Nevada; however, surveys conducted in the 1980s and 1990s documented a population decline, with population estimates of only 300 to 400 individuals (Serena 1982, Harris et al. 1987, Bombay 1999, Bombay et al. 2003b). These individuals occur in only a few large meadow systems, with several smaller sites supporting only a few (i.e., 1–3) flycatcher territories.

Riparian ecosystems in the Sierra Nevada have a long history of human-induced disturbances to natural ecological and hydrological processes. Beginning in the mid-1800s, lower-elevation meadows and riparian areas were converted to reservoirs, drained for agriculture, or served as transportation corridors to support the mining and logging industries (McKelvey and Johnston 1992, Kattelmann and Embury 1996, Larson 1996, Menke et al. 1996). Water-diversion structures associated with hydraulic mines, hydroelectric power, roads, or agriculture drastically altered hydrological processes (Larson 1996, Menke et al. 1996). The ubiquitous grazing of sheep denuded the landscape of grasses, shrubs, and forests throughout the Sierras, particularly in higher-elevation meadows (McKelvey and Johnston 1992, Menke et al. 1996). These practices initiated a cascading effect of erosion, stream channeling, and gullying, and disruption to natural disturbances (Kattelmann and Embury 1996, Larson 1996). Altered hydrology of montane meadows influences the water-holding capacity of the meadow flood plain; recruitment, growth, and reproduction of riparian vegetation; diversity and abundance of aquatic insects; and the multitude of aquatic and terrestrial vertebrates that rely on riparian systems (Ratliff 1985, Kattelmann and Embury 1996, Shafroth et al. 2002, Loheide et al. 2009). Wetland systems, particularly in the Lake Tahoe basin, experienced the largest wholesale loss of riparian communities during peak urbanization in the 1900s (Raumann and Cablk 2008).

In response to increasing concerns over population declines, we studied flycatchers from 1997 to 2008 in montane meadows in the Sierra Nevada, California (Fig. 1). Additionally, we compared reproductive success of flycatchers from the long-term study regions with that of a larger population of flycatchers in the Sierra Nevada located north of our primary study area. We used estimates from this region, Warner Valley, as a baseline because populations of flycatchers may be stable or increasing in this region (King and King 2003, Humple and Burnett 2004). Our objectives were to obtain descriptive information on the distribution, abundance, and breeding ecology of the flycatcher across multiple years and regions, and to identify potential factors constraining population size and reproductive success. We examined multiple hypotheses concerning the impact that weather and habitat characteristics have on nest survival. Our general hypotheses were based on the knowledge that terrestrial mammals are the primary nest predators in our system and that various characteristics of the meadows and riparian vegetation would reduce accessibility and detection of nests by these predators (Cain et al. 2003, Cocimano et al. 2011). We predicted that meadow wetness, for which we used annual snowfall and temperatures as an index, would reduce accessibility of nests (Picman et al. 1993, Fletcher and Koford 2004). We predicted that because of area and forest–meadow edge effects, nest predation would be higher in smaller meadows as a result of predator movement patterns and proximity of nests to forests. Furthermore, we consider the impact that habitat characteristics have on nest survival, predicting that increased horizontal and vertical cover would reduce predation rates.

Our long-term, multiple-region study provided an opportunity to examine natural annual variation among study areas while accounting for fluctuations in weather, which often confound studies at smaller temporal or spatial scales. Here, we examine annual variation in abundance within the study regions and how years with above-average weather events could influence observed changes in regional abundances. We relate information from our study on dispersal patterns and reproductive success to better understand how population sizes vary after stochastic weather events.

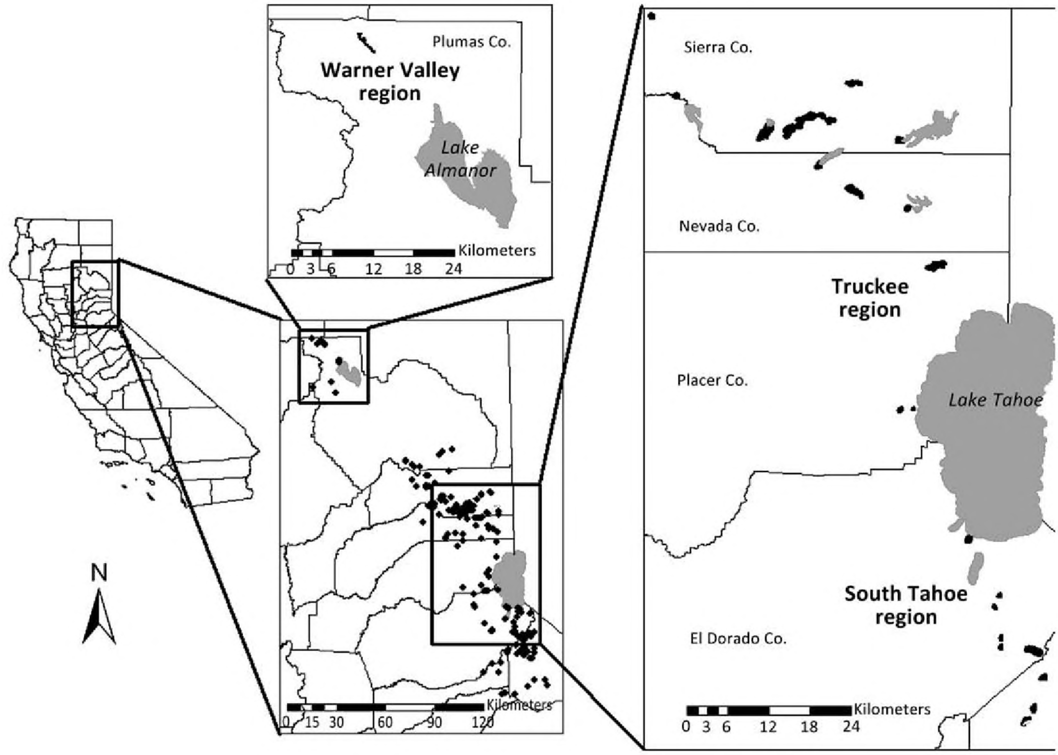

FIG. 1. Location of Willow Flycatcher study locations in California.

STUDY AREA

In 1997 and 1998, we conducted occupancy surveys in montane meadows in the central Sierra Nevada 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 (Bombay et al. 2003b). From these surveys, we selected sites for long-term monitoring from meadows identified as occupied. These sites included three of the four meadows that supported the largest numbers of breeding territories of flycatchers (*E. t. brewsteri* and *E. t. adastus*) within the Sierra Nevada (Serena 1982, Harris et al. 1987, Green et al. 2003). Study sites differed among years because of differences in annual funding, accessibility of properties, and reoccupation by flycatchers of meadows adjacent to our study sites (Mathewson 2010).

We grouped study sites into two regions (South Tahoe and Truckee) based on latitude (Fig. 1). Although meadows in the Sierra Nevada are unique because of local-scale heterogeneity in abiotic characteristics (Loheide et al. 2009), vegetative characteristics, and land-management practices, study sites within each region were similar with respect to landscape-scale effects. Study sites in the Truckee region were patchily distributed across the landscape and ranged in size from 10 to 162 ha and ranged in elevation from 1,700 to 2,100 m. Study sites in the South Tahoe region ranged in size from 6 to 98 ha at elevations of 1,900 to 2,400 m. These sites were ~40 km south of study sites in the Truckee region. The U.S. Department of Agriculture, Forest Service (USFS), California Department of Fish and Game (CDFG), or private landowners managed these study sites.

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 low-gradient streams and rivers, were adjacent to lakes, or were entirely spring fed (Weixelman et al. 2011). 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 et al. 2009). There is a north–south gradient in climate, with sites farther north receiving more precipitation (Fites-Kaufman et al. 2007). Riparian deciduous shrubs typically paralleled active and abandoned stream and river channels and lake edges but were sometimes scattered in large clumps across the meadows or were concentrated in spring-fed areas. The riparian shrub community was predominantly composed of Geyer Willow (*Salix geyeriana*) and Lemmon's Willow (*S. lemmonii*) in the South Tahoe and Truckee regions. 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, surrounded by coniferous forest dominated by Lodgepole Pine (*Pinus contorta*), with stands of Quaking Aspen (*Populus tremuloides*) interspersed (Weixelman et al. 1999).

In 2003, we established an additional study region along Warner Creek (Warner Valley Wildlife Area, Plumas County, California), to provide comparative data on the reproductive success of flycatchers breeding outside of the long-term study regions in the South Tahoe and Truckee regions. Located 125 km north of the Truckee region, Warner Valley is one of five meadows in the northern Sierra Nevada reported to contain a high number of breeding territories (Green et al. 2003, King and King 2003, Humple and Burnett 2004). Warner Valley is an extensive 250-ha meadow, of which we monitored 80 ha divided into four study sites based on natural vegetative and topographic divisions (i.e., where portions of the meadow narrowed because of upland conifer forest). We monitored flycatchers in the Warner Valley region from 2003 to 2005 and in 2008. Study sites ranged in size from 15 to 24 ha at elevations of 1,550 to 1,590 m. Compared to meadows in our South Tahoe and Truckee regions, this meadow is lower in elevation, with warmer temperatures and less snowpack, resulting in a longer growing season (Fites-Kaufman et al. 2007). In Warner Valley, the vegetation community was similar to that of our other study sites but the riparian shrub community was predominantly Mountain Alder (*Alnus tenuifolia*) mixed with Lemmon's and Geyer willows. Additionally, Lodgepole Pine and Quaking Aspen were more predominant within the meadow vegetative community than at sites farther south. The CDFG and private landowners managed these study sites primarily for recreational purposes (Lake Almanor Watershed Assessment Report 2007).

METHODS

FIELD METHODS

We monitored flycatchers using a standardized protocol, also used in the Sierra Nevada by the USFS and CDFG, that incorporated use of vocalization playback to determine occupancy, abundance, and locations of territories within study meadows (Bombay et al. 2003a). We modified this protocol to include at least one visit in July to differentiate between territorial and nonterritorial (i.e., floater) males. We located flycatcher territories using playback of conspecific calls and observing adult behaviors. We monitored territories every 2 to 7 days by locating the male and subsequently searching for females. Once we detected females, we focused our efforts on monitoring the female during territory visits. Additionally, because flycatchers exhibit facultative polygyny (Sedgwick and Knopf 1989, Davidson and Allison 2003), we continued to search the area for additional females.

We used standard nest-searching techniques (Martin and Geupel 1993) to locate and monitor nests. We monitored nests every 2 to 6 days, depending on estimated stage transition dates. We checked nest contents during every nest visit using a mirror or direct observation. After approximately day 10 of the nestling stage, we did not approach the nest but instead observed it with binoculars from a distance to reduce the chance of force-fledging the young. Although this method reduced our ability to count accurately all nestlings in the nests during the last few days of the nesting period, we revisited all nest locations after the estimated fledging date to estimate the number of young fledged and to determine nest fate.

Since 1997, we have banded all nestlings at our study sites once they reached approximately 7–9 days of age. We used a cohort banding method whereby each nestling was fitted with one colored band to denote year and a second colored band to denote natal meadow (Mathewson 2010); in 2007, we began banding nestlings with individually unique band combinations (Koronkiewicz et al. 2005). During the 12 years of the present study, we implemented various techniques for banding adults in collaboration with other local researchers (Mathewson 2010). In 2005, we began using standard target-netting methods (Sogge et al. 2001) to capture adult flycatchers periodically during the season and band them with unique color combinations. We attempted to resight all birds at our study sites throughout the season as well as flycatchers detected by USFS, CDFG, or other agencies during annual surveys or site visits and within the same counties as our study sites (Alpine, Amador, El Dorado, Nevada, Placer, Plumas, Sierra, and Yuba; Mathewson 2010).

