

## SURVIVAL AND MOVEMENTS OF FLEDGLING WILLOW AND DUSKY FLYCATCHERS

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**Abstract.** Estimates of productivity usually ignore survival during the postfledging period, the time between a bird's leaving its nest and departure for migration or movement to an area for wintering. During the first 1–3 weeks after fledging, young birds are limited in mobility, making them vulnerable to fatality, especially from predation. To help fill this information gap, we examined the period of postfledging dependence of the Willow (*Empidonax traillii*) and Dusky (*E. oberholseri*) Flycatchers in the central Sierra Nevada, California. For fledglings we examined factors that influenced survival, movements, and habitat use and home-range size. We observed family groups daily during the postfledging dependence period and resighted individual band combinations. Fledglings' survival ranged from 46% to 76% and varied by year and species. Fledglings moved on average 45 m from the nest per day during the dependence period. We detected family groups in their natal meadows from 13 to 33 days. We detected Willow Flycatchers in riparian shrubs 94% of the time, along the upland forest edge for the remaining 6%. We detected Dusky Flycatchers in riparian shrubs 70% of the time, in upland forest for the remaining 30%. For both years of our study combined, mean 95% home-range sizes were  $1.80 \pm 1.44$  (SD) ha for the Willow Flycatcher and  $1.82 \pm 1.70$  ha for the Dusky Flycatcher. Mean 50% core areas were  $0.33 \pm 0.27$  ha for the Willow Flycatcher and  $0.38 \pm 0.44$  ha for the Dusky Flycatcher.

**Key words:** *Dusky Flycatcher, fledgling movements, habitat use, home range, postfledging, Willow Flycatcher.*

### Supervivencia y Movimientos de Volantones de *Empidonax traillii* y *E. oberholseri*

**Resumen.** Los estimados de productividad usualmente ignoran la supervivencia durante el periodo posterior al emplumamiento, el tiempo entre que un ave deja el nido y que parte en migración o se mueve a un área para invernar. Durante las primeras 1–3 semanas luego de emplumar, las aves jóvenes tienen una movilidad limitada, haciendo que sean vulnerables a una fatalidad, especialmente por depredación. Para ayudar a llenar este vacío de información, examinamos el periodo de dependencia posterior al emplumamiento en *Empidonax traillii* y *E. oberholseri* en la Sierra Nevada central, California. Para los volantones, examinamos los factores que influenciaron la supervivencia, los movimientos, el uso de hábitat y el tamaño del ámbito hogareño. Observamos diariamente grupos familiares durante el periodo de dependencia posterior al emplumamiento y realizamos observaciones repetidas de combinaciones individuales de anillos. La supervivencia de los volantones fluctuó entre 46% y 76% y varió por año y especie. Los volantones se movieron en promedio 45 m desde el nido por día durante el período de dependencia. Detectamos grupos familiares en sus prados natales desde 13 a 33 días. Detectamos la presencia de *E. traillii* en arbustos ribereños el 94% de las veces y a lo largo del borde del bosque en la zona alta no inundable el 6% restante. Detectamos a *E. oberholseri* en los arbustos ribereños el 70% de las veces y en las tierras altas no inundables el 30% restante. Combinando los dos años de nuestro estudio, los tamaños medios 95% del ámbito hogareño fueron  $1.80 \pm 1.44$  (DE) ha para *E. traillii* y  $1.82 \pm 1.70$  ha para *E. oberholseri*. Las áreas núcleo medias 50% fueron  $0.33 \pm 0.27$  ha para *E. traillii* y  $0.38 \pm 0.44$  ha para *E. oberholseri*.

## INTRODUCTION

Understanding population demography and factors that limit population growth are critical in conserving species with declining populations. Reproductive success affects population dynamics (Holmes et al. 1992, Johnson and Geupel 1996, Chase et al. 1997), but our ability to estimate actual

productivity is limited (Powell et al. 1999). Most studies of avian productivity have focused on nest success or number of young fledged, indices that do not capture all the components of productivity (Powell et al. 1999, Anders and Marshall 2005, Mattsson et al. 2007). Often productivity estimates do not include field-based estimates of survival during the

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postfledging period, defined as the time between a bird's leaving the nest and its departure for migration or settling into an area for winter (Anders et al. 1998). The first 1–3 weeks of the postfledging period are called the dependence period, when young rely primarily on their parents for food and protection. During the dependence period, young birds are somewhat limited in mobility, making them vulnerable to fatality, especially from predation (Anders et al. 1997, Naef-Daenzer et al. 2001, Yackel Adams et al. 2006). Regardless of the importance of the postfledging period, it is often regarded as the least understood component of the avian life cycle (Morton et al. 1991, Baker 1993, King and Belthoff 2001), and reliable estimates are scarce (Faaborg et al. 2010).

