

GOLDEN-CHEEKED WARBLER NEST SUCCESS
AND NEST PREDATORS IN URBAN AND RURAL LANDSCAPES

A Thesis
presented to
the Faculty of the Graduate School
University of Missouri-Columbia

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

By
JENNIFER L. REIDY
Frank R. Thompson III, Thesis Supervisor

MAY 2007

© Copyright by Jennifer L. Reidy 2007

All Rights Reserved

The undersigned, appointed by the Dean of the Graduate School, have examined the thesis entitled:

GOLDEN-CHEEKED WARBLER NEST SUCCESS AND NEST PREDATORS IN
URBAN AND RURAL LANDSCAPES

presented by Jennifer L. Reidy

a candidate for the degree of Master of Science

and hereby certify that in their opinion it is worthy of acceptance

Dr. Frank Thompson

Dr. John Faaborg

Dr. Josh Millsbaugh

ACKNOWLEDGMENTS

First, I would like to thank Mike Stake, who employed me long ago on his own master's project studying Golden-cheeked Warblers and whose friendship and encouragement ultimately led me down the path to where I am today. And it was Mike who inspired me with the idea to pursue this topic for my masters' degree, for which I am truly grateful as this endeavor has been both a gratifying professional and personal journey. I also thank Mike for leading me to the University of Missouri and my graduate advisor Dr. Frank Thompson. I could not have hoped for a better supervisor, as Dr. Thompson's door was always open and his ear ready to listen to all my ideas, sane or otherwise. He patiently guided me through this process and taught me how to develop my critical and analytical skills (although I still wish I made a better student of statistics!) and I hope to make him proud in all my future endeavors.

I am grateful to John Cornelius of the Fort Hood Natural Resources Branch and Tim Hayden of the U. S. Army Construction Engineering Research Laboratory for securing the funding to undertake this project. I thank John for believing in me and my project idea and his steady determination to fund research and conservation projects for endangered species. Charles Pekins, Gil Eckrich, Scott Summers and the many others based at Fort Hood were great to work with and I appreciate their interest in me and this project. Rebecca Peak of The Nature Conservancy provided invaluable data collection on Fort Hood, without which part of this project would have been impossible. Rod Sandoval of The Nature Conservancy and Patty Ramirez of the City of Austin provided

me with aerial imagery of my study plots which was essential in the field and in analyzing the landscape metrics. Don Koehler and Helen Becker of the City of Austin provided access to my Austin sites and other logistical support for which I am thankful. Thanks also to The Nature Conservancy and the University of Missouri for the use of video camera systems.

A huge thank you goes out to Bill Dijak of the Forest Service's North Central Research Station for the considerable help he provided me with the ArcGIS work – without his assistance, I would have been in school a few more months figuring out how to write code for GIS! Karen Decker of the Department of Fisheries and Wildlife was a tremendous help in acquiring field housing and vehicles and taking care of my bills while I was away, which was a huge relief for me.

Field work was pretty intensive and I am lucky to have hired some great assistants, who were hard-working and dedicated in the field, and fun and easy-going back at home. Richard Aracil, Kyla Ercit, Nicole Flood, and Michael Wickens provided assistance locating and monitoring nests with me in Austin and Scott Stollery alone got to locate and monitor nests on Fort Hood. I demanded a lot of these folks, especially Kyla and Michael in 2006, and they delivered in good cheer! I am glad to call these individuals friends now. Also thank you to Cindy Sperry who conducted point counts in Austin – I will get to this data soon!

I was privileged to have Dr. John Faaborg and Dr. Josh Millsbaugh serve as my graduate committee. Thanks to Dr. Faaborg to providing a forum for all us “bird geeks” to share and critique our own work as well as others and for organizing trips to tropical Mexico. Everyone in the avian ecology group was invaluable in developing my critical

thinking skills and providing great friendship. I especially thank my lab mates Shane Pruett, Chad Rittenhouse, and Wes Bailey for their advice and encouragement and my best mate from school, Courtney Kerns for being a great friend. David Jachowski provided much good humor and banter during those few nights as my roommate.

Chris Merkord planted the love of birds and birding in me a long time ago and for that I am eternally grateful.

Thanks to my family for their support during this long process. Lastly, I'd like to extend my gratitude to my boys, Randy Cartwright and Snowball (my cat), for struggling through the process with me and providing constant encouragement and love the entire way.

TABLE OF CONTENTS

ACKNOWLEDGMENTS.....	ii	
LIST OF TABLES.....	vii	
LIST OF FIGURES.....	viii	
ABSTRACT.....	x	
CHAPTER 1		
FACTORS AFFECTING GOLDEN-CHEEKED WARBLER NEST SUCCESS IN URBAN AND RURAL LANDSCAPES.....		1
ABSTRACT.....	1	
INTRODUCTION.....	2	
STUDY AREA.....	6	
METHODS.....	8	
Nest Monitoring.....	8	
Nest-site and Nest-patch measurements.....	9	
Landscape Metrics.....	9	
DATA ANALYSIS.....	10	
RESULTS.....	13	
DISCUSSION.....	15	
CONSERVATION IMPLICATIONS.....	20	
LITERATURE CITED.....	21	
APPENDIX A.....	46	

CHAPTER 2

SOURCES OF NEST MORTALITY AND PREDATORS OF GOLDEN-CHEEKED WARBLERS IN AN URBAN LANDSCAPE.....	51
ABSTRACT.....	51
INTRODUCTION.....	52
STUDY AREA.....	55
METHODS.....	56
Nest searching and monitoring.....	56
Video cameras.....	57
Nest survival and camera effects.....	58
Cause-specific mortality.....	59
RESULTS.....	60
Nest survival and camera effects.....	61
Cause-specific mortality.....	61
Egg and nestling mortality.....	63
DISCUSSION.....	64
CONSERVATION IMPLICATIONS.....	68
LITERATURE CITED.....	70

CHAPTER 3

SNAKE PREDATION ON NESTING ADULT GOLDEN-CHEEKED WARBLERS.....	77
ABSTRACT.....	77
LITERATURE CITED.....	82

LIST OF TABLES

Table	Page
1.1. <i>A priori</i> candidate models, model variables and descriptions, and predicted direction (PD) used to evaluate nest success rates in Austin, Texas and Fort Hood, Texas during 2005-2006. In addition to single models and the global and null model, we examined additive combinations of the temporal model with one or two other models.....	27
1.2. Support for the models summing to a cumulative $w_i \geq 0.90$ predicting Golden-cheeked Warbler nest survival in Austin, Texas and Fort Hood, Texas during 2005-2006. Models are ranked from most supported to least based on Akaike's information criteria (AIC_c), ΔAIC_c , and Akaike weights (w_i). AIC_c is based on $-2 \times \log$ likelihood ($-2L$) and the number of parameters (K) in the model.....	29
1.3. Model-averaged parameter estimates, unconditional standard errors (SE), and the odds ratios (OR) and associated lower (LCL) and upper (UCL) 95% confidence intervals for factors hypothesized to effect Golden-cheeked Warbler nest survival in Austin, Texas and Fort Hood, Texas during 2005-2006.....	30
2.1. Support for models with and without video camera monitoring predicting Golden-cheeked Warbler nest survival in Austin, Texas from 2005-2006 based on 537 camera monitored and 384 non-camera monitored intervals. Models are ranked based on Akaike's information criteria (AIC_c), ΔAIC_c , and Akaike weights (w_i). AIC_c is based on the $-2 \times \log$ -likelihood ($-2L$) and the number of parameters (K).....	74
2.2. Cause-specific daily and period mortality rates and 95% confidence intervals (CI) for Golden-cheeked Warblers nests in Austin, Texas during 2005-2006 (537 intervals) and Fort Hood, Texas during 1997-2002 and 2005 (736 intervals).....	75
3.1. Temporal features of rat snake predation on female Golden-cheeked Warblers at the nest in Austin, Texas during 2005-2006 and Fort Hood, Texas during 1997-2002	84

LIST OF FIGURES

Figure	Page
1.1. Predicted daily and period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of Julian date in Austin, Texas and Fort Hood, Texas during 2005-2006.....	31
1.2. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of year in Austin, Texas and Fort Hood, Texas during 2005-2006.....	32
1.3. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of nest stage in Austin, Texas and Fort Hood, Texas during 2005-2006.....	33
1.4. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of nest height in Austin, Texas and Fort Hood, Texas during 2005-2006.....	34
1.5. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of nest cover in Austin, Texas and Fort Hood, Texas during 2005-2006.....	35
1.6. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of distance from main trunk (m) in Austin, Texas and Fort Hood, Texas during 2005-2006.....	36
1.7. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of slope in Austin, Texas and Fort Hood, Texas during 2005-2006.....	37
1.8. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of proximity to edge (0 if nests > 30 m and 1 if \leq 30 m) in Austin, Texas and Fort Hood, Texas during 2005-2006.....	38
1.9. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of open edge density	

	(m/ha) within a 100-m radius of the nest in Austin, Texas and Fort Hood, Texas during 2005-2006.....	39
1.10.	Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of trail density (m/ha) within a 25-m radius from the nest in Austin, Texas and Fort Hood, Texas during 2005-2006.....	40
1.11.	Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of percent of open area within a 1-km radius from the nest in Austin, Texas and Fort Hood, Texas during 2005-2006.....	41
1.12.	Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of percent of developed area within a 1-km radius from the nest in Austin, Texas and Fort Hood, Texas during 2005-2006.....	42
1.13.	Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of site in Austin, Texas and Fort Hood, Texas during 2005-2006.....	43
1.14.	Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of building density (#/ha) within a 500-m radius from the nest in Austin, Texas and Fort Hood, Texas during 2005-2006.....	44
1.15.	Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of road density (m/ha) within a 500-m radius from the nest in Austin, Texas and Fort Hood, Texas during 2005-2006.....	45
2.1.	Daily and period predation rates and 95% confidence intervals by snakes, birds, mammals, and ants at Golden-cheeked Warbler nests in Austin, Texas (white bars) during 2005-2006 and on Fort Hood, Texas (gray bars) during 1997-2002 and 2005.....	76

GOLDEN-CHEEKED WARBLER NEST SUCCESS IN URBAN AND RURAL LANDSCAPES AND URBAN NEST PREDATORS

Jennifer L. Reidy

Dr. Frank R. Thompson, III, Thesis Supervisor

ABSTRACT

The Golden-cheeked Warbler (*Dendroica chrysoparia*) is an endangered songbird that breeds exclusively in the juniper-oak woodlands of central Texas. We studied nesting success of Golden-cheeked Warblers from 2005-2006 on Fort Hood, situated in a rural landscape, and in Austin, a rapidly growing city. We hypothesized that temporal, nest-site, nest-patch, edge, landscape, and urban factors affected nest success and used an information-theoretic approach to evaluate models representing our hypotheses. We found the most support for the model with temporal and edge factors. Nest success declined throughout the season and with increasing amounts of open edge within 100 m of the nest. There was little support for nest-site, nest-patch, landscape, or urban features. The overall daily survival rate was 0.962 (0.943-0.974), resulting in a 25-day period survival of 0.374 (0.230-0.520). Nest survival was almost identical between Fort Hood (0.9615) and Austin (0.9614), and higher than the predicted survival rate needed to be self-sustaining (0.25-0.30) indicating that urban sites can provide as high quality breeding habitat as rural sites.

We monitored 61 Golden-cheeked Warbler nests in Austin, Texas, from 2005 to 2006 with time-lapse video cameras to determine sources of mortality and identify predators in an urban landscape. The overall period mortality rate was 0.631 and the predation rate was 0.541. Eight nests were depredated by Texas rat snakes (*Elaphe*

obsoleta lindheimeri), six by birds, including four by Western Scrub-Jays (*Aphelocoma californica*) and two by Cooper's Hawks (*Accipter cooperii*), three by Fox squirrels (*Sciurus niger*), and one by fire ants (*Solenopsis* sp.). We compared predators and predation rates in Austin to those from a previous study on Fort Hood and this study. The period predation rate in Austin (0.541) was slightly lower than on Fort Hood (0.599). The predator composition was similar between Austin and Fort Hood, except the dominant avian predator differed between the two landscapes. Western Scrub Jays were the dominant avian predator in Austin and American Crows (*Corvus branchyrynchos*) were dominant on Fort Hood. Nest abandonment, hatching success and nestling survival did not differ between Austin and Fort Hood. We compared nest success of 39 nests in Austin monitored without video cameras to those monitored with cameras and found no support for an effect of video surveillance on nest survival.

We monitored 116 females and 128 nests with video cameras to identify nest predators of Golden-cheeked Warblers on Fort Hood, Texas from 1997-2002 and in Austin, Texas from 2005-2006. Six female Golden-cheeked Warblers were depredated during 892 camera-monitored intervals during the portion of the nesting cycle when females were sitting on the nest through the night, resulting in a daily predation rate of 0.007. Females were captured 67% of the time they were present at the time of snake predation and 75% of the time they were present at night. Assuming a daily nest survival of 0.962 and that the female would attempt a second nest if the first nest failed, we estimated annual mortality on adult females due to predation on the nest was 12.2%. Snake predation represents an important source of adult mortality for nesting Golden-cheeked Warblers.

CHAPTER 1
FACTORS AFFECTING GOLDEN-CHEEKED WARBLER NEST SUCCESS
IN URBAN AND RURAL LANDSCAPES

ABSTRACT

The Golden-cheeked Warbler (*Dendroica chrysoparia*) is an endangered songbird that breeds exclusively in the juniper-oak woodlands of central Texas. We studied nesting success of Golden-cheeked Warblers from 2005-2006 on Fort Hood, situated in a rural landscape, and in Austin, a rapidly growing city. We hypothesized that temporal, nest-site, nest-patch, edge, landscape, and urban factors affected nest success and used an information-theoretic approach to evaluate models representing our hypotheses. We found the most support for the model including temporal and edge factors. Nest success declined throughout the season and with increasing amounts of open edge within 100 m of the nest. There was little support for nest-site, nest-patch, landscape, or urban features. The overall daily survival rate was 0.962 (0.943-0.974; 95% confidence intervals), resulting in a 25-day period survival of 0.374 (0.230-0.520). Nest survival was almost identical between Austin (0.3741) and Fort Hood (0.3747). Nest success was likely adequate for a self-sustaining population. Because we found strong support suggesting a negative effect associated with increasing open habitat within and around Golden-cheeked Warbler breeding patches, we recommend preserving large contiguous blocks of appropriate breeding habitat.

INTRODUCTION

The Golden-cheeked Warbler (*Dendroica chrysoparia*) is a federally endangered neotropical migrant songbird whose current breeding range is restricted to 24 counties (U.S. Fish and Wildlife Service 1996) in central and south-central Texas (Jette et al. 1998). The Golden-cheeked Warbler is a habitat specialist relying on peeling Ashe juniper (*Juniperus ashei*) bark for nest construction and various oaks for foraging; therefore breeding habitat is restricted to mature Ashe juniper-oak woodlands (Pulich 1976, Ladd and Gass 1999) associated with the Edwards Plateau and Lampasas Cut Plain (Riskind and Diamond 1988).

Golden-cheeked Warblers nest in closed-canopy woods, dominated by a high density of Ashe junipers and a variety of oaks (*Quercus* sp.), with nest patches characterized as having dense juniper cover above 2 m from the ground (Dearborn and Sanchez 2001). They typically occupy steep slopes far from edges and large patches dominated by mature Ashe juniper and a variety of deciduous trees (DeBoer and Diamond 2006). Golden-cheeked Warbler presence is best predicted by the percentage of woodland cover and largest woodland patch index at several spatial scales and least predicted by mean-nearest neighbor (distance between woodland patches) and edge density (Magness et al. 2006). How these habitat attributes relate to Golden-cheeked Warbler nest success is unknown though. Because presence and abundance in a habitat type does not necessarily correlate to nest success or productivity (Van Horne 1983, Vickery et al. 1992, Pidgeon et al. 2003), it is critical to establish how habitat characteristics affect nest success.

Recent studies of avian communities (Rodewald and Yahner 2001, Knutson et al. 2004, Peak et al. 2004) and single species or populations (Martin and Roper 1988, Tarvin

and Garvin 2002, Bailey 2005, Driscoll et al. 2005, Bakermans and Rodewald 2006) have shown that nest success can be affected at multiple spatial scales. Knowledge of which scale and what factors most affect nest success of a species or population can aid managers and biologists in prioritizing habitat management decisions (Thompson et al. 2002, Driscoll et al. 2005), particularly for endangered species. As the human population continues to grow, it is increasingly important to incorporate factors associated with human development into nesting studies and assess how these features impact nesting success, especially for sensitive species (Marzluff 2001). Studies of nest success should consider effects at multiple scales (Stephens et al. 2003), because large-scale effects often constrain small-scale effects (Chalfoun et al. 2002, Thompson et al. 2002).