Environmental Variables

We obtained historical weather variables from the Western Regional Climate Center (Reno, Nevada). We selected data from weather stations near our study regions that provided historical and consistent data across all years and that were at an elevation similar to that of our study meadows within each region. We calculated the deviation of each annual weather measurement from the mean value over a 50-year period (1958–2008), which represents a period of climatic change in the western United States marked by increased temperature variability, increased mean temperatures, and reduced spring runoff from snowpack (Stewart et al. 2005). We defined winter as November through March, and we estimated spring snowfall from April and May.

We outlined meadow-scale features visually using color digital orthoquad photos (DOQQs) and ARCVIEW GIS, version 3.2. In 2007, we groundtruthed our estimated delineation of trees and shrubs by comparing GPS coordinates recorded at study sites that represented the edge of trees and shrubs to boundaries represented on DOQQs to increase our ability to delineate meadow features accurately using digital orthoquads. We measured meadow area as a categorical variable because the range of area of our study sites was a bimodal distribution with sites either 2 to 41 ha (small meadows) or 70 to 162 ha (large meadows), thus providing a useful division into relatively small and large meadows. To represent meadow shape standardized for meadow size, we calculated the ratio of the meadow perimeter in relation 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. Also using GIS, we estimated the minimum distance from the nest to the continuous forest edge, a measure of within-patch forest edge effects.

At the nest scale, we measured nest height (ht), an index of over-nest cover (cover), and distance to shrub edge (edge). Nest height was the distance from the ground to the base of the nest, over-nest cover was the vertical distance between the rim of the nest and the outside edge of the majority of the willow cover, and distance to shrub edge was from the side of the nest to the nearest edge of the willow or willow clump. We recorded all vegetation measures after we confirmed that a nest failed or fledged young.

Population Trend Analysis

We defined an adult male as territorial if we detected him at a location for ≥10 days and after 30 June, to allow comparisons among survey sites and monitoring sites across the years of our study. We assumed that we detected all territorial males in our study sites because males vocalized from exposed perches and their songs and calls are distinctive. Detectability of females varied with the nesting stage; activity is at a maximum during courtship and nest construction (Ettinger and King 1980), with an increased likelihood of missing females once nest incubation begins. For this reason, we assumed that the likelihood of detecting females was similar across years to allow us to compare trends in numbers of females. We did not adjust the counts of males or females for detection probability because we monitored sites every 2 to 7 days throughout the season, and thus we assumed that season-long detection probability was near 1. We acknowledge, however, that opting to not include a detection adjustment introduced some degree of negative bias in our estimates of number of adults.

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

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

Dispersal

We estimated dispersal distances of returning juveniles (second-year [SY] individuals) from their natal nest location to a central point in the meadow where they were first sighted in subsequent breeding seasons. We calculated natal meadow fidelity as the proportion of returning SY individuals that returned but dispersed out of their natal meadow. For breeding dispersal, we estimated breeding-site fidelity from a subsample of individually banded adults. We examined changes in breeding-site locations beginning with the year in which the adults received individual band combinations. Because our banding methods changed during our study (Mathewson 2010), we assumed equal survival and detection probability for all years and individuals and did not consider breeding status or individual age.

Breeding Biology

For all analyses, we included only those nests for which we observed ≥1 egg or nestling, because we could not distinguish between empty nests that females abandoned during building or prior to laying from those that failed early in the laying period. We considered nest contents (i.e., clutch size) to be accurate if we located the nest before day 4 of incubation, to reduce inaccuracies associated with early brood loss.

Nesting phenology.—We converted dates into Julian dates for analyses. We considered nest initiation date to be day 1 of the laying period, and we assumed that females laid 1 egg day^{-1}. For use in analyses and to compare the length of the nest stages among study regions, we calcululcated the mean length of each nesting stage using only nests for which we had accurage dates of stage transitions. For estimating the mean incubation period, we included only nests that we had observed during laying and on hatch day. For estimating mean length of the nestling period, we included only nests that we observed on hatch day and at fledging. We compared differences in mean length of incubation and nestling periods between the Truckee and Warner Valley regions using *t*-tests (sample sizes for South Lake region were too small). To estimate nest initiation dates for nests found after incubation began, we backdated by using known nest transition dates (i.e., hatching) or by estimating the age of nestlings; we calculated nest initiation date using the average length of each nest stage. To examine temporal trends within seasons, we 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 differences in nesting-season onset and length, we determined the distribution of nest initiation dates within each region and year. We used the 10th percentile of nest initiation dates for presumed first nest attempts as an index for the seasonal onset of nesting. We used the standard deviation of first nest attempts as a measure of the period of nest initiation dates, which represents an index of the length of the breeding season (Chase et al. 2005). We used these indices to reduce the influence of extreme values in the analysis. We examined the influence of weather variables on nesting-season onset using the 10th percentile of the distribution of nest initiation dates each year within a study region.

Clutch size and nesting attempts.—For clutch size estimates, we included nests only if we located and observed the contents of the nest prior to day 4 of incubation, because we could not account for partial loss of nest contents in nests found at older ages. Additionally, we included nests with 4 eggs, regardless of when we located the nest, because 4 is the maximum number of eggs known to be laid by flycatchers (McCabe 1991, Sedgwick 2000) and because we never observed more than 4 eggs in a nest in our study area. We also excluded nests that contained eggs from Brown-headed Cowbirds because female cowbirds commonly remove single or multiple eggs.

Although we attempted to find all nests by monitoring females throughout the season, we could not always accurately determine which nests were first nest attempts. Thus, using multiple criteria, we identified a subset of nests presumed to be first nest attempts. First, we considered all nests with 4 eggs to be first nest attempts. Female flycatchers lay a maximum clutch size of 4 eggs, and this number usually declines to ≤3 eggs in renest attempts; however, some females lay only 3 eggs in first nest attempts (McCabe 1991, Sedgwick 2000). Furthermore, we determined that only 15% ($n = 104$) of females in our study laid 4 eggs in known renest attempts and, of these 16 renests, 81.3% of them followed a nest attempt that failed during the egg-laying stage. Thus, we assumed that any 4-egg nests that were renests but misidentified as first nest attempts occurred early in the season and only minimally biased our estimates of nest initiation date. Second, we identified a standard interval within which the majority of females lay the maximum clutch size of 4 eggs (Mathewson 2010). We assumed that any nests initiated after this interval were renests for which we had not located the female's first nest, and we removed those nests from our subset. Additionally, we assumed that any nests found within this interval, for which we did not have any observed behavioral information suggesting otherwise, could potentially be first nest attempts, and we included them in our subset for presumed first nest attempts. Third, we included in our subset of presumed first nest attempts any nests that failed for which that female renested.

For each female, we assigned a nest-attempt number based on assumptions of presumed first nest attempts and on nest initiation order. We defined the probability of renesting as the probability that a female would renest given that we found her previous nest and that it failed. On the basis of our banding data, we assumed that the likelihood of females switching between territories within a year was rare, and this provided us the ability to assign multiple nesting attempts to females.

Parasitism and predation.—To determine nest parasitism rates, we estimated the minimum proportion of parasitized nests by including only those nests that we located within the first 4 days of incubation. By eliminating nests found during later stages, we reduced the chance that we would falsely count a nest as unparasitized when, in fact, parasitism had occurred. For example, nest predators could remove cowbird eggs during partial predation events before we found the nest. Additionally, we observed cowbird eggs buried within the lining of nests underneath flycatcher eggs (H. A. Mathewson pers. obs.). We assumed that a nest was successful if we located ≥1 flycatcher fledgling or if the nest was active at least until day 12 of the nestling stage, after which the young are capable of force-fledging (McCabe 1991, Sedgwick 2000, H. L. Loffland pers. obs., H. A. Mathewson pers. obs.). We attributed the total loss of nest contents prior to day 12 of the nestling stage to nest predation. Additionally, we attributed the loss of ≥1 egg or nestling prior to day 12 of the nestling period to partial predation or removal by cowbirds. We attributed nest losses to weather events if adults abandoned nests or if we found dead nestlings in the nest after severe snowstorms or thunderstorms.

REPRODUCTIVE SUCCESS ANALYSIS

We calculated fecundity as the number of young produced per female detected within each study region, assuming a 50:50 nestling sex ratio (Paxton et al. 2002). We included females for which no nests were located, on the assumption that all females attempted to nest; however, we excluded females from territories that we did not continuously monitor during the season. If we located a family group (fledglings and adults) for a female that we had not continuously monitored or for a nest that we had not monitored, we included these data but used the mean number of young fledged per successful nest in that study year and region. We adjusted the number of young in these cases because detection of individual fledglings was low and varied with study year and region, although detection probability of a family group was high (Vormwald et al. 2011). Our estimate was a maximum estimate of fecundity because we used the number of young last seen in the nest prior to fledging; thus, we did not account for mortality during the last few days of nesting.

We examined the influence of weather variables on nesting-season onset using the 10th percentile of the distribution of nest initiation dates each year within a region. We 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, we excluded all region–years of data that did not meet the threshold of 11 nests: 1997 in the Truckee region, 2006 in Warner Valley, and 1997 and all years after 2001 in the South Tahoe region. We used generalized linear modeling and type II sums of squares to evaluate the contribution of individual variables to total variance in annual nest initiation. We examined residuals and predicted values to determine the influence of any potential outliers, but we did not remove any values ad hoc because extreme variations in weather events were important to our study.

Nest survival model development and evaluation.— To facilitate comparisons with previous research on flycatchers, we estimated Mayfield nest success (Mayfield 1961, 1975) for all study years and regions. To model daily nest survival in relation to multiple predictor variables, we used a logistic-exposure approach (Shaffer 2004, Shaffer and Thompson 2007) and Akaike's information criterion (AIC; Akaike 1973) to evaluate candidate models. We used a hierarchical modeling approach (Stephens et al. 2003, Hood and Dinsmore 2007) in which we determined the most predictive temporal effects model that considered nest age, date, and year, against which we compared the relative strength of predictor variables from the set of weather models and habitat models. For the set of habitat models, this approach involved a two-step process because data for nest-scale effects were available only for a subset of our study years. We considered models with ΔAIC < 4 to be competitive models (Burnham and Anderson 2002). 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, we calculated model-averaged parameter estimates, unconditional standard errors, and 95% confidence intervals. We examined goodness-of-fit of predicted models by graphically comparing predicted values against observed values (Shaffer and Thompson 2007). To acquire the observed predicted daily survival rate for continuous predictor variables, we grouped observations into several classes and then estimated the daily survival rate for each class. Precision of observed estimates was often low because of small sample sizes within each class.

For the temporal model, we considered models that included a categorical year effect; a linear, quadratic, and cubic effect of nest age; and a linear and quadratic effect of date. By allowing nest age and date to vary, we could better understand how nest survival changed over time; holding either effect constant or considering only a linear effect could mask important ecological patterns (Grant et al. 2005, Pasinelli and Schiegg 2006). Survival may change in a nonlinear manner with nest age because of changes in cues available to predators with transitions to different nesting stages and as nestlings age (Grant et al. 2005, Stake et al. 2005). Additionally, we considered a quadratic effect of date because survival may fluctuate during the breeding season as a result of variation in predator abundances and activity (Grant et al. 2005, Sperry et al. 2008). We considered a decreasing linear trend in survival because we hypothesized that predation would increase with declining water levels in meadows (Picman et al. 1993, Fletcher and Koford 2004).

