POSTFLEDGING SURVIVAL AND MOVEMENTS OF WILLOW AND DUSKY

FLYCATCHERS IN THE CENTRAL SIERRA NEVADA

A Thesis

by

LISA M. VORMWALD

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2010

Major Subject: Wildlife and Fisheries Sciences

Postfledging Survival and Movements of Willow and Dusky Flycatchers in the Central

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ABSTRACT

Postfledging Survival and Movements of Willow and Dusky Flycatchers in the Central

Sierra Nevada. (August 2010)

Lisa M. Vormwald, B.S., University of Delaware

Chair of Advisory Committee: Dr. Michael L. Morrison

Understanding factors limiting population growth is critical for species exhibiting declining populations. Reproductive success has an important effect on population dynamics; however, our ability to accurately estimate productivity is limited. Studies on avian breeding biology have focused on nest survival; however, surviving to fledging does not ensure survival to the end of the breeding season. Furthermore, our understanding of habitat selection by birds based on the nesting cycle may not adequately represent the breeding habitat requirements because habitat use often changes after the young leave the nest. My goal was to examine the postfledging dependence period of two flycatcher species in the central Sierra Nevada: the California state endangered willow flycatcher (*Empidonax traillii*) and the dusky flycatcher (*E. oberholseri*). My focus was to estimate fledgling survival and examine factors that influence survival, evaluate postfledging movements and habitat use, and estimate post-breeding home range sizes of postfledging flycatchers. I monitored nests of both flycatcher species, individually color banded nestlings, and observed family groups daily once the young fledged. Flycatcher fledgling survival ranged from 46% to 76% and

varied by year and species. Survival was lowest during the first week of the postfledging dependence period for both species. Fledgling flycatchers moved on average ~45m per day during the dependence period. I detected family groups in the natal meadows from 13 to 33 days. I detected willow flycatchers in riparian shrub vegetation 94% of the time, with the remaining detections being along the upland forest edge. Dusky flycatchers were more likely to use upland forest vegetation after leaving the nest, as I detected them in riparian shrub vegetation 70% of the time. For both years combined, mean 95% home range sizes were 1.80 ± 1.44 ha for willow flycatchers and 1.82 ± 1.70 ha for dusky flycatchers. Mean 50% core areas were 0.33 ± 0.27 ha for willow flycatchers and 0.38 ± 0.44 ha for dusky flycatchers. My results suggest that using fledgling survival throughout the dependence period to assess reproductive output is more accurate than using nesting data alone. Furthermore, postfledging family groups used a larger area of habitat than what is typically estimated from territory mapping singing males. Future research should continue to stress the importance of gaining knowledge about the postfledging period, especially for species with declining populations.

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INTRODUCTION

Understanding population demography and factors that limit population growth are critical in conserving species that exhibit declining population trends. Reproductive success affects population dynamics (Holmes et al. 1992, Johnson and Geupel 1996, Chase et al. 1997), but our ability to estimate productivity is limited. The majority of studies on avian breeding biology have focused on nest success or number of young fledged; however, surviving to fledging does not ensure that juveniles will survive to the end of the breeding season. Therefore, fledging survival prior to dispersal may be a better measure of reproductive success for population models (Keedwell 2003). There is a need for field-based estimates of fledgling survival because they are scarce (Anders et al. 1997). Furthermore, existing studies suggest that current estimates used in population modeling are overestimates (Anders and Marshall 2005). Collecting postfledging survival data will lead to more accurate estimates of population stability.

The postfledging period, generally defined as the time between leaving the nest and departure for migration or settling into wintering areas (Anders et al. 1998), is often regarded as the least understood component of the avian life cycle (Morton et al. 1991, Baker 1993, King and Belthoff 2001). The first 2-3 weeks of postfledging period is usually labeled as the dependence period, where young rely heavily on their parents for food and protection. During the dependence period, young birds are somewhat limited in mobility making them vulnerable to mortality, especially from predation

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This thesis follows the style of the Journal of Wildlife Management.

(Anders et al. 1997, Rivera et al. 1998, Naef-Daenzer et al. 2001, Kershner et al. 2004, King et al. 2006). Information on the postfledging period is limited due to constraints associated with observing and locating birds once they have left the nest. Advances in radio-telemetry technology have provided an additional tool for studying various aspects of the postfledging period of small birds, leading to a recent increase in interest of this topic. Studies have addressed habitat selection and use (Anders et al. 1998, Cohen and Lindell 2004, King et al. 2006), biological and temporal factors (Gardali et al. 2003, Adams et al. 2006, Wells et al. 2007), dispersal behavior (Rivera et al. 1998, Adams et al. 2001, Kershner et al. 2004, Guzy and Ribic 2007), parental care (Rivera et al. 2000, Wheelwright et al. 2003) and cause-specific mortality (Anders et al. 1997) during the postfledging period.

Many biological and temporal factors could be responsible for postfledging survival. For example, larger brood sizes could result in lower survivorship by reducing individual feeding rates of the parents to offspring or by attracting more attention from predators through begging vocalizations. One temporal factor, the date of fledging, is associated with juvenile survival in some species. Some studies documented higher survival for individuals that fledged early in the season (Krementz et al. 1989, Naef-Daenzer et al. 2001), whereas others reported higher survival later in the season (Green and Cockburn 2001, Adams et al. 2006). These contradictory results illustrate the need for additional postfledging studies, so that we can better understand limiting factors affecting fledgling survival.

Our understanding of habitat selection by birds based on the nesting cycle may not adequately represent breeding habitat requirements because habitat use may change after the young leave the nest (King et al. 2006). Both predator avoidance (Cohen and Lindell 2004, King et al. 2006) and food availability (Anders et al. 1998, Rivera et al. 1998) may be possible explanations for movement patterns and habitat use reported in postfledging studies. Habitat quality and availability during the postfledging period is potentially critical to the survival of fledglings because young birds must build up fat reserves for migration (Moore et al. 1993). If the fledgling survival is affected by habitat characteristics, then postfledging habitat use has important conservation implications. Several postfledging studies have examined forest and grassland habitat types but little is known about species in wetlands and riparian systems, where resource limitations, and therefore survival probabilities, may be highly variable (Wells et al. 2007).

Differences in postfledging movements vary across ecosystem types, as seen in recent literature on forest and grassland species. For example, wood thrushes (*Hylocichla mustelina*) displayed stationary and drifting home ranges (Anders et al. 1998). Post-fledging movement patterns in wood thrushes and Swainson's thrushes (*Catharus ustulatus*) also have been categorized as having multiple dispersal sites after leaving the natal site (Rivera et al. 1998, Fink 2003, White et al. 2005). For Swainson's thrushes, White (2005) associated these different movement types with parental care strategies. For grassland birds, post-fledging movements relates to distances moved during the dependence period by lark buntings (*Calamospiza melanocorys*) and total dispersal distances of juvenile eastern meadowlarks (*Sturnella magna*) (Kershner et al.