Our understanding of habitat selection by birds during nesting may not adequately represent habitat requirements for breeding as a whole because habitat use may change after the young leave the nest (Pagen et al. 2000, King et al. 2006, Vitz and Rodewald 2006). Predator avoidance (Anders et al. 1997, Naef-Daenzer et al. 2001) and food availability (Anders et al. 1998, Vega Rivera et al. 1998, Yackel Adams et al. 2006) are possible explanations for movement patterns and changes in habitat use reported after fledging. Several studies have examined movement of juveniles in forests (Anders et al. 1998, Pagen et al. 2000, Mitchell et al. 2010) and grasslands (Kershner et al. 2004, Yackel Adams et al. 2006, Berkeley et al. 2007, Suedkamp Wells et al. 2007), but little is known about species in wetlands and riparian systems.

Our goal was to investigate the period of postfledging dependence of two neotropical migrants that breed through much of the mountainous western United States: the Willow Flycatcher (*Empidonax traillii*), listed as endangered by the California Department of Fish and Game, and the Dusky Flycatcher (*E. oberholseri*). The Willow Flycatcher is a riparian obligate species whose population in California (Saracco and DeSante 2008) has declined primarily because of degradation and alteration of habitat, including the advent of the Brown-headed Cowbird (*Molothrus ater*; Green et al. 2003). In contrast, Dusky Flycatcher populations are increasing in California, likely because of silvicultural practices (Sedgwick 1993, Saracco and DeSante 2008). Although Dusky Flycatchers nest within meadows, they also nest widely in the forests of the Sierra Nevada. We worked with the Dusky Flycatcher to increase the sample size of postfledging movements and because we wondered if there are differences in movements and habitat use that might help explain why the abundance of the Dusky Flycatcher is apparently increasing while that of the Willow Flycatcher is decreasing.

We located fledglings daily to estimate their survival and to examine factors that influence survival, evaluated postfledging movements and habitat use, and estimated the sizes of postfledging flycatchers' home ranges. In the Sierra Nevada, Willow Flycatchers usually fledge after 14 or 15 days in the nest (Mathewson 2010), whereas Dusky Flycatchers usually fledge at ages from 15 to 17 days (Green et al. 2003, Cain and Morrison

2003). Fledglings of both species often remain together on the same perch near the nest for the first few days after leaving the nest. During the dependence period, fledglings' begging calls are common and especially intense when a fledgling is fed or an adult perches near a fledgling (Sedgwick 1993, 2000).

## STUDY AREA

We worked in six wet montane meadows (hereafter meadows) within the Little Truckee River drainage in Tahoe National Forest in Sierra County, California. These meadows are oriented north–south along the east side of the Sierra Nevada crestline at elevations between 1967 and 2013 m; they range in size from 24 to 106 ha. Willows (*Salix* spp.) constitute the majority of the riparian shrub community and are distributed along streams and in clumps scattered throughout the meadows. The meadows are surrounded primarily by lodgepole pines (*Pinus contorta*), but some stands of mountain alder (*Alnus tenuifolia*) and aspen (*Populus tremuloides*) grow along their edges (Bombay et al. 2003). During the past 10 years, these six meadows supported between 19 and 28 Willow Flycatcher territories each year (Mathewson 2010). Although the average number of territories is unknown, Dusky Flycatchers are common and nest in these meadows (Cain and Morrison 2003).

## METHODS

### NEST SEARCHING AND MONITORING

We located and monitored flycatcher nests during the breeding seasons (May through August) in 2008 and 2009. Using standard territory mapping techniques (Ralph et al. 1993), we followed flycatchers to provide a basis for nest searching. To minimize disturbance we located nests by observing behavioral cues of adults prior to searching the vegetation physically (Martin and Geupel 1993). We did not approach nests during the building stage, and we approached nests only after the female was away from the nest. We recorded the GPS coordinates (Garmin GPS 72, 3-m accuracy, Garmin, Ltd., Olathe, KS) of each nest and marked the location by placing colored flagging tape at least 6 m away. We checked nest contents every 3 to 5 days and recorded the number of eggs or nestlings until the nest failed or young fledged from the nest. Evidence of nest predation included missing eggs or missing nestlings that were less than 12 days old, too young to have fledged.

### BANDING AND RESIGHTING

On day seven to nine, we temporarily removed nestlings from the nest for banding. We marked all nestlings with a color-anodized U.S. Fish and Wildlife Service aluminum numbered band on the right leg and a double pin-striped color-anodized band (Koronkiewicz et al. 2005) on the left leg to create a unique combination of bands.