To the best model approximating temporal effects, we added the weather-effects model that included winter snow, spring snow, winter snow with a 1-year time lag, and temperatures in June and July. We constructed 42 models that included all main effects, combinations of weather variables, and additive combinations of variables selected from our temporal model and each main effect of weather or combination of weather variables. We based our weather models on the general hypothesis that decreased meadow wetness would result in increased nest predation rates because of accessibility to nests by terrestrial predators (Picman et al. 1993, Cain et al. 2003, Fletcher and Koford 2004, Cocimano et al. 2011). Within this context, we predicted increased nest survival following years with increased winter snowfall or spring snowfall, or with decreased temperatures in June or July. Additionally, we considered the direct effects that weather may have on predator abundances by considering a time-lag effect of snowfall in the previous winter because small mammal populations often fluctuate with resources over a 2-year period (Rotenberry and Wiens 1989, Schmidt and Ostfeld 2003).

We examined nest survival as a function of multiple habitat variables at the meadow and nest scales selected for their hypothesized association with differences in predator activity or abundances. We hypothesized that meadow-scale factors, such as riparian shrub cover and amount of core area, affected nests similarly within meadows (Burke and Nol 2000, Albrecht 2004, Pasinelli and Schiegg 2006). After accounting for collinearity among variables ($r > 0.7$; Graham 2003), we selected models that included meadow size (size; small [2–41 ha] or large [70–162 ha]), proportion of shrub cover (shr), meadow shape (pta), and distance from forest (forest) for use in our analyses. Elimination of collinear variables did not alter our original hypotheses, because we assumed that collinearity suggested that variables represent the same or similar influences on nest predator activity and abundance. For a subset of data from 2005 to 2007, we examined nest-scale measures that we hypothesized represented fine-scale effects on the ability of predators to detect or gain access to nests (Albrecht 2004, Pasinelli and Schiegg 2006). We included models for main effects of over-nest cover (cover), nest height (ht), and distance from nest to riparian shrub edge (edge) as well as interactions between them and additive combinations. We hypothesized that the effect of nest-scale variables may differ with patch size (Albrecht 2004); therefore, we included interactions between patch size and over-nest cover, nest height, and distance from nest to riparian shrub edge. We *z*-standardized all covariates for these analyses. Results are presented as means ± SD unless otherwise noted.

Results

Weather Trends

Our study coincided with a period of winter and spring snowfall above the 50-year mean until 2000, when the Sierra Nevada and California experienced below-mean drought years (Roos 2008; Fig. 2A–C). 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 throughout our study. Temperatures in June and July were above the 50-year mean for all regions (Fig. 3A–C), with some exceptions in years associated with above-average spring snowfall, notably in 1998, 1999, and 2005.

For weather variables used in our nest survival analysis from the South Tahoe and Truckee regions, winter snowfall was significantly correlated with temperatures in June ($r^2 = -0.67$, $P < 0.001$, $n = 24$) but was not related to snowfall in spring ($r^2 = -0.15$, $P = 0.47$, $n = 24$). Temperatures in June were not significantly correlated with spring snowfall ($r^2 = -0.11$, $P = 0.61$, $n = 24$) or temperatures in July ($r^2 = -0.04$, $P = 0.87$, $n = 24$). Because of the statistical association between winter snowfall and temperatures in June, we eliminated from our sets of candidate models any predicted combined effects of winter snowfall and June temperatures.

Population Trends

We detected flycatchers in 19% of the 104 meadows at which we conducted occupancy surveys in 1997 and 1998 (Bombay 1999). We detected flycatchers at 52% ($n = 21$) of sites for which we had historical records of flycatchers. Those sites that were unoccupied were primarily located in the South Tahoe region, where historical records indicated a flycatcher population that was locally common in large meadows in the Upper Truckee and Carson River watersheds (Bombay 1999, and citations therein). However, we detected only 12 male flycatchers in the South Tahoe region during these initial surveys. From 1997 to 2008, we documented a declining trend in the South Tahoe region population; the annual rate of change in number of territories declined by 17.9 ± 0.21% overall (Fig. 4A), and the number of females at our long-term study sites declined by 8.3 ± 0.5% overall (Fig. 4B). We documented a maximum of three territories at any single site in the South Tahoe region.

In the Truckee region, we detected flycatchers at all sites with historical flycatcher records, and we located birds in sites with unknown historical status. Site abundance fluctuated annually, but the mean annual rate of decline in number of territories was 6.1 ± 0.087% (Fig. 4A). Females declined at a mean rate of 6.4 ± 0.14% (Fig. 4B). In Warner Valley, territory numbers have fluctuated from 32 to 40 year^{-1} (Fig. 4A), and the mean rate of decline of territories was 1.9 ± 0.26%. From 2 years of data available to determine the change in number of females, there was a 31.3% increase from 2003 to 2004 and a decline of 9.5% from 2004 to 2005 (Fig. 4B).

From 1998 to 2008, we detected a higher proportion of unmated males in the Truckee region (26.0%; $n = 468$ males total) than in the South Tahoe region (20.9%; $n = 67$). The proportion of unmated males was substantially less in the Warner Valley region (8.6%; $n = 151$). Compared with the same period from 2003 to 2008, the proportion of unmated males was 31.1% ($n = 271$ males) in the Truckee region and 38.5% ($n = 26$) in the South Tahoe. There was an increasing trend in the proportion of unmated males in the South Tahoe and Truckee regions from 1997 to 2008, assuming a constant detection probability of males and females (Mathewson 2010). From 1998 to 2008, the proportion of territories that had a polygynous male was similar in the South Tahoe (7.5%; $n = 67$ males total) and Truckee regions (6.3%; $n = 486$). From 2003 to 2008, polygyny was higher in the Warner Valley region (15.2%; $n = 151$ males total) compared with the same period in the South Tahoe (7.7%; $n = 26$) and Truckee (8.1%; $n = 271$) regions.

Dispersal

For returning SY individuals that we could assign to a natal meadow (i.e., we were able to obtain a confirmed color-band identification), natal meadow fidelity was 34.3% ($n = 70$) and mean natal dispersal distance was 5.65 ± 7.20 km ($n = 70$). Considering only individuals that dispersed out of their natal meadows, the mean natal dispersal distance was

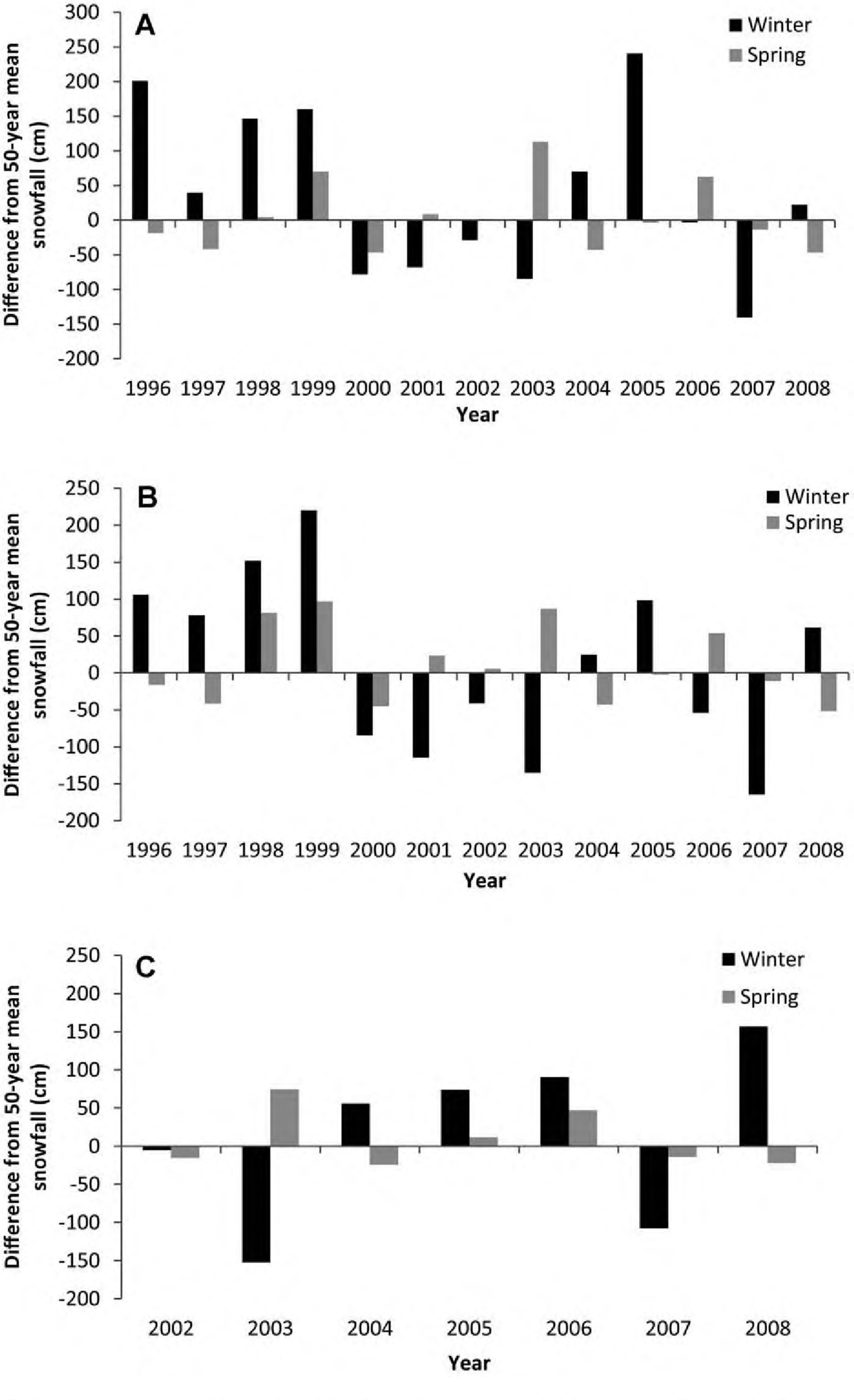

FIG. 2. Differences in winter (November–March) and spring (April–May) snowfall from the 50-year mean for the (A) South Tahoe, (B) Truckee, and (C) Warner Valley study regions in the Sierra Nevada, California. Data are from the Western Regional Climate Center, Reno, Nevada.

