POST-FLEDGING ECOLOGY OF AN ENDANGERED SPECIES: THE GOLDEN-CHEEKED WARBLER

BY

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THESIS

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ABSTRACT

Understanding associations between habitat and the demography of endangered wildlife is essential for effective management. Habitat and demography relationships are further complicated when different habitat features may have different impacts across various life-stages of an individual. I investigated the survival, behaviors and habitat use of endangered Golden-cheeked Warbler (Setophaga chrysoparia) fledglings in Texas. I monitored nests until fledging and tracked fledglings for at least four weeks after leaving the nest. I estimated survival rates for fledglings during the first four weeks out of the nest, analyzed how habitat and behavioral factors affect survival, and described temporal changes in habitat and behaviors as fledglings aged. Fledgling survival was much higher than expected, and higher than many other species during the dependent post-fledging stage. General habitat use did not change much over time, as fledglings appear to have ample habitat available, but focal tree use switched from juniper to oak as fledglings aged. Fledglings also began to forage more as parental care, especially by females, declined over time. Foraging success was higher in areas with more oak habitat. Habitat with a 70/30 ratio of juniper-oak appears to be sufficient not only for nesting but also for fledgling survival and foraging ability. Conserving habitat with a juniper-oak dominated matrix will be of utmost importance to promote survival of fledglings.
ACKNOWLEDGEMENTS

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DEDICATION

To those who pushed me to pursue my passions.

To my family and friends who have supported me no matter the distance.

To all the researchers who have passed on their knowledge.

To all women scientists in the field.

To endangered and threatened species.
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CHAPTER 1: GENERAL INTRODUCTION

Understanding associations between habitat and the demography of endangered wildlife is essential for effective management. The age or life-stage of an individual adds complexity to these associations because young often choose habitat that differs from adults (King et al. 2006). Among avian species, juveniles may select habitats to enhance survival by providing protection from predators and exposure (Cox et al. 2014) and to find suitable foraging habitat (Dittmar et al. 2014, Small et al. 2015). These relationships are further complicated by fledglings balancing foraging skills and reductions in parental care as they age. Thus, correlations between habitat and survival during different life stages are key in the management of endangered species.

Factors driving variation in survival rates often differ between juveniles and adults. Most survival estimates for songbirds are based on return rates of adults (Thomson et al. 1999) and often inaccurately assess post-fledging survival. Understanding post-fledging survival can improve management plans for species, especially since it is an easier component of the life cycle to manage (e.g., instead of wintering habitat management; Cox et al. 2014). Excluding this life cycle stage can bias survival estimates negatively, therefore limiting our ability to make predictions about population dynamics that are crucial for conservation and management planning. Recently, there has been a surge of research on post-fledging survival, mostly in species of lesser conservation concern (Anders et al. 1997, Fink 2003, Schmidt et al. 2008, Jenkins et al. 2016, Ausprey and Rodewald 2011), but are valuable to our understanding of this life-stage.

For birds, the post-fledging stage can be particularly sensitive to low survival (Cox et al. 2014). A bird in post-fledging stages does not necessarily mean low survival rates, but other post-fledging studies reveal alarmingly low survival rates during post-fledging (e.g., 0.23 in
Hooded Warblers; *Setophaga citrina*, Rush and Stutchbury 2008). Fledglings are subject to higher predation and exposure risks, both of which can be affected by habitat (Anders et al. 1998, Yackel Adams et al. 2006, and Cox et al. 2014). For example, Anders et al. (1998) found that young Wood Thrushes (*Hylocichla mustelina*) preferred areas of greater understory density and exhibited higher survival rates in these habitats than individuals not using similar habitats. Young birds may be using different habitat than nesting habitat to forage, or to reduce mortality from exposure and predation. Fledglings may retreat to areas with different cover types (Streby and Andersen 2013) or greater understory density to hide from mobile predators (e.g., raptors or corvids, Anders et al. 1998). Thus, understanding how fledglings use and move within their habitat could explain survival variation from adults and survival and habitat associations become more important when managing endangered species.

The Golden-cheeked Warbler (*Setophaga chrysoparia*), is an endangered neotropical migrant that breeds only in the contiguous juniper-oak forests of central Texas (Pulich 1976, U.S. Fish and Wildlife Service 1990a, Ladd and Gass 1999). Many studies have evaluated how extensive habitat loss and fragmentation affect their demography (Jetté et al. 1998, Reidy et al. 2008, Duarte et al. 2014, Reidy et al. 2016). Based on return rates, adult survival estimates range between 0.25-0.75 among years (Duarte et al. 2014), but we lack information on post-fledging survival estimates, along with their habitat preferences and behavior. Therefore, there is a need to study the post-fledging stage of Golden-cheeked Warblers because previous estimates do not incorporate post-fledging survival. We need robust studies on Golden-cheeked Warbler post-fledging ecology, such that habitat and species management plans are based on the entirety of the breeding season—incorporate post-fledging survival, habitat use, and behaviors—to ensure the viability of Golden-cheeked Warbler populations.
The first chapter of this thesis examines the survival of Golden-cheeked Warbler fledglings and how habitat use and behaviors during the last week of life affects fledgling survival. The second chapter explores temporal changes in Golden-cheeked Warbler fledgling behaviors, parental care, and associations to habitat use to bolster understanding of post-fledging ecology and management efforts in protected areas of this species.

REFERENCES


Fink, M. L. 2003. Post-fledging ecology of juvenile Wood Thrush in fragmented and contiguous
landscapes. Ph.D. dissertation, University of Missouri, Columbia, MO, USA.


CHAPTER 2: SURVIVAL OF GOLDEN-CHEEKED WARBLER FLEDGLINGS

ABSTRACT

Understanding variation in survival rates can guide conservation efforts, especially for endangered species. Post-fledging survival in migratory songbirds can be strongly influential on a species’ population dynamics. We tracked fledglings of the endangered Golden-cheeked Warbler (Setophaga chrysoparia) in central Texas. We followed fledglings using telemetry for at least four weeks. Daily survival rate during the post-fledging stage was surprisingly high at 0.989 (95% CI = 0.975-0.995). We did not observe any age or seasonal effects on survival during the fledgling stage. The best predictor for fledgling survival was the proportion of juniper trees in the local habitat used by individuals (β: 0.057, 95% CI = -0.008-0.121). Juniper likely provides better shelter/concealment than other tree types for fledglings. Continuing to preserve habitat with a mixed forest dominated by juniper will likely sustain populations of Golden-cheeked Warblers throughout their range.

INTRODUCTION

Survival rates within the post-fledging period tend to be especially low in migratory songbirds (Cox et al. 2014, Naef-Daenzer and Grüebl 2016). In juvenile Wood Thrushes (Hylocichla mustelina) and Northern Cardinals (Cardinalis cardinalis), mortality is common during the early post-fledging period when young are relatively immobile and remain dependent on parents for food (0.95 daily survival rate, Anders et al. 1997; 0.84 daily survival rate, Ausprey and Rodewald 2011). Importantly, fledgling survival can be especially influential on the viability of endangered species with small or isolated populations (Faaborg et al. 2010, Cox et al. 2014, Todd et al. 2003). The availability of specific habitats may be key in the survival of individuals during the post-fledging period (Anders et al. 1998, Naef-Daenzer and Grüebl 2016). Fledgling songbirds frequently use habitats differing from nests (King et al. 2006). Often fledglings prefer relatively dense understory (Anders et al. 1998) and ground vegetation (Jones et al. 2017), likely because these habitats provide cover from predators. Several studies suggest that fledgling ability to find denser areas within available habitat can increase their survival (Ausprey and Rodewald 2011, King et al. 2006, Jones et al. 2017).

We studied post-fledging survival of Golden-cheeked Warblers (Setophaga chrysoparia), an endangered species that breeds only in Texas. Golden-cheeked Warblers are closely associated with mixed juniper-oak habitat found throughout the Edwards Plateau region of central Texas (Pulich 1976, U.S. Fish and Wildlife Service 1990, Ladd and Gass 1999). Golden-cheeked Warblers builds cryptic, open-cup nests constructed with peeling bark of mature, Ashe juniper (Juniperus ashei) trees – a behavior that results in specific habitat requirements. Habitat loss prompted the Golden-cheeked Warbler’s emergency listing as endangered in 1990 (USFWS 1990), and its recovery plan includes delineating breeding habitats and demography. Golden-cheeked Warblers prefer specific habitat features for nesting, and variation in habitat can affect
nest survival (Campbell 2003, Reidy et al. 2017). Nest failure is usually attributed to predation, and the most common nest predators are Texas rat snakes (*Elaphe obsolete linheimeri*; >50% nest predation) and avian species (>30% nest predation; Stake et al. 2004). After young fledge from the nest, little is known about their survival and the factors that affect Golden-cheeked Warbler fledgling survival.