2004). Local vegetation conditions are important factors affecting home range size and movements during the post-fledging period for juvenile dickcissels (*Spiza americana*) and eastern meadowlarks (*Sturnella magna*) (Suedkamp Wells 2005).

My goal was to investigate the postfledging dependence period of two Neotropical migrants that breed throughout much of the mountainous western United States: willow flycatcher (*Empidonax traillii*) and the dusky flycatcher (*E. oberholseri*). Research in the central Sierra Nevada has examined various aspects of the breeding ecology of these two flycatcher species, including habitat selection (Bombay et al. 2003), behavioral activities (Soroka and Morrison 2005), predation (Cain et al. 2003, Cain et al. 2006), dispersal and demography (Mathewson et al. 2008), and nest success (Cain and Morrison 2003, Mathewson et al. 2008). However, no attempt has been made to study the postfledging period, which could be an important component of future conservation and management needs. My objectives were to locate fledglings daily in order to estimate fledgling survival and examine factors that influence survival, evaluate postfledging movements and habitat use, and estimate post-breeding home range sizes of postfledging flycatchers in montane meadows of the central Sierra Nevada.

METHODS

Study species

My study species are both Neotropical migrants with similar life histories, although there are a few important differences between them. The willow flycatcher is a riparian obligate species that has experienced population declines in California (Sauer et al. 2003), due primarily to degradation and alteration of habitat (Green et al. 2003). The two willow flycatcher subspecies present in the Sierra Nevada (*E. t. adastus* and *E. t. brewsteri*) were listed as state endangered by the California Department of Fish and Game in 1990 (Green et al. 2003). In contrast, dusky flycatcher populations are increasing in California, which is likely due to silvicultural practices (Sedgwick 1993, Sauer et al. 2003). However, like willow flycatchers, dusky flycatcher populations occurring in riparian systems may be vulnerable to a variety of potential impacts such as channelization, recreational development, grazing, agriculture and conversions that are commonly associated with these habitat types (Sedgwick 1993). Furthermore, although the dusky flycatcher is not a riparian-obligate species, riparian areas may be important breeding areas in some regions (Cain and Morrison 2003), as much of the research on this species has been conducted in upland habitats.

During the breeding season, both flycatcher species often nest and forage in the same riparian shrub communities. Both species build small cup nests in shrubs, however dusky flycatchers are not substrate specific like willow flycatchers. Dusky flycatchers also begin breeding activity a couple weeks earlier than willow flycatchers (Cain and Morrison 2003). Willow flycatchers usually fledge after 14-15 days in the nest, while

dusky flycatchers usually fledge from 15-17 days (Green et al. 2003, Cain and Morrison 2003). Fledglings of both species often huddle together on the same perch first few days after leaving the nest. Fledgling begging calls during the dependence period are common and especially intense when a fledgling is fed or an adult perches near a fledgling (Sedgwick 1993, Sedgwick 2000).

Study area

I conducted research in wet montane meadows that are part of a long-term willow flycatcher demographic study in the central Sierra Nevada. Meadows used for the long-term research extend from Highway 88 in Alpine County (south of Lake Tahoe), north to Lassen Volcanic National Park, California. However, my study focused on sites in the central region, north of Lake Tahoe but south of the Feather River in Plumas County (Mathewson 2010). Meadows have a north south distribution along the east side of the Sierra Nevada crestline at elevations between 1900 m and 2700 m and range in size from 20 ha to 106 ha. Willows (*Salix spp.*) constituted the majority of the riparian shrub community and are distributed along streams and in clumps scattered throughout the meadows. The meadows are primarily surrounded by lodgepole pines (*Pinus contorta*) but some stands of mountain alder (*Alnus tenifolia*) and aspen (*Populous tremuloides*) also occur along the meadow edges (Bombay et. al. 2003).

I monitored all willow flycatcher nests and a random sample of dusky flycatcher nests in 6 study sites (hereafter, meadows) within the Perazzo Meadow Complex in Sierra County. These meadows are all in the Little Truckee River drainage in Tahoe National Forest, which is located approximately 32 km northwest of Truckee,

California. During the past 10 years, these six meadows supported between 19 and 28 willow flycatcher territories each year (Mathewson et al. 2008). Although the average number of territories is unknown, dusky flycatchers commonly occur and nest in these meadows (Cain and Morrison 2003).

Study design

Nest searching and monitoring. – I located and monitored flycatcher nests during the breeding seasons (May through August) in 2008 and 2009. I followed flycatchers using standard territory mapping techniques (Ralph et al. 1993) to provide a basis for nest searching activities. To minimize disturbance I located nests by observing behavioral cues of adults prior to physically searching (Martin and Geupel 1993). I did not approach nests during the building stage, and I only approached nests after the female was away from the nest. I record the GPS coordinates (Garmin GPS72) for each nest and marked the location by placing colored flagging tape at least 6 m away. I 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 (Rourke et al. 1999). I visited each nest during or immediately after the expected time of hatching to help determine nest fate and age of nestlings. I also recorded any evidence of nest predation or brood parasitism at each nest check. Evidence of nest predation included missing eggs or missing nestlings that were less than 12 days old and were too young to have fledged. I observed flycatcher nests daily with binoculars starting on day 12-14 in order to estimate fledge date and nest outcome.

Banding, resighting, and radio telemetry. – I marked all flycatcher nestlings with a color anodized USFWS 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. I banded nestlings on day 7 to 9, when nestlings were of adequate size to accept the band but too young to prematurely fledge. I target mist-netted and individually banded adult flycatchers as necessary to facilitate parental care observations (Sogge et al. 2001). My goal was to band at least one adult in each territory so that I could differentiate between the sexes and note their parental care activities.

Several postfledging studies on songbirds have equipped the fledglings with radio transmitters (Anders et al. 1997, Adams et al. 2001, Cohen and Lindell 2004, Berkeley et al. 2007, Wells et al. 2007), whereas others have equipped the adults with transmitters and used them to locate the individually banded fledglings (Bayne and Hobson 2001, Rush and Stutchbury 2008). In 2008, I attached transmitters to nestling dusky flycatchers approximately five days prior to fledging. I used transmitter model LB-2N with a battery life of three weeks from Holohil Systems (Carp, Ontario). These transmitters weighed 0.42g which was just over 3% of the anticipated body weight of a 12g fledgling flycatcher. The Ornithological Council (1997) recommends a transmitter weight not to exceed 5% of the total weight of an individual bird while the United States Bird-Banding Laboratory recommends no more than 3% (although exceptions are provided). I attached transmitters with thin cotton using the leg-harness method (Rappole and Tipton 1991). No negative effects were reported when this attachment method was used on migratory wood thrush when radio tagged birds were compared

with banded-only birds (Powell et al. 1998). However, adults of some species have been observed removing radio-tagged young from the nest (Mattsson et al. 2006). During my study, attaching radio transmitters to nestlings before day 12 decreased the amount of possible data collection after the young left the nest (i.e. almost one week of battery life used in the nest), but attachment on or after day 12 often caused premature fledging of the tagged individual or the entire brood, which likely inadvertently decreased fledgling survival. Because of these concerns, I did not use radio telemetry on dusky flycatchers in 2009.