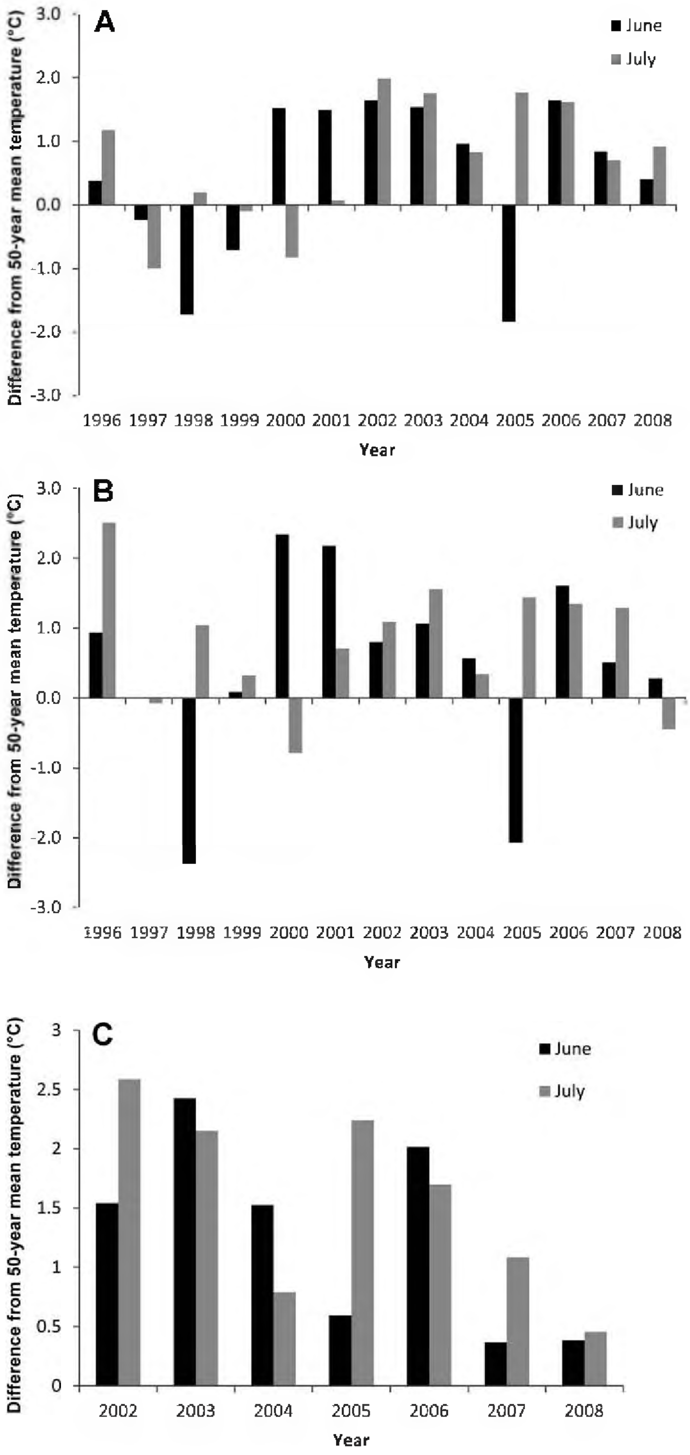

FIG. 3. Differences in June and July temperatures from the 50-year mean for the (A) South Tahoe, (B) Truckee, and (C) Warner Valley study regions in the Sierra Nevada, California. Data are from the Western Regional Climate Center, Reno, Nevada.

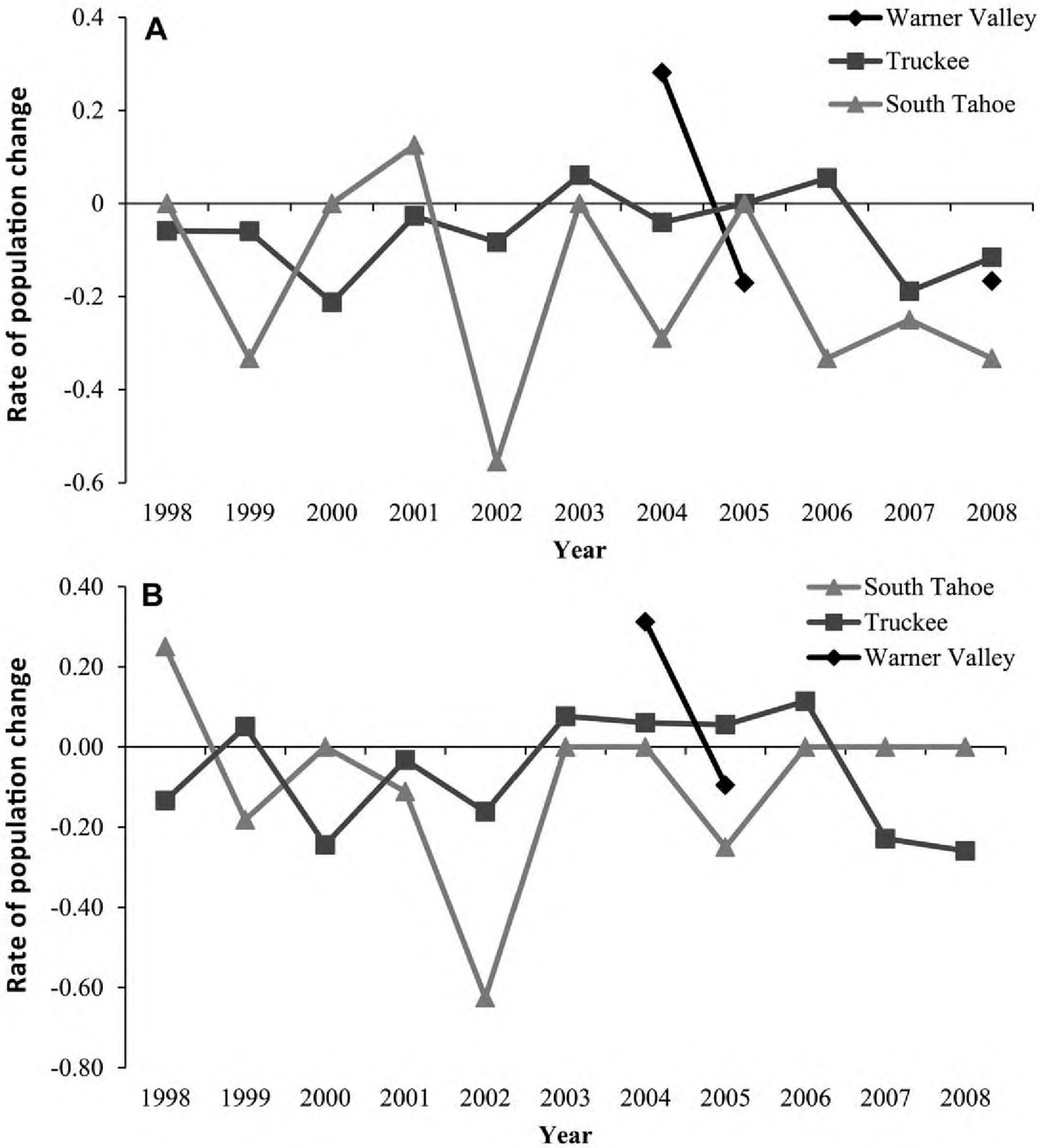

FIG. 4. Rates of population change for (A) male and (B) female Willow Flycatchers detected in the South Lake, Truckee, and Warner Valley study regions in the Sierra Nevada, California.

8.36 ± 7.36 km (n = 46), and the dispersal distance for 76% of these individuals was <10 km from their natal meadows. There was one long-distance natal dispersal event of 134 km documented for a female flycatcher that fledged in Warner Valley and returned as an SY to breed in the Truckee region. Based on 38 uniquely banded individuals captured in 2005 through 2007 and resighted in the year following banding, the return rate for breeding adults was 73.7% (n = 38), of which 89.3% (n = 34) returned to the previous year's breeding site.

BREEDING BIOLOGY

From 1997 to 2008, we found 83 nests in South Tahoe, 519 in the Truckee region, and 243 in Warner

Valley. We found the majority of nests during the building or egg-laying period (58.8%; $n = 792$); for nests found after the egg-laying period, the mean nest age was 7.38 days (95% CI: 6.46–8.31).

Nesting phenology.—Between the Truckee sites and Warner Valley, there was no significant difference in mean incubation length ($t = 1.34$, $P = 0.186$) and in mean nestling length ($t = 1.055$, $P = 0.314$). Incubation period in the Truckee region was 13.6 ± 0.352 days ($n = 30$), and mean nestling period was 14.7 ± 0.707 days ($n = 9$). Because the sample size for the nestling period was small, we compared the mean length of the nestling period with the mean value from all nests for which we had known fledging dates. We calculated the length of the nestling period using standard measures of nestling aging (i.e., we backdated to estimate the hatch date using nestling age) and determined that the mean period length (14.6 ± 1.391 days; $n = 26$) was not different from that of the smaller sample size. In Warner Valley, mean incubation period was 13.2 ± 0.616 days ($n = 20$) and mean nestling period was 14.3 ± 0.5 days ($n = 4$). Using the same standards for backdating from known fledging dates, the mean nestling period also did not vary (14.1 ± 0.539 days; $n = 11$).

There was no discernible trend among years in nesting-season onset, defined as either the mean annual nest initiation date or the 10th percentile of nest initiation dates for presumed first nest attempts. However, the mean 10th percentile of nest initiation dates in Warner Valley was 6.3 days earlier than in the Truckee region and 7.3 days earlier than in the South Tahoe region (Table 1). Nest initiation in the Truckee region was 1.0 days earlier than in the South Tahoe region. The length of the nest initiation period for flycatcher breeding seasons, based on the standard deviation of nest initiation dates for each study year, was 6.3 days ($n = 8$ years) in South Tahoe, 7.6 days ($n = 12$ years) in Truckee, and 10.8 days ($n = 4$ years) in Warner Valley (Table 1). Differences in June temperatures from the 50-year mean explained 58% of variation in nesting-season start date compared with spring snowfall and July temperatures ($r^2 = 0.592$, $P < 0.001$, $n = 22$; Fig. 5).

Clutch size and nesting attempts.—Maximum clutch size for flycatchers at all study sites was 4 eggs, and the mean (± SE) annual clutch sizes for nests at all study sites were similar in each study region (South Tahoe: 3.6 ± 0.31, $n = 11$ years; Truckee: 3.5 ± 0.13, $n = 12$ years; Warner Valley: 3.6 ± 0.25, $n = 5$ years). Clutch size declined significantly with date of nest initiation (South Tahoe: $r^2 = 0.116$, $P = 0.02$, $n = 48$; Truckee: $r^2 = 0.267$, $P < 0.001$, $n = 306$; Warner Valley: $r^2 = 0.147$, $P < 0.001$, $n = 133$). For females with known renesting attempts (first nest failed), 15% ($n = 104$) laid 4 eggs in a known renest, and 81% ($n = 16$) of these renest attempts followed a previous nest attempt that failed during the egg-laying stage.

The proportion of females that renested after a failed nesting attempt fluctuated among years within study regions (Mathewson 2010). Nest initiation date for renests occurred no later than 4 August in South Tahoe, 3 August in Truckee, and 7 August in Warner Valley. In all regions combined, the estimated mean nest initiation date for females that renested (first nest failed) was 6.0 days earlier than that for non-renesting females ($t = 7.05$, df = 1 and 510, $P < 0.001$, $n = 510$). Similarly, mean

TABLE 1. Mean nest initiation dates of presumed first nest attempts and fledging dates of Willow Flycatchers in the South Tahoe, Truckee, and Warner Valley regions in the Sierra Nevada, California, 1998–2008.

Region	Years[a]	Number of nests	Min.	10%	Mean	90%	Max.	SD
Incubation								
South Tahoe	8	48	22 June	24 June	29 June	5 July	8 July	6.3
Truckee	12	326	20 June	23 June	1 July	10 July	21 July	7.6
Warner Valley	4	127	11 June	17 June	28 June	12 July	23 July	10.8
Fledge								
South Tahoe	4	22	23 July	24 July	29 July	4 Aug	6 Aug	9.6
Truckee	12	220	18 July	21 July	31 July	14 Aug	19 Aug	5.5
Warner Valley	4	103	10 July	15 July	25 July	7 Aug	16 Aug	9.6

[a] Estimates for each study region are for years with ≥4 nests. For South Tahoe region, nest incubation estimates are for 1997–2001 and 2003–2005. For South Tahoe region, fledge estimates are for 1997–2000. Estimates for Truckee are for 1997–2008, and estimates for Warner Valley are for 2003–2005 and 2008.