Golden-cheeked Warblers are unique in that they are likely one of the earliest breeding neotropical migrants in North America (Ladd and Gass 1999). Nest initiation begins in mid-March and concludes by the end of May, while fledging begins in mid-April and continues through early June. Nest survival has been well studied for Golden-cheeked Warblers in two large populations. At the Fort Hood Military Installation (hereafter “Fort Hood”), nest period survival can range from 0.24 to 0.59 and declines as the breeding season progresses (Peak and Thompson III 2014). Nest survival estimates near Austin in comparison to Fort Hood from 2005-2006 are essentially the same (both 0.40, but 95% CI = 0.270-0.526 and 0.261-0.528, respectively; Reidy et al. 2009). During the nesting season, the suite of nest predators includes snake species, avian species, and to a lesser extent mammalian species (Stake et al. 2004). Nest survival declines as snake activity increases during the breeding season (Sperry et al. 2008), likely due to the fact that snakes are the most common nest predator for Golden-cheeked Warblers. Multiple taxa of predators also frequently depredate fledglings of other species (Anders et al. 1997, Naef-Daenzer et al. 2001, King et al. 2006, Sperry et al. 2008), but survival threats to Golden-cheeked Warbler fledglings remain unclear.

To better understand survival during post-fledging stages, the goals of this study are twofold: to document post-fledging survival throughout the breeding season and assess how habitat and behavior influence post-fledging survival. Because post-fledging survival during the
dependent stage is typically low, we expect low survival rates during the first week out of the
nest, but higher survival rates after the first week. We conducted our research within the largest
population of Golden-cheeked Warblers at the Fort Hood Military Installation; the installation

MATERIALS AND METHODS

Study Sites
We conducted fieldwork during the 2017 and 2018 breeding seasons (March-June) on the Fort
Hood Military Installation (hereafter, “Fort Hood”) in central Texas, USA. Fort Hood
encompasses large tracts of intact forest deemed high-quality forest habitat (Peak 2007). Forest
habitat consists primarily of Ashe juniper (*Juniperus ashei*), plateau live oak (*Quercus
*fusiformis*), Texas red oak (*Quercus buckleyi*), shin oak (*Quercus sinuata*), and Texas ash
(*Fraxinus texensis*). In addition to military training, land use on the base includes cattle grazing
and habitat management for recreation and conservation of endangered species (Cornelius et al.
2007). Management for the Golden-cheeked Warbler includes habitat maintenance (reduce
habitat lost to military activity below a specific threshold) and cowbird removal via trapping and
shooting (Cornelius et al. 2007). We conducted research on two study sites in 2017 and three in
2018 (Fig. 1).

Field Data Collection

*Nest Location and Monitoring*. From March through May, we collaborated with Fort Hood’s
personnel to mist net, band, and map the locations of arriving males (the latter using handheld
Garmin eTrek GPS and Trimble GPS systems). We monitored all singing males within our sites
to assess paired status and observe females with paired males. We observed behavioral cues of
females to find and monitor nests (daily) to estimate nest survival rates. We monitored nests to either failure or fledging (≥1 young leaving the nest), and when nests were about to fledge, we checked nests twice daily until fledglings were seen outside of the nest. We determined if a nest successfully fledged by empty or partially empty nests and by finding fledglings nearby being fed by the banded adult associated with that nest.

Radio Telemetry. Once fledglings were out of the nest, we hand-captured one fledgling per brood, recorded mass (± 0.1g), and banded it with one USGS band and one to three color bands to create a unique color combination. We outfitted each fledgling with a 0.31-g radio transmitter (AG337 PicoPip, Biotrack) using the backpack method (Rappole and Tipton 1991) with modifications from Streby et al. (2015). Any other siblings caught from the same nest were also recorded and banded with a USGS and color band combination to identify it from the radiotagged fledgling. Backpacks weighed ≤3% and ≤5% of each bird’s body mass in 2017 and 2018, respectively. We attached eight transmitters in 2017 and 15 transmitters in 2018, for a total of 23 transmitters. Transmitters operated for 32 days on average, and radio transmitters had a range between 800 and 1,000 m. Longer transmitter life allowed us to examine most of the dependent post-fledging period, approximately four weeks after leaving the nest (Pulich 1976). During the first week post-fledging, we tracked fledglings twice a day since the first few days after fledging are usually more sensitive to mortality for many bird species (Cox et al. 2014). In the following weeks, we tracked fledglings once daily and recorded any coincidental observations while searching for other fledglings and monitoring nests.

We tracked fledglings daily via homing methods using Yagi antennas and hand-held receivers (R1000, Communication Specialists, Orange, CA, USA) until the transmitter died or
the fledgling died. We assumed an individual was dead if 1) the transmitter was found with scratches and bite marks; 2) the transmitter was found intact, but the body or body parts (i.e., feathers) were found with the transmitter; or 3) the transmitter signal was lost when the bird was <14 days post-fledge and the fledgling was not found with the family group for 7 days afterward or within 3 km of the site. Once we located a fledgling, we observed that individual for at least 10 minutes, being careful while approaching fledglings to reduce the impact of our presence on the fledgling or adult. We recorded the transmitter frequency, color band combination, location with handheld GPS units, fledgling’s status (live or dead), estimated height of the fledgling, adult presence and distance from fledgling, adult provisioning frequency, total parental feedings by sex, sibling presence and count, start and end times of the observation, date, and any additional notes about condition of the fledgling. We tracked fledglings daily in a randomized order. We tracked each fledgling either in the morning or afternoon, and we alternated morning and afternoon tracking each day for each bird. If we did not detect a signal in the area of the previous location, we scanned adjacent vegetation up to 100 m away from that location for no longer than 30 min. If we did not find the fledgling, we used a vehicle to circle the area via roads, searching an area up to 3 km. One fledgling moved into an inaccessible area (i.e., active archery hunting area) on day 28 preventing us from tracking this individual until the battery or individual died.

*Habitat Measurements.* To characterize habitat at the last known location before mortalities, we took vegetation measurements following a method modified from the BBIRD Field Protocol (Martin et al. 1997) for at least three weeks after fledging. We sampled vegetation approximately one week after the original fledgling observation at each location to reduce potential disturbance. Each sampling point was the center of a 5 m radius circular plot. At each point, we estimated
canopy cover 1 m from the center using a concave densiometer and estimated vertical vegetation coverage 5 m from the center using a canvas coverboard in each cardinal direction understory. We used a coverboard similar to that used by Jenkins et al. (2016). The coverboard was painted with a checkerboard pattern divided into three regions: low (0-0.3 m), middle (0.3-1.0 m), and upper (1.0-2.0 m). We counted the number of checker-squares in each region covered ≥50% by green vegetation. We visually estimated herbaceous ground cover up to 30 cm in height in each quadrant of the circular plot to the nearest five percent. Finally, we recorded tree species and measured diameter at breast height (4.5 ft, “DBH”) of all trees within the circular plot that were ≥ 3 cm. Due to logistical constraints, we could not sample every location after three weeks of age, but we believe our vegetation sampling of at least the first three weeks adequate for modeling habitat associations during the dependent fledgling stage.

Modeling and Analyses

To reduce the number of correlated variables, we ran a Principal Components Analysis (PCA) on the 13 vegetation variables (Table A2). We retained two principal components that explained 26.0% and 19.2% of the total sample variation, respectively. Factor loadings indicated that Component 1 characterized density of the understory (via coverboard measurements and ground cover estimates, hereafter “understory density”) while Component 2 characterized tree canopy cover (mean size of trees and canopy cover, hereafter “canopy cover”). To characterize habitat use before fledgling death, we took the factor score of each fledgling on the last day alive or last measurement available and calculated the mean proportion of each tree type category and fledgling height during the last week the fledgling was alive. We used these mean values as covariates to explain fledgling survival. There is most likely temporal variation within habitat
use over time and using the last week of data available for each individual is our attempt to capture how habitat variation affects survival.