Locating fledglings without the use of radio telemetry lacks the rigor of obtaining many unbiased locations, 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 observations, however, Rush and Stutchbury (2008) reported a resighting probability of 84%, and suggested observing fledglings for a full four week period to obtain accurate estimates of survival using this method. Willow and dusky flycatcher fledglings can be located relatively easily because of their loud begging calls throughout the dependence period (personal observation). Therefore, with the exception of 10 radio tagged dusky flycatcher fledglings in 2008, I located and resighted all individuals daily to estimate survival. Willow flycatchers were located using only begging calls during both years because of their current protected status.

Postfledging observations. – I conducted daily nest checks starting on day 12 of the nestling period using adult behavior and/or binoculars from a distance to determine

nest status. If the nest had not fledged yet (all nestlings still present in the nest), I returned the following day, and continued daily visits until they fledged. Once the young fledged, I conducted a 30 minute to two-hour observation period per day with each flycatcher family group (adults and fledglings). Observation periods occurred between 06:00 and 18:00 to ensure that fledgling birds could be visually located.

To begin the observation period, I approached the nest area or the area of last detection and systematically searched using visual and audio cues and/or radio-telemetry by homing in to locate flycatcher family groups. For the radio tagged dusky flycatcher fledglings I used a TRX-1000s receiver and a 3-element Yagi antenna (Wildlife Materials, Carbondale, Illinois). Upon first detection of a fledgling, I recorded its location. I attempted to resight each fledgling in the family group by its colored bands while also noting the number and sex of the adults caring for it. Once all individuals were resighted and at least 30 minutes had passed, I 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, I counted it as a resight for each individual.

I continued daily visits to locate the family group until the young were no longer detected in the natal meadow for at least 3 consecutive days, as long as the young were old enough to have reached the independence stage (≥ 2 weeks). After this point I assumed that the young were either independent of their parents and ceased begging calls and/or they dispersed out of the natal meadow. If during a visit I detected adults but not fledglings, I returned for the next several days to try to locate fledglings. If I did not

detect adults or fledglings, I expanded my searches outward from the nest area until I found them or until I sufficiently surveyed the natal meadow and surrounding forest edge. In this case, if I failed to detect any members of the family group after 3-5 days, I ceased my searches.

DATA ANALYSIS

Fledgling survival

I analyzed fledgling survival using Program MARK (White and Burnham 1999) which provides parameters such as survival and recapture estimates for marked animals from biological studies, which allowed me to address resighting. I analyzed each fledgling's recapture history using Cormack-Jolly-Seber models generated in Program MARK. Program MARK weights models using Akaike's Information Criterion (AIC) as a function of the equation:

$$AIC = -2 \ln(L) + 2q$$

where the model likelihood or fit of the model to the data is denoted as L while q is the number of parameters in the model. Selecting the model with the lowest AIC weight out of all candidate models should result in the selection of the model best fitting the data to which it has been applies (Williams et al. 2001). To determine if the survivorship of fledglings was influenced by certain factors I incorporated specific covariates in the modeling process (White and Burnham 1999). I used the logit link function in the models where the logit function creates a linear function of the response variable of the CJS models, in this case survival (ϕ) or recapture (p). The logit function then addressed the probability of the response as a vector of the explanatory variables through the equation:

$$\text{Logit}\ (\phi) = \beta_0 + \beta_1\ (\text{covariate})$$

$$\phi = \frac{e^{\beta 0\ +\ \beta 1\ (\text{covariate})}}{1 + e^{\beta 0\ +\ \beta 1\ (\text{covariate})}}$$

For each survival analysis, I constructed a set of candidate models representing my hypotheses on the causes of variation in fledgling survival. I selected variables that had been reported in the literature to affect fledgling survival, as well as variables I thought may be important for survival based on my field observations. The possible sources of variation I considered were:

1) *Year*. I included year because annual variation is a common source of variation in survival rates, which could result from factors such as changes in weather patterns and fluctuations in predator or prey densities.

2) *Ordinal date of fledging*. I included date in season of the fledging event to account for any possible effects of temporal variation.

3) *Brood size.* I included the number of nestlings in the nest just prior to fledging to test for any possible confounding effects on fledgling survival. As brood size increases, feeding rates for each individual may decrease, which could result in lower survivorship. In addition, a larger and therefore louder family group may attract more attention from predators; thereby lowering survivorship.

I grouped years together but analyzed each species separately. I used capture histories that included 21 intervals (days) for willow flycatchers and a 28 intervals (days)

for dusky flycatchers because dusky flycatchers typically stayed longer in the natal meadows.

Postfledging movements and habitat use

I calculated the mean linear distance moved by each family group from the nest site per observation period using the GPS waypoints collected for daily fledgling locations. I collected waypoints in the Universal Transverse Mercator (UTM) system, which consisted of two values, an Easting and a Northing. I subtracted each of the coordinates collected for the first detection of the observation period from the UTM coordinates collected for the nest site. Then I fit the resultant values into the equation D = (square root $(A^2 + B^2)$), where A represents the Easting, B represents the Northing, and D is the distance between the waypoint and the nest.

I projected fledgling locations onto color orthoquad maps (2005) in ArcGIS 9.3 to evaluate habitat use of family groups after the young fledge from the nest. Three major vegetation types were found in my study area: riparian shrub community, upland forest, and mountain shrub steppe. I determined the percentage of each vegetation type used by each family group 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 group.

Postfledging home ranges

Home range was first defined as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt 1943). It is also recognized that "home range" is a concept, not an entity (Morris 1988); therefore, in this

study I defined home range as the area used by family groups during the postfledging

dependence period. I used the fixed-kernel method to calculate home ranges (95% of the

utilization distribution) and core areas (50%) using Home Range Tools for ArcGIS

(Rodgers et al. 2005) in ArcGIS version 9.3 (ESRI, Inc., Redlands, CA). I used kernel

estimators because they have been ranked as the best method for estimating home range

size and are capable of calculating utilization distributions (Kernohan et al. 2001). The

fixed-kernel method is preferred because it is a measurement of the intensity of use,

excluding areas used minimally (White and Garrott 1990, Seaman 1999). I restricted my

sample to those individuals with ≥30 detections because simulation research has

suggested that is the minimum sample size required for stable home range estimates

using 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., href) (Silverman 1986; Worton 1989, 1995). I

used the "href" method for smoothing because it is effective if the underlying utilization

distribution is unimodal (i.e., "singlepeaked") (Worton 1995). Although it might

oversmooth the utilization distribution for some animals because they have multiple

centers of activity, my family groups generally displayed a main center of activity with a

few outside points.