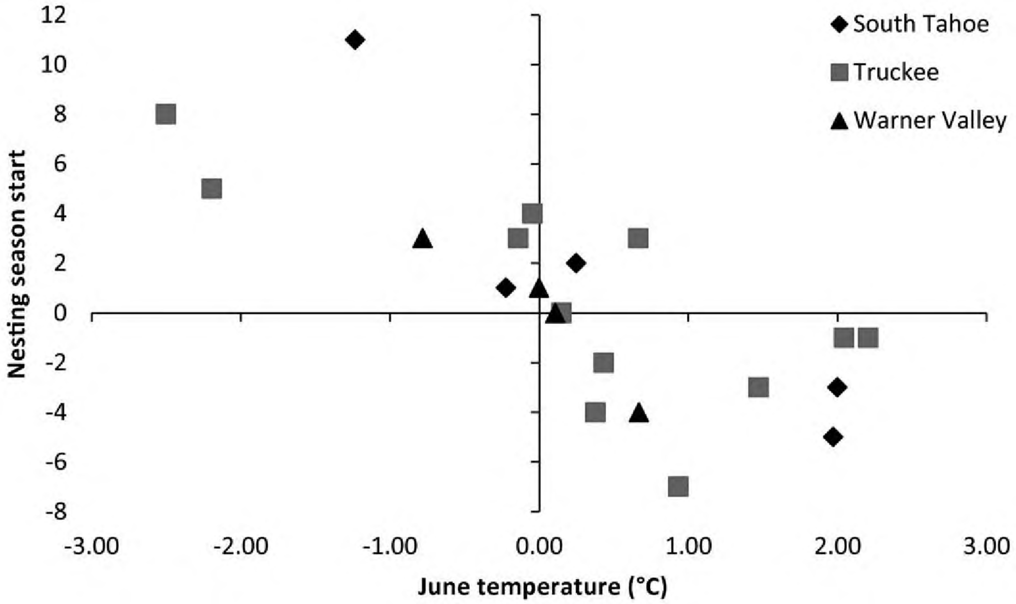

FIG. 5. Relationship between seasonal onset of nesting in Willow Flycatchers and June temperatures for 1997–2001 in the South Tahoe region, 1997–2008 in the Truckee region, and 2003–2008 in the Warner Valley region in the Sierra Nevada, California.

nest failure dates of first nest attempts for females that renested were 15.4 days earlier than those for females that did not attempt to renest ($t = 13.78$, df = 1 and 254, $P < 0.001$, $n = 254$). In all study regions, only 3 ($n = 158$) females renested that had a nest fail after 19 July, which, in the Truckee and South Tahoe regions, was only 30 days after the mean annual date when 10% of females in all years initiated nesting. We documented only two cases of females renesting after successfully fledging young (i.e., double brooding), both of which occurred in Warner Valley (we confirmed these attempts because both females were uniquely color-banded).

Parasitism and predation.—The mean annual Brown-headed Cowbird parasitism rate of nests was 18.4% in the South Tahoe region ($n = 11$ years), 11% ($n = 12$) in the Truckee region, and 8.4% ($n = 5$) in the Warner Valley region (Mathewson 2010). Predation was the primary cause of complete nest failure in 74% ($n = 324$) of nests, whereas abandonment (5.3%), unknown causes (12%), nestling mortality (2%), weather events (2%), and unhatched clutches (4.5%) accounted for the remaining nest losses. For nests that we assumed accurate clutch-size estimates, we documented partial predation in 111 nests (22.1%; $n = 503$), of which 55.9% ($n = 111$) subsequently failed, and the percentage of all nests that were partially depredated was similar for all regions (South Tahoe: 28%, $n = 50$; Truckee: 22%, $n = 313$; Warner Valley: 20%, $n = 140$).

REPRODUCTIVE SUCCESS

Mayfield nest success for all years combined was 33.8% ($n = 70$ nests) in the South Tahoe, 40.5% ($n = 434$ nests) in the Truckee, and 51.5% ($n = 198$ nests) in Warner Valley regions (Fig. 6). Annual fecundity estimates declined in the South Tahoe from 1997 to 2004 (Fig. 7), after which we detected ≤ 3 females year^{-1}. Fecundity estimates in the Truckee region fluctuated annually, showing no discernible trend; however, seasonal estimates did not exceed 2.19 young female^{-1} (Fig. 7). Mean annual fecundity estimates were 23% higher in Warner Valley (1.76 ± 0.243; $n = 4$) than in Truckee (1.43 ± 0.413; $n = 11$) and 40% higher than in South Tahoe (1.26 ± 0.645; $n = 10$).

The best approximating model for temporal and weather effects on daily nest survival rates was a cubic effect of nest age, and model-averaged estimates for a cubic effect of nest age were significant ($\beta = 4.42$; 95% CI: 1.57–7.26). Model prediction of a cubic trend in nest age concurred with observed values based on grouping data into nest age intervals

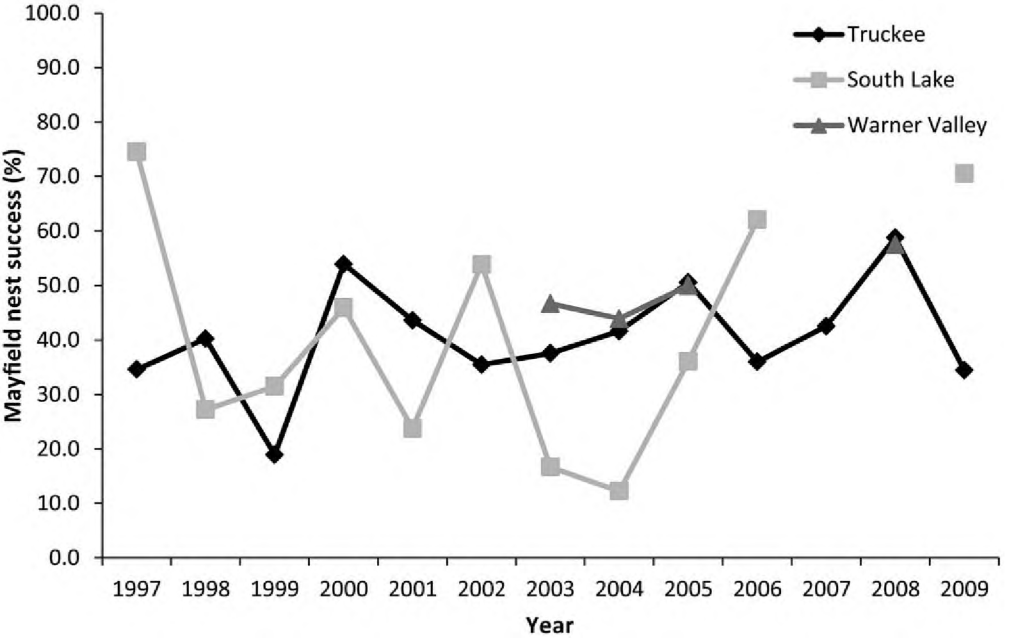

FIG. 6. Mayfield nest success for Willow Flycatchers breeding in three study regions in the Sierra Nevada, California.

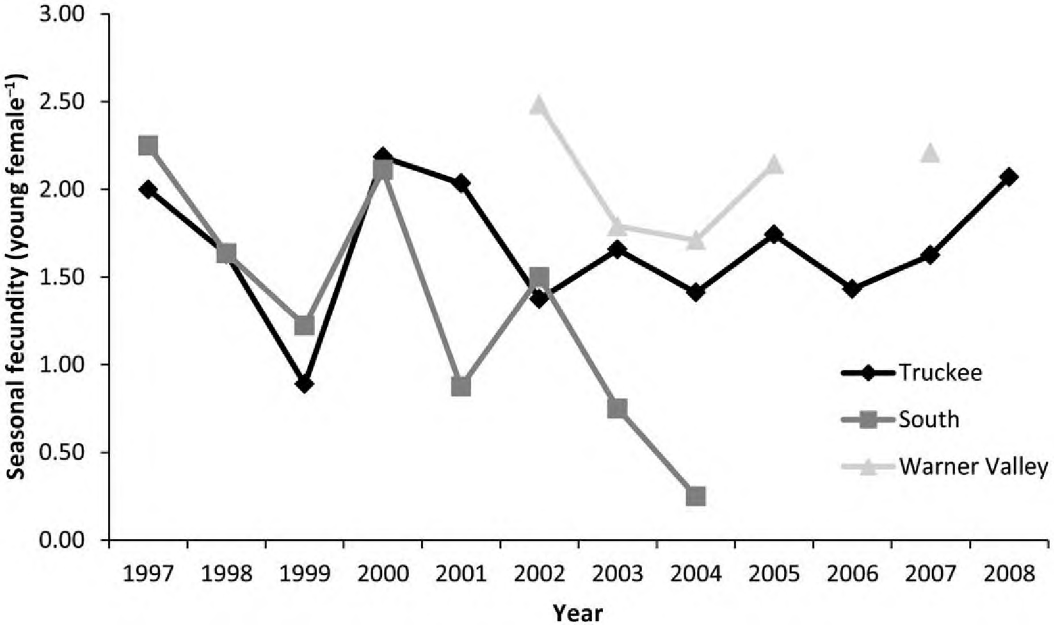

FIG. 7. Fecundity estimates for Willow Flycatchers breeding in South Tahoe, Truckee, and Warner Valley study regions in the Sierra Nevada, California.