**Fledgling Survival Models.** To estimate fledgling survival, we used a step-wise approach with known-fate models in Program MARK. We converted radio telemetry data into daily encounter histories for each fledgling. One individual was depredated within 24 h of tagging was censored from later steps in the analysis using individual covariates since we did not have habitat measurements for this individual nor a final death location. First, we used a known-fate model with staggered entry to account for individuals entering the monitored population throughout the season. We used this approach to find any age or seasonality effects on survival. With this design, we created a constant survival model and various age-structure models based on observed mortality events.

In the first model set, we used a staggered entry design with the first parameter estimate fixed to 1. The staggered entry design accounted for individuals entering the population throughout the season. Constant survival was the top model, so our second step was to test individual habitat and behavior covariates on survival. We used a same-entry design for this model set since day of season did not affect fledgling survival. We tested univariate models of year, sex of parental care (majority of care by male, female or split between both parents), average height of the fledgling, last height the fledgling was observed, nest height of the fledgling, mass at tagging, total number of siblings, the top two components from our PCA (understory density and canopy cover), and three separate proportions of tree types in the habitat (juniper species, oak species, and non-oak deciduous species). We also tested these individual covariates against a null and global model. The global model with the maximum number of
parameters did not converge because of low sample sizes and few birds dying (eight), so we did not include it in the candidate models.

RESULTS
We attached transmitters to 23 fledglings; 8 in 2017 and 15 in 2018. We tracked fledglings between 1-39 days, but on average we tracked fledglings 28.8 ± 2.5 days. Surviving fledglings were tracked for 32 days on average, approximately the life of the battery. Fledging dates for our study period ranged from April 17 to May 21. We confirmed the status of fledglings alive or dead for 552 observations. We recorded eight mortalities; 2 in 2017, and 6 in 2018. Three individuals in 2018 died directly after a substantial weather event (rain lasting 24 hours followed by cool temperatures) one of which the body was found intact (assumed exposure mortality), while the other two were not found intact. While the exact cause of mortality for those two individuals is unclear, it seems likely that exposure or predation during or after storms is a substantial source of mortality. We found damaged transmitters for two additional individuals and the final three were assumed depredated based on those individuals disappearing at a young age and not present with the adults or in a 3 km radius of the site.

In our model set to determine age and seasonality effects during post-fledging, two of our age and seasonality models resulted in ΔAICc <2, but the constant survival model held the most weight (Table B3). Daily survival rate (DSR) under the constant model was 0.985 (95% CI = 0.971-0.993) and period survival for the average 28-day observation period was 0.654 (95% CI = 0.442-0.815).

In the model set investigating the role of habitat for fledgling survival, the proportion of juniper appeared to be the most important factor affecting DSR (Table 1). As the amount of
juniper increased, survival also increased slightly (12.5% increase in period survival for every 20% increase in juniper composition; Fig. 2). DSR for the top model was 0.989 (95% CI = 0.975-0.995) with 28-day period survival rate of 0.734 (95% CI = 0.492-0.869). There was greater uncertainty (i.e., wider confidence intervals) in DSR when juniper proportion was low but individuals that died were found in habitat with less juniper (Fig. 3). The beta 95% confidence interval overlapped 0 for the top model most likely due to our small sample size (Table 1).

**DISCUSSION**

We have provided the first estimates for Golden-cheeked Warbler post-fledging survival. Golden-cheeked Warbler fledgling survival estimates were much higher than expected in comparison to other species’ fledglings (Cox et al. 2014, Naef-Daenzer et al. 2016). Golden-cheeked Warbler fledgling survival (0.734) was in the upper range of post-fledging survival estimates for other songbirds (0.23-0.87; Cox et al. 2014). Fledglings had high period (28-day) survival and did not exhibit any declines due to age or day of the season, commonly referred to as “bottleneck” effects (Naef-Daenzer et al. 2016).

We did not record fledgling predators, but nesting studies have found that Texas Rat Snakes and avian predators were the most common causes of nest mortality (Stake et al. 2004). We suggest that predation of fledglings is most likely due to avian predators. Avian predators can vary across urban-to-rural gradients (Reidy et al. 2009) and consist of American crows (*Corvus brachyrhynchos*), Woodhouse’s Scrub-Jay (*Aphelocoma woodhouseii*; formerly Western Scrub Jay) and Cooper’s Hawks (*Accipiter cooperii*), for Golden-cheeked Warblers (Stake et al. 2004). Most transmitters were found with damage (i.e., bite-marks, scratches, bent antenna) and
some body feathers indicating raptor predation as the main predation threat for fledglings. None of the transmitters were found in fecal material, which we assume would indicate snake predation. Texas Rat Snakes may then pose a higher threat to nesting success than fledgling survival. Although we did not see predation events, we assume fledglings face higher survival risks from avian predators. Fledglings are more mobile – able to escape terrestrial predators (e.g., snakes) – once out of the nest, and more aerial predators (i.e., raptors) may be a more significant threat to fledglings (Anders et al. 1997).

Additionally, the three mortalities after the substantial rainstorm in 2018 indicate that long-lasting weather events are a potential threat to survival. One individual was four days out of the nest and succumbed to exposure as it was located on the ground with saturated body feathers. Recently fledged young have poor thermoregulatory skills, which may have been more important for this individual’s survival. The low temperatures following the rain could have exaggerated the effects of the fledgling being unable to warm itself, especially because of dampened body feathers from rain. While highly unlikely, the other two individual deaths could have been predated during or right after the storm, but it is more likely that they were scavenged after dying from exposure or starvation. The latter two fledglings were both 14 days out of the nest on separate sites, more capable of flying to escape predators. Those two individuals could have been weakened or slowed by wet plumage and less able to escape predators. All three individuals were cared for by the male, which may result in lower energy input from the parent since males typically feed fledglings less (see Ch. 3) lowering the fledgling’s ability to keep warm and/or avoid predators. Adults may also not be feeding fledglings during heavy rain, which could cause fledglings to starve during long-lasting, heavy rains. Dittmar et al. (2014) also found that weather can be a major threat to survival for Black-capped Vireo juveniles on Fort Hood as three
individuals died directly after a storm lasting several days. If a single severe weather event can cause multiple mortalities, then total mortalities may increase as climate change will likely lead to more severe weather in the future (Greenough et al. 2001). Golden-cheeked Warbler fledglings still survived at a much higher rate than expected, suggesting that the post-fledging stage is currently not limiting the Golden-cheeked Warbler population at Fort Hood.

Another factor to consider is that Fort Hood contains a large expanse of seemingly high-quality Golden-cheeked Warbler habitat (Peak 2007, Reidy et al. 2018), so adults and fledglings may have access to plentiful habitat and abundant prey resources. Fledgling survival related to habitat appears to be less influential most likely because of widespread habitat available on Fort Hood. We found a positive relationship between daily survival rate to the proportion of juniper in the habitat, but fledglings do not substantially change general habitat use over time (see Trumbo Ch. 2). Dense juniper could provide resources needed for fledgling survival by acting as a shelter from predators and weather. We occasionally observed fledglings flying to and orienting themselves under thicker juniper tree branches when light rain occurred during our behavioral observations. This behavior could prevent exposure to plumage-drenching rains that could otherwise lower fledgling mobility. Fledglings appear to stay within nesting habitat, so other factors besides habitat features (i.e., behavior) may influence their survival from predation. Generally, nests can have a higher likelihood of predation since they are stationary and parental activity and audible nestlings can attract more predators (Haskell 1994). In contrast, a fledgling may remain quieter in response to adults (less begging) and predators (Magrath et al. 2006) during its first week out of the nest and relocate itself to avoid predators (to dense vegetation).

In regions where Golden-cheeked Warbler habitat is more fragmented and of lower quality (more edge habitat; Reidy et al. 2009), nest and fledging survival may not be as high.
Predator suites for Golden-cheeked Warbler nests vary on urban-rural gradients (Reidy et al. 2009), and these predators could vary in abundance depending on habitat connectivity (e.g., Texas Rat Snakes; Sperry et al. 2008) and timing of the breeding season. Golden-cheeked Warbler fledglings at Fort Hood have higher survival rates that fledglings of many other species (0.23 period survival in Hooded Warblers, Rush and Stutchbury 2008; 0.35 period survival in Lark Buntins Calamospiza melanocorys, Yackel Adams 2006) and their survival rate is at the higher end of the range reported by Cox et al. (2014).