RESULTS

Fledgling survival

Willow flycatchers. – In 2008, I monitored 13 willow flycatcher nests, eight (62%) of which fledged at least one young. I individually banded 21 nestlings from these eight nests, and I resighted 17 (81%) of the fledglings on multiple days ($\bar{x} = 10 \pm 2.5$, range $= 5 - 14$) throughout the dependence period. Two individuals were never resighted although their siblings were, one was resighted but not after 3 days postfledging even though its sibling was resighted on multiple days, and the last fledgling was last resighted two days postfledging but was unable to fly and appeared to have a broken leg. In addition, one of the fledglings was resighted 8 days postfledging but was unable to fly, so I did not include it in any movement or habitat analyses. Based on this information, I estimated that 16 of the 21 (76%) fledglings survived the dependence period.

In 2009, I monitored 21 nests, five (24%) of which fledged at least one young. I individually banded 13 nestlings from these five nests, and resighted 6 (46%) of the fledglings on multiple days ($\bar{x} = 6 \pm 2.0$, range $= 4 - 9$) throughout the dependence period. For one nest, on day 15 of the nestling period, one nestling was found dead in the nest, and the other two were never detected. A second nest fledged and one individual was seen 2 days postfledging but none of the three fledglings were ever detected again. The last fledgling was never resighted out of the nest although its sibling was resighted on multiple days. Based on this information, I estimated that 6 of the 13 (46%) fledglings survived the dependence period.

I found that a model with a time-dependent variation by week (7 days) in survival probability and a constant recapture probability was the one with lowest AIC value and received 51% of model support (Table 1; Model 1). Models including covariates of year, brood size, and ordinal date of fledging had higher AIC values (Table 1, Models 4-6). The results of the best-fitting model (Model 1; Fig 1) indicated that fledgling survival was lowest during the first week postfledging, and increased during the second week. Estimated survival probabilities for each week were 0.95, 1.00, and 0.78 for each week respectively, while the constant recapture probability was 0.56 (Table 2).

Table 1. Model selection for the effects of time, year, brood, and ordinal date of fledging on the postfledging survival of willow flycatchers.

	Model	AICc	Delta AICc	AICcWeight	No. Par.
1	Weekly survival, constant recapture	645.75	0.00	0.51	3
2	Weekly survival, early/late recapture	646.54	0.79	0.34	4
3	Weekly survival, weekly recapture	648.18	2.43	0.15	5
4	Survival (year), constant recapture	669.23	23.48	0.00	3
5	Survival (brood), constant recapture	675.22	29.47	0.00	3
6	Survival (fledge), constant recapture	675.24	29.49	0.00	3

Table 2. Weekly survival and resighting probabilities for willow flycatchers during the

21-day postfledging period.

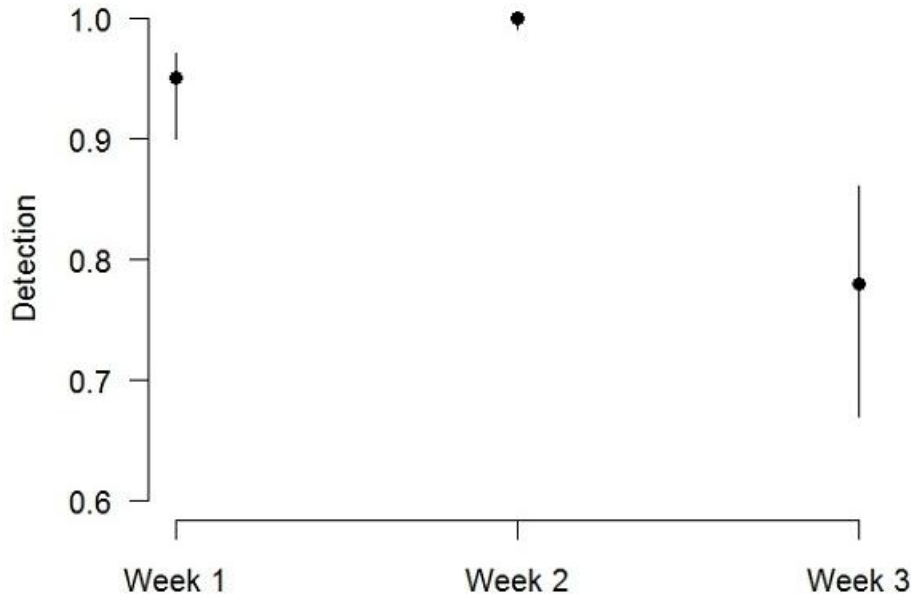| Days postfledging	Survival Probability	95% CI	Resighting Probability	95% CI
1-7	0.95	0.90 - 0.97	0.56	0.50 - 0.61
8-14	1.00	0.99 - 1.00	0.56	0.50 - 0.61
15-21	0.78	0.67 - 0.86	0.56	0.50 - 0.61

Fig. 1. Estimated survival probabilities by week with 95% confidence intervals for

willow flycatchers.

Dusky flycatchers.- In 2008, I monitored a total of 50 dusky flycatcher nests in

2008, 25 of which successfully fledged at least one young. I individually banded a total

of 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. Six were each resighted once on the first day they fledged, but then never resighted or detected again. Two fledglings were found dead on the ground with an unknown cause death, and one was found in an underground burrow (see below). In addition, one of the fledglings was resighted twice, last five days postfledging, but was never resighted or detected again even though its two siblings where resighted on 16 and 18 days respectively. Based on this information, I estimated that 32 (65%) fledglings survived the dependence period.

In 2008, I attached radio transmitters to 10 nestling dusky flycatchers. Of these, only four birds were located daily throughout the dependence period. Two transmitters fell off the individuals a few days after they fledged from the nest. I found one transmitter attached to fledgling remains in an underground burrow. I found one intact dead nestling on the ground not far from the nest, with an unknown cause of death. The remaining four transmitters were found on the ground or the signal was lost completely, but the individuals were never resighted.

In 2009, I monitored a total of 48 nests, of which 30 fledged at least one young. I individually banded 55 nestlings from 18 successful nests and I 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 two days postfledging. In addition, one individual was resighted four days postfledging but was unable to fly, and was never

detected again. Based on this information, I estimated that 37 of the 55 (67%) fledglings survived the dependence period.

I found that a model with a time-dependent variation by week (7 days) in survival probability and recapture probability 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 (Model 1; Fig 2) indicated that fledgling survival was lowest during the first week postfledging, and increased during the second and third week. Estimated survival probabilities for each week were 0.94, .99, 0.95, and 0.81 for each week respectively, while recapture probabilities were 0.55, .67, 0.59, and 0.54 for each week respectively (Table 4).

Table 3. Model selection for the effects of time, year, brood size, and ordinal date of fledging on the postfledging survival of dusky flycatchers.