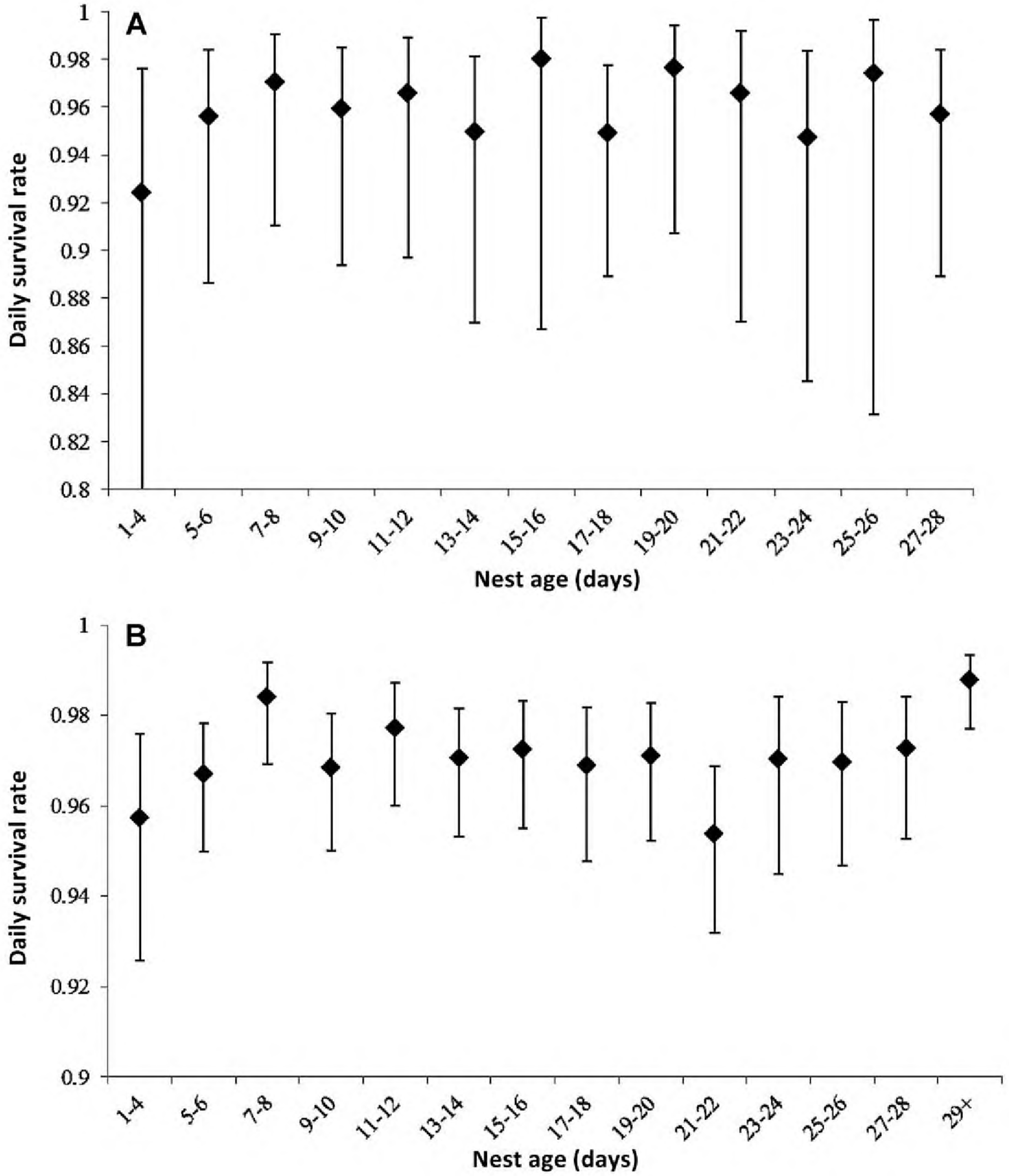

FIG. 8. Observed values and 95% confidence intervals of the effect of nest age on daily nest survival rate of Willow Flycatchers in the (A) South Lake region and (B) Truckee region in the Sierra Nevada, California, 1997–2008. We estimated values using the logistic-exposure model based on grouping the data into age intervals.

(Fig. 8). After adding effects of weather to the nest age model, the best-fit models included the effects of spring snow (total $\text{AIC}_{\omega} = 0.72$) and a cubic trend in nest age (Table 2). Although model-averaged estimates indicated some variation in the direction of the effect of spring snow on daily nest survival rates ($\beta = -0.11$; 95% CI: –0.26 to 0.05), daily nest survival generally decreased with increased snow in the spring. The probability of nest survival was lowest on the first day of nest initiation and increased until approximately the first few days of the incubation period, when it remained relatively steady,

Table 2. Model-selection results for logistic-exposure models of the effect of nest age and weather variables on daily survival rate of Willow Flycatcher nests in the Sierra Nevada, California, 1998–2008. Factors included in this model were nest age (age; quadratic effect: age2; cubic effect: age3), spring snowfall (spring), winter snowfall (snow) and winter snowfall in year $t - 1$ (snow1), temperatures in June, and temperatures in July. The number observed was 499 and the effective sample size was 8,568. Models with $\Delta AIC_c < 5$ are presented.

Model	k	Log likelihood	AIC_c	ΔAIC_c	w_i
Age3 + spring	5	–740.64	1,491.29	0.000	0.318
Age3 + spring + june	6	–739.98	1,491.97	0.676	0.227
Age3 + snow1 + spring	6	–740.07	1,492.15	0.854	0.207
Age3 + snow	5	–742.37	1,494.75	3.460	0.056
Age3 + snow + snow1	6	–741.83	1,495.66	4.368	0.036
Age3 + snow1	5	–742.85	1,495.71	4.417	0.035
Age3	4	–743.90	1,495.80	4.507	0.033
Age3 + june + july	6	–741.95	1,495.91	4.618	0.032
Age3 + july	5	–743.00	1,496.01	4.720	0.030
Age3 + june	5	–743.19	1,496.40	5.103	0.025

declining slightly until approximately day 5 or 6 of the nestling period. Probability of survival increased after about day 7 or 8 of the nestling period.

For meadow-scale landscape effects on daily nest survival, several models received support in explaining daily nest survival, but no single model was significantly competitive. For the seven models with $\Delta AIC_c < 4$, meadow shape (pta) received a total $AIC_\omega = 0.577$ and distance to forest edge (forest) a total $AIC_\omega = 0.410$; however, the effect sizes and 95% CIs from model averaging indicated weak effects from these measures. For meadow and nest-scale measures from the 2005–2007 data set, the best approximating model included an interaction between meadow size and over-nest cover (Table 3). Model-averaged estimates were not significant ($\beta = -0.61$; 95% CI: –1.53 to 0.31), but model-predicted estimates indicated that nests in large meadows were more likely to survive with increasing amounts of over-nest cover (Fig. 9). Observed estimates of daily nest survival at varying levels of over-nest cover supported the trends in the predicted models (Fig. 10).

Discussion

During the 12 years of our study, we detected a population decline in flycatchers in meadows in the Sierra Nevada, California. Declines were strongest in the South Tahoe region, resulting in local extirpation of flycatchers in most of our long-term monitoring sites. In the Truckee region, populations declined during the first 3 years of our study (1997–2000) and then appeared stable until a decline in the last 2 years (2007 and 2008) of the study. Consistent with other long-term studies on passerines (e.g., Holmes and Sherry 2001), our results indicated that multiple factors likely influenced annual population sizes of flycatchers in the Sierra Nevada. Late-spring storms and low temperatures at the start of the breeding season appeared to influence reproduction by delaying nesting, thus reducing the likelihood of renesting. Although weather parameters were not significant in directly influencing nest survival analyses, our

Table 3. Model-selection results for logistic-exposure models of the effect of meadow and nest-scale variables on daily survival rate of Willow Flycatcher nests in the Sierra Nevada, California, 2005–2007. Factors included in this model were 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 (ht). The number observed was 643 and the effective sample size was 2,456. Models with $\Delta AIC < 5$ are presented.

Model	k	AIC_c	ΔAIC_c	w_i
Size * cover	4	415.79	0	0.336
Size * cover + ht	5	417.23	1.43	0.164
Size * cover + edge	5	417.77	1.97	0.125
Ht * cover	4	418.96	3.17	0.069
Size * cover + ht + edge	6	419.19	3.43	0.060
Ht * cover + size	5	419.52	3.75	0.051
Ht * cover + edge	5	420.75	4.95	0.029

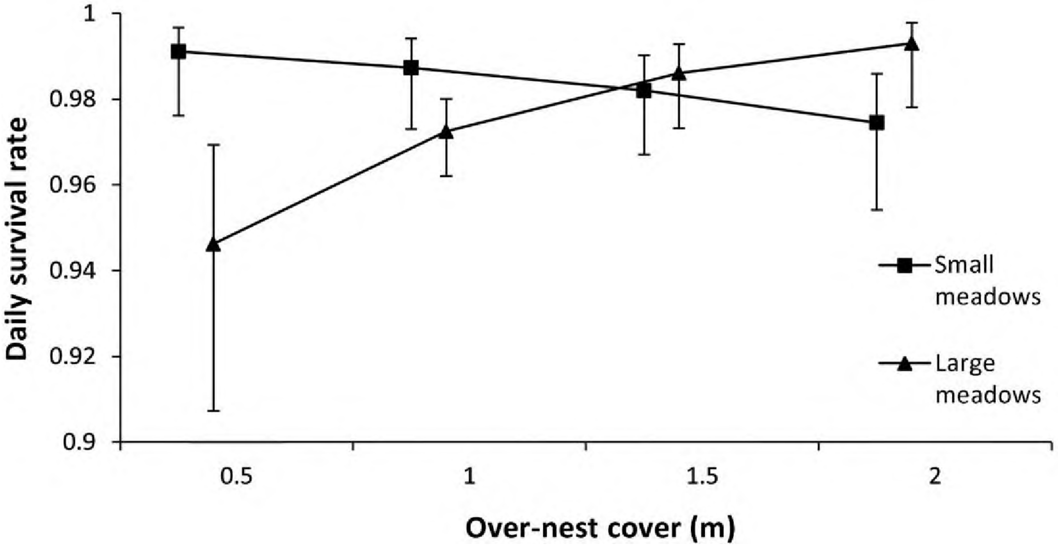

FIG. 9. Predicted values and 95% confidence intervals using the logistic-exposure model of the effect of over-nest cover in relation to small and large meadows on daily nest survival rate of Willow Flycatchers in the Sierra Nevada, California, 2005–2007.

results suggested a weak negative relationship with increased snowfall. Furthermore, the relationship between nest survival and over-nest vegetation could be explained by the potential indirect effects of weather on riparian vegetation. Evidence from our dispersal data implied that flycatchers in our study regions had high natal- and breeding-site fidelity, which suggests that recruitment across these study regions might be limited and that populations in the South Tahoe region might not rebound. Populations in Warner Valley exhibited annual fluctuations in abundance but remained relatively stable, providing us with a benchmark against which we compared reproductive parameters to infer potential constraints on breeding flycatchers. Higher nest success compounded with less severe temporal constraints may explain the stable population trends in Warner Valley.

Population Trends

Flycatcher abundances were lower in the South Tahoe region than in our other study areas at the beginning of the study, and although our own surveys and those conducted by others have detected individuals in adjacent small meadows, the total number of flycatchers detected in the region in recent years never exceeded 5 males. In the South Tahoe region, residential and commercial development starting >100 years ago removed or altered many large (>100 ha) meadow systems known to support flycatchers (Ray 1903, 1913; Raumann and Cablk 2008). If still intact, these large systems likely could have served as source habitat to the current population (Pulliam 1988, Donovan and Thompson 2001, Kus et al. 2003, Sogge et al. 2003), but we did not detect any breeding activity during intermittent surveys at these larger meadows. The majority of large meadows that still exist in the region have degraded hydrologic and vegetative conditions, and the remaining mesic, willow-dominated meadows tend to be of small or moderate size and support only a few (e.g., 1 to 3) territories per site. Many of the occupied meadows in the South Tahoe region are adjacent to densely populated residential or recreation areas that can considerably affect ecosystem functions (Schlesinger et al. 2008). Other occupied meadows are scattered at higher elevations, where the effective breeding season is short. These small meadows were unable to sustain a local population of flycatchers, likely because of high predation rates coupled with stochastic events, such as late-spring storms in the late 1990s. Although it is common for flycatcher distributions within populations to be scattered among small patches of habitat (Kus et al.