**MANAGEMENT IMPLICATIONS**

When selecting areas of habitat to conserve or manage for Golden-cheeked Warblers it is extremely important to consider the continuity and tree compositions of that habitat for both nesting requirements and success and post-fledging survival. Also, because dependent fledgling survival is much higher than apparent survival estimates used in population viability analyses (Duarte et al. 2016), there need to be more robust survival estimates examining dependent and independent fledgling survival, juvenile survival during migration to and from the wintering grounds, and juvenile wintering ground survival. Because dependent fledgling survival is higher than overall juvenile apparent survival estimates (Duarte et al. 2014, 2016), we may miss possible variation in juvenile survival rates where population bottlenecks may occur. To continue effective conservation of Golden-cheeked Warblers we recommend that further study of juvenile demographics occur during independence and at the wintering grounds. We recognize limitations in the ability to study this period, but as technology advances, we will hopefully have the tools to further our understanding of full life-cycle demographics for Golden-cheeked Warblers.
Additionally, continued protection of large, connected juniper-oak forest habitat similar to Fort Hood will be vital for the continued survival of this species during the breeding season.
Table 1. This model set shows results for habitat and behavioral covariates that affect survival of fledglings. The constant model represents no habitat or behavior covariate effects on survival. The table shows AICc, Delta AICc, AICc weight, model likelihood, number of parameters, deviance, estimated coefficients ($\beta$), and confidence intervals.

<table>
<thead>
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<th>Model</th>
<th>AICc</th>
<th>Delta AICc</th>
<th>AICc Weights</th>
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<th>Num. Par</th>
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<td>Understory Density (PC1)</td>
<td>77.609</td>
<td>1.420</td>
<td>0.099</td>
<td>0.492</td>
<td>2</td>
<td>73.587</td>
<td>-0.578</td>
<td>-1.554 - 0.398</td>
</tr>
<tr>
<td>Mass</td>
<td>77.633</td>
<td>1.444</td>
<td>0.098</td>
<td>0.486</td>
<td>2</td>
<td>73.611</td>
<td>1.031</td>
<td>-0.612 - 2.674</td>
</tr>
<tr>
<td>Total Siblings</td>
<td>78.136</td>
<td>1.947</td>
<td>0.076</td>
<td>0.378</td>
<td>2</td>
<td>74.114</td>
<td>0.390</td>
<td>-0.382 - 1.162</td>
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<tr>
<td>Average Height during Last Week</td>
<td>78.194</td>
<td>2.005</td>
<td>0.074</td>
<td>0.367</td>
<td>2</td>
<td>74.172</td>
<td>-0.682</td>
<td>-2.046 - 0.681</td>
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<tr>
<td>Year</td>
<td>78.378</td>
<td>2.189</td>
<td>0.068</td>
<td>0.335</td>
<td>2</td>
<td>74.356</td>
<td>-0.665</td>
<td>-2.314 - 0.984</td>
</tr>
<tr>
<td>Sex of Parental Care</td>
<td>78.394</td>
<td>2.205</td>
<td>0.067</td>
<td>0.332</td>
<td>2</td>
<td>74.372</td>
<td>-0.361</td>
<td>-1.213 - 0.492</td>
</tr>
<tr>
<td>Last Known Height</td>
<td>78.534</td>
<td>2.345</td>
<td>0.062</td>
<td>0.310</td>
<td>2</td>
<td>74.512</td>
<td>-0.132</td>
<td>-0.483 - 0.219</td>
</tr>
<tr>
<td>Canopy Cover (PC2)</td>
<td>78.538</td>
<td>2.349</td>
<td>0.062</td>
<td>0.309</td>
<td>2</td>
<td>74.516</td>
<td>-0.251</td>
<td>-0.934 - 0.432</td>
</tr>
<tr>
<td>Nest Height</td>
<td>78.619</td>
<td>2.430</td>
<td>0.060</td>
<td>0.297</td>
<td>2</td>
<td>74.597</td>
<td>-0.139</td>
<td>-0.534 - 0.256</td>
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</table>
Figure 1. A map outlining the extent of our study area, Fort Hood Military Installation. Yellow delineates Golden-cheeked Warbler habitat and the other colors indicate our study sites during 2017 and 2018. Adapted from Macey and Grigsby (2018, annual report).
Figure 2. The model for proportion of juniper in the habitat used by fledglings during 2017-2018. As the proportion of juniper increases fledgling daily survival rate (DSR) also appears to slightly increase. This model held the most weight in the final model set (\( w_i = 0.202 \)). Mean DSR was 0.989 (95% CI = 0.975-0.995) and the beta estimate was 0.057 (95% CI = -0.008 to 0.121). LCI is the lower confidence interval and UCI is the upper confidence interval.
Figure 3. The proportion of oak, juniper, and non-oak deciduous habitat in which birds survive or die. More fledglings died in oak habitat than in juniper habitat. Standard error bars are shown.
REFERENCES


Cox, A. W., F. R. Thompson III, A. S. Cox, and J. Faaborg. 2014. Post-fledging survival in


warbler (Dendroica chrysoparia) on Fort Hood, Texas. USACERL Technical Report.


CHAPTER 3: FLEDGLING BEHAVIORS, ADULT PARENTAL CARE, AND HABITAT USE OF GOLDEN-CHEEKED WARBLERS

ABSTRACT

Most juvenile birds are dependent on their parents for food for multiple days after fledging the nest but quickly become mobile and nutritionally independent. As parental care declines fledglings (young from the day they leave the nest until 32 days), must then support themselves by finding appropriate foraging habitat that also offers protection from predators. The post-fledging period of birds is a time of relatively high mortality and understanding the factors that lead to high mortality is especially important for endangered species. We documented the behavior of fledgling Golden-cheeked Warblers (i.e., foraging, movement, parental care; *Setophaga chrysoparia*) and investigated the relationships with habitat (i.e., canopy cover, vegetation density, tree composition) during the 2017 and 2018 breeding seasons. Fledglings foraged more and moved greater distances as they aged, and they also increased begging as they aged. Parents fed fledglings for at least four weeks after leaving the nest, however, the number of feedings per hour decreased, with a marked change around 21 days of age. Fledglings begin to forage for themselves the second week out of the nest and increased foraging rates as they aged. Parents split the brood at fledging and they remained separated for an average of 12 days before the fledglings rejoined. Parents fed fledglings 12.38 ± 0.44 times per hour, and females fed more often early in the life of a fledgling, but decreased feeding rates over time, while males maintained a constant feeding rate as the fledglings aged. General habitat (habitat within 10 meters of the radio-tagged individual) of fledglings was approximately 70/30% juniper-oak in tree composition, but fledglings changed their focal tree usage from junipers to oaks as they aged. Fledglings were also more successful at foraging in oaks. Adult Golden-cheeked Warblers
are a habitat specialist (juniper-oak forest), and it appears that fledglings use the same habitat; however, oaks may be particularly important for foraging early in the life of Golden-cheeked Warblers.

INTRODUCTION

Understanding how avian behaviors are influenced by the environment is crucial for understanding how to conserve appropriate habitat for sustaining populations (Faaborg et al. 2010). Much is known about which habitat adult birds prefer to nest in (Holmes 1981, Faaborg et al. 2010), and the habitats that promote the greatest nest success (Martin 1993, Robinson et al. 1995, Batáry and Báldi 2004, Bakermans et al. 2012). One aspect that is also important to understanding the behavior and reproductive success of birds is post-fledging behavior. Upon fledging from their nest birds rapidly develop and begin exhibiting behaviors such as long-distance movements and foraging. Fledglings depend on parents immediately after leaving the nest and presumably remain close to the nest and in habitats similar to where the adults placed the nest before dispersing (movements greater than 600 m away from the nest; Jenkins et al. 2017a). As the fledglings age, they can move to different habitats than adults use for nesting (King et al. 2006) potentially to habitats where they can forage independently (Sullivan 1989) and find cover from predators (Jenkins et al. 2017a). Exploring relationships among fledgling behavior, parental care, and habitat use of fledglings may prove useful in understanding this critical period in a species’ life.