Factors at the nest-site, nest-patch, habitat, and landscape scale can affect nest success (Thompson et al. 2002). Potentially important factors at the nest-site scale include cover around the nest, nest height, nest tree height, nest tree species, distance from the main branch or trunk, and nest tree girth (Martin and Roper 1988, Filliater et al. 1994, Burhans et al. 2002). Nest-patch features typically include vegetation or landscape characteristics in the immediate area of the nest, often defined by a 5 m or 11.3 m radius (Martin and Roper 1988), and include variables such as stem count, degree of slope, canopy height, and canopy cover (Kilgo et al. 1996, Dearborn and Sanchez 2001, DeBoer and Diamond 2006). Factors at the habitat scale can include patch size, proximity to edge, the total amount of edge (edge density), or habitat type (Thompson et al. 2002). Large-scale effects include those at the landscape and biogeographic scales (Thompson et al. 2002). Landscape features, such as percentage of open habitat and developed habitat surrounding Golden-cheeked Warbler habitat, could impact nest success by affecting the presence and

abundance of predators (Chalfoun et al. 2002, Tewksbury 2006). Features associated specifically with human development, such as road and building density, can also affect productivity by changing the predator composition and abundance (Haskell et al. 2001) or altering adult behavior (Gutzwiller et al. 1998).

Golden-cheeked Warblers nest in mature woodlands, but due to the fragmented nature of the historic range of Ashe juniper (along steep canyons and ravines) (Kroll 1980, Diamond 1997), Golden-cheeked Warblers are often found close to an edge (Coldren 1998), where Golden-cheeked Warbler woodland abuts another land use, often grasslands. While edge density at multiple scales was not found to affect presence-absence of Golden-cheeked Warblers (Magness et al. 2006), nest success decreased with increasing edge density (boundary between forest and other land uses) within 100 m of the nest on Fort Hood (Peak in press). Different types of edge resulting from different surrounding land uses may have different impacts on the Golden-cheeked Warbler's productivity in appropriate habitat patches. Patch occupancy by Golden-cheeked Warblers was lower for sites abutting urban edges than those abutting rural edges, but territory placement, pairing success, and inferred reproductive success (based on evidence of young) were not (Coldren 1998). Stake (2003) found no support for nest-site (canopy cover, canopy height, stem density, nest substrate) or territory (male age, slope) factors affecting nest predation of Golden-cheeked Warblers on Fort Hood.

Habitat loss resulting from urbanization and agriculture clearing is considered the main threat to the Golden-cheeked Warbler's population viability (U.S. Fish and Wildlife Service 1992). Little information exists on how these large-scale effects impact productivity of Golden-Cheeked Warblers in residual habitat patches. In Travis County,

Golden-cheeked Warbler presence was positively associated with agriculture and grassland surrounding wooded habitat and negatively associated with increasing amounts of residential and commercial development (Arnold et al. 1996, Coldren 1998). However, inferred reproductive success was higher in territories closer to residential development than agriculture and grassland, and territory sizes were smaller near residential areas and grassland than those near agriculture (Coldren 1998). Nest success has been shown to decrease with increasing amounts of agriculture/grazing (Rodewald 2002, Knutson et al. 2004) and human development (Bakermans and Rodewald 2006, Burhans and Thompson 2006) in the landscape. Additionally, Brown-headed Cowbird (*Molothrus ater*) parasitism can be higher in areas near agriculture (Morse and Robinson 1999, Ford et al. 2001) or grazing (Goguen and Mathews 2000) and in areas of human settlement (Burhans and Thompson 2006, Tewksbury 2006).

Urban and suburban growth is high in many parts of the Golden-cheeked Warbler's breeding range (U.S. Fish and Wildlife Service 1992) and their productivity may suffer from features associated with urban sprawl in key areas such as Austin, San Antonio, and Kerrville (Pulich 1976). Blue Jays (*Cyanocitta cristata*) exhibit a strong positive association with residential areas outside Austin (Arnold et al. 1996). A negative correlation between presence of Golden-cheeked Warblers and presence of Blue Jays in the urban bird community was documented in one study in Travis County (Engels and Sexton 1994), but not in a separate study in the same county (Arnold et al. 1996). However, Western Scrub-Jays (*Aphelocoma californica*) are the dominant corvid in the native urban community around western Austin and have greater propensity to co-exist with Golden-cheeked Warblers (Sexton 1987). Elevated abundance of these two jay species associated

with increased residential development living in or in close proximity to Golden-cheeked Warbler habitat (Sexton 1987, Arnold et al. 1996) could be detrimental to productivity of urban Golden-cheeked Warblers. Additionally, residential areas support high numbers of nut-producing trees which was shown to artificially inflate populations of Fox squirrels (*Sciurus niger*; Sexton 1987), a known nest predator of Golden-cheeked Warblers (Stake et al. 2004).

In addition to habitat features, temporal variables can influence nest success. Temporal factors include variables such as year, nest stage, Julian date, and nest age. Although the temporal variables year, Julian date, and stage did not receive support in a previous study on Golden-cheeked Warbler nest predation (Stake 2003), other studies have shown strong support for a temporal effect on nest success (Winter 1999, Burhans et al. 2002, Peak et al. 2004, Bailey 2005, Grant et al. 2005).

We studied nesting success of Golden-cheeked Warblers in juniper-oak habitat embedded in a suburban landscape (Austin) and a rural landscape (Fort Hood). We hypothesized that temporal factors and factors at the nest-site, nest-patch, and landscape scales (including urban and edge effects) affected nest success. We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate support for alternative hypotheses that were represented by nest survival models that included covariates for the hypothesized effects.

STUDY AREA

We conducted this study during the spring and early summer of 2005 and 2006 on multiple sites located in Austin (Travis County) and Fort Hood Military Reservation (Bell and Coryell Counties), both located in central Texas and separated by approximately 70

miles (112 km). These sites were within core Golden-cheeked Warbler breeding habitat. The Austin sites were Emma Long Metropolitan Park (30°20'N, 97°50'W), Forest Ridge Preserve (30°23'N, 97°47'W), and Jester Preserve (30°23'N, 97°47'W); these sites are located in northwest Austin and owned and managed by the City of Austin. The Fort Hood sites included Belton Lake Outdoor Recreation Area (31°08'N, 97°34'W), Training Area (TA) 32 (31°09'N, 97°35'W), TA 51 (31°16'N, 97°47'W), and TA 70 (31°04'N, 97°51'W); these sites are owned by the Department of Defense, but Golden-cheeked Warbler monitoring was performed by The Nature Conservancy.

Golden-cheeked Warbler habitat on the Austin sites was composed of mature juniper-oak woods along steep limestone canyons and densely wooded plateaus. Though Golden-cheeked Warbler habitat was fairly contiguous, fragmentation by residential development has resulted in loss of breeding habitat (Engels 1995). All sites contained a network of closed-canopy trails and contained at least one major open-canopy (>10 meters wide) trail cutting through. Limited public access was allowed to some of the trails during Golden-cheeked Warbler breeding season; however, most of the land was set aside as a breeding preserve. Additionally, there was a section of Emma Long open to mountain and motorized biking. Golden-cheeked Warbler habitat on the Fort Hood sites consisted of steep slopes with flat mesas composed of scrubby juniper-oak woodlands, broken by numerous trails and openings, particularly along the mesa tops, separated by wide open grasslands leased for cattle grazing. The trails were frequented mostly by field biologists during the breeding season. Belton Lake Outdoor Recreation Area was open to mountain biking. Brown-headed Cowbirds were intensively managed on Fort Hood during the duration of this study, but management in the Austin area was limited to a few select sites.

Dominant vegetation was Ashe juniper, Plateau live oak (*Quercus fusiformis*), Texas red oak (*Q. texana*), shin oak (*Q. sinuata*), elms (*Ulmus* spp.), hackberry (*Celtis* spp.), Texas ash (*Fraxinus texensis*), and Texas persimmon (*Diospyros texana*) (Guilfoyle 2002). Post Oak (*Q. stellata*) was common on the uplands of Fort Hood, but completely absent from the Austin sites (J. L. Reidy pers. obs.).

METHODS

Nest Monitoring

We searched for and monitored Golden-cheeked Warbler nests from mid-March through mid-June 2005 and 2006. Most nests were found by tracking an adult to the nest, but several nests were located by systematically searching through a small area thought to contain the nest. We recorded the nest location using Garmin global positioning units (GPS; Garmin International, Olathe, Kansas) with an accuracy to ~3 m and relocated nests by hanging plastic flagging with directions (distance and bearing, plus description of location in tree) > 3 m from the nest. All nest flags were placed so that the nest was viewable from that point, while also being far enough away to not disturb the birds or attract predators. We monitored nests every 1-3 days after incubation began until the nest fledged or failed. A subset of nests on both sites was monitored with video cameras (see Chapter 2). Nests were considered fledged if we documented fledging by video surveillance or located fledglings at or near the nest site by sight or sound. Nests were considered failed if no nest activity was documented during monitoring and there was no evidence (described above) or possibility (nestlings too young) of fledging. We attempted to find re-nests following nest failures.

Nest-site and nest-patch Measurements

We measured characteristics of the nest-site (nest height, nest cover, and distance to main trunk) and nest-patch (percent of slope and proximity to edge) in late May or early June. We measured the nest height in meters from the ground to the rim of the nest with a clinometer. We visually estimated percent of nest cover (concealment around the nest) one meter above and below the nest and from the side in each cardinal direction and averaged these estimates for one measure of nest cover. We estimated the distance from the nest along the nest branch to the main trunk in meters (distance to main trunk). We measured percent slope by sighting downhill in the steepest direction with a clinometer. To determine proximity to edge, we measured the distance to the nearest trail, road, or clearing ≤ 50 m from the nest with meter tape.

Landscape metrics

We used ArcGIS 9 (Environmental System Research Institute, Redlands, California) to calculate all landscape measurements. We defined the study areas for the landscape analyses as a 2-km buffer around all nest locations. We digitized habitat patches in four habitat classes, using a minimum mapping unit of 30 meters: wooded (probable Golden-cheeked Warbler habitat), developed (buildings, parking lots, roads, etc.), open (includes any open, undeveloped land including grazing land), and water (rivers and ponds large enough to show up in imagery). We also digitized paved roads, trails (including dirt roads) through warbler habitat, and buildings. We calculated the percent of developed (percent developed) and open (percent open) habitat within 1 km of every nest; density of wooded edge abutting open land (m/ha) within 100 m of each nest (open edge density); trail density (m/ha) within 25 m of the nest; and road density (m/ha) and building density

(number of buildings/ha) within 500 m of the nest. We chose these scales because we believe they were representative of the biologically relevant scale for the respective attribute for this species and they captured variability in the attribute among sites. Images of the study sites overlaid with roads, buildings, and habitat polygons are provided in Appendix 1.

DATA ANALYSIS

We used an information-theoretic approach to evaluate support for models representing our hypotheses concerning factors affecting nest success of Golden-cheeked Warblers. We used the logistic exposure method (Shaffer 2004) to model factors hypothesized to affect nest success and to estimate daily nest survival rates. This approach models the success or failure of nests during each interval between nest checks and allows consideration of time-specific covariates that can vary among intervals, such as nest stage and date. Nest losses to all sources were classified as failures. Nests that were abandoned prior to laying or depredated prior to being confirmed as active were excluded. We fit models with PROC GENMOD (SAS Version 9.1, SAS Institute, Cary, North Carolina) by using a binomial response distribution (interval nest fate = 1 if successful, and 0 if failed) and providing the user-defined logit link function ($g(\theta)=\log_e(\theta^{1/t}/[1-\theta^{1/t}])$) where t = the length of the interval (Shaffer 2004).

The temporal model included the variables year, Julian date (cubic effect), and the nest stage (Table 1). We chose to evaluate the effect of date with a cubic effect because it permits flexibility in the shape of the curve and covers the range of possible date effects (Grant et al. 2005). We hypothesized that nest success would decrease through the season and in later nest stages, but that year would not affect nest success (Table 1). The nest-site

model included the variables nest height, nest cover, and distance to main trunk. We hypothesized that nest success would increase with increases in nest height, nest cover, and distance to main trunk (Table 1). The nest-patch model included the variables slope and proximity to edge. We predicted that nest success would increase with increases in degree of slope and proximity to edge (Table 1). The edge model included the variables open edge density in a 100-m radius and trail density in a 25-m radius. We hypothesized that nest success would decrease with increases in open edge density and trail density (Table 1). The landscape model included the variables percent open and percent developed within a 1-km radius of the nest. We hypothesized that nest success would decrease with increases in percent open and percent developed habitat (Table 1). The urban model included the variables site, building density within 500 m, and road density within 500 m of the nest. We predicted that nest success would decrease with increases in road and building density and if the nest was at the urban site (Table 1).

In addition to the above models, candidate models included combinations of the temporal model with one or two other models, because we hypothesized that nest-site, nest-patch, edge, landscape, or urban factors could affect nest survival in an additive manner in addition to temporal effects. We only added effects from one or two of the models at a time to temporal effects so that the number of parameters did not become excessive. We included temporal effects in every additive model because we considered these to be nuisance parameters that we wanted to control for while investigating support for other effects (Grant et al. 2006). The candidate models also included a global model with all covariates and a null model with only an intercept (Table 1).

We calculated tolerance values for covariates in the global model to detect multicollinearity before proceeding with model selection (Allison 1999). We examined the overdispersion parameter for evidence of lack of fit (Burnham and Anderson 2002). We evaluated support for 23 candidate models using Akaike's Information Criteria for small sample sizes (AIC_c) to rank the competing models from most supported to least (Burnham and Anderson 2002). The "best approximating model" was the model where AIC_c was minimized (Δ_i was zero) (Burnham and Anderson 2002). The models were ranked by the Akaike weights (w_i), which represents the probability that a model is the best model of those hypothesized for the data (Burnham and Anderson 2002). We report $-2 \times$ likelihood ($-2L$), AIC_c , ΔAIC_c , and w_i for the models representing a cumulative $w_i \geq .90$ (Burnham and Anderson 2002). Because no single model in this set had the majority of support, we report the model-averaged estimates of coefficients, standard errors, odds ratio and their associated 95% confidence intervals (CI), and model-averaged weight for the final model set. We calculated the relative importance value (RIV) for the effects by summing the w_i for each model that included those effects for the models representing $w_i \geq 0.90$ (Burnham and Anderson 2002, Grant et al. 2006). Because we chose to include temporal effects in all combinations, we only report the relative importance values of the habitat models. To compare the importance of all effects, we also report the weight of all single models.

We estimated model-averaged daily and period survival rates as a function of explanatory variables of interest. For continuous variables, we varied the value of the factor of interest at incremental levels spanning the range of observed values while holding the other variables at their median value (to control for their effects). Categorical variables were held constant at levels representing the proportions of the observations at each

category level, with the exception of nest stage, which was set at proportions representing time spent in each stage (3, 12, and 10 days for the laying, incubating, and nestling stages, respectively, based on video observation). We used a 25-day nesting cycle to compute period survival rates.

RESULTS

We monitored 207 nests (58 in 2005 and 149 in 2006). We excluded 12 nests from analyses because contents were never confirmed, resulting in 195 nests for analyses and 1568 monitoring intervals. One hundred of the analyzed nests were in Austin (32 in 2005 and 68 in 2006) and 95 (23 in 2005 and 72 in 2006) on Fort Hood. Mean interval length between nest checks was 1.47 days (± 0.704 ; SE). One hundred and twenty-five nests (64%) successfully fledged ≥ 1 young.

The overdispersion parameter of $c=0.98$ indicated no evidence of lack of fit. Seven models accounted for a cumulative $w_i \geq 0.90$ (Table 2). We found the most support for our hypothesis that temporal and edge effects affected nest survival; the most supported model included the temporal and edge variables ($w_i=0.412$). The second most supported model included temporal, nest-patch, and edge factors ($w_i=0.161$), which was slightly better than the third-ranked model with only temporal factors ($w_i=0.135$). Temporal factors occurred in six of the seven models. Edge factors were supported in five of the seven models with a RIV of 0.724. Nest-site (RIV=0.034), nest-patch (RIV=0.203), and landscape (RIV=0.080) factors appeared in some of the top seven models, but overall received little support. Urban effects did not appear in the top seven models (RIV=0). The temporal model had the most support of the single models with a w_i of 0.135, followed by the edge model (0.037), nest-

patch model (0.007), landscape model (0.003), and the nest-site and urban models both with a w_i of 0.001.