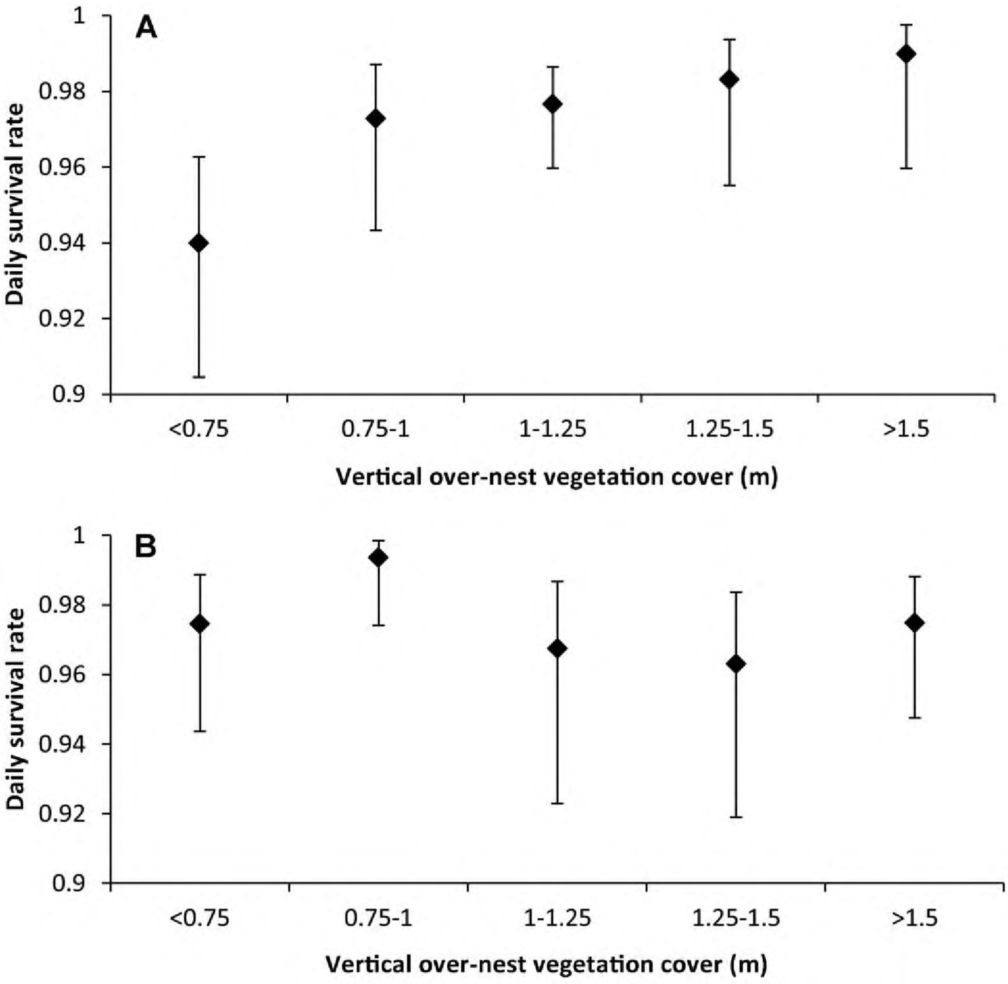

FIG. 10. Observed values and 95% confidence intervals of the effect of over-nest cover in relation to (A) small and (B) large meadows on daily nest survival rate of Willow Flycatchers in the Sierra Nevada, California, 2005–2007. We estimated values using the logistic-exposure model based on grouping the data into height interval.

2003, Sogge et al. 2003), the presense of larger habitat patches with extensive suitable breeding habitat is necessasry for the persistence of a population through the production of individuals available to disperse to smaller, adjacent areas (Pulliam 1988, Kus et al. 2003, Sogge et al. 2003). This pattern is consistent with the distribution of meadows in the Truckee region, where small meadows supporting ≤3 territories were interspersed with several meadows ≥100 ha believed to support the highest number of flycatcher territories in the Sierra Nevada (Sanders and Flett 1989, Green et al. 2003). In the Truckee region, abundance of flycatchers declined across the years of our study, but there were considerable annual fluctuations in territory and female numbers within meadows as birds moved among available meadows in the study region.

When site fidelity and regional return rates are high, as in our study system, low reproductive success across a region will interrupt dispersal dynamics and result in local population reductions (Donovan and Thompson 2001, Hoover 2003). Our estimate of natal philopatry at the site scale (i.e., meadow) was higher than estimates reported for flycatchers elsewhere (Sedgwick 2004, Paxton et al. 2007), and returning juveniles dispersed within a short distance (<8 km) from natal locations. Low reproductive success in the

South Tahoe region suppressed juvenile recruitment within the region and potentially reduced breeding-site fidelity and adult return rates, especially of female flycatchers. Our estimates from the Truckee region for breeding (adult) site fidelity and adult return rates were higher than estimates for flycatchers elsewhere in their range (Sedgwick 2004, Paxton et al. 2007). Breeding adult flycatchers might use information from previous breeding seasons to determine whether to disperse to different sites in subsequent breeding seasons, which is a common pattern observed in flycatchers (Sedgwick 2004, Paxton et al. 2007) and in other species (Hoover 2003, Pärt and Doligez 2003).

The proportion of unmated males increased in the South Tahoe region as females failed to return in subsequent years, even though site persistence was maintained by a few returning males. Although variable among years, the proportion of unmated males in the Truckee region also increased. In several small meadows in the Truckee region, we observed declines in site occupancy by females, while a single territorial male consistently returned for several years, which suggests that females were more likely to disperse from areas with low reproductive success—a common pattern exhibited in passerines. Populations with estimates of >30% of unmated males are considered to be at a higher risk of extinction (Dale 2001), and estimates from the South Tahoe region and several meadows in Truckee exceeded this proportion. Given these dispersal dynamics, the likelihood of repopulation of the South Tahoe region will depend on long-distance dispersal of individuals from other population centers. However, we observed little movement of individuals between the South Tahoe and Truckee regions, indicating that the distance to larger meadows in the Truckee region (e.g., Perazzo meadows) was too great for dispersing individuals to sustain a population of flycatchers in the South Tahoe region. Although populations fluctuated, uncertainties about the persistence of flycatchers in the Truckee and South Tahoe regions are warranted, especially if current habitat quantity and quality continue to decline.

Populations of flycatchers may be stable or increasing in Warner Valley, which is consistent with the results of other studies (King and King 2003, Humple and Burnett 2004). Surveys conducted in Warner Valley from 1998 to 2001 estimated 30 to 35 territorial males (King and King 2003), which is in accordance with our abundance estimates. Territory densities were twice as high as those in the Truckee region and almost 4× the density in the South Tahoe region (Mathewson 2010). The meadows in the Warner Valley region differed in their hydrology and vegetative community and were at lower elevation than our long-term study regions. These meadows experienced a longer and earlier growing season, without the constraints of cold early-season temperature and early and late-summer storms (Ratliff 1985). Furthermore, constraints imposed by lowered water tables across the season on vegetative growth might be relaxed at lower elevations because of earlier onset of reproductive stages of the vegetation (Loheide et al. 2009). Historically, this region did not experience the level of human-induced disturbances that degraded conditions in meadows in the Lake Tahoe Basin and in the Truckee region (Lake Almanor Watershed Assessment Report 2007).

FACTORS INFLUENCING REPRODUCTIVE SUCCESS

Our fecundity estimates were at or below the reported fecundity values for flycatchers elsewhere, including values of 0.99–2.0 in Arizona (Davidson and Allison 2003, Paxton et al. 2007); 1.44 at Kern River, California (M. Whitfield unpubl. data, cited in Stoleson and Finch 2003); and 1.45–2.13 in Oregon (Altman et al. 2003). In a 10-year study on flycatchers at two large study sites in Arizona, Paxton et al. (2007) estimated mean annual fecundity of 1.6 and 2.0 fledglings adult female^{-1}, estimates that are comparable to our minimum and maximum estimates in the Warner Valley region. Although fecundity estimates from our Truckee region fluctuated around 1.5 fledglings adult female^{-1}, our fecundity estimates were likely biased high because we used the maximum number of potential fledglings from a nest to standardize our estimates. By using this standard, we did not account for mortality of young during the last few days of nesting or during the first few days postfledging, which may be considerable in some years (Vormwald et al. 2011). Determining whether fecundity estimates are adequate for sustaining a population requires estimates of juvenile and adult survival for calculating population growth rates (Faaborg et al. 2010b); preliminary demographic analysis of our study populations suggested that fecundity in the Truckee region would need to increase for the flycatcher population to maintain stability or experience population growth (Mathewson 2010).

Weather.—Weather appeared to influence flycatchers through a direct influence on timing of nest initiation and, thus, length of the breeding season. Low temperatures in June were correlated with delayed initiation of the breeding season and reduced opportunities for renesting. Flycatchers are long-distance migratory birds and are predominantly insectivorous (Wiesenborn and Heydon 2007). Low temperatures or late-season storms likely delay initiation of nesting because of limitations on the activity and availability of insects (Harper and Peckarsky 2006, Finn and Poff 2008), delayed onset of leaf eruption in willow and other riparian shrubs (Briskie 1995), and increased physiological demands resulting from reduced temperatures and resources. The nesting season for flycatchers is already constrained because of migratory behavior; the birds are late-spring migrants, and when flycatchers initiate nesting many co-occurring species are already 2 to 4 weeks into breeding. Furthermore, they initiate fall migration earlier than other species (Sanders and Flett 1989, Yong and Finch 1997). Single-brooded species with relatively short breeding seasons are also constrained by necessary preparation for fall migration (Marshall et al. 2002, Murphy 2004).

Flycatchers are further constrained by both cold fronts from the north and monsoonal thunderstorms from the south at the end of the breeding season, but flycatchers in lower elevations such as Warner Valley do not experience storms until later in August and are not affected as often by monsoonal thunderstorms that concentrate at higher elevations. On several occasions, we found nestlings dead in a nest following cold fronts in early August in the Truckee and South Tahoe regions. Vormwald et al. (2011) found lower nest success and postfledging survival in 2009 following a cold front in early August in the Truckee region. Results from a study on relative insect abundances at our study sites detected significant decreases in insects at the beginning of August and that temperatures at low-elevation sites might not be so cold that they adversely affect insect populations (H. A. Mathewson unpubl. data).

The primary limitations on renesting opportunities were associated with timing of nest initiation and failure of the initial nest attempt. Nesting delays reduced the likelihood of renesting if the previous nest failed. Our study indicated that mid-July might be the maximum date for a failed nest attempt after which females do not attempt renesting. This suggests that seasonal delays in the onset of the nesting season may have strong effects on reproductive success. Simulation models indicate that limiting nesting attempts to 1 might make bird populations unsustainable even if nest success is high (Donovan and Thompson 2001). Compared with the South Tahoe and Truckee regions, Warner Valley had longer periods of nest initiation, higher nest success and fecundity, and lower parasitism rates. A longer breeding season is likely due to elevational differences among study regions; breeding seasons in the lower-elevation northern sites started earlier and lasted longer. Even a few days' difference in nesting can have profound effects on reproductive success. For example, Marshall et al. (2002) demonstrated that a difference of 5 days in nest initiation might interact with high predation or parasitism rates and cause a reduction in fecundity of 0.25 young female^{-1}.

Brown-headed Cowbird parasitism.—Parasitism was limited to a few sites in our study regions; however, these sites supported some of the highest abundance of flycatcher territories in the region (i.e., Perazzo meadows; Green et al. 2003). Parasitism rates were high in our South Tahoe region compared with those in other species at high elevations (Purcell and Verner 1999, Smith et al. 2005, Borgmann and Morrison 2010). Parasitism rates for a population of flycatchers in southern California would need to be ≤10% for the population to experience growth (Uyehara and Narins 1995, Whitfield et al. 1999). Although parasitism rates were low in several of our study years, parasitism should not be dismissed as a potential limiting factor on flycatchers without further investigation of the additive effect that brood parasitims can have with other limiting factors such as increased predation risk (Rothstein et al. 2003; but see Kus 2002).