	Model	AICc	Delta AICc	AICcWeight	No. Par.
1	Weekly survival, weekly recapture	2281.26	0.00	0.97	8
2	Weekly survival, constant recapture	2289.32	8.06	0.02	5
3	Weekly survival, early/late recapture	2290.46	9.20	0.01	6
4	Survival (year), weekly recapture	2316.04	34.78	0.00	6
5	Survival (brood), weekly recapture	2316.89	35.63	0.00	6
6	Survival (fledgedate), weekly recapture	2316.89	35.63	0.00	6

Table 4. Weekly survival and resighting probabilities for dusky flycatchers during the

28-day postfledging period.

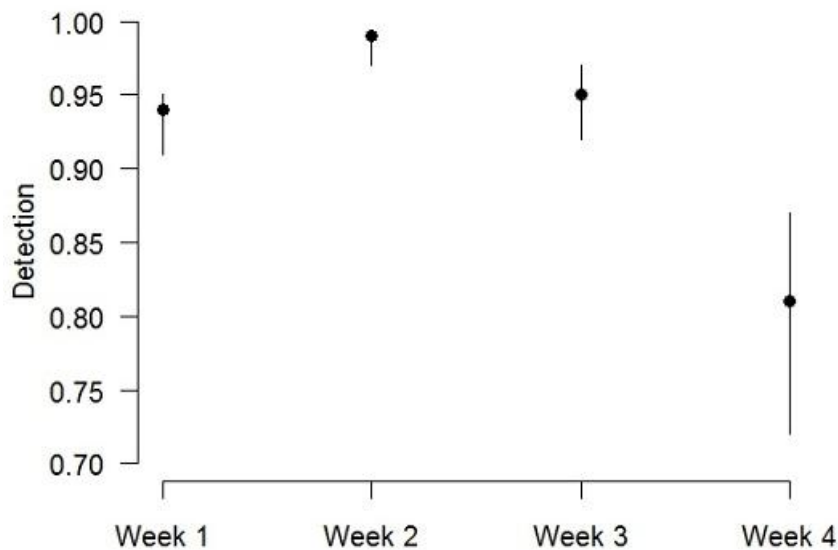| Days postfledging	Survival Probability	95% CI	Resighting Probability	95% CI
1-7	0.94	0.91 - 0.95	0.55	0.50 - 0.59
8-14	0.99	0.97 - 0.99	0.67	0.62 - 0.71
15-21	0.95	0.92 - 0.97	0.59	0.53 - 0.65
22-28	0.81	0.72 - 0.87	0.54	0.42 - 0.65

Fig. 2. Estimated survival probabilities by week with 95% confidence intervals for

dusky flycatchers.

Postfledging movements and habitat use

Movements. - In 2008, I located and followed 7 willow flycatcher family groups

for an average of 18.7 ± 1.70 days (range = 16 – 21d) in the natal meadow (Fig. 3). The

average daily linear distance moved by those family groups from the nest site was 48 ± 51 m (Table 5; Fig. 4). For dusky flycatchers, I located 18 family groups for an average of 21.4 ± 5.4 days (range = 6–28) in the natal meadow (Fig 3). The average linear distance moved by those family groups from the nest site was 45 ± 43 m (Table 5; Fig. 5). In 2009, I located and followed 3 willow flycatcher family groups for an average of 14.7 ± 0.58 days (range = 14–15) in the natal meadow (Fig 3). The average daily linear distance moved by those family groups from the nest site was 23 ± 18 (Table 5; Fig. 4). For dusky flycatchers, I followed 13 family groups for an average of 22.1 ± 5.3 days (range = 13–33d) in the natal meadow (Fig. 3). The average linear distance moved by those family groups from the nest site was 45 ± 45 m (Table 5; Fig 5).
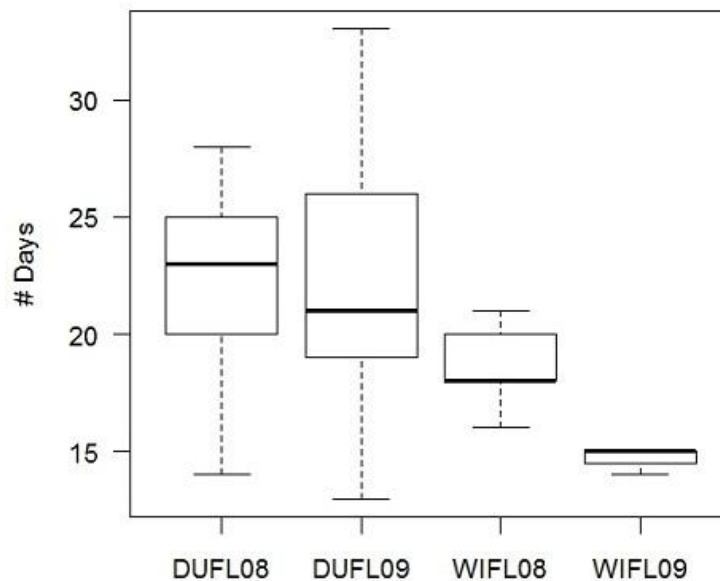
Fig. 3 Box plot of the number of days postfledging willow (WIFL) and dusky (DUFL) flycatcher family groups were detected in their natal meadows in 2008 and 2009.

Table 5. Range and average daily linear distances moved from nest sites by postfledging flycatcher family groups.