Habitat types (e.g., forest, shrub, edge) differ between nesting and fledging stages for several species (King et al. 2006, Burke et al. 2017). As fledglings age, they select habitat that may conceal them from predators and/or improve opportunities for foraging (Dittmar et al. 2014,
Parental care may complicate habitat choices for fledglings as they may need to stay near the nest to receive parental care. Fledglings can begin to forage by the first or second week in some species (Marchetti and Price 1989, Weathers and Sullivan 1989, Wheelwright and Templeton 2003), but are unlikely to fully support themselves (Weathers and Sullivan 1989). As fledglings begin to forage on their own, they may have the opportunities to use different habitats. Habitat use between recently fledged young, (still under parental care) and after fledglings begin foraging but are not nutritionally independent, most likely differ and continue to change as they age (Anders et al. 1998, King et al. 2006). This may be a critical transition point during which fledglings may move to new habitats and exhibit different behaviors, all while attempting to avoid predators, forage, and stay near enough to parents to receive parental care. Finding what habitat features are important to fledglings can help us better understand their ecology and conserve appropriate habitat to increase survival of not only adults and nests, but also fledglings.

We studied the behavior of Golden-cheeked Warbler fledglings (from fledging to 35 days old), parents, and the habitat use of fledglings (*Setophaga chrysoparia*). Listed as endangered in 1990 due to habitat loss and fragmentation (USFWS 1990), the Golden-cheeked Warbler is a neotropical migrant that breeds only within central Texas (Pulich 1976, Ladd and Gass 1999). The Golden-cheeked Warbler breeds relatively early and is strictly tied to mature juniper-oak forests since it constructs most of its nest from the peeling bark of older Ashe juniper (*Juniperus ashei*, hereafter “juniper”) trees. General nesting habitat is dominated by juniper followed by oak species (Genus *Quercus*). Golden-cheeked Warblers typically place nests in juniper trees but also multiple oak species and other deciduous species (Ladd and Gass 1999). Adults forage in oaks early in the breeding season when lepidopteran larvae are abundant on freshly budding trees and
forage among junipers as arthropods increase in abundance later in the breeding season (Quinn 2000, Marshall et al. 2013). Many studies have extensively characterized behaviors and breeding habitat for adult Golden-cheeked Warblers (Dearborn and Sanchez 2001, Stake et al. 2004, Peak and Thompson III 2014, Reidy et al. 2017) as outlined in their recovery plan (USFWS 1992, 2014); however, information is lacking on fledgling behaviors and habitat during post-fledging stages.

Our overarching goal was to better understand changes in post-fledging behaviors, parental care, and habitat use over time for the Golden-cheeked Warbler. Using radio telemetry, behavioral observations, and vegetation sampling we address three questions about their post-fledging ecology: 1) How do fledgling behaviors such as movement, foraging rates, and begging change as they age (i.e., fledgling development)?, 2) How do parental care and parental behavior change with fledgling age?, 3) Do fledglings change their habitat use as they age and are these changes due to fledgling foraging success and/or parental care?

MATERIALS AND METHODS

Study Sites

We studied Golden-cheeked Warbler behavior during 2017 and 2018 breeding seasons on the Fort Hood Military Installation (hereafter, “Fort Hood”) in central Texas, USA. The primary use of land on Fort Hood is military training, followed by cattle grazing and fish and wildlife habitat management for recreation and conservation (Cornelius et al. 2007). Fort Hood utilizes multiple management techniques for endangered species management, including habitat restoration and Brown-headed Cowbird (Molothrus ater) removal via trapping and shooting (Cornelius et al. 2007). Fort Hood encompasses large tracts of intact forest throughout the installation. Forest
habitat consists of mostly juniper, plateau live oak (*Quercus fusiformis*), Texas red oak (*Quercus buckleyi*), shin oak (*Quercus sinuata*), and Texas ash (*Fraxinus texensis*).

**Field Data Collection**

*Radio Telemetry.* Upon fledging, we hand-captured one individual per brood and banded it with one USGS and one to three color bands to create a unique color combination. We outfitted each fledgling with a 0.31-g radio transmitter (Lotek PicoPip) using the backpack method (Rappole and Tipton 1991) with modifications from Streby et al. (2015). Any other siblings caught from the same nest were also banded with a USGS and color band combination to identify it separately from the transmittered fledgling. Backpacks weighed ≤3% and ≤5% of each bird’s body mass in 2017 and 2018, respectively. We attached eight transmitters in 2017 and 15 transmitters in 2018, for a total of 23 transmitters.

We tracked fledglings daily, homing directly to each individual using Yagi antennas and hand-held receivers (R-1000, Communication Specialists, CA, USA) until the transmitter died, or the fledgling died. The life expectancy of the transmitters was 32 days on average. This allowed us to examine all of the dependent post-fledging period (Pulich 1976). We were able to detect the radio transmitters to a range of 800 to 1,000 m. We located fledglings once daily and recorded additional information if we had incidental observations while searching for other fledglings. We assumed an individual was dead if 1) the transmitter was found with scratches and bite marks; 2) the transmitter was found intact, but the body or body parts (i.e., feathers) were found with the transmitter; and 3) the transmitter signal was lost when the bird was <14 days post-fledge and the fledgling was not found with the family group for 7 days afterward or within 3 km of the site.
Once we located a fledgling, we observed that individual for at least 10 minutes, being careful to reduce the impact of our presence on fledgling or adult behavior. We were able to determine which color-banded adults fed which individuals within the brood, allowing us to document brood division. We recorded the transmitter frequency, color band combination, location with handheld GPS units, fledgling’s status (live or dead), estimated height of the fledgling, tree species the fledgling was found in (hereafter “focal tree”), adult presence, adult provisioning frequency (by parent), successful foraging event by fledglings, sibling presence and count, start and end times of the observation, date, and any additional notes about condition of the fledgling. For successful fledgling foraging attempts, we did not record individual prey items since we were usually not close enough to the fledgling to accurately identify individual prey, but we did observe fledglings capturing various types of arthropods (i.e., caterpillars, moths, flies, walking sticks, ants). We tracked fledglings daily in a randomized order. If a signal was not detected in the area from the previous location, we scanned adjacent vegetation up to 100 m away from that location for no longer than 30 min. If we did not find the fledgling, we used a vehicle to circle the area via roads, searching an area up to 3 km away from the previous location of that fledgling. We were unable to track one fledgling who moved into an inaccessible area (i.e., active archery hunting area) on day 28.

**Activity Observations.** In 2018, we performed 10-minute detailed activity observations once daily for at least the first three weeks after tagging a fledgling. During these sessions, we used a stopwatch to record start and end times for behaviors to the nearest second. Behaviors were categorized with a number for perching/resting, flight (aerial movement ≥ 2 m), movement (non-flight hopping), active foraging, preening, begging, singing, and being fed by parents. Up to
three behaviors could occur at one time (i.e., perching, begging, fed by a parent) so we recorded co-occurring behaviors.

_Habitat Measurements._ To characterize general fledgling habitat use and to compare with available habitat we took vegetation measurements at each fledgling location and a paired random location in a random azimuthal direction 20-50 m away from the fledgling location. We followed a vegetation sampling method modified from the BBIRD Field Protocol (Martin et al. 1997) for at least three weeks after fledging. We sampled vegetation approximately one week after the original fledgling observation at each location to reduce potential disturbance to the fledglings. Each fledgling and random location was the center of a 10 m diameter circular plot. At each location, we estimated canopy cover 1 m from the location in each cardinal direction using a concave densitometer. We also estimated understory vegetation density (hereafter “vegetation density”) 5 m from the center using a canvas coverboard in each cardinal direction. We used a coverboard similar to that used by Jenkins et al. (2017a). The coverboard was painted with a checkerboard pattern divided into three regions: low (0-0.3 m), middle (0.3-1.0 m), and upper (1.0-2.0 m). We counted the number of checker-squares in each region covered ≥ 50% by green vegetation. We visually estimated herbaceous ground cover up to 30 cm in height in each quadrant of the circular plot to the nearest five percent. Finally, we recorded tree species and measured diameter at breast height (4.5 ft, “DBH”) of all trees within the circular plot that were ≥ 3 cm. We quantified these variables because fledglings may be using a wide range of vertical structure in forest habitat. Due to logistical constraints, we could not sample every location after three weeks of age, but we believe our vegetation sampling period to be adequate for modeling habitat associations during the dependent fledgling stage.
Statistical Analysis

We performed all analyses using R version 3.5.2 “Eggshell Igloo” (R Core Team 2018). To visualize finer scale trends during the observation period we utilized “loess” smoothing on data for activity rates, movement distances, total parental provisioning rates, and focal tree use probabilities. All factors were considered statistically significant at $P \leq 0.050$, and marginally significant at $P \leq 0.070$.