As our results indicate, flycatchers in this region are limited in their number of nesting attempts because of temporal constraints; thus, parasitism of any single nest can greatly affect the reproductive success of a nesting female. Furthermore, low reproductive success might influence site fidelity by breeding adults to the extent that high parasitism rates in a meadow would result in local extirpation of nesting flycatchers (Hoover and Reetz 2006). Increased parasitism rates are positively associated with livestock grazing (Goguen and Mathews 2001) and proximity to residential areas (Borgmann and Morrison 2010), so the persistence of flycatcher populations in these regions will rely on management practices that can counteract the negative effects of these land uses.

Nest survival.—Nest predation was the primary cause of nest failure in our population, and we found considerable annual variation in nest survival, a pattern observed in many long-term studies of passerines (Sillett et al. 2000, Holmes and Sherry 2001, Knutson et al. 2007). Mammals are likely the primary nest predators in our study regions (Cain 2001). We detected Deer Mice (*Peromyscus maniculatus*), Short-tailed Weasels (*Mustela erminea*), Long-tailed Weasels (*M. frenata*), Douglas Squirrels (*Tamiasciurus douglasii*), and chipmunks (*Tamias* spp.) at or near songbird nests in our study sites. Other regularly detected nest predators in our study regions include accipiters (*Accipiter* spp.), Steller's Jays (*Cyanocitta stelleri*), and garter snakes (*Thamnophis* spp.) (Cain et al. 2003). Brown-headed Cowbirds also are common and considered a nest predator because they remove eggs or nestlings from other species' nests to induce females to renest (Arcese et al. 1996, Hoover and Robinson 2007).

Nest survival analyses indicated that most flycatcher nests failed during the egg-laying and nestling periods. Nest survival was lowest during egg laying, when nest attendance by adults is low (Soroka and Morrison 2005), ostensibly because nest predators quickly locate nests placed in poor locations (Sedgwick and Iko 1999, Martin et al. 2000). Nest survival was high once incubation began but steadily declined until approximately day 6 of the nestling period. Increases in predation from hatch until approximately halfway through the nestling period are common for many passerines (Grant et al. 2005, Purcell 2006) and are commonly attributed to changes in adult and nestling behavior (Soroka and Morrison 2005). Given that over-nest concealment was a strong predictor of nest survival in large meadows in our system, we suggest that high shrub cover might offset negative effects of increased parental activity (Weidinger 2002) during the vulnerable early-nestling stage. Some of the common nest predators in our study area, such as weasels, snakes, raptors, and Brown-headed Cowbirds, use visual cues for foraging (Fitzgerald 1977, Uyehara and Narins 1995). Thus, increasing over-nest cover might improve nest success.

Our results did not support our prediction that annual snowfall or summer temperatures would directly influence nest survival. Instead we found that finer-scale variables, such as within-season nest age, meadow size, and over-nest vegetation cover, were better predictors of variation in individual nest survival. Our inclusion of weather variables as predictors was based on the assumption that snowfall or temperatures influence meadow wetness, an assumption that we did not directly test here. Because our study included multiple meadows with varying land-use history and hydrological characteristics, the annual variation in weather patterns likely did not contribute to meadow wetness consistently across all sites. Furthermore, weather patterns have far more influences on the system than simply the amount and duration of water across meadows that might influence the predator community. Other long-term studies have shown that the predators themselves are limited by multiple factors, such as food supply, that are, in turn, influenced by variation in weather patterns.

These results do not negate the overall premise that standing water in meadows affects predation because the nestling period, which our results suggested influenced nest survival, coincides with the hottest periods of the summer, when water is reduced or no longer present to impede access to riparian shrubs by some mammalian predators (Cain et al. 2003, Cocimano et al. 2011). Concurrent research conducted during our study indicated that the primary nest predators were chipmunks and squirrels, and they are significantly more active in meadows with less water cover (Cain 2001, Cocimano et al. 2011) and are generally associated with drier, forested habitats. Consistent with our result that over-nest concealment influences nest survival in large meadows, snowfall and precipitation might still influence nest survival indirectly through inter-annual changes in vegetative age and structure. 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). Flycatchers in our Sierra Nevada study area nest almost exclusively in willows or alders (King and King 2003, present study), although they have shown more flexibility in nesting substrates in other Sierra study areas (McCreedy and Heath 2004). Willows are intolerant of drought and rely on groundwater rather than shallow soil water for establishment, growth, and reproduction (Stromberg et al. 1996, Lite and Stromberg 2005, Hultine et al. 2010). The effects of drought conditions on willows may not be evident until the water table is low; in some systems, this threshold may require more than 1 year of reduced water supplies (Horton et al. 2001, Rood et al. 2003, Hultine et al. 2010). During drought conditions, limited water availability can result in considerable reduction in vegetative cover (Lite and Stromberg 2005).

In the Truckee region, the effect of over-nest cover on daily nest survival was minimal in small meadows, but it positively influenced daily nest survival in large meadows. Large meadows (>70 ha) in our system have expanses of large, open areas of grassland, often with water sources and shrubs concentrated toward the center of the meadow or along one side. In large meadows, riparian shrubs provide cover for mammalian predators that avoid open grassland areas because of susceptibility to their own predators. For example, short-tailed and long-tailed weasels are significantly more active in larger meadows in our study region (Cain et al. 2003). 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). In smaller meadows, riparian shrubs cover the majority of the meadow extending to the forest edge, thus providing continuous cover for movement of terrestrial predators across the forest–meadow boundary. This continuation of vegetative cover might reduce concentrations of mammals within the shrub matrix. Additionally, extensive, open grasslands in the larger meadows might enhance activity and abundance of some nest predators, such as snakes that concentrate at grassland and shrub interfaces (Davison and Bollinger 2000) or Brown-headed Cowbirds (Brodhead et al. 2007). Functionally, the grassland–riparian shrub ecotones represent an edge effect that is reduced in smaller meadows where riparian shrubs are continuous with the surrounding forest. Inconsistent with our prediction that the forest–riparian shrub interface would negatively influence nest survival (Batary and Baldi 2004), we found no effect of distance to forest edge on nest survival. In small patches, edge effects may prevail throughout the patch so that distance to edge would not explain variation in nesting success (Thompson et al. 2002).

Our study demonstrates the necessity of long-term monitoring and comparative analyses for examining trends in populations and evaluating factors constraining reproductive productivity. It is evident from our results that the effects of weather patterns on breeding phenology and productivity should be accounted for when studying species in these montane meadow systems, as demonstrated in the mountainous regions in northeastern North America (Holmes 2011). Although the extreme winters of 1998 and 1999 influenced both the South Tahoe and Truckee study regions, our results demonstrate the inability of a small population to rebound following stochastic events leading to the near extirpation of flycatchers in that region. Abundances in the Truckee region were similarly depressed following these winters but remained at a sustainable level for several years until drought conditions began in 2006, demonstrating how two different extremes in weather patterns can similarly influence populations. Given these observed patterns, the ambiguity in our nest survival analyses and the absence of a general relationship with linear changes in weather parameters is not surprising. Future research on factors that influence reproductive success in riparian, intermountain regions should consider the complexity of the system that we demonstrated here and include consideration of synergistic effects of weather and habitat characteristics on population dynamics.

Management and Conservation Implications

Loss and degradation of montane meadows, specifically the riparian shrub community, is the primary factor contributing to population declines of flycatchers in our study regions. Dispersal dynamics indicated that suitable breeding habitat, characterized by dense riparian shrubs, must be available across the landscape for persistence of populations. Even without the loss of montane meadows, degradation of the habitat within them results in increased nest predation, which disrupts dispersal dynamics through reduced juvenile recruitment and adult site fidelity. Reversing population declines or maintaining population stability of flycatchers in these study regions depends on active restoration of hydrological processes to montane meadows. In our study regions, degradation of riparian habitat is of particular concern in larger meadows where historical grazing, water diversions, urbanization, timber harvesting, and mining have resulted in extensive gullying and subsequent reduction in groundwater tables that reduce establishment and growth of riparian vegetation (Auble et al. 1994, Stromberg et al. 1996, Stromberg 2001, Lite and Stromberg 2005). Land managers in the Sierra Nevada are thus challenged with the need to improve current conditions in montane meadows, riparian areas, and surrounding landscapes to improve nest survival rates and to buffer against negative effects of parasitism and constraints imposed by elevation factors and weather events (Horton et al. 2001, Anders and Post 2006, Loheide et al. 2009).

Given the dispersal patterns and high natal- and breeding-site fidelity of flycatchers in our study area, restoration of montane meadows proximate to existing populations should be prioritized over isolated sites. It is likely that a behavioral mechanism, such as conspecific attraction or postbreeding prospecting, contributes to the landscape-scale clustering of flycatcher territories observed in our study regions (H. A. Mathewson unpubl. data).

Reducing disturbances (i.e., grazing and recreation) to nesting birds through the end of July will positively influence reproductive success. In some grazing regimes in meadows in the Sierra Nevada, livestock are introduced around mid-July, which has been presumed adequate to allow flycatchers to breed undisturbed. However, our results suggested that the end of July remained a critical time because of increased failure rates of nestlings and renesting attempts. Vegetative concealment influences nesting success and browsing, and tunneling into willows by cattle reduces foliage and opens up the willow matrix (Brookshire et al. 2002). Poorly managed livestock grazing can reduce the ability of meadows to withstand flooding events by removal of streamside vegetation and can alter size and foliar density in mature willow stands, as well as reduce survival of seedlings (Auble et al. 1994, Stanley and Knopf 2002, Scott et al. 2003). Flycatchers in Oregon have experienced population increases when livestock were removed from sites following many years of season-long, intensive livestock grazing (Taylor and Littlefield 1986). Flycatchers have also recently reoccupied a site in Mono County after changes in water-diversion practices and the removal of livestock (McCreedy and Heath 2004). Alternatively, in Colorado riparian vegetation, flycatchers and other shrub-nesting bird populations were not significantly affected by light, late-season grazing (Stanley and Knopf 2002).

During the course of our study, western North America has experienced a considerable shift in weather patterns, most notably the shift from El Niño to La Niña in 2000 (Stewart et al. 2005). Prior to 2000, winter and spring snowfall was above the 50-year mean, but conditions shifted to below-average snowfall after 2000 (Roos 2008). Research indicates that weather patterns in the Sierra Nevada are shifting, and the direction of change will exacerbate preexisting factors that hinder the persistence of mesic conditions in montane meadows and other riparian systems. Specifically, human-induced disturbances have resulted in stream degradation, gullying, changes in plant communities, and encroachment of upland woody vegetation (Vale 1981, Scott et al. 2003, Opdam and Wascher 2004, Ewers and Didham 2006). Restoration and conservation activities should prioritize reducing human-induced disturbances and improving the hydrological and geomorphic processes conducive to maintaining high groundwater tables and mesic conditions for the duration of the dry summers typical of this region. Currently, restoration has begun at several meadows in the South Tahoe and Truckee regions. Continued monitoring of flycatchers in and adjacent to these sites is critically important for evaluating the effectiveness of restoration practices on flycatcher populations (Donovan et al. 2002).

Availability of habitat that promotes productivity is a primary factor limiting songbird populations (Faaborg et al. 2010b). Flycatchers, as well as numerous other species, depend on riparian systems in western North America. Restoration activities that manage for dense, continuous riparian vegetation in meadows will increase bird abundance and diversity (Sabo et al. 2005, Gardali et al. 2006) and may reduce predation pressure on nesting birds (Ellis et al. 2009). Improving conditions of riparian habitat may offset the limitations imposed by shortened breeding seasons at higher elevations and buffer against natural stochasticity in the environment.

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