The overall daily survival rate was 0.962 (0.943- 0.973) and the overall period survival rate was 0.374 (0.230-0.520). Model-averaged survival rates and odds ratios indicated several temporal and edge variables had large effects but confidence intervals tended to be large and overlapped 1 due to model selection uncertainty (Table 3). Survival was highest for nests initiated early in the season (late March) and lowest for nests initiated late in the season (June). Nest survival declined sharply from late March through April, rebounded slightly from early to mid May, and dropped again after May 20 through early June (Fig. 1). Nest survival was higher in 2005 than 2006 (Fig. 2), with nests in 2005 having 43% greater odds of surviving than nests in 2006 (Table 3). The incubation and nestling stages had similar daily survival rates, but the survival rate during the laying stage was much lower (Fig. 3), with 35% lower odds of surviving compared to the nestling stage (Table 3). The odds ratios for almost all the habitat variables showed small effects and all had confidence intervals that overlapped 1 (Table 3). Increasing nest height (Fig. 4), nest cover (Fig. 5), and distance to main trunk (Fig. 6) did not affect nest survival. There was a slight positive trend in nest survival with increasing degree of slope (Fig. 7). Nests greater than 30 m from an edge had slightly higher survival than nests closer than 30 m (Fig. 8) with 6% greater odds of succeeding (Table 3). Nest survival was negatively affected by increasing open edge density (Fig. 9), with 0.6% lower odds of surviving with every 1m/ha increase (Table 3), but positively affected by trail density (Fig. 10), with 0.1% greater odds of surviving with each 1m/ha increase. However, due to model-selection uncertainty, the confidence intervals for both these variables became increasingly broad as the density

increased. The estimate for open edge density in the top model (including only temporal and edge effects) was -0.0076 (-0.0139 to -0.0013), indicating 0.8% lower odds of surviving with every m/ha increase in open edge. The amount of open (Fig. 11) and developed area (Fig. 12) within 1 km of the nest had a very small positive affect on nest survival, but the odds did not differ much from 1 (Table 3). Austin and Fort Hood had almost identical survival rates (Fig. 13), with no effect of building density (Fig. 14) or road density (Fig. 15). The odds were 0.6% lower for nest survival with every building per hectare increase within the 500-m radius around the nest (Table 3).

DISCUSSION

We found the strongest support for our hypothesis that temporal and edge factors affected nest survival, as indicated by support for the models and the magnitude of the variable effects. While we included temporal variables in all the additive models, the temporal model was the most supported single model and temporal effects occurred in the top five models. Nest-site, nest-patch, and landscape effects all appeared in one or two of the top models, but the addition of these effects to the temporal and edge effects resulted in only small model improvements as indicated by the small increase in model likelihood and ΔAIC_c of > 1.88 (Table 2).

Other studies have observed lower nest survival during the laying stage than the nestling stage. Peak et al. (2004) found lower nesting success during the laying stage in three species of songbirds in Missouri, and Black-capped Vireos (*Vireo atricapilla*) on Fort Hood had lower nesting success during the laying stage (Cimprich 2004, Cimprich 2005, Bailey 2005). In a separate study on Golden-cheeked Warblers conducted exclusively on Fort Hood, overall nest success was lowest during the laying stage from 2003-2005 (our

analysis included a small subset of the 2005 nests used in this analysis; Peak 2005). This pattern may be the result of a combination of early predation and abandonment. The probability of abandonment declines as the nesting cycle progresses (Best 1978, Clark and Robertson 1981, Grant et al. 2005). Female Golden-cheeked Warblers abandon nests more in the building stage than after the onset of laying and rarely after they have begun incubating (Pulich 1976, Stake 2003, Peak 2004, Peak 2005, this study). While almost no activity occurs at the nest during the laying stage, substantial activity occurs during the building stage. Predators may locate the nest during the building stage, and make return visits to check on nest contents. Based on video observation (Stake et al. 2004, this study), corvids and snakes are known to make return visits to nests, even if the nest is found empty during the initial visit. Because we did not set up video cameras on nests prior to incubation, we do not know how or if nest predators differ between the laying stage and the incubating/nestling stages. Nor do we know if Brown-headed Cowbirds negatively influenced Golden-cheeked Warbler nest survival because nests were usually placed high in the dense canopy, precluding us from inspecting contents of the majority of nests on Fort Hood and many in Austin. However, most Golden-cheeked Warbler nests were initiated in late March and early April, before cowbirds typically begin laying in this region (S. Summers, The Nature Conservancy, pers. comm., Bailey 2005). We only documented one parasitized nest in Austin and we did not detect any cowbird fledglings being fed by warblers in Austin or Fort Hood. However, much higher parasitism rates have been documented in other areas of the breeding range (Pulich 1976). Because Fort Hood intensively manages Brown-headed Cowbirds (Summers and Norman 2005) and the Austin sites do not support substantial cowbird populations (Sexton 1987, J. L. Reidy, University

of Missouri, unpub. data), we believe parasitism fails to explain the observed pattern in higher laying stage failure.

Nest survival was very high early in the season, dropping rapidly and leveling off to moderate levels mid-season, and declining to the lowest rate late in the season (Fig. 1). This decrease in survival could be related to changes in the abundance or behavior of the predator community or alternative prey during the season. It does not appear to be related to changes in nest stage or to changes in the adults' behavior (related to nest stage) because we controlled for stage when predicting date effects. Golden-cheeked Warblers are an early breeding songbird in the central Texas region and may be a significant source of prey for nest predators early in the season. As the season progresses and other songbirds begin breeding, nest predators may shift to nests that are easier to locate, resulting in the slight increase in nest survival in May. As the initial nest cycle of alternative prey begins tapering off in June, warblers still re-nesting may become more targeted. Similar studies on Fort Hood showed a negative linear trend on nest success as the date progressed (Bailey 2005, Peak 2005). Stake (2003) found more support for temporal variables affecting nest predation when he examined snakes separately from other predator groups. We may be better able to explain these temporal patterns of nest predation when we have more knowledge about the behavior of the chief predator, Texas rat snakes (*Elaphe obsoleta lindheimeri*).

Nest survival declined substantially with increasing amounts of open edge abutting Golden-cheeked Warbler habitat. This effect also occurred in a separate analysis of edge effects on Fort Hood (Peak in press). Inferred reproductive success was higher in unfragmented patches than fragmented patches on Fort Hood (Maas 1998). Higher

numbers of potential avian nest predators were found within 100 m of an edge in Travis County (Arnold et al. 1996). Snakes and corvids were the main predator groups of Golden-cheeked Warblers (Stake et al. 2004, this study) and both groups respond positively to increasing edge and fragmentation. Black rat snakes (*Elaphe obsoleta obsoleta*) prefer edges (Weatherhead and Charland 1985, Durner and Gates 1993, Blouin-Demers and Weatherhead 2001), and while this may be for thermoregulatory reasons, it nonetheless increases their chances of locating birds' nests. Texas rat snakes and Great Plains rat snakes (*Elaphe guttata emoryi*) are common throughout the warbler's breeding range and are abundant in several habitat types, including woods and pastures and suburban areas (Tennant 1998), although currently no study has addressed habitat preferences for either species. Abundance of corvids such as Blue Jays and Western Scrub-Jays is positively associated with increasing development in the warbler's breeding range (Sexton 1987), while abundance of American Crows is positively associated with increasing open edge (Verbeek and Caffrey 2002). The abundance of these edge-associated predators could be responsible for the observed negative open edge effect. Corresponding to this, we also found that nests closer to an edge were more likely to fail than more interior nests. These edges included soft (such as trails or narrow roads) and hard edges (such as cattle grazing areas or residential developments), so we do not know the effect of proximity to each edge type separately. We also observed a positive effect of increasing trail density close to the nest. These trails represent small canopy gaps that receive some human visitation, including mountain biking. The presence of humans may deter many predatory species from using the trails as travel lanes. Small canopy breaks may also increase structural heterogeneity in the vicinity of the nest, creating more understory vegetation for a predator

to search. There is limited evidence that nest predation is lower near trails (Miller and Hobbs 2000); this artificial nest study concluded avian predators such as corvids and grackles were the leading nest predator both close to and away from trails. Higher trail densities close to the nest may reduce overall abundance of predators. Predator groups likely respond to presence of trails or humans differently and this response may also differ from their response to different degrees and types of fragmentation.

Nest success was the same between the two landscapes and compares favorably to previous nest success estimates from Fort Hood, which ranged from 0.96-0.97 from 2003-2006 (Peak 2003, Peak 2004, Peak 2005, Peak 2006). Nest success was higher than from a small nest sample from an earlier study conducted in the western portion of the warbler's range (Pulich 1976). We conducted a post-hoc analysis to determine if landscape, edge, and urban effects measured at different scales than we hypothesized had an effect on nest survival. We evaluated alternative models with the effect of percent open and percent developed within a 500- and 1,000-m radius from the nest, the amount of open and developed edge in a 100-, 500-, and 1,000-m radius, and the building and road density in a 500- and 1,000-m radius. The percent open was more important at the 500 m scale (and was a negative effect), but the percent developed affected nest survival more at the 1,000 m radius. Open edge was most influential at the 100 m scale and the developed edge was not important at any scale examined. Building density affected survival more at the 500 m scale than the 1,000 m, but road density mattered more at the 1,000 m than the 500 m (and had a positive effect). Including these variables at the most supported scale for each attribute had little impact on model support or our conclusions. We suggest that different

features affect nest survival at different scales, but even at the most supported scales, effects had wide confidence intervals.

CONSERVATION IMPLICATIONS

Nest success of Golden-cheeked Warblers was generally high and was the same in the urban site and the rural site. Based on population modeling and sensitivity analyses by Donovan and Thompson (2001) for demographic parameters of a neotropical migrant songbird, we suggest Golden-cheeked Warbler populations in Austin and Fort Hood are not limited by low production. Urban patches like those we studied can be important habitat. Preserving large blocks of contiguous mature juniper-oak woodlands to reduce the amount of open edge may increase nest success. Future researchers should explore the behavior and activity patterns of known Golden-cheeked Warbler nest predators and how these predators change across landscapes within the Golden-cheeked Warbler's range, as this may enable managers to determine if management practices can reduce the risk of predation. Researchers should also further examine the effect of proximity to different types of edge on the Golden-cheeked Warbler's productivity, since we found evidence to suggest that these features of the landscape negatively impact nest success.

LITERATURE CITED

- Allison, P. D. 1999. Logistic regression using the SAS system: theory and application. SAS Institute, Cary, North Carolina.
- Arnold, K. A., C. L. Coldren, and M. L. Fink. 1996. The interactions between avian predators and Golden-cheeked Warblers in Travis County, Texas. Texas Transportation Institute report number TX-96/1983-2. Texas A&M University, College Station, Texas, USA.
- Bailey, J. W. 2005. Hierarchical nest-site selection and the effects of habitat characteristics on Black-capped Vireo nest survival. M.S. thesis, University of Missouri, Columbia, Missouri.
- Bakermans, M. H., and A. D. Rodewald. 2006. Scale-dependent habitat use of Acadian Flycatcher (*Empidonax vireescens*) in central Ohio. *Auk* 123:368-382.
- Best, L. B. 1978. Field Sparrow reproductive success and nesting ecology. *Auk* 95:9-22.
- Blouin-Demers, G., and Weatherhead, P. J. 2001. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology* 83:2882-2896.
- Burhans, D. E., D. D. Dearborn, F. R. Thompson III, and J. Faaborg. 2002. Factors affecting predation at songbird nests in old fields. *Journal of Wildlife Management* 66:240-249.
- _____, and F. R. Thompson III. 2006. Songbird abundance and parasitism differ between urban and rural shrublands. *Ecological Applications* 16:394-405.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Chalfoun, A. D., F. R. Thompson III, and M. J. Ratnaswamy. 2002. Nest predators and fragmentation: a review and meta-analysis. *Conservation Biology* 16:306-318.
- Cimprich, D. A. 2004. Monitoring of the Black-capped Vireo during 2004 on Fort Hood, Texas. *In* Endangered species monitoring and management at Fort Hood, Texas: 2004 annual report. The Nature Conservancy, Fort Hood Project, Fort Hood, Texas, United States.
- Cimprich, D. A. 2005. Monitoring of the Black-capped Vireo during 2005 on Fort Hood, Texas. *In* Endangered species monitoring and management at Fort Hood, Texas: 2005 annual report. The Nature Conservancy, Fort Hood Project, Fort Hood, Texas, United States.
- Clark, K. L., and R. J. Robertson. 1981. Cowbird parasitism and evolution of anti-

- parasite strategies in the Yellow Warbler. *Wilson Bulletin* 93:249-258.
- Coldren, C. L. 1998. The effects of habitat fragmentation on the Golden-cheeked Warbler. Ph.D. dissertation, Texas A & M University, College Station, Texas.
- Dearborn, D. C., and L. L. Sanchez. 2001. Do Golden-cheeked Warblers select nest locations on the basis of patch vegetation? *Auk* 118:1052-1057.
- DeBoer, T. S., and D. D. Diamond. 2006. Predicting presence-absence of the endangered Golden-cheeked Warbler (*Dendroica chrysoparia*). *The Southwestern Naturalist* 51:181-190.
- Diamond, D. D. 1997. An Old-growth definition for western juniper woodlands: Texas Ashe juniper dominated or codominated communities. USDA Forest Service General Technical Report SRS-15.
- Donovan, T. M., and F. R. Thompson III. 2001. Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. *Ecological Applications* 11:871-882.
- Driscoll, M. J. L., T. Donovan, R. Mickey, A. Howard, and K. K. Fleming. 2005. Determinants of Wood Thrush nest success: a multi-scale, model selection approach. *Journal of Wildlife Management* 69:699-709.
- Durner, G. M., and J. E. Gates. 1993. Spatial ecology of black rat snakes on Remington Farms, Maryland. *Journal of Wildlife Management* 57:812-826.
- Engels, T. M., and C. W. Sexton. 1994. Negative correlation of Blue Jays and Golden-cheeked Warblers near an urbanizing area. *Conservation Biology* 8:286-290.
- Engels, T. M. 1995. The conservation biology of the Golden-cheeked Warbler. Ph.D. dissertation, University of Texas, Austin, Texas.
- Filliater, T. S., R. Breitwisch, and P. M. Nealen. 1994. Predation on Northern Cardinal nests: does choice of nest site matter? *Condor* 96:761-768.
- Ford, T. B., D. E. Winslow, D. R. Whitehead, and M. A. Koukel. 2001. Reproductive success of forest-dependent songbirds near an agricultural corridor in south-central Indiana. *Auk* 118:864-873.
- Goguen, C. B., and N. E. Mathews. 2000. Local gradients of cowbird abundance and parasitism relative to livestock grazing in a western landscape. *Conservation Biology* 14:1862-1869.
- Grant, T. A., T. L. Shaffer, E. M. Madden, and P. J. Pietz. 2005. Time-specific variation

- in passerine nest survival: new insights into old questions. *Auk* 122:661-672.
- _____, E. M. Madden, T. L. Shaffer, P. J. Pietz, G. B. Berkey, and N. J. Kadrmas. 2006. Nest survival of Clay-colored and Vesper Sparrows in relation to woodland edge in mixed-grass prairies. *Journal of Wildlife Management* 70:691-701.
- Guilfoyle, M. P. 2002. Black-capped Vireo and Golden-cheeked Warbler populations potentially impacted by USACE reservoir operations. U.S. Army Engineer Research and Development Center EMRRP Technical Notes Collection TN EMRRP-SI-28.
- Gutzwiller, K. J., H. A. Marcum, H. B. Harvey, J. D. Roth, and S. H. Anderson. 1998. Bird tolerance to human disturbance in Wyoming montane forests. *Condor* 100:519-527.
- Haskell, D. G., A. M. Knupp, and M. C. Schneider. 2001. Nest predator abundance and urbanization, p. 243-258. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [eds.], *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston.
- Jette, L. A., T. J. Hayden, and J. D. Cornelius. 1998. Demographics of the Golden-cheeked Warbler (*Dendroica chrysoparia*) on Fort Hood, Texas. USACERL Technical Report 98/52.
- Kilgo, J. C., R. A. Sargent, B. R. Chapman, and K. V. Miller. 1996. Nest-site selection by Hooded Warblers in bottomland hardwoods of South Carolina. *Wilson Bulletin* 108:53-60.
- Knutson, M. G., G. J. Niemi, W. E. Newton, and M. A. Friberg. 2004. Avian nest success in Midwestern forests fragmented by agriculture. *Condor* 106:116-130.
- Kroll, J. C. 1980. Habitat requirements of the Golden-cheeked Warbler: management implications. *Journal of Range Management* 33:60-65.
- Ladd, C., and L. Gass. 1999. Golden-cheeked warbler (*Dendroica chrysoparia*). *In* A. Poole and F. Gill [eds.], *The birds of North America*, no. 420. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, D.C.
- Maas, D. S. 1998. Effects of habitat fragmentation on demographics of Golden-cheeked Warblers. M.S. thesis, University of Oklahoma, Norman, Oklahoma.
- Magness, D. R., R. N. Wilkins, and S. J. Hejl. 2006. Quantitative relationships among Golden-cheeked Warbler occurrence and landscape size, composition, and structure. *Wildlife Society Bulletin* 34:473-479.