Individual Fledgling Behaviors as Fledglings Develop

To assess within fledgling variation in behavior over time we used general linear mixed models for activity rates (proportion of time spent in individual behaviors). We derived each fledgling’s daily activity rates as a proportion (%) of the 10 min observation period, so activity rates for all behaviors do not add up to 100%. Activity rates included percent time spent perching, moving, begging, flying, and foraging. Each model consisted of one behavior as the response variable with age as the predictor variable. We used the frequency of the fledgling’s transmitter as the individual identity to account for non-independence in our models.

Parental Care and Behavior with Fledgling Development

To assess variation in parental care over time we used general linear mixed models for continuous response variables (feedings per hour). We modeled the response of total hourly provisioning rates of both parents by age of fledgling. We also modeled the provisioning rates by sex of the parent with fledgling age, the response of total hourly provisioning rates to the amount of time the fledgling spent begging, and the provisioning rates by sex of parent over time (Julian
date). Finally, we modeled whether fledgling foraging rate was affected by parental care (hourly feeding rates)

_Habitat Associations with Fledgling Behavior and Parental Care_

We compared used and available habitat locations to understand if fledglings are using areas with specific vegetation structures and compositions. We used a student’s t-test to compare means between focal and random vegetation variables over the entire sampling period.

To understand habitat associations with fledgling activity rates and parental care we used general linear mixed models. We first modeled change in general habitat use by fledgling age to understand trends with fledgling development. We then modeled responses in fledgling behavior (including activity rates) and parental behavior and care to changes in general habitat. For fledgling hourly foraging rates in response to their focal tree, we used a generalized linear mixed model with a Poisson distribution to account for multiple zeros in the data.

**RESULTS**

**Changes in Fledgling Behavior with Development**

On average, we observed fledglings for 12.45 ± 0.21 min per observation, resulting in ~146 hours of fledgling observations. Distance from the fledgling’s nest and the distance from the previous day’s observation increased with age ($P < 0.001$; $n = 701$ and $n = 666$, respectively; Fig. 4). On average, fledglings moved 44.20 ± 2.61 m between daily observations during the first week, but by the fourth week moved 252.22 ± 35.86 m between daily observations. As fledglings aged, they became more active (i.e., movement, foraging, and flight; Fig. 5) and increased
successful foraging rates \((P < 0.001, t = 4.70; \text{Fig. 6})\). Fledglings foraging rates were not affected by parental feeding rates \((P = 0.43, t = -0.79, n = 705)\).

**Changes in Parental Care and Behavior with Fledgling Development**

One parent was often more closely associated with a given fledgling(s) \((93.18 \pm 0.01 \% \text{ of observations})\) or feeding the fledgling \((76.50 \pm 0.02 \% \text{ of observations; \text{Fig. 7}})\). The parents divide the brood immediately after fledging and on average the siblings were brought back together (rejoined) at 12.19 days after fledging. Parental hourly feeding rates declined over time and had a marked drop when the fledgling was 21 days old \((P < 0.001, F = 17.06, n = 705, \text{Fig. 8a})\). On average parents fed fledglings 13.2 ± 0.46 times per hour. Females fed fledglings more than males \((P < 0.001, t = 8.59)\), but females decreased their hourly feeding rates as fledglings aged \((P < 0.001, F = 41.29, \text{Fig. 8b})\). Parents fed fledglings regardless of the distance away from their nest \((P = 0.974, n = 704)\), and increased feeding rates as fledglings spent more time begging \((P < 0.001, F = 29.79, \text{Fig. 8c})\), but still fed young less as they aged. After the third week of age, females had similar feeding rates to males \((4.37 \pm 1.12 \text{ and } 4.02 \pm 1.15 \text{ feedings per hour, respectively; } P = 0.828)\) and males did not change feeding rates when broods rejoined \((P = 0.117, F = 2.46)\).

**Associations between Habitat Use and Fledgling Behavior and Parental Care**

Fledglings used specific habitat attributes that differed from random samples among ground cover, canopy cover, vegetation density, oak proportion and non-oak deciduous proportion \((P < 0.050, \text{Fig. 9})\). Mean percent differences between used and random sample points throughout the observation period are shown in Figure 9.
The fledgling’s focal tree species changed over time, from juniper to oak (juniper: \( P < 0.001, F = 51.15, n = 706 \) and oak: \( P < 0.001, F = 30.13, n = 706 \); Fig. 10). Fledglings decreased general juniper habitat use \( (P = 0.014, n = 563) \) and increased general oak/deciduous habitat use over time \( (P = 0.014, n = 563) \); Fig. 11). As fledglings aged, they used areas with greater ground cover \( (P = 0.002, n = 563) \) and areas with greater vegetation density \( (P = 0.037, n = 563) \); however, the amount of canopy cover did not change \( (P = 0.375, n = 563) \). Fledglings spent more time perched in areas with greater canopy cover \( (P = 0.017, t = 2.42, n = 227) \) and begged less in areas with greater canopy cover \( (P = 0.010, t = -2.61, n = 227) \); Fig. 12). Parental feeding rates were not influenced by tree type proportions in the general habitat, but fledglings foraged more successfully in general habitat with less juniper and more oak (Juniper: \( P = 0.040, t = -2.06, n = 563 \); Oak: \( P = 0.070, t = 0.01, n = 563 \); Fig. 13). Foraging rate was also significantly influenced by focal tree use. Fledglings were more successful while foraging in oak compared to junipers \( (P < 0.001); \) Juniper: \( z\)-value = -7.132, Oak: \( z\)-value = 5.658). Fledglings captured almost twice as much prey per hour when using oaks instead of junipers (Juniper: 9.94 ± 0.34 and Oak: 18.10 ± 4.10 prey captures per hour).

**DISCUSSION**

Although Golden-cheeked Warblers are a generally well-studied system for breeding ecology, this is the first research to investigate the behaviors of fledglings. As is true in many altricial birds upon leaving the nest, Golden-cheeked Warbler fledglings become substantially more active as they age, and parents reduce provisioning rates to young. Fledglings still appear to at partially rely on parents longer than expected. Fledglings also modified their habitat potentially to avoid predators and find appropriate foraging habitat.
Initially, fledglings may remain inactive to reduce detection by predators (Magrath et al. 2006) early after leaving the nest. Since fledglings have poor mobility the first week out of the nest, they may be more responsive to alarm calls from parents (Magrath et al. 2006) and stay quiet (not beg). Also, as might be expected, the parents reduced the number of feeding trips as the fledglings aged. We notice that at approximately day 21 there was a marked reduction in feeding rates similar to other species that reduce or stop feeding by the second or third week (Weathers and Sullivan 1989, Wheelwright et al. 2003, Middleton et al. 2007). Interestingly, while the number of parental feeding rates declined, begging of the fledglings continued. This could be due to the fact that we observed parental feeding rates increase as time spent begging increased. It should be noted that we were not always able to determine if begging was elicited by an adult approaching with food or if begging resulted in an adult attending a fledgling. Since many adult birds cannot directly assess the quality or “hunger” of a fledgling, they will feed a fledgling more often if it begs (Trivers 1981). The fledgling may see a benefit to begging if it uses less energy to beg and receive food than it would to forage for prey itself. Fledglings, however, could incur a cost if continued begged attracts the attention of nearby predators (Trivers 1981, Magrath et al. 2006), so decreasing begging and increasing foraging might be advantageous to survival during the first week for fledging Golden-cheeked Warblers. Golden-cheeked Warblers fledglings spent up to 60% of their time foraging after the fourth week out of the nest, but it was not affected by the decline in parental provisioning rates.