In several studies, postfledging songbirds have been equipped fledglings with radio transmitters (Anders et al. 1997,

Yackel Adams et al. 2001, Cohen and Lindell 2004, Berkeley et al. 2007, Suedkamp Wells et al. 2007), whereas in others the adults have been equipped with transmitters, used to locate the individually banded fledglings (Bayne and Hobson 2001, Rush and Stutchbury 2008). In 2008, we attempted to follow fledgling Dusky Flycatchers with radio transmitters. However, because nestlings equipped with transmitters frequently fledged prematurely because of handling or possible accidental ejection from the nest by the parents (see Mattsson et al. 2006), we decided to suspend our attempts (see details in Vormwald 2010). Locating fledglings without the use of radio telemetry lacks the rigor of the many unbiased locations telemetry yields, but it is a noninvasive alternative that can provide much useful information on juvenile birds (Lukacs et al. 2004, Mattsson et al. 2006). Using resighting to estimate survival may lead to missed observations of newly fledged young despite intense observation; however, Rush and Stutchbury (2008) reported a probability of resighting of 84% for the Hooded Warbler (*Wilsonia citrina*) and suggested observing fledglings for 4 full weeks to obtain accurate estimates of survival with this method. Willow and Dusky Flycatcher fledglings can be located relatively easily because of their loud begging calls throughout the dependence period. Therefore, we located and resighted all individuals daily to estimate survival.

#### POSTFLEDGING OBSERVATIONS

Starting on day 12–14, we observed flycatcher nests daily with binoculars to estimate date of fledging and nest outcome. If the young had not fledged yet (i.e., all nestlings still present in the nest), we returned the following day and continued daily visits until they fledged. Once the young fledged, we observed each family of flycatchers (adults and fledglings) for 30 min to 2 hr per day; the time varied because of logistical considerations (e.g., meadow wetness, shrub coverage). Observations took place between 06:00 and 18:00 to ensure that fledglings could be located visually.

To begin the observation period, we approached the nest area or the area of last detection and searched systematically, using visual and audio cues to locate flycatcher families. Upon first detecting a fledgling, we recorded its location and attempted to resight each fledgling in the family by its colored bands while also noting the number and sex (if known) of the adults caring for it. Once all individuals were resighted and at least 30 min had passed, we recorded a second GPS location where the group was last seen and noted the primary vegetation type used during the observation period. If a complete brood of fledglings was seen together on a branch, we counted it as a resighting of each individual.

We continued daily visits to locate the family until we had not detected the young in the natal meadow for at least 3 consecutive days, as long as the young were old enough to have reached the independence stage ( $\geq 2$  weeks). After this point we assumed that the young were either independent of their parents and ceased begging calls or they dispersed out

of the natal meadow. If during a visit we detected adults but not fledglings, we returned for the next 3–5 days to try to locate fledglings. If we did not detect adults or fledglings, we expanded our searches outward from the nest area until we found them or until we surveyed the natal meadow and surrounding forest edge (i.e., 50–100 m into forest edge, according to the topography) sufficiently. In this case, if we failed to detect any members of the family after 3–5 days, we ceased our searches.

#### DATA ANALYSIS

*Fledgling survival.* We analyzed each fledgling's recapture history with Cormack–Jolly–Seber (CJS) models generated in program MARK (White and Burnham 1999). For survival analysis, we constructed a set of candidate models representing our hypotheses of the causes of variation in fledgling survival. We considered (1) year, which we included because annual variation is a common source of variation in survival rates and could result from factors such as changes in weather patterns and fluctuations in predator or prey densities (Yackel Adams et al. 2006, Schmidt et al. 2008); (2) ordinal date of fledging, which we included to account for seasonal effects (Anders et al. 1997, Naef-Daenzer et al. 2001); (3) weekly age class (Anders et al. 1997); and (4) brood size prior to fledging, which we included to test for any possible confounding effects on fledgling survival. As brood size increases, the rate at which each chick is fed may decrease, which could result in lower survivorship. In addition, a larger and therefore louder family may attract more attention from predators, lowering survivorship. We used capture histories that included 21 intervals (days) for the Willow Flycatcher (Mathewson 2010) and 28 intervals (days) for the Dusky Flycatcher (Cain and Morrison 2003); the intervals differ because Dusky Flycatchers typically nested earlier. Because brood-level factors could influence survival probability, we recalculated estimates post hoc by randomly selecting a single fledgling per brood and compared its survival rate to that of the complete brood with CONTRAST (Hines and Sauer 1989). We found no significant differences (all  $P > 0.17$ ) in survival rates; therefore, we present estimates from the complete dataset.

*Postfledging movements and habitat use.* We calculated the mean linear distance each family moved from the nest site per observation period from the GPS waypoints recorded for the fledglings' daily locations. We recorded waypoints in the Universal Transverse Mercator (UTM) system, and we subtracted each of the coordinates for the first detection of the observation period from the UTM coordinates of the nest. We fit the values into the equation  $D = (A^2 + B^2)^{1/2}$ , where  $A$  represents the easting,  $B$  represents the northing, and  $D$  is the distance between the waypoint and the nest.

To evaluate habitat use of family groups after the young fledged, we projected fledglings' locations onto aerial digital color ortho-quarter quadrangle images in a geographic information system (GIS; National Agricultural Imagery Program

2005, U.S. Dept. of Agriculture; ArcGIS 9.3, ESRI, Redlands, CA). The three major vegetation types in our study area are riparian shrub community, upland forest, and mountain shrub steppe. We determined the percentage of each vegetation type used by each family by classifying each location by vegetation type, then dividing the number of locations in each vegetation type by the total number of locations for that family.