- Martin, T. E., and J. J. Roper. 1988. Nest predation and nest site election of a western population of the Hermit Thrush. *Condor* 90:51-57.
- Marzluff, J. M., R. Bowman, and R. Donnelly. 2001. A historical perspective on urban bird research: trends, terms, and approaches, p 1-17. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [eds.], *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston.
- Miller, J. R., and N. T. Hobbs. 2000. Recreational trails, human activity, and nest predation in lowland riparian areas. *Landscape and Urban Planning* 50:227-236.
- Morse, S. F., and S. K. Robinson. 1999. Nesting success of a neotropical migrant in a multi-use, forested landscape. *Conservation Biology* 13:327-337.
- Peak, R. G. 2003. Demography of the Golden-cheeked Warbler on Fort Hood, Texas, 2003. *In* *Endangered species monitoring and management at Fort Hood, Texas: 2003 annual report*. The Nature Conservancy, Fort Hood Project, Fort Hood, Texas, USA.
- _____. 2004. Demography of the Golden-cheeked Warbler on Fort Hood, Texas, 2004. *In* *Endangered species monitoring and management at Fort Hood, Texas: 2004 annual report*. The Nature Conservancy, Fort Hood Project, Fort Hood, Texas, United States.
- _____. 2005. Demography of the Golden-cheeked Warbler on Fort Hood, Texas, 2005. *In* *Endangered species monitoring and management at Fort Hood, Texas: 2005 annual report*. The Nature Conservancy, Fort Hood Project, Fort Hood, Texas, United States.
- _____. 2006. Demography of the Golden-cheeked Warbler on Fort Hood, Texas, 2006. *In* *Endangered species monitoring and management at Fort Hood, Texas: 2006 annual report*. The Nature Conservancy, Fort Hood Project, Fort Hood, Texas, United States.
- _____. In press. Edge density negatively effects Golden-cheeked Warbler nest survival on Fort Hood Military Reservation. *Condor*.
- _____, F. R. Thompson III, and T. L. Shaffer. 2004. Factors affecting songbird nest survival in riparian forests in a Midwestern agricultural landscape. *Auk* 121:726-737.
- Pidgeon, A. M., V. C. Radeloff, and N. E. Mathews. 2003. Landscape-scale patterns of Black-throated Sparrow (*Amphispiza bilineata*) abundance and nest success. *Ecological Applications* 13:530-542.
- Pulich, W. M. 1976. *The Golden-cheeked Warbler: a bioecological study*. Texas Parks

and Wildlife Department, Austin, Texas.

Riskind, D. H., and D. D. Diamond. 1988. An introduction to environments and vegetation, p. 1-16. *In* B.B. Amos and F.R. Gehlbach [eds.], *Edwards Plateau vegetation*. Baylor University Press, Waco, Texas.

Rodewald, A. D. 2002. Nest predation in forested regions: landscape and edge effects. *Journal of Wildlife Management* 66:634-640.

_____, and R. H. Yahner. 2001. Avian nesting success in forested landscapes: influence of landscape composition, stand and nest-patch microhabitat, and biotic interactions. *Auk* 118:1018-1028.

Sexton, C. W. 1987. A comparative analysis of urban and native bird populations in central Texas. Ph.D. dissertation, University of Texas, Austin, Texas.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. *Auk* 121:526-540.

_____, and F. R. Thompson III. In press. Making meaningful estimates of nest survival with model-based methods. *Studies in Avian Biology*.

Stake, M. M. 2003. Golden-cheeked Warbler nest predation. M.S. thesis, University of Missouri, Columbia, Missouri.

_____, J. Faaborg, and F. R. Thompson III. 2004. Video identification of predators at Golden-cheeked Warbler nests. *Journal of Field Ornithology* 75: 337-344.

Stephens, S. E., D. N. Koons, J. J. Rotella, and D. W. Willey. 2003. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. *Biological Conservation* 115:101-110.

Summers, S. G., and G. L. Norman. 2005. Brown-headed Cowbird removal at Fort Hood, Texas. *In* *Endangered species monitoring and management at Fort Hood, Texas: 2005 annual report*. The Nature Conservancy, Fort Hood Project, Fort Hood, Texas, United States.

Tarvin, K. A., and M. C. Garvin. 2002. Habitat and nesting success of Blue Jays (*Cyanocitta cristata*): importance of scale. *Auk* 119:971-983.

Tennant, A. 1998. *A field guide to Texas snakes*. Gulf Publishing, New York.

Tewksbury, J. J., L. Garner, S. Garner, J. D. Lloyd, V. Saab, and T. E. Martin. 2006. Tests of landscape influence: nest predation and brood parasitism in fragmented ecosystems. *Ecology* 87:759-768.

Thompson, F. R., III, T. M. Donovan, R. M. DeGraff, J. Faaborg, and S. K. Robinson.

2002. A multi-scale perspective of the effects of forest fragmentation on birds in eastern forests. *Studies in Avian Biology* 25:8-19.
- U.S. Fish and Wildlife Service. 1992. Golden-cheeked Warbler (*Dendroica chrysoparia*) recovery plan. Albuquerque, New Mexico.
- _____. 1996. Balcones Canyonlands National Wildlife Refuge proposed additions; final land acquisition compliance document. U.S. Fish and Wildlife Service, Albuquerque, New Mexico.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893-901.
- Verbeek, N. A. M., and C. Caffrey. 2002. American Crow (*Corvus brachyrhynchos*). In A. Poole and F. Gill [eds.], *The birds of North America*, no. 647. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, D.C.
- Vickery, P. D., M. L. Hunter, Jr., and J. V. Wells. 1992. Is density an indicator of breeding success? *Auk* 109:706-710.
- Weatherhead, P. J., and M. B. Charland. 1985. Habitat selection in an Ontario population of the snake, *Elaphe obsoleta*. *Journal of Herpetology* 19:12-19.
- Winter, M. 1999. Nesting biology of Dickcissels and Henslow's Sparrows in southwestern Missouri prairie fragments. *Wilson Bulletin* 111:515-527.

Table 1. *A priori* candidate models, model variables and descriptions, and predicted direction (PD) used to evaluate nest success rates in Austin, Texas and Fort Hood, Texas during 2005-2006. In addition to single models and the global and null model, we examined additive combinations of the temporal model with one or two other models.

Model	Variables	Description	PD
Temporal	Julian date	Cubic effect of date	-
	Nest stage	Laying, incubation, nestling	-
	Year	2005 or 2006	=
Nest-site	Nest height	Height of nest above ground	+
	Nest cover	Average of over, under, and four side cover estimates	+
	Distance to main trunk	Distance from nest to main trunk along nest branch	+
Nest-patch	Slope	Percent grade in steepest direction from the nest	+
	Proximity to edge	Proximity to nearest canopy break/edge measured with meter tape	+
Edge	Open edge density	Density of open habitat edge in 100-m radius around nest	-
	Trail density	Density of open-canopy trails in 25-m radius around nest	-
Landscape	Percent open	Percent of open habitat within 1-km radius around nest	-

Landscape	Percent developed	Percent of developed habitat within 1-km radius around nest	-
Urban	Site	Austin or Fort Hood	-
	Road density	Density of roads within a 500-m radius around nest	-
	Building density	Density of buildings within a 500-m radius around nest	-
Global	All variables listed above		
Null	Intercept only		

Table 2. Support for the models summing to a cumulative weight (w_i) ≥ 0.90 predicting Golden-cheeked Warbler nest survival in Austin, Texas and Fort Hood, Texas during 2005-2006. Models are ranked from most supported to least based on Akaike's Information Criteria (AIC_c), ΔAIC_c , and Akaike weights (w_i). AIC_c is based on $-2 \times \log$ likelihood ($-2L$) and the number of parameters in the model (K).

Model	-2L	K	AIC_c	ΔAIC_c	w_i
Temporal + Edge	-269.157	9	556.394	0.000	0.412
Temporal + Nest-patch + Edge	-268.080	11	558.278	1.884	0.161
Temporal	-272.288	7	558.625	2.231	0.135
Temporal + Edge + Landscape	-268.774	11	559.666	3.272	0.080
Temporal + Nest-patch	-271.452	9	560.983	4.589	0.042
Edge	-277.609	3	561.228	4.834	0.037
Temporal + Nest-site + Edge	-268.635	12	561.410	5.016	0.034

Table 3. Model-averaged parameter estimates, unconditional standard errors (SE), and the odds ratios (OR) and associated lower (LCL) and upper (UCL) 95% confidence intervals for factors hypothesized to effect Golden-cheeked Warbler nest survival in Austin, Texas and Fort Hood, Texas during 2005-2006.

Parameter	Level	Estimate	SE	OR	LCL	UCL
Jul		-2.6828	1.3637	0.06837	0.004	1.046
Jul2		0.0207	0.0108	1.02091	0.999	1.043
Jul3		-0.0001	0.0000	0.99995	1.000	1.000
Stage	L	-0.4348	0.5360	0.64739	0.222	1.891
Stage	I	0.0526	0.2748	1.05398	0.608	1.826
Year	2005	0.3607	0.3135	1.43428	0.766	2.685
Nest height		0.0003	0.0038	1.00029	0.993	1.008
Cover		0.0003	0.0007	1.00028	0.999	1.002
Distance to main trunk		-0.0035	0.0095	0.99649	0.978	1.016
Slope		0.0027	0.0060	1.00272	0.991	1.015
Proximity to edge	0	0.0578	0.1241	1.05955	0.827	1.358
Open edge density		-0.0057	0.0043	0.99429	0.986	1.003
Trail density		0.0009	0.0012	1.00093	0.999	1.003
Percent open		0.0009	0.0023	1.00089	0.996	1.005
Percent developed		0.0012	0.0037	1.00123	0.994	1.009
Road density		-0.0003	0.0011	0.99968	0.998	1.002
Building density		-0.0056	0.0257	0.99442	0.945	1.047
Site	Austin	-0.0017	0.0190	0.99830	0.961	1.037

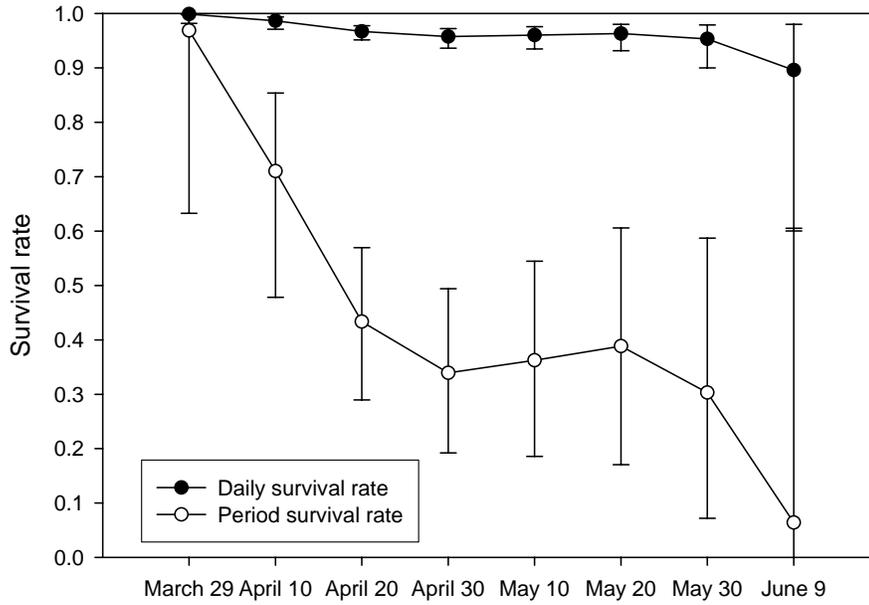


Fig. 1. Predicted daily and period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of Julian date in Austin, Texas and Fort Hood, Texas during 2005-2006.

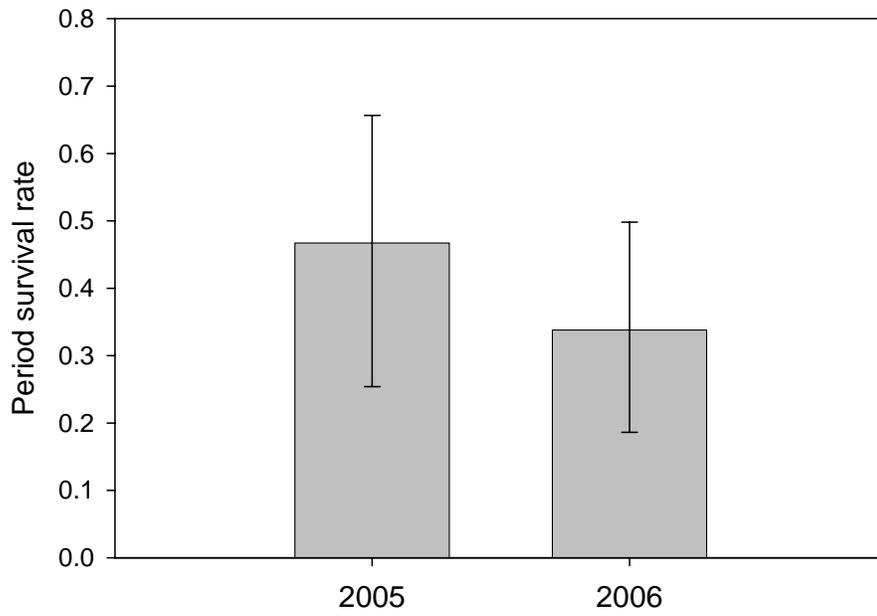


Fig. 2. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of year in Austin, Texas and Fort Hood, Texas during 2005-2006.

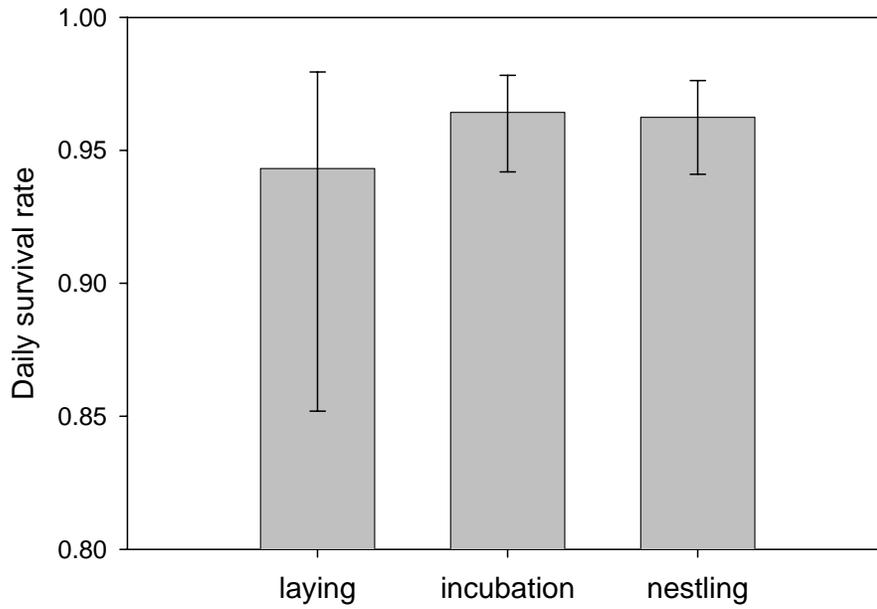


Fig. 3. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of nest stage in Austin, Texas and Fort Hood, Texas during 2005-2006.

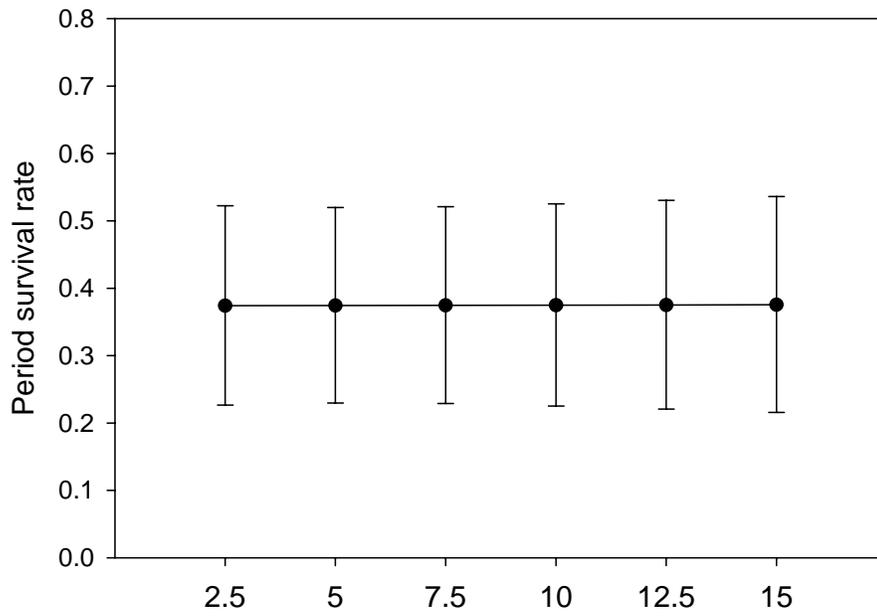


Fig. 4. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of nest height in Austin, Texas and Fort Hood, Texas during 2005-2006.