The parents fed fledglings for at least 35 days out of the nest, which is longer than the dependent period first noted by Pulich (1976). The duration of the dependent period in temperate songbird species can vary between two (Leonard et al. 1991, Middleton et al. 2007) and six weeks (Sullivan 1989, Ogden and Stutchbury 1997), but longer post-fledging care can improve
fledgling survival (Grüebler and Naef-Daenzer 2010, Dybala et al. 2013). Golden-cheeked Warblers split the brood between adults, and this behavior has also been noted in other species (Black-throated Blue Warbler, *Setophaga caerulescens*, Black 1975; Hooded Warbler, *Setophaga citrina*, Odgen and Stutchbury 1997; Savannah Sparrow, *Passerculus sandwichensis*, Wheelwright et al. 2003). We found that fledgling survival was relatively high in this system regardless of the sex of parental care (Chapter 2), but we expect that adults are splitting broods to increase the chances of at least some of the fledglings surviving if attacked by a predator (Smith 1978, McLaughlin and Montgomerie 1985, Tarwater and Brawn 2008). It may be that the adults “rejoin” the brood around 12 days of age because the fledglings are more mobile, and the risk of predation is reduced. Bringing the fledglings together at this age would be less risky than keeping them together upon fledging since a predator could prey on all the fledglings in one predation event. Rejoining the brood would also allow one parent to feed multiple or all fledglings easier (McLaughling and Montgomerie 1985) and is likely why we observed differences in male and female feeding rates.

We observed sex-specific differences in parental feeding rates which can vary among species (Ogden and Stutchbury 1997; Middleton et al. 2007). Female Golden-cheeked Warblers decreased provisioning rates as the fledgling aged, matching feeding rates of males after the third week. Females may invest more resources in young during the first few weeks to bolster survival and reduce feeding rates to initiate a second nest (or double brood). In Western Bluebirds (*Sialia mexicana*) and Hooded Warblers, the female often leaves all the fledglings to be cared for by the male once she initiates a second nest (With and Balda 1990, Ogden and Stutchbury 1997). Delaying when the brood rejoins and initiating a second nest until fledglings are more mobile and start to forage would allow the male to take care of all the fledglings easier and reduce the
likelihood of losing the entire brood to a single predation event. We saw a similar pattern in our system where the male would take responsibility for feeding the entire brood by the third week if the female initiated a second nest. Golden-cheeked Warbler females may also be gathering food and resources for themselves to begin migration, reducing feeding visits to the young. Typically, adult Golden-cheeked Warblers begin southerly migration between mid-June and late July (Ladd and Gass 1999) which is earlier than most breeding songbirds. Since female songbirds are likely contributing more energetically to reproduction (nest-building, egg-laying, incubation, etc.; Mainwaring and Hartley 2013, Walsberg 1983, Carey 1996), they may have depleted energy resources after nesting. The female may reduce provisioning as the end of the breeding season approaches (late May-early June) to replenish her energy reserves. While males can take care of the entire brood, even though they generally feed the young less, they exhibit stable feeding rates regardless of the number of siblings when broods rejoin (usually up to four fledglings).

Fledglings change their habitat use over time, as they are moving to areas with more oak/deciduous forest and specifically using oak trees. Fledgling survival was positively influenced by increasing amounts of juniper in the habitat (Ch. 2) and is likely why we saw fledglings using juniper trees more often when they first fledged. As fledglings aged, they switched focal tree use to oaks and moved to areas that had slightly more oak in the surrounding habitat. The importance of oaks is highlighted by the fact that fledglings are more successful at foraging in areas with more oak trees and while in oaks. Oaks may have less structurally complex leaf structures than junipers (junipers have denser branches and needles) allowing for easier foraging for fledglings and may provide higher abundances of arthropods, although arthropods possibly decline among oak species as the breeding season progresses (Marshall et al. 2013). Adult Golden-cheeked Warblers appear to forage more in junipers by May (Marshall et
al. 2013), contrary to our findings for fledglings. Foraging differences between adults and fledglings may occur to reduce foraging competition or because it is easier for fledglings to improve foraging skills in oak trees. Fledglings may still be trying to avoid predators while foraging (Marchetti and Price 1989), so nearby junipers may provide quick cover if a predator is encountered. Overall, fledglings stayed in general habitat with juniper-oak ratios similar to nesting habitat (Klassen et al. 2012, but see Long et al. 2016).

Dependent Golden-cheeked Warbler fledglings are likely using similar tree compositions in general habitat that adults use for nesting since our study sites were designated as nesting habitat (Macey and Grigsby 2018) and individuals typically remained in our sites. Additionally, canopy cover at fledgling-use locations was similar to previous research on nesting locations (Dearborn and Sanchez 2001). Since fledglings generally remain in suitable nesting habitat and parents feed young up to five weeks out of the nest, adults may be influencing fledgling habitat decisions to promote their survival (i.e., staying in areas with high canopy cover). Fledglings may remain in natal areas possibly to prolong parental care and remain in sheltered areas to reduce predation. It seems likely then that dependent fledglings rely on similar habitat to nesting and continued preservation of this habitat will promote both nesting and fledgling survival. It remains unclear what habitat older, independent fledglings may use as they disperse. Further research into both habitat use and survival for independent stages will be important in the future as habitat loss and fragmentation continues in unmanaged areas of Golden-cheeked Warblers.

**MANAGEMENT IMPLICATIONS**

Land management discussions on pre-settlement habitat conditions vacillate between a grassland-dominated or extensive forest ecosystem within the Edwards Plateau Region or the
Hill Country in Texas. Fire is an extremely limiting factor for juniper as burning can cause crown fires and reduces seedling and sapling junipers and canopy cover (Reidy et al. 2016). Fire was likely used by Native Americans in surrounding regions not including the Edwards Plateau Region but is still argued that “cedar brakes” or juniper forests would have only existed on steep barren slopes and canyon areas where fires could not reach (O’Donnell 2019, unpublished data), therefore limiting the range of Golden-cheeked Warblers. Historical accounts in this region support the idea that expansive juniper-oak forests were common and that increased fires during European settlement reduced Golden-cheeked Warbler habitat (O’Donnell 2019, unpublished data). Management then needs to consider how to reduce further loss and fragmentation of juniper-oak habitat while urban expansion continues in this region. Smaller patches of Golden-cheeked Warbler habitat appear to be more prone to decreased nest survival (Peak and Thompson III 2014), and we have provided evidence that early post-fledging stages also need adequate amounts of juniper-oak habitat to facilitate transitions to independence as fledglings increase movement and foraging behavior. Fort Hood typically limits disturbance to mature juniper-oak habitat, which seems to work well for this population of Golden-cheeked Warblers. Wherever possible, contiguous habitat should be managed for the largest patch size and least disturbance, especially by controlling browsing animals, promoting reforestation (Peak and Thompson III, 2014), and carefully managing prescribed fire (Reidy et al. 2016).