	Year	*n*	Min. (m)	Max. (m)	Mean (m)	*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
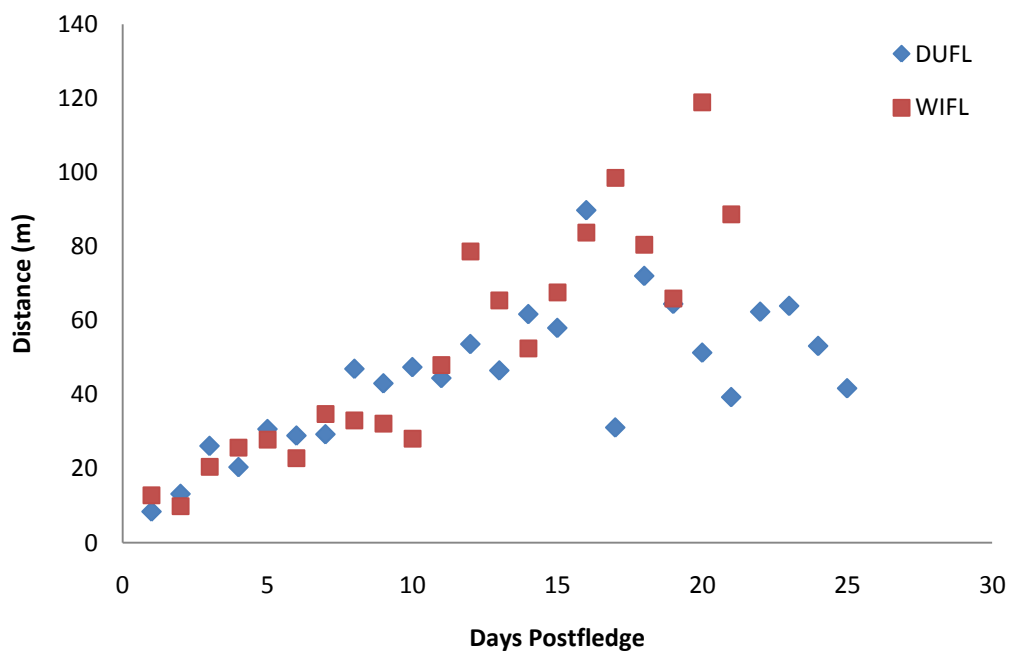
Fig. 4 Average daily linear distance moved from the nest site by postfledging family groups of willow and dusky flycatchers in 2008.
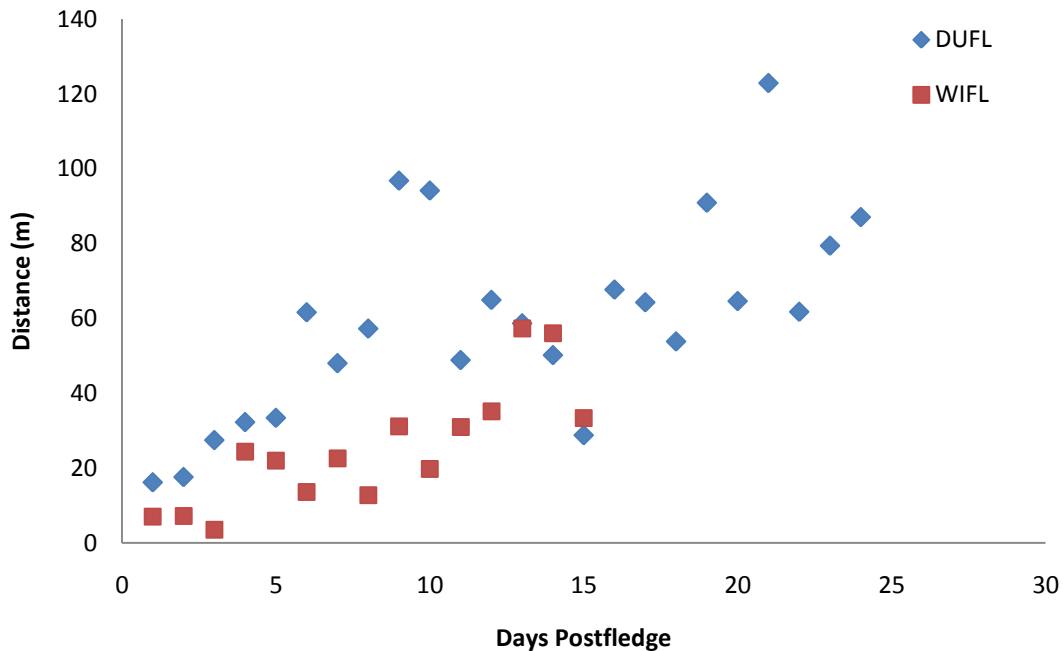
Fig. 5 Average daily linear distance moved from the nest site by postfledging family groups of willow and dusky flycatchers in 2009.

Habitat use. - In both years I located willow flycatcher family groups primarily in willow vegetation with occasional sightings along a forest edge towards the end of the dependence period. In 2008, I followed 7 family groups for a total of 234 location ($\bar{x} =$ 33.4 ± 2.7, range = 30 –38), of which 220 locations (94%, $\bar{x}$ = 31.4 ± 3.6, range = 26– 38) were in riparian shrub vegetation within the meadow. The remaining points were located in the upland forest surrounding the meadow. In 2009, I followed 3 family groups for a total of 82 locations ($\bar{x}$ = 27.3 ± 3.1, range = 24 –30), of which 77 points (94%, $\bar{x}$ = 25.7 ± 1.5, range = 24–27) were in riparian shrub vegetation 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.

For both years I located dusky flycatcher family groups primarily in willow
vegetation although there were also frequent sightings along a forest edge. Two family
groups, one from each year, moved to the forest edge only a few days after fledgling and
stayed there for the remainder of the dependence period. In 2008, I followed 12 family
groups for a total of 432 locations ($\bar{x} = 36 \pm 6.7$, range = 24 –48), of which 300 locations
(69%, $\bar{x} = 25 \pm 11.2$, range = 11–48) were in riparian shrub vegetation within the
meadow. The remaining points were located in the upland forest surrounding the
meadow. In 2009, I followed 11 family groups for a total of 456 locations ($\bar{x} = 41.5 \pm$
10.1, range = 30 –58), of which 325 points (71%, $\bar{x} = 29.6 \pm 12.7$, range = 6–56) were in
shrub vegetation 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.

Postfledging home ranges

I calculated home ranges and core areas for a total of 10 willow flycatcher and 23
dusky flycatcher family groups in 2008 and 2009. Schoener's ratio values for some
family groups indicated high levels of positive serial autocorrelation, but when I
subsampled the locations in an attempt to attain independence among points, I still did
not achieve independence for all groups. I concluded that this statistical measure was
not biologically relevant, and I did not want to eliminate biologically important
information by subsampling (Reynolds and Laundre 1990, McNay et al. 1994, Barg et

al. 2005). Despite the fact that my data did not meet the assumption of statistical independence, kernel estimates core areas and home ranges of the flycatchers provided models that matched our field observations, and I believe the points were biologically independent.

Average home range sizes and core areas were similar across species in 2008, but contours were nearly twice as large for dusky flycatchers compared to willow flycatchers in 2009 (Tables 6 & 7). For both years combined, mean 95% home range sizes were 1.8 ± 1.4 ha for willow flycatchers and 1.7 ± 1.2 ha for dusky flycatchers. Mean 50% core areas were 0.3 ± 0.2 ha for willow flycatchers and 0.4 ± 0.4 ha for dusky flycatchers (Figs. 6 & 7).

Both species most often displayed central patterns which were characterized by the clustering of points around the central natal area with occasional trips away from the central area in a non-linear fashion. However, one dusky flycatcher family group in 2008 showed a home range pattern with multiple centers of activity, unlike the other groups I sampled. Therefore, the href method of choosing a smoothing parameter resulted in an extremely large home range estimate (7.6 ha) compared to the other estimates in either year. Therefore, I adjusted h to 50% of href which gave a more reasonable estimate based on field observations.

Table 6. Range and average sizes of 95% home range fixed kernel estimates of

postfledging flycatcher family groups.