*Postfledging home ranges.* We defined home range as the area used by a family group during the postfledging dependence period. To calculate home ranges (95% of the utilization distribution) and core areas (50%), we used the fixed-kernel method in Home Range Tools for ArcGIS (Rodgers et al. 2005) in ArcGIS version 9.3 (ESRI, Inc., Redlands, CA). The fixed-kernel method is preferred over other home-range methods because it calculates a utilization distribution that represents the intensity of use, or the relative amount of time at a location (Van Winkle 1975, Kernohan et al. 2001), and it produces less biased results (Worton 1995, Seaman and Powell 1996, Seaman et al. 1999). We restricted our sample to those family groups with  $\geq 30$  detections because simulation research has suggested that 30 is the minimum sample size required for stable range estimates by kernel estimators (Seaman et al. 1999).

Choosing an appropriate smoothing parameter (i.e., bandwidth) is the most important step in deriving a kernel density estimator (Worton 1989), but there is no agreement on how to approach this problem (Barg et al. 2005). The smoothing parameter ( $h$ ) determines the spread of the kernel that is centered over each observation. An automated method of choosing a value for  $h$  is to use the optimum value with reference to a known standard distribution (i.e.,  $h_{ref}$ ) (Worton 1989, 1995). We used the " $h_{ref}$ " method for smoothing because it is effective if the underlying utilization distribution is unimodal and our family groups generally remained around a main center of activity, straying to few outside points (Worton 1995).

We considered the biological independence of our location data as more relevant to our study's objectives than achieving statistical independence (de Solla et al. 1999, Barg et al. 2005). Addressing autocorrelation by subsampling may have eliminated biologically important information. We consider our sampling design to have achieved biological independence of sampling points because we recorded location points at 30-min intervals, twice a day, for at least 15 days. These intervals allowed the family group to traverse its utilization range (Lair 1987, de Solla et al. 1999, Barg et al. 2005).

## RESULTS

### FLEDGLING SURVIVAL

*Willow Flycatcher.* In 2008, we monitored 13 Willow Flycatcher nests, eight (62%) of which fledged at least one young. We banded 21 nestlings and resighted 17 (81%) of the fledglings on multiple days ( $\bar{x} = 10 \pm 2.5$  SD, range 5–14) throughout the dependence

period. Two individuals were never resighted (although their siblings were), another was resighted for only 3 days after fledging even though its sibling was resighted on multiple days, and a fourth fledgling was last resighted 2 days after fledging but was unable to fly and appeared to be injured. In addition, one of the fledglings was resighted 8 days after fledging but was unable to fly, so we did not include it in any movement or habitat analyses. On the basis of this information, we estimated that 16 of the 21 (76%) fledglings survived the dependence period.

In 2009, we monitored 21 nests, five (24%) of which fledged at least one young. We banded 13 nestlings and resighted 6 (46%) of the fledglings on multiple days ( $\bar{x} = 6 \pm 2.0$ , range 4–9) throughout the dependence period. In one nest, on day 15 of the nestling period, one nestling was found dead, and the other two were never detected. At a second nest the young fledged, and one was seen 2 days after fledging, but none of the three fledglings was ever detected again. At a third nest one fledgling was never resighted out of the nest although its sibling was resighted on multiple days. On the basis of this information, we estimated that 6 of the 13 fledglings (46%) survived the dependence period.

We found that a model with a time-dependent variation by week (7 days) in survival probability and a constant recapture probability best fit the data (Table 1, model 1). Models including covariates of year, brood size, and ordinal date of fledging were less supported (Table 1, models 4–6). The results of the best-fitting model indicated that fledgling survival increased slightly between the first and second weeks and then declined sharply in the last week monitored (Table 2).

*Dusky Flycatcher.* In 2008, we monitored 50 Dusky Flycatcher nests, 25 of which successfully fledged at least one young. We banded 49 nestlings from 18 successful nests and resighted 33 (67%) of the fledglings on multiple days ( $\bar{x} = 11.2 \pm 4.5$ , range 2–19) throughout the dependence period. Seven fledglings were never resighted or detected out of the nest, and six were each resighted once on the first day they fledged but then never resighted or detected again. Two fledglings were found dead from an unknown cause, and one was found in an underground burrow (see below). In addition, one of the fledglings was resighted twice, the last time on day 5, but it was

TABLE 1. Model selection for the effects of time, year, brood, and ordinal date of fledging on the postfledging survival of Willow Flycatchers, Sierra Nevada, California, 2008–2009. Effective sample size = 260.

| Model                                   | $\Delta AIC_c$    | weight | $K$ |
|---|-------------------|--------|-----|
| 1 Weekly survival, constant recapture   | 0.00 <sup>a</sup> | 0.51   | 3   |
| 2 Weekly survival, early/late recapture | 0.79              | 0.34   | 4   |
| 3 Weekly survival, weekly recapture     | 2.43              | 0.15   | 5   |
| 4 Survival (year), constant recapture   | 23.48             | 0.00   | 3   |
| 5 Survival (brood), constant recapture  | 29.47             | 0.00   | 3   |
| 6 Survival (fledge), constant recapture | 29.49             | 0.00   | 3   |

<sup>a</sup>Lowest value of  $AIC_c = 645.75$ .