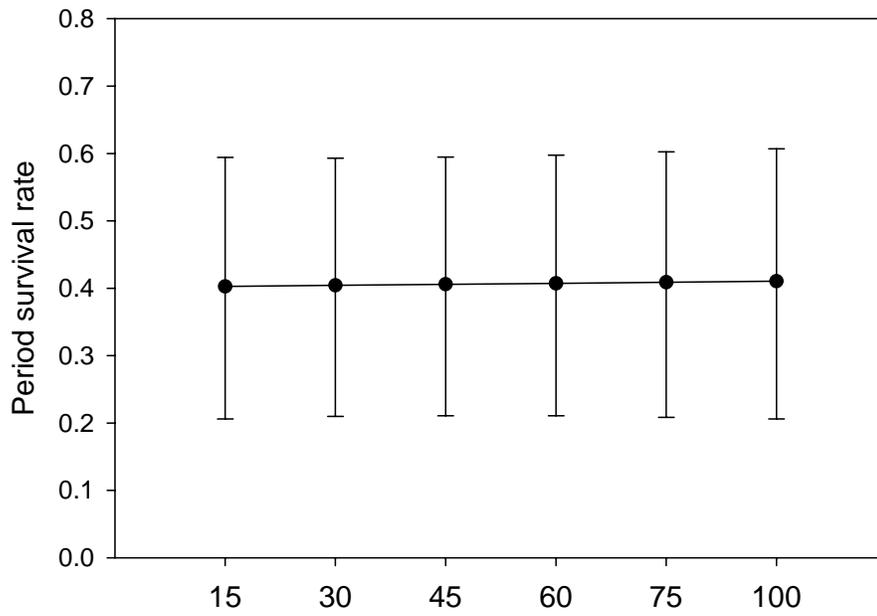


Fig. 5. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of nest cover in Austin, Texas and Fort Hood, Texas during 2005-2006.

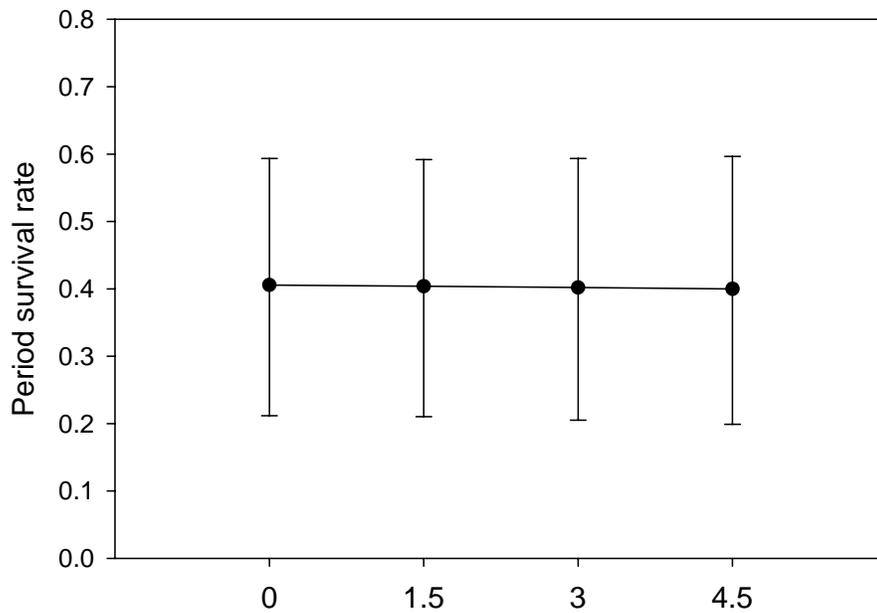


Fig. 6. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of distance from main trunk (m) in Austin, Texas and Fort Hood, Texas during 2005-2006.

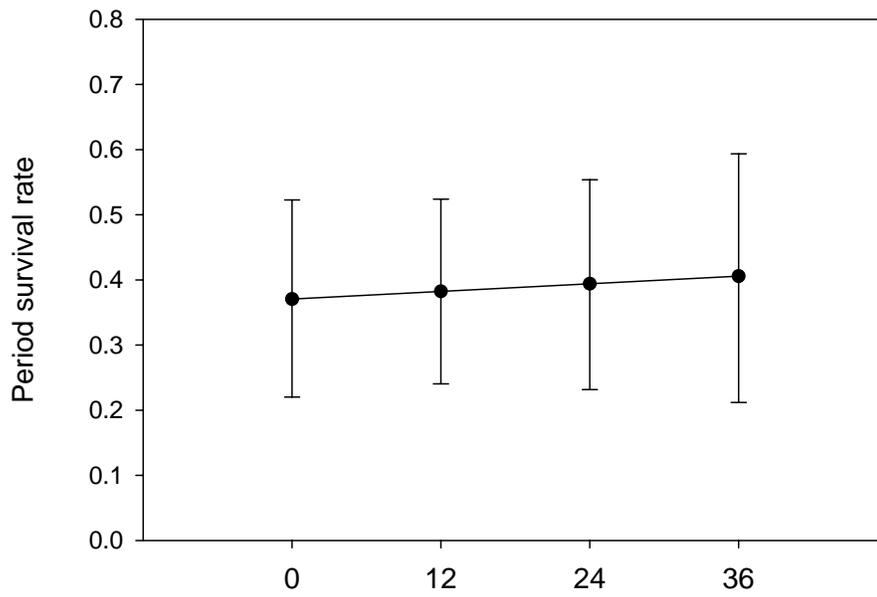


Fig. 7. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of slope in Austin, Texas and Fort Hood, Texas during 2005-2006.

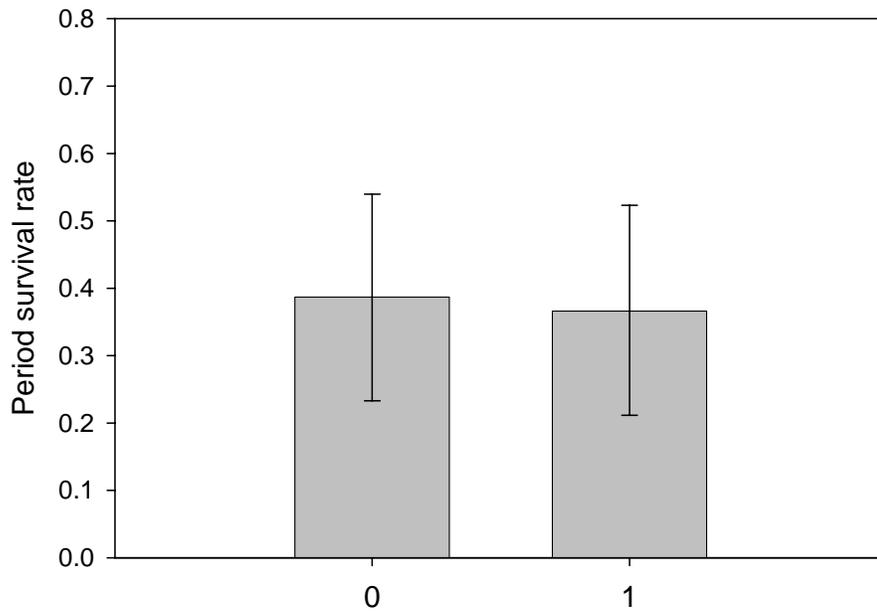


Fig. 8. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of proximity to edge (0 if nests > 30 m and 1 if ≤ 30 m) in Austin, Texas and Fort Hood, Texas during 2005-2006.

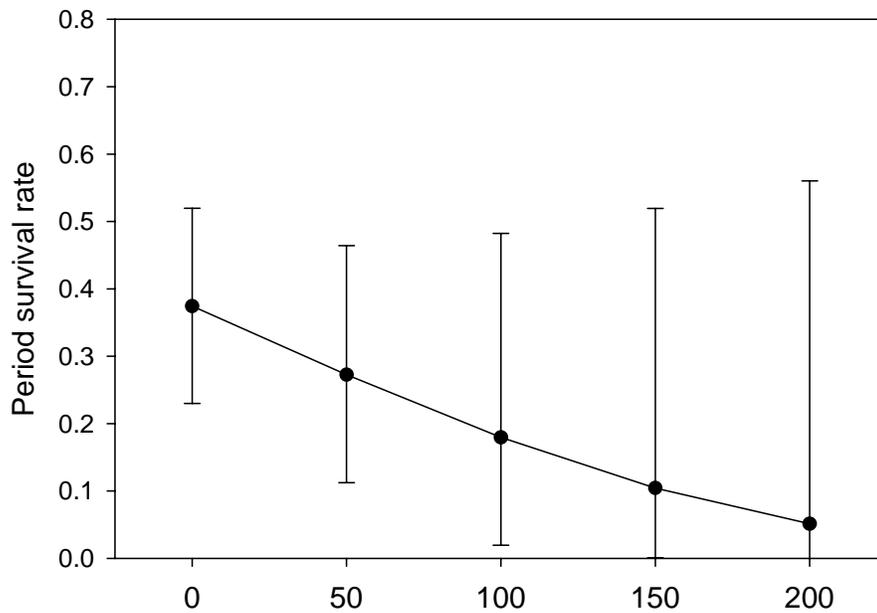


Fig. 9. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of open edge density (m/ha) within a 100-m radius of the nest in Austin, Texas and Fort Hood, Texas during 2005-2006.

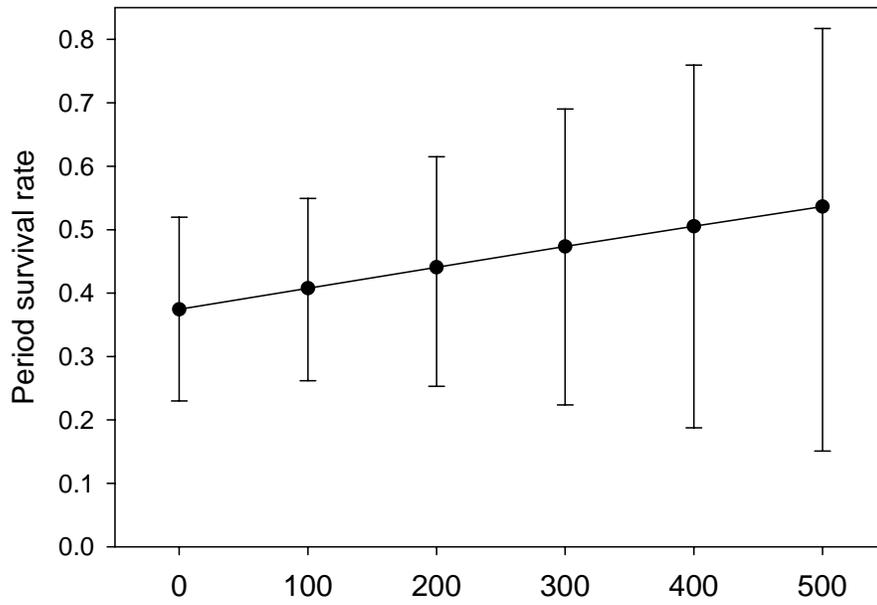


Fig. 10. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of trail density (m/ha) within a 25-m radius from the nest in Austin, Texas and Fort Hood, Texas during 2005-2006.

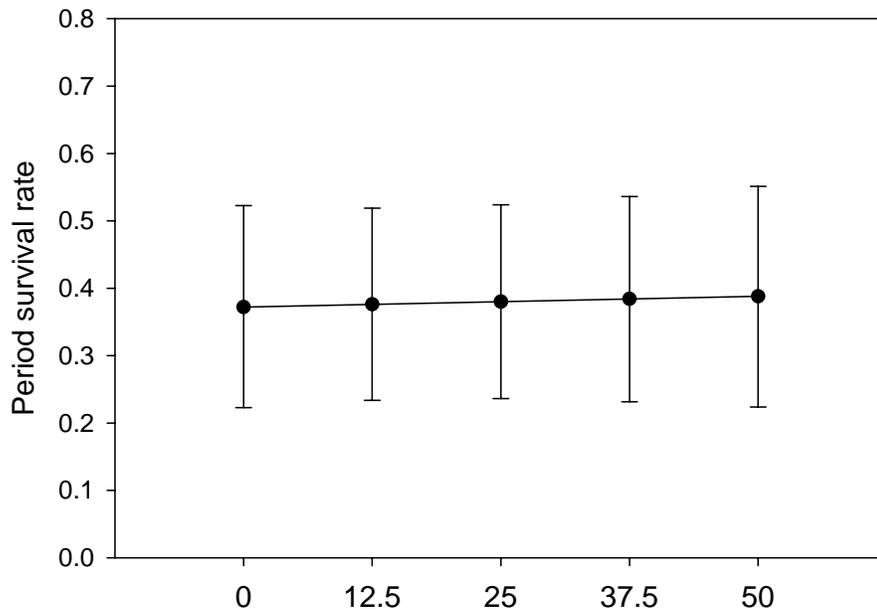


Fig. 11. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of percent of open area within a 1-km radius from the nest in Austin, Texas and Fort Hood, Texas during 2005-2006.

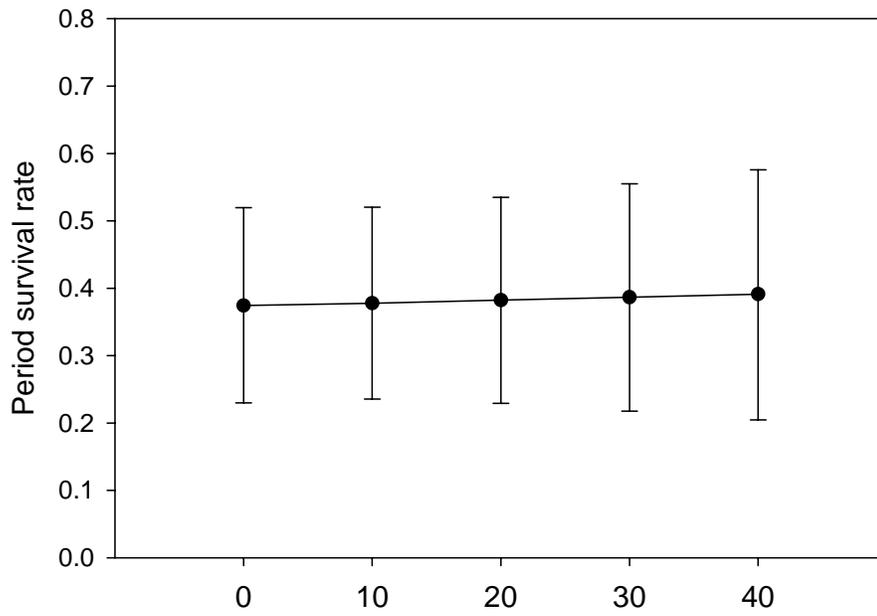


Fig. 12. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of percent of developed area within a 1-km radius from the nest in Austin, Texas and Fort Hood, Texas during 2005-2006.

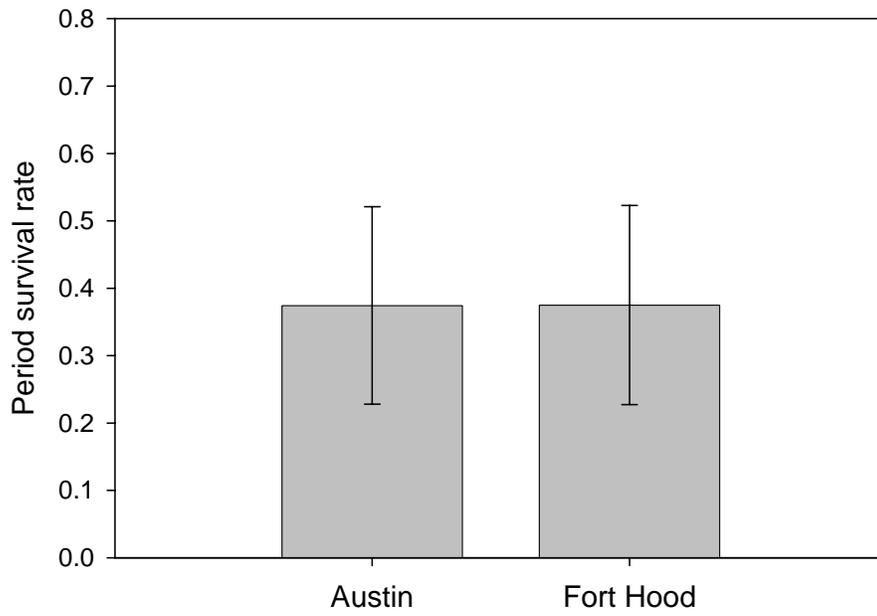


Fig. 13. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of site in Austin, Texas and Fort Hood, Texas during 2005-2006.

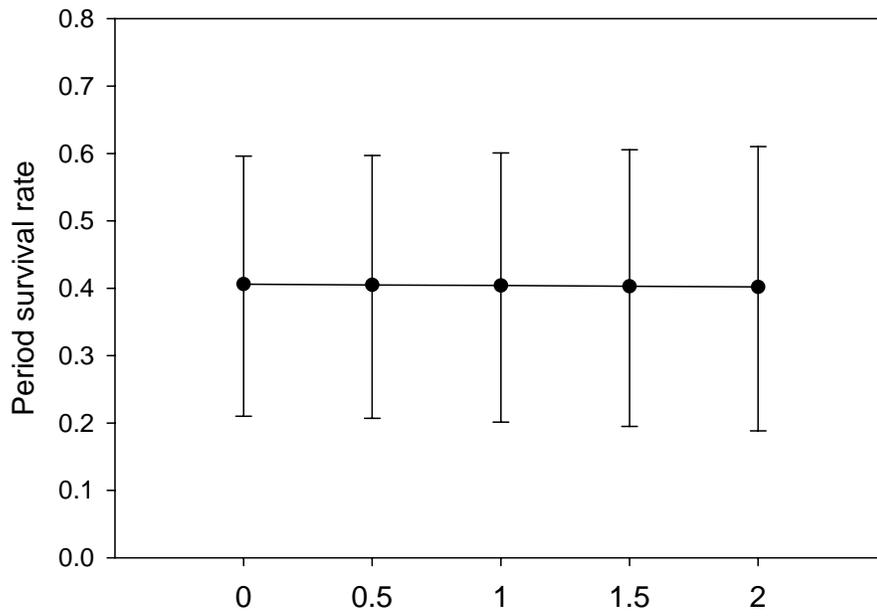


Fig. 14. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of building density (#/ha) within a 500-m radius from the nest in Austin, Texas and Fort Hood, Texas during 2005-2006.