	Year	*n*	Min (ha)	Max. (ha)	Mean (ha)	*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
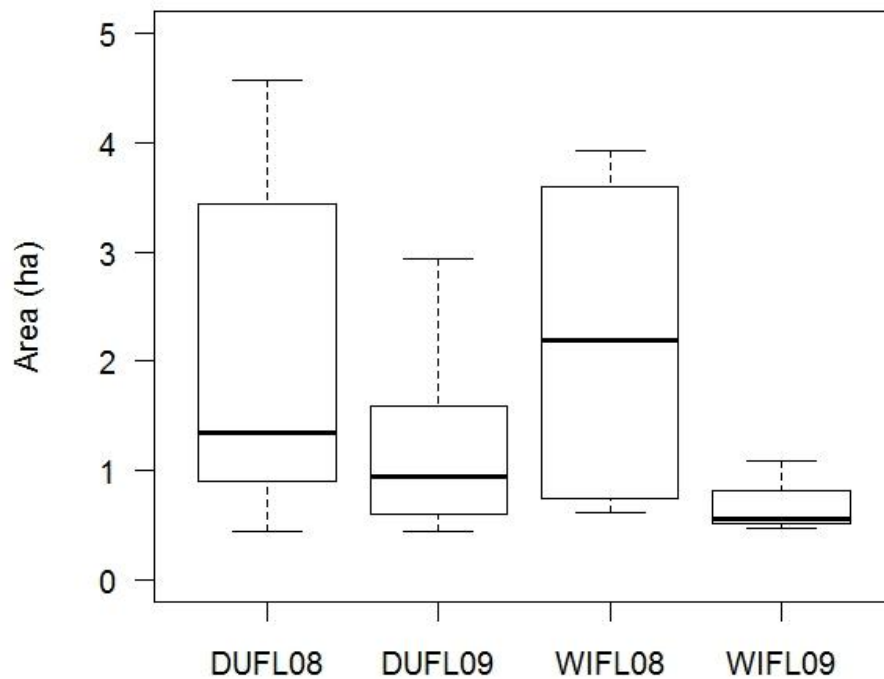
Fig. 6 Box plot of 95% home range estimates for willow (WIFL) and dusky (DUFL)

flycatchers in 2008 and 2009.

Table 7. Range and average sizes of 50% core area fixed kernel estimates of
postfledging flycatcher family groups.

	Year	*n*	Min (ha)	Max. (ha)	Mean (ha)	*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

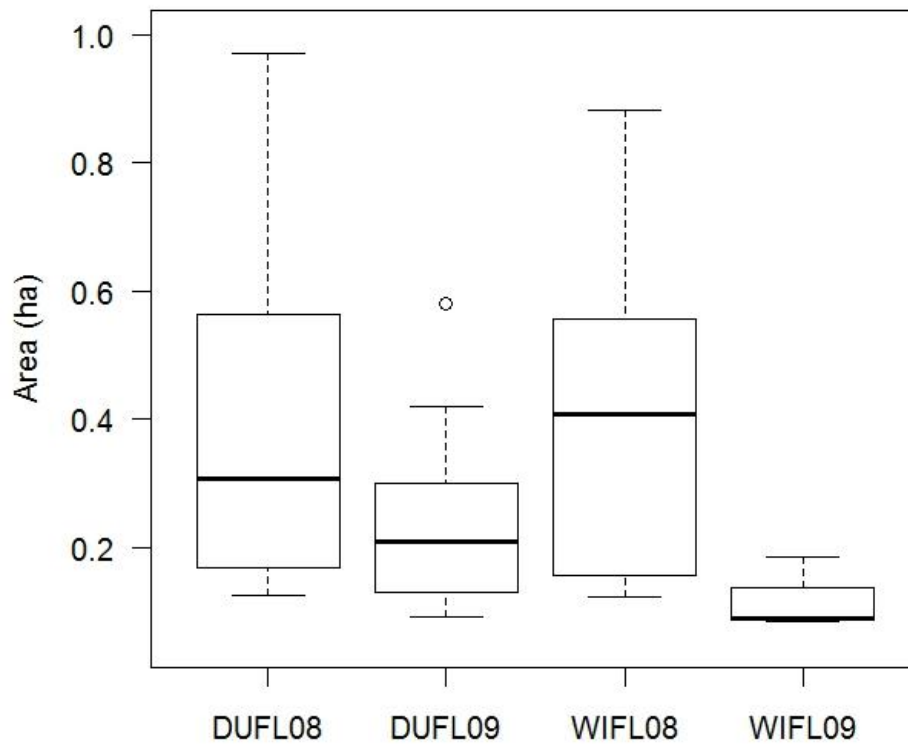**Fig. 7** Box plot of 50% core area estimates for willow and dusky flycatchers in 2008 and
2009.

DISCUSSION AND SUMMARY

Postfledging survival

In general, I found that flycatcher fledgling apparent survival ranged from 46% to 76%, which is within the range found in other studies. Willow flycatcher fledging survival was lower in 2009 than 2008, while dusky flycatcher survival was similar between years. With years combined, survival probabilities were similar between species and resighting probabilities was slightly higher for dusky flycatchers. A model with a time-dependent variation by week in survival probability best fit the data for both species, suggesting that survival was lowest during the first week after leaving the nest, followed by an increase in survivorship with age. Lower survival estimates in the last week of the periods likely reflect dispersal from the natal grounds or the end of the dependence period, not a decrease in survivorship. Similarly, resighting probabilities were lowest during the first week after leaving the nest when young were the least mobile and more difficult to locate, and increased with age until they began to reach independence and disperse. I did not find support for effects of year, brood size, or the ordinal date of fledging on fledgling survival for either species.

Robinson et al. (1993) proposed that 2.23 young/female/season was the minimum fecundity value needed to maintain stable populations of small passerines. Annual fecundity estimates of the willow flycatcher population in my study area were already below this suggested minimum *prior* to considering fledgling survival (Mathewson et al 2008). Although my research shows annual variation, some young are likely lost in the postfledging stage each year, which decreases annual fecundity.

Therefore, my results should encourage researchers to consider the postfledging period in population estimates, especially for species exhibiting a declining population trends.

It is difficult to make sufficient comparisons between years for willow flycatchers because I was only able to follow 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 and/or lower detection probabilities of the already fledged family groups. Three willow flycatcher nests in the late nestling stage failed after the cold front, with dead nestlings left in the nest. In addition, one of three nestlings on day 14 was found dead in a nest, while its siblings were never detected, although they were old enough to have fledged. Unlike dusky flycatchers, willow flycatchers that lose a nest late in the season rarely have time to renest because they arrive later to the breeding grounds (Green et al. 2003, Mathewson 2010). The majority of dusky flycatcher nests had already fledged by this date, and, therefore, were not likely affected. Furthermore, two of the three willow flycatcher family groups could not be located after 6 August. It is unlikely that all fledglings in these three groups died due to cold temperatures, but the groups may have moved away from the natal meadow sooner and therefore were difficult to relocate. The high winds and cold temperatures associated with this cold front could have led to low detections for multiple days in a row, during which time the family groups could have gradually moved out of the area. Future studies could involve examining how various weather variables may affect postfledging survival and movements, especially at high elevation sites where late summer cold fronts may occur.

My finding of annual variation in fledgling survival for willow flycatchers cautions against extrapolating results of short-term studies when assessing the stability of bird populations over longer periods and across large geographic areas (e.g., James et al. 1996). Varying estimates of fledgling survival may stem from differences in geographic location, time, and habitat association (Krementz et al. 1989, Anders et al. 1997, Vega Rivera et al. 1998). As suggested in other studies (Rush and Stutchbury 2005, Wells 2007), ideally postfledging survival should be quantified for each species over multiple years in order to use the estimates to calculate the population stability.