TABLE 2. Weekly survival and recapture probabilities for Willow Flycatchers during the 21-day postfledging period, Sierra Nevada, California, 2008 and 2009.

| Days postfledging | Survival probability | 95% CI    | Recapture probability | 95% CI    |
|-------------------|----------------------|-----------|-----------------------|-----------|
| 1–7               | 0.95                 | 0.90–0.97 | 0.56                  | 0.50–0.61 |
| 8–14              | 1.00                 | 0.99–1.00 | 0.56                  | 0.50–0.61 |
| 15–21             | 0.78                 | 0.67–0.86 | 0.56                  | 0.50–0.61 |

never resighted or detected again even though its two siblings were resighted on days 16 and 18, respectively. On the basis of this information, we estimated that 32 fledglings (65%) survived the dependence period.

In 2009, we monitored 48 nests, of which 30 fledged at least one young. We banded 55 nestlings from 18 successful nests and resighted 38 (69%) of the fledglings on multiple days ( $\bar{x} = 11.9 \pm 5.2$ , range 2–22) throughout the dependence period. Eight individuals were never resighted out of the nest, and nine were seen only once out of the nest but not after 2 days postfledging. In addition, one individual was resighted 4 days postfledging but was unable to fly and was never detected again. From this information, we estimated that 37 of the 55 fledglings (67%) survived the dependence period.

Of the six models evaluated, we found that a model with a time-dependent variation by week (7 days) in survival and recapture probabilities was the one with lowest AIC value (Table 3; model 1). Models including covariates of year, brood size, and ordinal date of fledging had much higher AIC scores (Table 3, models 4–6). The results of the best-fitting model indicated that fledgling survival was lowest during the first week after fledging and increased during the second and third weeks (Table 4).

#### POSTFLEDGING MOVEMENTS AND HABITAT USE

**Movements.** In 2008, we located and followed seven families of the Willow Flycatcher for an average of  $18.7 \pm 1.70$  days (range 16–21) in the natal meadow (Fig. 1). The average daily linear distance moved by those family groups from the nest site was  $48 \pm 51$  m (Table 5; Fig. 2). Of the Dusky Flycatcher, we located 18 families for an average of  $21.4 \pm 5.4$  days (range 6–28) in the natal meadow (Fig. 1). The average linear distance moved by those family groups from the nest site was  $45 \pm 43$  m (Table 5; Fig. 3).

In 2009, we located and followed three Willow Flycatcher families for an average of  $14.7 \pm 0.58$  days (range 14–15) in the natal meadow (Fig. 1). The average daily linear distance they moved from the nest site was  $23 \pm 18$  m (Table 5; Fig. 2). We followed 13 families of the Dusky Flycatcher for an average of  $22.1 \pm 5.3$  days (range 13–33) in the natal meadow (Fig. 1). The average linear distance they moved from the nest site was  $45 \pm 45$  m (Table 5; Fig. 3).

**Habitat use.** In 2008, we followed seven Willow Flycatcher families for a total of 234 locations ( $\bar{x} = 33.4 \pm 2.7$ , range 30–38), of which 220 (94%,  $\bar{x} = 31.4 \pm 3.6$ , range

TABLE 3. Model selection for the effects of time, year, brood size, and ordinal date of fledging on the postfledging survival of Dusky Flycatchers, Sierra Nevada, California, 2008–2009. Effective sample size = 260.

| Model                                     | $\Delta AIC_c$    | weight | $K$ |
|---|-------------------|--------|-----|
| 1 Weekly survival, weekly recapture       | 0.00 <sup>a</sup> | 0.97   | 8   |
| 2 Weekly survival, constant recapture     | 8.06              | 0.02   | 5   |
| 3 Weekly survival, early/late recapture   | 9.20              | 0.01   | 6   |
| 4 Survival (year), weekly recapture       | 34.78             | 0.00   | 6   |
| 5 Survival (brood), weekly recapture      | 35.63             | 0.00   | 6   |
| 6 Survival (fledgedate), weekly recapture | 35.63             | 0.00   | 6   |

<sup>a</sup>Lowest value of  $AIC_c = 2281.26$ .