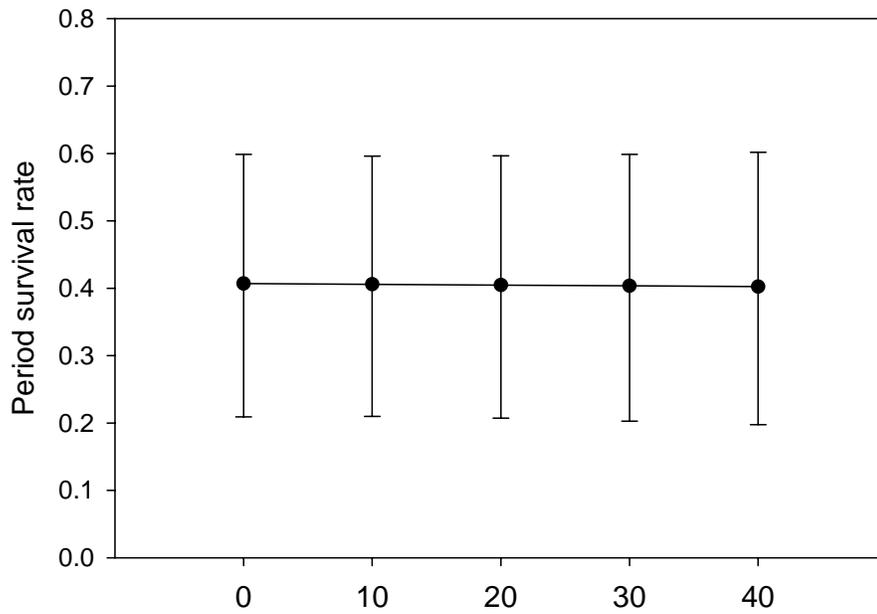
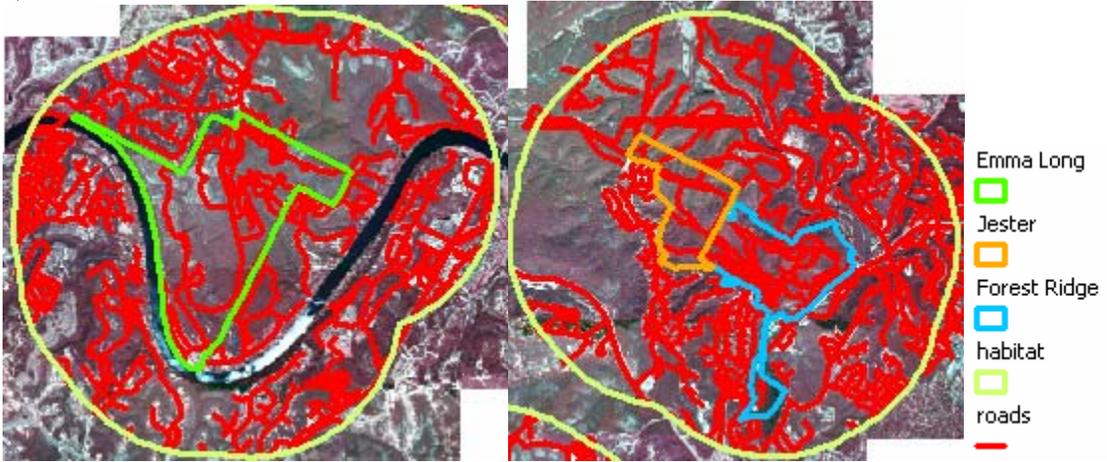


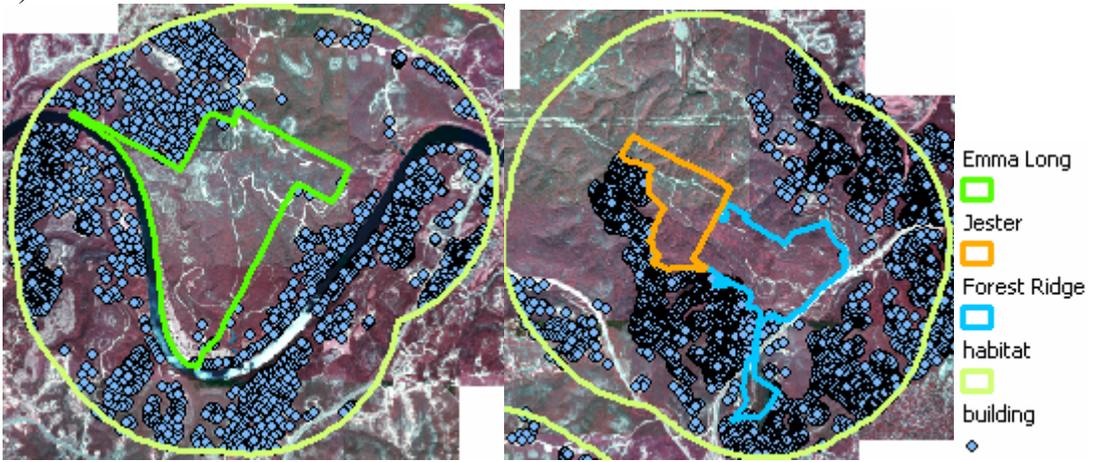
Fig. 15. Predicted period survival rates and 95% confidence intervals for Golden-cheeked Warbler nests as a function of road density (m/ha) within a 500-m radius from the nest in Austin, Texas and Fort Hood, Texas during 2005-2006.

Appendix A. Aerial photos of the study sites overlaid with GIS landscape metrics (resolution 1:100,000): a) Austin study sites with roads and trails outlined, b) Austin study sites with buildings highlighted, c) Austin study sites with habitat polygon classifications, d) Fort Hood study sites with roads and trails outlined, e) Fort Hood study sites with buildings highlighted, f) Fort Hood study sites with habitat polygon classifications.

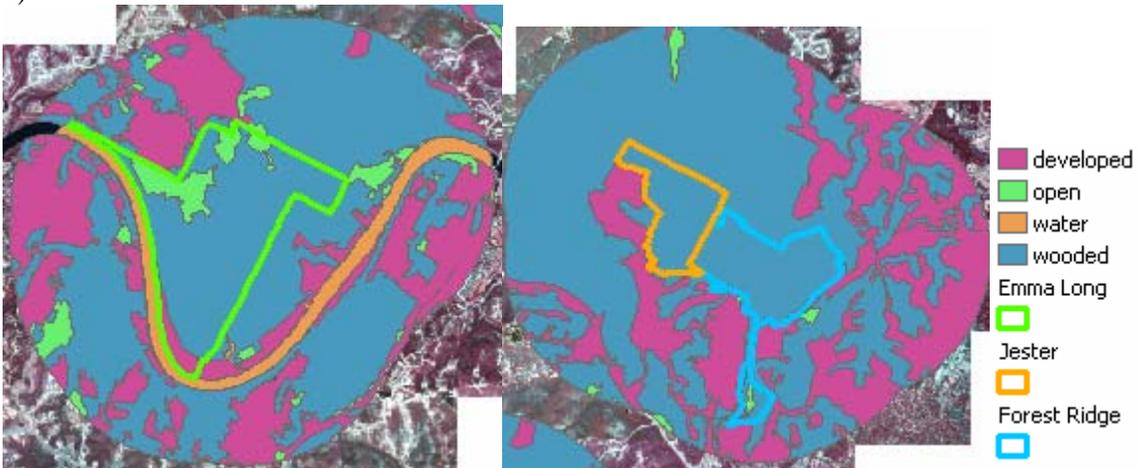
a)



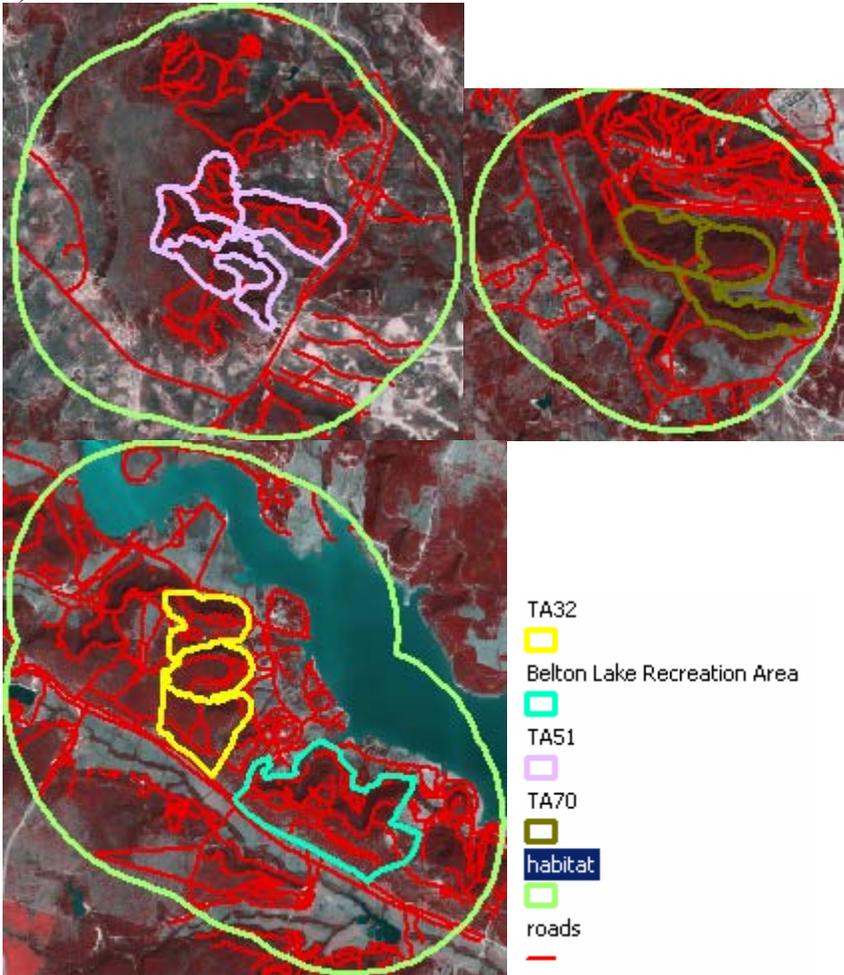
b)



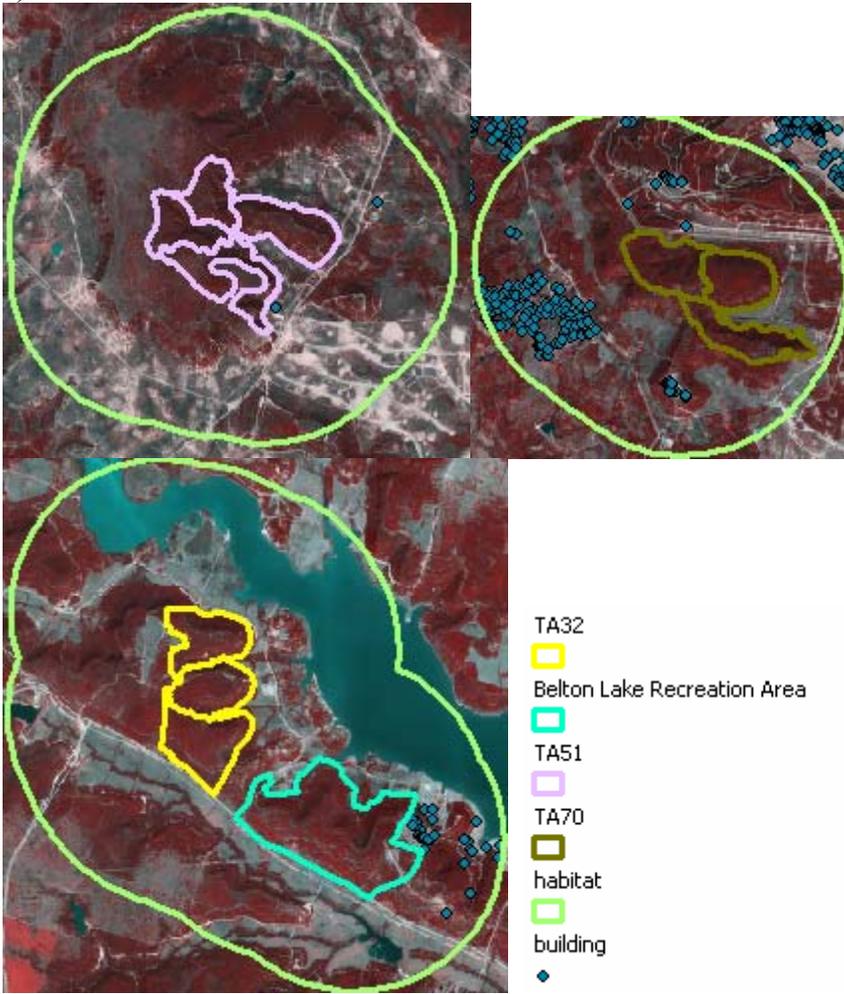
c)



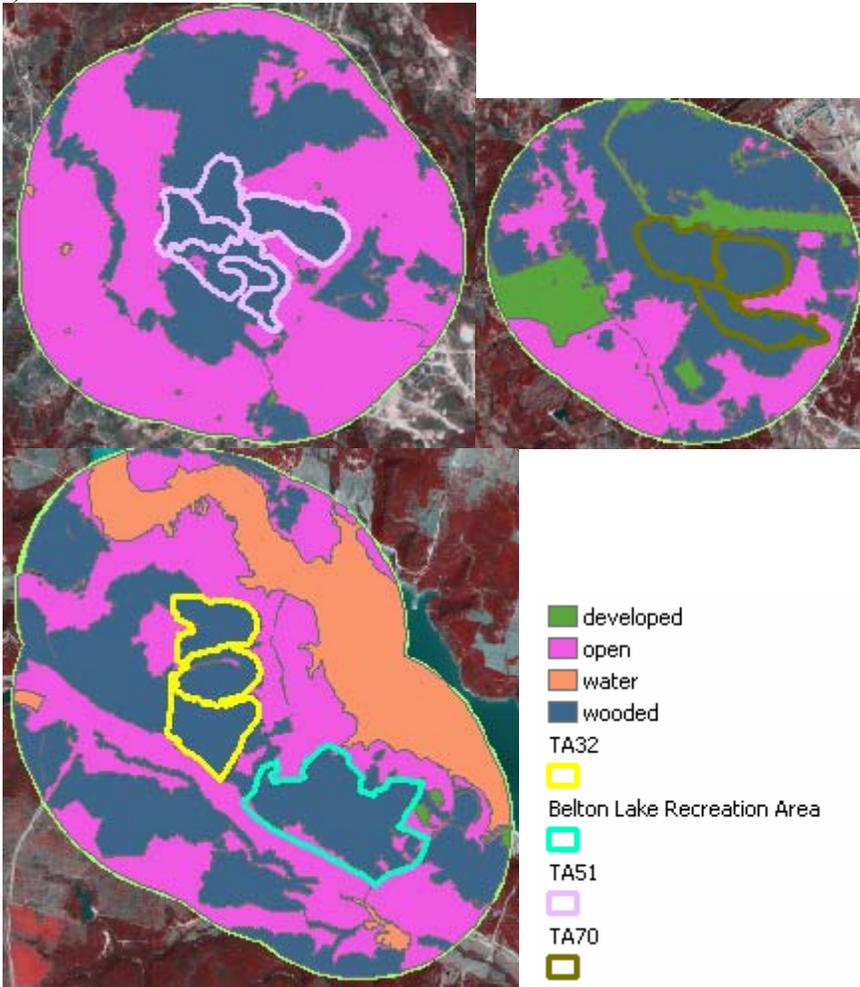
d)



e)



f)



CHAPTER 2

**SOURCES OF NEST MORTALITY AND PREDATORS OF
GOLDEN-CHEEKED WARBLERS IN AN URBAN LANDSCAPE**

ABSTRACT

We monitored 61 Golden-cheeked Warbler (*Dendroica chrysoparia*) nests in Austin, Texas, from 2005 to 2006 with time-lapse video cameras to determine sources of mortality and to identify predators in an urban landscape. The overall period mortality rate was 0.631 and the predation rate was 0.541. Eight nests were depredated by Texas rat snakes (*Elaphe obsoleta lindheimeri*), six by birds, including four by Western Scrub-Jays (*Aphelocoma californica*) and two by Cooper's Hawks (*Accipiter cooperii*), three by fox squirrels (*Sciurus niger*), and one by fire ants (*Solenopsis* sp.). We compared predators and predation rates in Austin to those from a previous study on Fort Hood, Texas and this study. The daily predation rate in Austin (0.0335) was slightly lower than on Fort Hood (0.0367). The predator composition was similar between Austin and Fort Hood. However, the dominant avian predator differed between the two landscapes. Western Scrub Jays were the dominant avian predator in Austin and American Crows (*Corvus branchyrynchos*) were the dominant avian predator on Fort Hood. Nest abandonment, hatching success and nestling survival were similar between Austin and Fort Hood. We compared success of 39 nests in Austin monitored without video cameras to those monitored with cameras and found no support for an effect of video surveillance on nest survival.