Additionally, it may become important in future research to examine older/independent fledglings if habitat loss and fragmentation continues. Since fledglings remain in close proximity to and are attended frequently by the parents during the first four weeks out of the nest, continued protection of this habitat type should allow continued parental care and provide appropriate shelter and foraging substrate for fledglings. Older fledglings may move to different
habitat types, however, as exhibited by Black-capped Vireo (*Vireo atricapilla*) fledglings on Fort Hood moving to riparian habitat types (Dittmar et al. 2014). Understanding further habitat use by all periods of post-fledging stages will remain important for proper conservation of the entire breeding season for Golden-cheeked Warblers.
Figure 4. Mean fledgling distance from the nest and distance between daily observations with standard error bars. Each time period consists of 5 days (e.g., period 1 is day 1-5). Fledglings increased movement distances over time and exhibited a sudden increase after day 35.
Figure 5. The percent of time over a 10 min observation period that fledglings spent moving, flying, foraging and begging differed significantly over time ($P < 0.001, n=255$). Loess smoothing was used to show fine-scale trends over the data.
Figure 6. Successful forage rates with 95% confidence intervals (gray shading). Foraging rate increased significantly with age \((P < 0.001, n = 396)\). The average successful hourly foraging rate overall was \(2.09 \pm 0.38\). The trend line is a linear model.
Figure 7. The ratio of parental care by sex of the parent is shown for each individual bird. All birds were care for by one parent at least until the broods rejoined. One individual (164.621) was the only surviving fledgling out of the nest and parents divided care evenly for this fledgling.
Figure 8. Parental hourly feeding rates for fledglings with 95% confidence intervals (gray shading). a) Hourly feeding rates by the parents significantly change over time ($P < 0.001$, $F = 17.06$, $n = 705$). The trend line is a loess model. b) Feeding rates by sex differ significantly ($P < 0.001$, $t = 8.58$) and females decrease feeding rates more than males (-0.15 feedings/hr/day and -0.02 feedings/hr/day, respectively). On average males and females fed fledglings 3.71 ± 0.34 and 8.22 ± 0.40 times per hour, respectively. The trend lines are linear models. c) As fledglings spent more time begging, the adults would increase hourly feeding rates ($P < 0.001$, $n = 227$; 13.99 ± 0.69 and 7.66 ± 0.99 feedings per hour, respectively). The trend line is a linear model.
Figure 9. Figures represent the mean values of each habitat variable as fledglings aged. Points are means and lines represent trends. 95% CI are shown in grey. a) Mean ground cover between use and random points differed by 8.0%, b) Mean canopy cover between use and random points differed by 9.0%, c) Mean vegetation density between use and random points differed by 3.6%. General habitat tree compositions for d) juniper, e) oak, and f) non-oak deciduous differed between use and random points by 3.0%, 2.4% and 1.3%, respectively. All trend lines are linear models.
Figure 10. The focal tree used by fledglings. Each line shows the probability a fledgling was found in each tree type as they aged (95% confidence intervals are in gray shading). a) Early in the fledging stage individuals were found in junipers significantly more often ($P < 0.001$, $n = 706$), but decreased and b) were found in oaks more as they aged ($P < 0.001$, $n = 706$). Fledglings also used non-oak deciduous species (“other”) but this relationship did not change as they aged ($P = 0.128$, $n=706$).
Figure 11. Fledglings changed surrounding habitat within 10 m of their location as they aged. a) Mean proportion of junipers in habitat was 74.67 ± 0.93 % and declined over time ($P = 0.014$, $F = 6.10$, $n = 563$). b) Mean oak proportion was 20.68 ± 0.84 % ($P = 0.135$, $F = 2.23$, $n = 563$). c) Mean proportion of non-oak deciduous trees was 4.64 ± 0.34% and increased over time ($P < 0.001$, $F = 11.99$, $n = 563$). Mean tree composition of each day add up to 100%. Trend lines are linear models.
Figure 12. The percent time spent perching and begging in relation to canopy cover. Time spent perching increases as canopy cover increases ($P < 0.017$, $F = 5.84$, n= 227) and time spent begging decreases as canopy cover increases ($P = 0.010$, $F = 6.82$, n= 227). Trend lines are linear models.
Figure 13. The successful foraging rate (# of successful foraging events per hour) of fledglings changed as tree composition of general habitat changed. Fledgling successful foraging rate increased and decreased as the composition of a) oak and b) juniper increased, respectively. Ninety-five percent confidence intervals are shown in gray shading.
REFERENCES


BBIRD Field Protocol. Montana Cooperative Wildlife Research Unit.


*chrysoparia* recovery plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.


CHAPTER 4: GENERAL CONCLUSION

Species management needs to incorporate all breeding season dynamics, including post-fledging ecology, into management techniques. Post-fledging survival can be a bottleneck in population dynamics for avian species and understand what factors affect survival and behaviors are important to understand species biology and further conservation.

In Chapter 2, my results revealed important demographics and habitat relationships during the post-fledging stage of Golden-cheeked Warblers. Nest survival for Golden-cheeked Warblers is relatively low, but our results are similar to previous nest survival data at Fort Hood and other locations. Golden-cheeked Warbler fledgling survival is relatively high in comparison to results from Cox et al. (2014) at 70% period survival. The amount of juniper in general fledgling habitat is positively influencing their survival and continued protection of habitat with juniper-oak forests will promote fledgling survival.

In Chapter 3, I characterized Golden-cheeked Warbler behaviors, habitat use, and parental care as fledglings develop. Fledglings exhibit more active behaviors as they age, of which foraging is particularly important. Immediately after leaving the nest, fledglings beg and move less often. Fledglings have low mobility this early after fledging but remaining still and quiet likely to avoid predators. As fledglings age, they become more mobile, and beg and forage more often. Parents also cared for fledglings at least four weeks after fledging, so parental care may be important for fledglings that are not skilled at foraging immediately after fledging. Parental care declines over time, so fledglings must learn to efficiently forage in their habitat as they mature.

Fort Hood contains large amounts of contiguous habitat, likely aiding high-quality habitat conditions for this species. Juniper-oak ratios in general habitat used by fledglings remained
relatively constant across our observation period (four weeks). Fledglings changed their focal
tree use as they aged, however, likely a result of moving into new habitat to find shelter and
appropriate foraging substrate. Fledglings also successfully foraged more often in general habitat
containing more oak, which could be due to easier foraging ability for fledglings or reduced
competition with adults. Promoting habitat with a general 70/30% juniper-oak ratio and higher
canopy cover and vegetation density should allow fledglings to find appropriate habitat to find
shelter from predators, forage, and receive parental care, overall enhancing their survival.

As continuing habitat loss and fragmentation are likely, managers will need to emphasize
the importance of habitat and its composition for Golden-cheeked Warblers. Fort Hood is a large
military installation containing large patches of contiguous habitat where we have observed high
fledgling survival rates and consistent general habitat use, with a shift in focal tree usage.
Although the proportion of juniper in general habitat positively influences survival, fledglings
are still moving into oaks, likely to find better foraging substrates. Fledglings may need juniper
as a dense shelter when they are less mobile to avoid predators, but gradually transition to using
oaks to balance foraging with predator avoidance. Once fledglings are older, moving into more
oak habitat, they have greater mobility, likely enabling them to avoid predators. It remains
unclear how fledgling survival and behaviors change when they are independent, relying on their
own foraging skills for food. It will also become important to understand post-fledging ecology
in smaller parcels of habitat throughout the breeding range of Golden-cheeked Warblers.
APPENDICES

APPENDIX A: VEGETATION VARIABLES USED IN ANALYSIS

Table 2. Vegetation variables that were included in covariate analysis for their influence on fledgling survival. Variables are divided into whether they were included in the PCA.

<table>
<thead>
<tr>
<th>Vegetation Variables</th>
<th>Included in PCA</th>
<th>Not included in PCA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ground Cover (%)</td>
<td></td>
<td>Proportion of trees that are juniper</td>
</tr>
<tr>
<td>Canopy Cover (%)</td>
<td></td>
<td>Proportion of trees that are oak species</td>
</tr>
<tr>
<td>Low Coverboard Region (% covered 0-30 cm in height)</td>
<td></td>
<td>Proportion of trees that are non-oak deciduous species</td>
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<tr>
<td>Middle Coverboard Region (% covered 30-100 cm in height)</td>
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</tr>
<tr>
<td>High Coverboard Region (% covered 100-200 cm in height)</td>
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<td>Total Tree Count</td>
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<td>Mean DBH of all trees</td>
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<tr>
<td>Total Juniper Count</td>
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<tr>
<td>Mean DBH of Junipers</td>
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<tr>
<td>Total Oak Species Count</td>
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<td>Mean DBH of Oaks</td>
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<tr>
<td>Total Non-oak Deciduous Species Count</td>
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<tr>
<td>Mean DBH of Non-oak Deciduous species</td>
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### APPENDIX B: FLEDGING SURVIVAL RESULTS

Table 3. The fledgling model set that we used for the initial staggered entry design to understand age and seasonal effects on fledgling survival during 2017-2018. This table contains AICc, Delta AICc, AICc weight, model likelihood, number of parameters, deviance, estimated coefficients (β), and confidence intervals for fledgling survival models.

<table>
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<tr>
<th>Model</th>
<th>AICc</th>
<th>Delta AICc</th>
<th>AICc Weights</th>
<th>Model Likelihood</th>
<th>Num. Par</th>
<th>Deviance</th>
<th>β (Mean)</th>
<th>95 % CI Lower</th>
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<td>1.349</td>
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<td>All Weeks</td>
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