TABLE 4. Weekly survival and recapture probabilities for Dusky Flycatchers during the 28-day postfledging period, Sierra Nevada, California, 2008–2009.

| Days postfledging | Survival probability | 95% CI    | Recapture probability | 95% CI    |
|-------------------|----------------------|-----------|-----------------------|-----------|
| 1–7               | 0.94                 | 0.91–0.95 | 0.55                  | 0.50–0.59 |
| 8–14              | 0.99                 | 0.97–0.99 | 0.67                  | 0.62–0.71 |
| 15–21             | 0.95                 | 0.92–0.97 | 0.59                  | 0.53–0.65 |
| 22–28             | 0.81                 | 0.72–0.87 | 0.54                  | 0.42–0.65 |

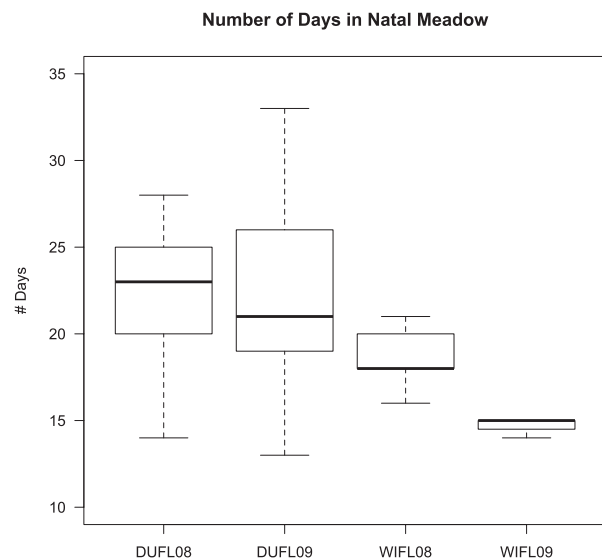


FIGURE 1. Median number and range of days family groups of the Willow (WIFL) and Dusky (DUFL) Flycatchers were detected after fledging in their natal meadows in the Sierra Nevada, California, 2008–2009.

26–38) were in riparian shrubs within the meadow; the remaining points were located in the upland forest surrounding the meadow. In 2009, we followed three Willow Flycatcher families for a total of 82 locations ( $\bar{x} = 27.3 \pm 3.1$ , range 24–30), of which 77 (94%,  $\bar{x} = 25.7 \pm 1.5$ , range 24–27) were

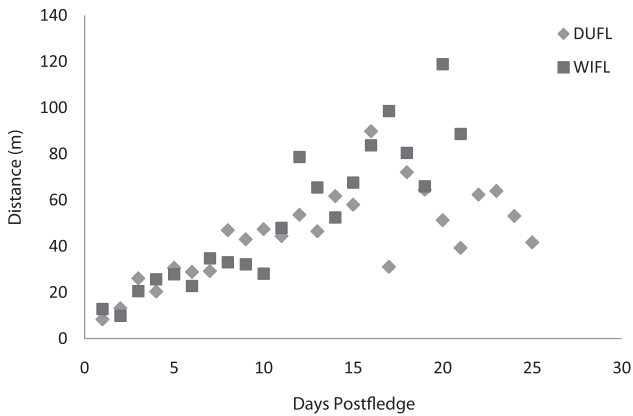


FIGURE 2. Average daily linear distance moved from the nest site after fledging by family groups of the Willow (squares) and Dusky (diamonds) Flycatchers, Sierra Nevada, California, 2008.

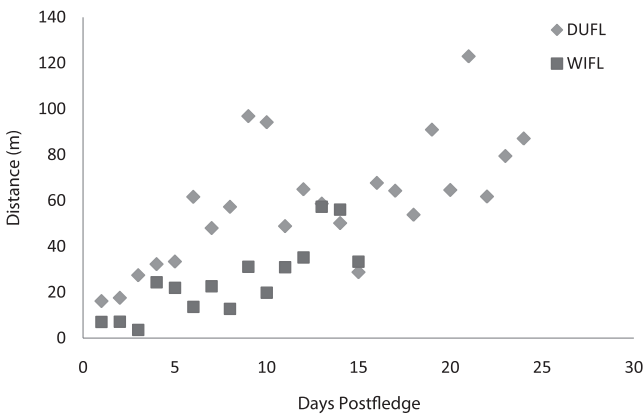


FIGURE 3. Average daily linear distance moved from the nest site after fledging by family groups of the Willow (squares) and Dusky (diamonds) Flycatchers, Sierra Nevada, California, 2009.

in riparian shrubs within the meadow; the remaining points were located in the upland forest surrounding the meadow. No family groups were detected in mountain shrub steppe in either year.

In 2008, we followed 12 Dusky Flycatcher families for a total of 432 locations ( $\bar{x} = 36 \pm 6.7$ , range 24–48), of which 300 (69%,  $\bar{x} = 25 \pm 11.2$ , range 11–48) were in riparian shrubs within the meadow; the remainder were in the upland forest surrounding the meadow. In 2009, we followed 11 Dusky Flycatcher families for a total of 456 locations ( $\bar{x} = 41.5 \pm 10.1$ , range 30–58), of which 325 (71%,  $\bar{x} = 29.6 \pm 12.7$ , range 6–56) were in shrubs within the meadow and the remainder were in the surrounding upland forest. No family groups were detected in mountain shrub steppe in either year.