INTRODUCTION

Native bird populations face increasing pressure of living in or co-existing beside human-dominated landscapes and whether populations can sustain themselves in the face of this pressure depends on interacting direct and indirect factors that ultimately drive population parameters (Marzluff 2001). One such parameter is productivity, and one component of productivity is nest success. Since predation is often the greatest source of nest failure for passerines (Ricklefs 1969), knowledge of levels of predation and the identity of nest predators could be important for avian conservation. There is little knowledge of nest success or nest predators of populations of native songbirds in urban landscapes. There is some evidence that nest predation is higher in urban sites than nearby rural or undeveloped sites (Borgmann and Rodewald 2004, Bakermans and Rodewald 2006), while other studies have not found this pattern (Morrison and Bolger 2002, Burhans and Thompson 2006). Only one study used video surveillance to identify nest predators in an urban setting (Morrison and Bolger 2002). In addition to predation effects, features associated with or caused by human disturbance may alter adult fitness or behavior (Gutzwiller et al. 1998, Fernández-Juricic et al. 2001, Verhulst et al. 2001), thus impacting nest productivity (Gill et al. 2001) through higher nest abandonment, lower hatching success, or lower nestling survival in urban populations when compared to their rural counterparts. Knowledge of nest survival and predation risk in urbanizing areas is especially important for endangered species at risk because of habitat loss due to development.

The Golden-cheeked Warbler (*Dendroica chrysoparia*) is a federally endangered neotropical migrant songbird that breeds in the canopy of mature juniper-oak woodlands in

central Texas (Ladd and Gass 1999). Urbanization along the I-35 corridor is destroying alarming amounts of Golden-cheeked Warbler habitat in the core of their range (Pulich 1976, Wahl 1990) and habitat loss due to urbanization is considered a major threat to the viability of the Golden-cheeked Warbler (U.S. Fish and Wildlife Service 1992). The Golden-cheeked Warbler recovery plan established research priorities, one of which is to determine the relationship of various predators to reproductive success, and to understand the relationship of predation rates to fragmentation and land use practices (U.S. Fish and Wildlife Service 1992, task 1.24).

Stake et al. (2004) documented nest predators of Golden-cheeked Warblers at Fort Hood, Texas an active military installation situated in a rural landscape where warbler habitat patches are surrounded by open grasslands used for grazing. Rat snakes (*Elaphe* spp.) were the leading predator, followed by a variety of bird species, fox squirrels (*Sciurus niger*), and fire ants (*Solenopsis invicta*). Avian predators included American Crow (*Corvus brachyrhynchos*), Brown-headed Cowbird (*Molothrus ater*), Western Scrub-Jay (*Aphelocoma californica*), and Cooper's Hawk (*Accipiter cooperii*). How the importance of nest predators of Golden-cheeked Warblers changes in response to landscape composition is unknown. Characteristics of a habitat patch or the surrounding landscape can affect nest predators (Thompson and Burhans 2003). For example, Golden-cheeked Warbler nests may be subject to different suites of avian nest predators in different landscapes, such as urban areas (Stake et al. 2004). Numerous studies have shown higher densities of corvid species in man-altered environments (Beissinger and Osborne 1982, Wilcove 1985, Blair 1996, Jokimäki and Huhta 2000, Haskell et al. 2001) or otherwise found corvid species to be insensitive to increased development (Bolger et al. 1997). Blue

Jays (*Cyanocitta cristata*) and Western Scrub-Jays responded positively to increased levels of suburbanization in Austin (Sexton 1987, Arnold et al. 1996). The response by Golden-cheeked Warblers to Blue Jays has been ambiguous - presence of Golden-cheeked Warblers was negatively associated with presence of Blue Jays in one study (Engels and Sexton 1994), but no association was found in another (Arnold et al. 1996). In fact, Arnold et al. (1996) found Golden-cheeked Warblers were often found in patches co-inhabited by at least one of the jay species on their sites in Travis County (near Austin). Increases in predator abundance in urban areas could mean increases in nest predation in urban areas. This pattern may explain the observed increase in nest predation of urban Acadian Flycatchers (*Empidonax vireescens*) in Ohio (Bakermans and Rodewald 2006).

Alternatively, there may be a shift in predators moving along the rural-urban gradient, resulting in similar overall predation rates but differences in predator-specific mortality. Predator communities changed across a forest-old field ecotone (Thompson and Burhans 2003), but no study has recorded the predator assemblage along the rural-urban gradient.

Video surveillance is an increasingly popular way to document nest predators (Brown et al. 1998, Thompson et al. 1999, Pietz and Granfors 2000, Stake and Cimprich 2003, Peterson et al. 2004, Stake et al. 2004, King and DeGraaf 2006). While these studies have discovered information about nest predators, they have focused on ground-nesting (Pietz and Granfors 2000, Renfrew and Ribic 2003) or shrub-nesting (Burhans and Thompson 1999, Morrison and Bolger 2002, Stake and Cimprich 2003, Small 2005, King and DeGraaf 2006) species, resulting in a knowledge gap for canopy-nesting songbirds. Most camera studies have been conducted in exurban or rural settings (but see Morrison and Bolger 2002 conducted along urban edge), while many bird populations are becoming

increasingly squeezed into encroaching suburbia (Marzluff 2001). Beyond determining sources and rates of nest predation, video surveillance also allows researchers to evaluate the relative importance of predator groups and species in different areas, and determine other sources of nest failure and the extent of partial losses, an often overlooked, but potentially significant component of nest success.

We monitored Golden-cheeked Warbler nests in Austin and Fort Hood with video cameras to determine sources of nest mortality and the importance of nest predator species. We evaluated whether camera monitoring affected nest success by comparing survival rates of nests in Austin monitored with and without cameras. We estimated cause-specific nest mortality rates for camera-monitored nests in Austin and compared them to estimates from the more rural landscape at Fort Hood based on results collected by Stake et al. (2004) and this study. We documented the occurrence of all sources of egg and nestling mortality for nests in Austin and Fort Hood to determine if differences existed in hatching success or nestling survival.

STUDY AREA

This study was conducted in northwest Austin (Travis County), in central Texas. Travis County contains more juniper-oak woodland than any other county (Wahl et al. 1990). Austin, however, is a rapidly growing city; the population size increased almost 50% from 1990-2000 ([www.censuscope.org](http://www.censusscope.org)), an annual growth rate of approximately 3.5% (www.ci.aus.tx.us). Our study sites were owned and managed by the City of Austin under the umbrella of the Balcones Canyonlands Preserve, which protects over 5,300 hectares (ha) of Golden-cheeked Warbler habitat. Our study sites were Emma Long Metropolitan Park (30°20'N, 97°50'W; 385 ha), Forest Ridge (30°23'N, 97°47'W; 294 ha),

and Jester (30°23'N, 97°47'W; 119 ha). The dominant habitat was mature juniper-oak woods along steep limestone canyons and densely wooded plateaus.

We also found and monitored nests located on Fort Hood (Bell and Coryell counties) in 2005 to increase the sample size from an earlier study identifying Golden-cheeked nest predators (Stake et al. 2004). Our study sites were Belton Lake Outdoor Recreation Area and Training Area 32 on the east side of the base (31°08'N, 97°34'W; each ~175 ha). Fort Hood is an active military installation located approximately 70 miles north of Austin. The habitat was scrubby juniper-oak woods on steep slopes and flat mesas separated by valleys leased for cattle grazing. Intensive cowbird control was practiced near the site in 2005.

METHODS

Nest searching and monitoring

We located and monitored nests from mid-March through mid-June 2005 and 2006 in Austin and 2005 on Fort Hood. Most nests were found by tracking an adult to the nest. We recorded the nest location using Garmin global positioning units (GPS; Garmin International, Olathe, Kansas) with an accuracy to ~3 m and marked them in the field with plastic flagging > 3 m from the nest with directions to the nest (distance and bearing, plus description of location in tree). Nests were monitored every two days after the onset of incubation, and more frequently around the expected hatching and fledgling dates. We determined eggs had hatched by verifying adults bringing food to the nest and feeding or if we recorded hatching by video surveillance. We considered young to have fledged only if we verified fledglings by sight or sound with the parents within the first few days of the expected fledge date (usually verified the day of or day after fledge) or if we recorded

fledging by video surveillance. We considered a nest depredated if eggs or nestlings too young to have fledged disappeared from the nest (or the nest itself was destroyed and weather could not be the cause), abandoned if the female deserted the nest (if abandonment was determined to have occurred before laying, the nest was not included in analyses), parasitized if we discovered evidence of cowbird contents in the nest, and unknown if we could not determine the fate of the nest (nests with unknown fates were not used in analyses).

Video cameras

We used miniature video camera systems with infra-red illumination (Fuhrman Diversified, Inc., Seabrook, Texas) to monitor a subset of nests. The cameras measured 32 x 32 x 60 mm and contained six infra-red light-emitting diodes (950 nm) that allowed for filming at night but were not visible to vertebrates. Cameras were clamped to the nest tree or branch with a 1-m long adjustable arm and positioned 30-50 cm above the nest to permit optimal viewing of nest contents during the day and night. The camera was connected by a 20-m long cable to a time-lapse video cassette recorder that was powered by a 12-volt deep cycle marine battery. The cable was routed to be inconspicuous to humans and potential predators and the recorder and battery were hidden and positioned as far from the nest as possible. We monitored nest activity daily with a portable monitor connected to the video recorder, allowing monitoring to be performed without disturbing the nest.

We set up video cameras at all nests possible, but not all nests were accessible and we often monitored more active nests than we had cameras for at one time. Nests in the egg stage were first priority for cameras, but nests in the nestling stage were used as needed. Cameras were typically set up in the afternoon. We deployed cameras only after

the onset of incubation to reduce chances of abandonment (Thompson and Burhans 2003, Stake et al. 2004). Therefore, we were only able to identify predators during the incubation and nestling stages. We removed the camera set-up if a female did not resume normal activity within two hours of departing the nest area after initial set-up. Cameras were taken down after the final outcome occurred (fledged or failed), but we monitored post-outcome nests if we did not have another nest ready for camera deployment to determine if potential predators visited the nest soon after nest activity concluded.

We used a time-lapse setting (~7 frames/sec) on the recorder enabling us to record 24-hrs on a single tape. Tapes were replaced daily and batteries were replaced and recharged every other day. We reviewed the end of each tape daily to determine activity at the nest and recorded standard monitoring information (date, time, stage, nest contents). If the nest contents changed since the previous day (e.g. hatched, fledged, depredated), we searched the tape and recorded pertinent information (e.g. hatching or fledging time(s), predation time, predator identity). We documented all changes for each egg and nestling in the nest. We identified predators to the lowest possible taxa. We watched all post-outcome footage and recorded any visits made to the nest by potential predators.

Nest survival and camera effects

We used the logistic exposure method (Shaffer 2004) to estimate daily survival of nests monitored with and without cameras in Austin. This method compensated for varying interval lengths between monitoring checks of camera and non-camera nests. We coded survival as 1 if the nest was successful for the interval and as 0 if the nest failed. Failure included abandonment, weather-related failure, predation (resulting in complete loss of nest contents) and parasitism (if the event resulted in loss of all warbler eggs or

nestlings). This allowed the information collected by traditional monitoring methods to be comparable to those gathered from video surveillance and produced a nest survival estimate equivalent to typical nest success studies.

We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate our *a priori* hypothesis that camera-monitored nests had the same nest success as non-camera monitored nests. We compared support for the *a priori* model with year, stage, Julian date and camera effects (camera present or not) to a null model with year, stage, and Julian date effects. This allowed us to control for temporal effects that may have affected nest survival while evaluating our hypotheses concerning camera effects. We examined the overdispersion parameter for the full model for evidence of lack of fit (Burnham and Anderson 2002). We ranked the models according to their Akaike information criteria (AIC) value, which is based on the maximum likelihood value and a penalty for the number of model parameters (Burnham and Anderson 2002). The most supported model is the model with the lowest AIC value for small sample sizes (AIC_c), and highest Akaike weight (w_i) (Burnham and Anderson 2002). We report the $-2 \times \log$ -likelihood ($-2L$), AIC_c , ΔAIC_c , and w_i (Burnham and Anderson 2002, Shaffer and Thompson in press). We used the most supported model to estimate nest survival. The nest success period was based on a 25 day nest cycle (3, 10, and 12 days for laying, incubation, and nestling stages, respectively).

Cause-specific mortality

We used program Micromort 1.2 (Heisey and Fuller 1985) to estimate cause-specific mortality rates in Austin with data from this study and on Fort Hood with data from this study and Stake et al. (2004). This method is similar to the Mayfield method (Mayfield 1961, 1975) but uses a maximum-likelihood approach and estimates standard

errors and confidence intervals based on Johnson (1979). While model-based approaches such as Dinsmore et al. (2002) and Shaffer (2004) are preferred for estimating nest survival, Micromort allowed us to directly estimate cause-specific nest mortality rates and associated standard errors and confidence intervals. We present daily and period mortality rates from Austin and Fort Hood (Stake et al. 2004 and this study).

RESULTS

We found and monitored 111 nests (35 in 2005 and 76 in 2006) in Austin for a total of 921 monitoring intervals. We monitored 61 Golden-cheeked Warbler nests with cameras in Austin (18 and 43 nests in 2005 and 2006, respectively) for a total of 537 monitoring intervals. Forty nests fledged young with no predators visiting the nest while it was active, 14 were depredated resulting in complete failure of the nest, 4 were partially depredated resulting in ≥ 1 nestling being force-fledged from the nest, 2 were abandoned (after camera acceptance), and 1 failed due to weather. We did not record any multi-predator events, but we found one parasitized nest that we later filmed being depredated. We monitored 50 nests without cameras in Austin (17 in 2005 and 33 in 2006) for a total of 384 monitoring intervals. We considered 22 nests fledged, 17 depredated, 3 abandoned prior to laying, and 7 had unknown fates.

We found and monitored nine nests on Fort Hood in 2005, for a total of 86 monitoring intervals. Seven nests were monitored with cameras, totaling 68 monitoring intervals. Five nests fledged (72%) with no predator visits while active, one nest (14%) was completely depredated, and one nest (14%) was partially depredated. Two nests were monitored without cameras for 18 intervals and we determined that both nests fledged young.

No female abandoned a nest due to initial presence of a camera, although we did remove cameras from five nests because females did not resume incubating within two hours of set-up. These instances occurred within the first couple days of incubation, and females returned after removal of cameras and accepted the camera during a subsequent attempt several days later.

Nest survival and camera effects

We monitored 61 nests with cameras and 39 (active and known fate) without. Examination of the overdispersion parameter ($c=0.983$) for the full model (with camera effects) indicated no lack of fit. The null model (without camera effects) received considerable support over the model with a camera effect (Table 1), but there was some model-selection uncertainty (the camera model had a $\Delta AIC_c = 1.8$). We used model-averaging to estimate nest survival for nests monitored with and without cameras. Nest success was similar for camera monitored nests (0.425; 95% CI 0.231-0.608) than non-camera monitored nests (0.407; 95% CI 0.225-0.583), but confidence intervals overlapped almost completely.

Cause-specific nest mortality

Nest mortality was 0.631 (0.437-0.760) in Austin. Predation was the greatest source of mortality, with few losses due to abandonment or weather (Table 2). The daily predation rate was 0.006 (169 camera intervals) and 0.046 (368 camera intervals) for eggs and nestlings, respectively. We recorded 18 predation events in Austin and 2 predation events on Fort Hood. Snakes were the dominant predator in Austin, followed by birds, mammals, and insects. Predation rates by predator groups were similar between Austin and Fort Hood (Fig. 1).

Texas rat snakes (*Elaphe obsoleta lindheimeri*) were responsible for eight predations in Austin and one predation on Fort Hood and were the only snake species recorded. All snake predations occurred in the nestling stage and resulted in the loss of 11.5% of the total nestlings, and 47.2% of the nestlings lost to predators in Austin. All snake predations were nocturnal, occurring between 20:30 and 23:52 from 18 April to 19 May. One unhatched egg was also consumed during a predation, representing 0.7% of the total eggs and 20% of the eggs lost to predators. One predation resulted in two young being force-fledged from the nest. Both fledglings from this nest were later re-sighted. Two nests fledged one young, leaving 3-4 young who were subsequently depredated by a snake (one in Austin and one on Fort Hood). Neither fledgling was re-sighted. Snakes caused complete failure in all other instances. Four predations happened early in the nestling stage when the young were < 4 days old and the female was still brooding; three of these instances resulted in the predation on the female.