Few studies have examined the effects or efficacy of affixing radio transmitters to small birds, and particularly young birds. To date, most investigators have reported few or no negative effects (Brigham 1989, Sykes et al. 1990, Neudorf and Pitcher 1997, Naef-Daenzer et al. 2001, Wells et al. 2003). As only one of my transmitter attachments was truly successful, the method of timing and harness attachment that I used was not effective. Similar results were seen in a study of Losisiana waterthrushes (*Seiurus motacilla;* Mattson et al 2006) where only one of 12 radio-tagged young was relocated more than 24 h after attaching the transmitter. Furthermore, the authors captured adults on videotape removing radio-tagged young from three nests. Although I did not directly observe this behavior, four of the young fledged prior to their siblings and did not survive; suggesting that removal of radio tagged young was a possibility. In addition, the force fledging of an entire brood after radio attachment occurred at two nests, which likely impacted survival of the young. Therefore, like Mattson et al (2006), I caution researchers intending to use these methods and recommend they consider various

options and methods. Other possible alternatives are (1) capturing fledglings in mist nets and attaching transmitters a week or more after fledging by which time contour feathers have grown and the likelihood of a parent removing the transmitter may be reduced, or (2) attempting to monitor fledglings without attaching transmitters, and a tagged adult would enhance this method.

Postfledging movements, habitat use, and home ranges

Movements. – I found that on average fledglings of both species primarily moved ca. 45 m per day and up to ca. 250 m from the nest during the dependence period. Distances moved were similar between years and species, with the exception of small sample sizes for willow flycatchers in 2009. This suggests that fledglings did not have to move very far to obtain needed resources. As expected, distance moved increased with age as young become more mobile and began feeding themselves, but movements back to the nest were also observed. On average, I detected dusky flycatchers in the natal meadow for more days than willow flycatchers.

Distances moved from the nest undoubtedly vary by species and vegetation associations. My findings of average daily distance moved per day by willow and dusky flycatchers was lower than what was reported for Western bluebirds (*Sialia mexicana*) during the 20 day dependence period (Wightman 2009), but similar to that found in hooded warblers (Rush and Stutchbury 2008), which is a similar sized bird. The maximum average distance moved of ca. 200 m found for willow and dusky flycatchers was also comparable to what was found for post-fledging white-crowned sparrows in montane meadows after three weeks postfledging (Morton et al. 1991).

It has been hypothesized that fledging earlier and thus staying longer in the natal meadow better prepares young for migration. Dusky flycatchers are likely to be able to take advantage of this as they tend to fledge earlier than willow flycatchers (Sedwick 1993, Cain and Morrison 2003). Overall, I found that flycatchers stayed in the natal meadows from 13-33 days, which was lower than the ages at independence for other neotropical migrants, including wood thrushes (32.5 + 0.6 days [Anders et al. 1998] or 28–36 days [Vega Rivera et al. 2000]) and hooded warblers [*Wilsonia citrina*], 37–51days, Evans Ogden and Stutchbury 1997). My estimates may be lower than other studies because I followed young only until dependence (i.e. they were no longer vocal) without the use of radio telemetry. It is possible that one or two of the flycatcher groups I monitored dispersed too quickly from the natal area to be adequately tracked using auditory cues only.

Habitat use. – Although other fledgling studies reported a change in habitat use after young left the nest, my data suggests that postfledging willow flycatchers generally do not switch to a different habitat type after leaving the nest, at least not during the dependence period. Dusky flycatcher fledglings were 25% more likely to be detected in upland forest vegetation than willow flycatchers, and therefore, more likely to use switch habitats after leaving the nest. This finding is likely related to what vegetation was available to each species and where the nests were located in relation to the forest edge, as dusky flycatchers in my study were more likely to nest closer to the forest.

Although willow flycatchers are considered riparian obligates, a recent telemetry study in central Utah on the non-endangered subspecies, *E. t. adastus*, found willow

flycatchers using non-riparian habitat, especially when nests were placed close to the edge of the riparian zone (Paxton et al. 2003). However, Cardinal (2005) found that post-breeding habitat use by *E. t. extimus* adults was restricted to the riparian floodplain, and although mature riparian shrub vegetation was used most, flycatchers were also observed using young and immature vegetation. Willow flycatcher females in my study area have been observed foraging in non-riparian shrub particularly during the incubation stage, and trips to the forest edge to forage for fledglings was also observed (personal observation). However, to what extent willow flycatchers use non-riparian shrub vegetation is still relatively unknown, but may be important for making management and restoration decisions for this declining species. Furthermore, the use of non-riparian shrub habitat after the postfledging dependence period may show different results and could be studied with the use of telemetry.

Home ranges. – Average home range sizes and core areas were similar across species in 2008, but not in 2009. Home ranges of dusky flycatchers were slightly smaller in 2009 than in 2008, although this could be a result of one or two large estimates in 2008. A small sample size of willow flycatcher family groups in 2009 likely explains the difference in home range sizes between years, however, core areas were similar between years for willow flycatchers.

Estimates of space needed and habitat use can help aide managers in making decisions about setting aside habitat for endangered species. Core areas used by postfledging willow flycatchers averaged 0.3 ± 0.3 ha over both years, and were comparable to territory sizes estimated by Bombay (1999) in the same study area. She

suggested managing for as many 0.5 ha areas with 0.25 ha of shrub cover to maximize the number of areas available for use as territories by willow flycatchers. However, I also found that willow flycatcher postfledging home ranges averaged 1.8 ± 1.4 ha, which suggests postfledging family groups use a much larger area than typically estimated from nesting activities.

As others have suggested, we should further examine movements and space use for various species in a variety of habitat types during the post-fledging period to better understand resource needs during this critical time period.

Conservation implications

Future research is needed to better understand postfledging survival, especially for species like the willow flycatcher, which are experiencing population declines. Future studies could examine fledging cause specific mortality using radio telemetry, which could lead to management of a particular predator. But more importantly, increased nest success and even productivity (i.e. clutch sizes) could produce more fledglings that could survive the dependence period, which could eventually increase juvenile recruitment. Therefore, researchers could focus on examining causes of nest failure and identifying nest predators as well.

One management practice that could have an impact on both nest success and fledgling survival is meadow restoration. Restoring the hydrology of the meadows could improve nest conditions by deterring nest predators (Cocimano 2009), increasing nest concealment, and inhibiting forest encourachment. Furthermore, restoring meadows to wetter conditions could increase arthropod abundance thereby increasing nestling weight

and possibly fledgling survival if larger fledglings are more likely to survive. Finally, restoration would increase vegetation growth, which could provide better cover and protection for fledglings. Of course, more research is needed to determine the effects of these practices.

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