TABLE 5. Range and average daily linear distances (m) moved from nest sites by family groups of postfledging flycatchers, Sierra Nevada, California, 2008–2009.

|                   | Year | n   | Min. | Max. | Mean | SD |
|-------------------|------|-----|------|------|------|----|
| Willow Flycatcher | 2008 | 119 | 1    | 261  | 48   | 51 |
|                   | 2009 | 41  | 1    | 61   | 23   | 18 |
| Dusky Flycatcher  | 2008 | 269 | 1    | 244  | 45   | 43 |
|                   | 2009 | 251 | 1    | 197  | 45   | 45 |

POSTFLEDGING HOME RANGES

We calculated postfledging home ranges and core areas for 10 Willow Flycatcher and 23 Dusky Flycatcher families in 2008 and 2009. In 2008 the average size of both species’ home ranges and core areas were similar, but in 2009 the contours for the Dusky Flycatcher were nearly twice as large as those for the Willow Flycatcher (Tables 6 and 7). For both years combined, mean 95% home-range sizes were  $1.8 \pm 1.4$  ha for the Willow Flycatcher and  $1.7 \pm 1.2$  ha for the Dusky Flycatcher. Mean 50% core areas were  $0.3 \pm 0.2$  ha for the Willow and  $0.4 \pm 0.4$  ha for the Dusky.

Both species central patterns were most often characterized by the clustering of points around the central natal area with occasional trips away from the central area in a nonlinear fashion. In 2008, however, one Dusky Flycatcher family, unlike the others we sampled, had multiple centers of activity. Therefore, the  $h_{ref}$  method of choosing a smoothing parameter resulted in an home-range estimate (7.6 ha) far larger than the other estimates in either year. Therefore, we adjusted  $h$  to 50% of  $h_{ref}$ , which gave a more reasonable estimate based on field observations.

DISCUSSION

Survival of fledgling Willow (0.740 over 21 days) and Dusky (0.716 over 28 days) Flycatchers was influenced by weekly age class since fledging. These estimates are higher than those for the Hooded Warbler (19% over 4 weeks; Rush and Stutchbury 2008), Lark Bunting (*Calamospiza melanocorys*) in Colorado (0.154 to 0.433 over 21 days; Yackel Adams et al. 2006), Wood Thrush (*Hylocichla mustelina*) in Missouri (0.423 over 8 weeks; Anders et al. 1997), and Western Bluebird (*Sialia mexicana*; 0.64 over 20 days; Wightman 2009) but similar to those for the Dickcissel (*Spiza americana*) in Missouri (0.563 over 30 days; Suedkamp Wells et al. 2007), Eastern Meadowlark (*Sturnella magna*) in Illinois (0.56–0.69 over 13 weeks; Kershner et al. 2004) and in Missouri (0.65 over 30 days; Suedkamp Wells et al. 2007), and Rose-breasted Grosbeak (*Pheucticus ludovicianus*; 0.62 over 21 days, Moore et al. 2010).

A model with a time-dependent variation by week in survival probability best fit the data for both species, with

TABLE 6. Range and average sizes (ha) of fixed-kernel estimates of 95% home ranges of family groups of postfledging flycatchers, Sierra Nevada, California, 2008–2009.

|                   | Year | <i>n</i> | Min. | Max. | Mean | SD  |
|-------------------|------|----------|------|------|------|-----|
| Willow Flycatcher | 2008 | 7        | 0.6  | 3.9  | 2.2  | 1.5 |
|                   | 2009 | 3        | 0.5  | 1.1  | 0.7  | 0.3 |
| Dusky Flycatcher  | 2008 | 12       | 0.5  | 4.6  | 2.0  | 1.5 |
|                   | 2009 | 11       | 0.4  | 2.9  | 1.3  | 0.9 |

low survival during the first week after leaving the nest, followed by increasing survivorship during the second week. Low survival during the first few days after leaving the nest is consistent with several studies of passerines (Anders et al. 1997, Kershner et al. 2004, King et al. 2006, Yackel Adams et al. 2006, Rush and Stutchbury 2008, Moore et al. 2010). Within the first few days after leaving the nest, fledglings are more susceptible to predators because of reduced flight capability and defense behaviors (Anders et al. 1997, King et al. 2006, Schmidt et al. 2008). Lower survival estimates in the last week of the period likely reflect dispersal from the natal grounds or the end of the dependence period, not a decrease in survivorship. Similarly, probabilities of resighting were lowest during the first week after young left the nest, when they were the least mobile and more difficult to locate, and increased with age as they became independent and dispersed out of our study sites. We did not find support for effects of year, brood size, or the ordinal date of fledging on survival of fledglings of either species.

Although our survival analysis did not support a year effect, for the Willow Flycatcher fledging rate and fledging survival were lower in 2009 than in 2008, while Dusky Flycatcher survival was similar in both years. It is difficult to compare the two years for the Willow Flycatcher because we were able to follow only three family groups in 2009. A cold front in early August 2009 with overnight temperatures below freezing may have been directly or indirectly responsible for a few late-stage nest failures or lower probabilities of detection of the family groups. The majority of Dusky Flycatchers had already fledged by this date and were likely not affected. Future studies could address how weather affects postfledging survival and movements, especially at high elevations where late summer cold fronts may occur. That is, if cold temperatures affect the Willow Flycatcher disproportionately, the average date of fledging of the Willow being later than that of the Dusky Flycatcher could explain, in combination with other negative factors (e.g., meadow drying, overall habitat loss), why the former is unable to maintain stable populations in the Sierra Nevada.

Flycatcher fledglings gradually moved away from the nest area during the dependence period, suggesting that resources were readily available. As expected, distance moved from the nest increased with age as young become more

TABLE 7. Range and average sizes (ha) of fixed-kernel estimates of 50% core areas of family groups of postfledging flycatchers, Sierra Nevada, California, 2008–2009.

|                   | Year | <i>n</i> | Min. | Max. | Mean | SD  |
|-------------------|------|----------|------|------|------|-----|
| Willow Flycatcher | 2008 | 7        | 0.1  | 0.9  | 0.4  | 0.3 |
|                   | 2009 | 3        | 0.1  | 0.2  | 0.1  | 0.1 |
| Dusky Flycatcher  | 2008 | 12       | 0.1  | 2.2  | 0.5  | 0.6 |
|                   | 2009 | 11       | 0.1  | 0.6  | 0.2  | 0.2 |

mobile and began feeding themselves, but movements back to the nest site were also observed. Increasing distance from the nest is well documented in studies of the Eastern Meadowlark (Kershner et al. 2004), Western Bluebird (Wightman 2009), Dickcissel (Berkeley et al. 2007), Hooded Warbler (Rush and Stutchbury 2008), and Ovenbirds and Worm-eating Warbler (Vitz and Rodewald 2010).

The core (50% fixed kernel) and natal (95% fixed kernel) home ranges of both flycatchers were similar. Core areas used by postfledging Willow Flycatchers were comparable to territory sizes estimated by Bombay (1999) in the same study area. To maximize the number of areas suitable as territories for the Willow Flycatchers, she suggested managing for as many areas of 0.5 ha with 0.25 ha of shrub cover as possible. However, we also found that the species' postfledging home range averaged  $1.8 \pm 1.4$  ha, implying that after fledging family groups use an area much larger than typically estimated during nesting. Home ranges based on postbreeding activity are also considerably larger than breeding territories for the Wood Thrush (Anders et al. 1998), Ovenbird, and Worm-eating Warbler (Vitz and Rodewald 2010). For adult Willow Flycatchers in Arizona, Cardinal (2005) estimated mean prenesting and nesting ranges of 9.9 ha and 0.38 ha, respectively, compared to  $143.2 \pm 83.5$  ha during the postbreeding season.

In our study area, meadows are patchily distributed, and both flycatchers appear to remain within or near their natal meadows, a pattern that has been described for Swainson's Thrush in riparian areas (White and Faaborg 2008) and the Ovenbird in fragmented forests (Bayne and Hobson 2001). Although other studies of fledglings have reported a change in habitat use after young left the nest, our data suggest that fledgling Willow Flycatchers remain in riparian vegetation during the dependence period. Dusky Flycatcher fledglings used riparian vegetation predominantly but were 25% more likely to be detected in upland forest than were Willow Flycatchers. This finding was not unexpected because Dusky Flycatchers are more likely to nest closer to the forest edge than are Willow Flycatchers, and they are not riparian obligates. In central Utah, Paxton et al. (2003) found Willow Flycatchers (*E. t. adastus*) using nonriparian habitat, especially when nests were placed close to the edge of the riparian zone. In contrast, Cardinal (2005) found that post-breeding adult southwestern Willow Flycatchers (*E. t. extimus*) were

restricted to the riparian floodplain. In our study area, we observed female Willow Flycatchers foraging at the forest edge, particularly during the incubation and fledgling stages. Therefore, the extent to which Willow Flycatchers use nonriparian shrubs is still poorly known, though important for decisions about management and restoration. Overall, however, it appears that the Willow Flycatcher is restricted primarily to riparian systems throughout the breeding period. Thus it would be expected to be affected negatively by poor meadow conditions (e.g., dry, with concomitantly low food resources) more than the Dusky Flycatcher, which is able to move readily into upland locations in search of food.

Estimates of the Willow Flycatcher's annual fecundity in our study area were already low without fledgling survival being considered (Mathewson 2010). Although it is promising that we found fledgling survival higher than reported by many other studies, our results should encourage researchers to consider the postfledging period in population estimates, especially for species with declining populations. As suggested in other studies (Rush and Stutchbury 2008, Suedkamp Wells et al. 2007), ideally postfledging survival should be quantified for each species over multiple years in order for the estimates to be used to calculate the population's stability. Our study provides an expanded understanding of how habitat is used by our focal species throughout the breeding season. Estimates of space needed and habitat use can aid managers in making decisions about setting aside habitat for endangered species.

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