Western Scrub-Jays depredated four nests in Austin, accounting for 67% of the total recorded avian predations and 22% of total predations. Cooper's Hawks depredated two nests in Austin, accounting for 33% of total avian predations, and 11% of the total predations. All avian predations in Austin were during the nestling stage resulting in the loss of 8.8% of the total nestlings, and 35.8% of nestlings lost to predators. An American Crow depredated one nest in the egg stage on Fort Hood. All avian predations were diurnal and occurred from 23 April to 18 May. We discovered one nest in Austin containing only a cowbird hatchling being attended to by both Golden-cheeked Warbler adults. This nest was subsequently depredated by a Western Scrub-Jay.

Fox squirrels were the only mammalian nest predator and depredated three nests. Squirrels depredated one nest in the egg stage and two in nestling stage, resulting in the loss of 3% of total eggs and 1.8% of total nestlings, and 80% of the eggs and 7.5% of the nestlings lost due to predators. Squirrel predations were diurnal and occurred from 16 April to 28 April. One predation event resulted in ≥ 1 young being force-fledged from the nest. One fledgling from this nest was subsequently re-sighted.

Fire ants, the only insect predator, depredated one nest in the afternoon on 14 May during the nestling stage, resulting in the loss of 1.8% of all nestlings and 7.5% of nestlings lost to predators. The six-day old nestlings were too young to escape the nest. Two nestlings hopped around so much they fell out of the nest. The remaining two nestlings died in the nest - one died within a few hours of the event and the other died the following morning. The adults made numerous trips to the nest following the attack until the evening of the next day, often bringing food and usually prodding the unresponsive young. The second night after the attack, the ants returned and consumed the dead young. The other nestlings' remains were never found.

We recorded five post-outcome visits in Austin by Texas rat snakes in ~87 hrs of observation. All visits were made the night after a successful fledging. All snakes made more than one visit to the nest and spent time investigating the nest. No other potential predators were documented in post-outcome footage. We did not record any post-outcome visits by potential predators in ~8 hrs of footage on Fort Hood.

Egg and nestling mortality

We monitored 130 eggs (39 and 91 in 2005 and 2006, respectively) and 217 nestlings (63 and 154 in 2005 and 2006, respectively) with cameras in Austin. One-

hundred and ten eggs hatched (85%) and 157 nestlings fledged (72%) from the nest. Predators consumed 5 eggs (3.8%) and 53 (24.4%) nestlings. One egg from four nests failed to hatch (3%). Twelve eggs (9%) representing three nests were abandoned. One nestling from three nests died in the nest from an unknown cause (1.4%). Four nestlings from one nest died in a storm event (1.8%).

We monitored 172 eggs (155 from Stake et al. 2004 and 17 from this study) and 231 nestlings (206 from Stake et al. 2004 and 25 from this study) on Fort Hood from 1997-2002 and 2005. One-hundred and nineteen eggs hatched (69%) and 173 nestlings fledged (75%) from the nest. Predators consumed 38 eggs (22%) and 54 nestlings (23%). One egg from six nests failed to hatch (3.5%). Four eggs from one nest (2.3%) were abandoned. One nestling from three nests died in the nest from unknown causes (1.3%).

DISCUSSION

Nest survival was similar in Austin to nest survival estimates from Fort Hood during the same time period (Peak 2005, Peak 2006) and higher than historical estimates from a study conducted in the western portion of the warbler's range and with no cowbird control (Pulich 1976). Video surveillance was an effective method for monitoring Golden-cheeked Warbler nests and determining cause-specific mortality. Nest survival was similar for nests monitored with and without cameras, which corresponds to results from other camera studies (Pietz and Granfors 2000, Stake and Cimprich 2003, Thompson and Burhans 2003). We were able to prevent abandonment due to presence of cameras after the initial set-up by removing cameras after a suitable time period lapsed if the female did not resume normal behavior. Placing video cameras at the nest allowed us to identify all predators that visited Golden-cheeked Warbler nests, document other sources of nest

failure accurately, and determine the frequency of partial failures (including unhatched eggs, nestlings that died in the nest, and partial predations). This additional information, particularly on partial predation, may provide better knowledge on productivity than nest success alone.

Nest survival, overall mortality (including individual eggs and nestlings), and losses due to predation were very similar between Austin and Fort Hood. There were too few failures due to abandonment or weather to effectively compare estimates, other than to note that failures due to either cause were rare. Predation by predator groups was similar between the two landscapes, but we found some interesting species-level differences (discussed below). There was a difference in predation by nest stage between the landscapes, with fewer predations in the egg stage in Austin compared with Fort Hood, which experienced similar predation between the egg and nestling stages (Stake et al. 2004). However, a camera study on Black-capped Vireo (*Vireo atricapillus*) nests on Fort Hood exhibited a similar pattern of increased predation during the nestling stage (Stake and Cimprich 2003). The occurrence of abandonment, hatching success and nestling survival were similar in both landscapes, suggesting that fitness of adults breeding in urban patches was not negatively affected by features attributed to increased human disturbance, at least at our sites, differently from a rural site.

Snakes were the dominant predator. While the predation rate attributed to snakes was slightly higher on Fort Hood (0.297) than Austin (0.255), the difference is not likely biologically meaningful (the confidence intervals largely overlapped). The predations we observed on attending females indicates that the previously noted adult predations (Stake et al. 2004) were not an anomaly and may be a substantial source of breeding season

mortality for this species. No other adult songbirds have been filmed being consumed by a snake while incubating or brooding at the nest, but an incubating female Black-capped Vireo was almost captured by a Texas rat snake on Fort Hood (Stake and Cimprich 2003). As further evidence of the importance of rat snakes to nest success of breeding songbirds in this area, we also recorded Texas rat snakes depredating two Blue-gray Gnatcatcher (*Poliophtila caerulea*) nests and one Northern Cardinal (*Cardinalis cardinalis*) nest on Fort Hood in 2005, and snakes were the only predator recorded in post-outcome footage in Austin.

The most notable difference in predator composition between Austin and Fort Hood was due to a shift in the dominant avian predator. Western Scrub-Jays were the chief avian predator in Austin, depredating four nests (period rate = 0.128), but only recorded once (period rate = 0.023) on Fort Hood (Table 2). Stake et al. (2004) suggested the avian predator community differed between the urban and rural sites. Western Scrub-Jays, however, accounted for 41% (7 of 17) of the avian predations on Black-capped Vireo nests on Fort Hood (Stake and Cimprich 2003), so it is unclear why there were not more Western Scrub-Jay predations on Golden-cheeked Warblers on Fort Hood. Western Scrub-Jays were also the primary nest predator of the shrub-nesting Least Bell's Vireo (*Vireo bellii*) in California (Peterson et al. 2004). American Crows were the dominant avian predator (period rate = 0.091) of Golden-cheeked Warbler nests on Fort Hood, but were never recorded depredating Golden-cheeked Warbler nests in Austin or Black-capped Vireo nests on Fort Hood. Crows were not frequently encountered on the Austin sites. No Blue Jay predations were recorded on either site on Golden-cheeked Warbler or Black-capped Vireo nests (Stake and Cimprich 2003), but Blue Jays were not commonly encountered on sites in

either landscape. Raptor predation was documented in both landscapes, suggesting that, while not common, it is not restricted to a rural landscape. Cooper's Hawks are becoming increasingly adapted to urban landscapes (Boal and Mannan 1998, Rosenfield et al. 2000), but since they tend to favor larger prey such as doves in urban areas (Estes and Mannan 2003), they may not pose a major threat to Golden-cheeked Warbler nests. Cowbirds did not pose a substantial threat to nest survival in either landscape, but cowbird management was practiced locally in Austin and intensively base-wide on Fort Hood. However, in both recorded cowbird events (1 in the egg stage and 1 in the nestling stage), the female cowbird caused complete failure of the nest. The nest found post-parasitism contained only one hatchling cowbird and we can only speculate that the loss of the warbler eggs or young was caused by a female cowbird. Cowbirds likely pose a greater threat in areas that do not manage cowbirds (Pulich 1976), particularly to re-nesting warblers who are more susceptible to the nest-searching female cowbirds, who lay eggs after most warbler nests have been initiated.

Squirrel predation rates were similar in Austin and Fort Hood. Squirrels have long been implicated as nest predators and some species are a dominant nest predator in other systems (Pietz and Granfors 2000, Miller 2002, Williams and Wood 2002, Renfrew and Ribic 2003). Although squirrels were common on both sites, they depredated few Golden-cheeked Warbler nests, signifying nests were probably found opportunistically. We noted that squirrel activity in Austin was higher in oaks (*Quercus* spp.) than in Ashe junipers (*Juniperus ashei*), so nests placed in junipers may be safer from squirrel predation than those placed in oaks. Interestingly, no fox squirrel predations were recorded on Black-capped Vireos, even though one was seen passing beneath the nest (Stake and Cimprich

2003) and only one fox squirrel was recorded on low shrub-nesting songbirds in Missouri (Thompson et al. 1999), signifying that this species of squirrel may not be a dominant nest predator.

Fire ant mounds were common on both sites in areas near open edges. While fire ants were an important predator of Black-capped Vireo nests (Stake and Cimprich 2003), they were the least important predator of Golden-cheeked Warbler nests, likely because Golden-cheeked Warblers typically nest ≥ 5 m high in dense woods. However, fire ants do exhibit arboreal tendencies (Kaspari 2000) and Golden-cheeked Warblers probably benefit more from increased distance from openings than from nest height. Both nests depredated by ants were placed close to an edge. Fire ants may pose a greater threat to nest survival in landscapes with more disturbance, canopy breaks and edge (Stiles and Jones 1998, Wetterer and Moore 2005).

CONSERVATION IMPLICATIONS

Nest mortality was moderate in the urban sites and we found no support that it differed significantly from rural sites. This provides evidence that urban preserves can provide valuable breeding habitat for Golden-cheeked Warblers, and that these endangered birds can reproduce as successfully in large urban patches as they can in large rural patches. Smaller patches (< 100 ha) with differing surrounding land uses are likely subject to different processes and warrant future research investigation. Predation was the primary cause of nest failure. Therefore, where productivity is considered inadequate to sustain populations, mitigation of nest predation may be the most efficient approach to increasing productivity. Additional information on predators, particularly Texas rat snakes and their

habitat preferences, may elucidate approaches to manipulate habitats in order to reduce predation on this species.

LITERATURE CITED

- Arnold, K. A., C. L. Coldren, and M. L. Fink. 1996. The interactions between avian predators and Golden-cheeked Warblers in Travis County, Texas. Texas Transportation Institute report number TX-96/1983-2. Texas A&M University, College Station, Texas, USA.
- Bakermans, M. H., and A. D. Rodewald. 2006. Scale-dependent habitat use of Acadian Flycatcher (*Empidonax vireescens*) in central Ohio. *Auk* 123:368-382.
- Beissinger, S. R., and D. R. Osbourne. 1982. Effects of urbanization on avian community organization. *Condor* 84:75-83.
- Blair, R. B. 1996. Land use and avian species diversity along an urban gradient. *Ecological Applications* 6:506-519.
- Boal, C. W., and R. W. Mannan. 1998. Nest-site selection by Cooper's Hawks in an urban environment. *Journal of Wildlife Management* 62:864-871.
- Bolger, D. T., T. A. Scott, and J. T. Roteneberry. 1997. Breeding bird abundance in an urbanizing landscape in coastal southern California. *Conservation Biology* 11:406-421.
- Borgmann, K. L., and A. D. Rodewald. 2004. Nest predation in an urbanizing landscape: the role of exotic shrubs. *Ecological Applications* 14:1757-1765.
- Brown, K. P., H. Moller, J. Innes, and P. Jansen. 1998. Identifying predators at nests of small birds in a New Zealand forest. *Ibis* 140:274-279.
- Burhans, D. E., and F. R. Thompson III. 2006. Songbird abundance and parasitism differ between urban and rural shrublands. *Ecological Applications* 16:394-405.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling nest survival. *Ecology* 83:3476-3488.
- Engels, T. M., and C. W. Sexton. 1994. Negative correlation of Blue Jays and Golden-cheeked Warblers near an urbanizing area. *Conservation Biology* 8:286-290.
- Estes, W. A., and R. W. Mannan. 2003. Feeding behavior of Cooper's Hawks at urban and rural nests in southeastern Arizona. *Condor* 105:107-116.
- Fernández-Juricic, E., M. D. Jimenez, and E. Lucas. 2001. Bird tolerance to human

- disturbance in urban parks of Madrid (Spain): management implications, p. 259-273. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [eds.], *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston.
- Gill, J. A., K. Norris, and W. J. Sutherland. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation* 97:265-268.
- Gutzwiller, K. J., H. A. Marcum, H. B. Harvey, J. D. Roth, and S. H. Anderson. 1998. Bird tolerance to human disturbance in Wyoming montane forests. *Condor* 100:519-527.
- Haskell, D. G., A. M. Knupp, and M. C. Schneider. 2001. Nest predator abundance and urbanization, p. 243-258. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [eds.], *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston.
- Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. *Journal of Wildlife Management* 49:668-674.
- Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651-661.
- Jokimäki, J., and E. Huhta. 2000. Artificial nest predation and abundance of birds along an urban gradient. *Condor* 102:838-847.
- Kaspari, M. 2000. Do imported fire ants impact canopy arthropods? Evidence from simple arboreal pitfall traps. *Southwestern Naturalist* 45:118-122.
- King, D. I., and R. M. DeGraaf. 2006. Predators at bird nests in a northern hardwood forest in New Hampshire. *Journal of Field Ornithology* 77:239-243.
- Ladd, C., and L. Gass. 1999. Golden-cheeked warbler (*Dendroica chrysoparia*). *In* A. Poole and F. Gill [eds.], *The birds of North America*, no. 420. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, D.C.
- Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds, p. 19-47. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [eds.], *Avian Ecology and Conservation in an urbanizing world*. Kluwer Academic, Boston.
- Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255-261.
- _____. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456-466.

- Miller, K. E. 2002. Nesting success of the Great Crested Flycatchers in nest boxes and in tree cavities: are nest boxes safer from nest predation? *Wilson Bulletin* 14:179-185.
- Morrison, S. A., and D. T. Bolger. 2002. Lack of an urban edge effect on reproduction in a fragmentation-sensitive species. *Ecological Applications* 12:398-411.
- Peak, R. G. 2005. Demography of the Golden-cheeked Warbler on Fort Hood, Texas, 2005. *In* Endangered species monitoring and management at Fort Hood, Texas: 2005 annual report. The Nature Conservancy, Fort Hood Project, Fort Hood, Texas, United States.
- _____. 2006. Demography of the Golden-cheeked Warbler on Fort Hood, Texas, 2006. *In* Endangered species monitoring and management at Fort Hood, Texas: 2006 annual report. The Nature Conservancy, Fort Hood Project, Fort Hood, Texas, United States.
- Peterson, B. L., B. E. Kus, and D. H. Deutschman. 2004. Determining nest predators of Least Bell's Vireo through point counts, tracking stations, and video photography. *Journal of Field Ornithology* 75:89-95.
- Pietz, P. J., and D. A. Granfors. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. *Journal of Wildlife Management* 64:71-87.
- Pulich, W. M. 1976. The Golden-cheeked Warbler: a bioecological study. Texas Parks and Wildlife Department, Austin, Texas.
- Renfrew, R. B., and C. A. Ribic. 2003. Grassland passerine nest predators near pasture edges identified on videotape. *Auk* 120:371-383.
- Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9:1-48.
- Rosenfield, R. N., J. Bielefeldt, and J. L. Affeldt. 2000. Urban nesting biology of Cooper's Hawks in Wisconsin, p. 41-44. *In* D. M. Bird, D. E. Varland, and J. J. Negro [eds.], *Raptors in human landscapes: adaptations to built and cultivated environments*. Academic Press, London.
- Sexton, C. W. 1987. A comparative analysis of urban and native bird populations in central Texas. Ph.D. dissertation, University of Texas, Austin, Texas.
- Shaffer, T. L. 2004. A unified approach to analyzing nest success. *Auk* 121:526-540.
- _____, and F. R. Thompson III. *In press*. Making meaningful estimates of nest survival.

Studies in Avian Biology.

- Small, S. L. 2005. Mortality factors and predators of Spotted Towhee nests in the Sacramento Valley, California. *Journal of Field Ornithology* 76:252-258.
- Stake, M. M., and D. A. Cimprich. 2003. Using video to monitor predation at Black-capped Vireo nests. *Condor* 105:348-357.
- _____, J. Faaborg, and F. R. Thompson III. 2004. Video identification of predators at Golden-cheeked Warbler nests. *Journal of Field Ornithology* 75:337-344.
- Stiles, J. H., and R. H. Jones. 1998. Distribution of red imported fire ant, *Solenopsis invicta*, in road and powerline habitats. *Landscape Ecology* 335:335-346
- Thompson, F. R., III, W. Dijak, and D. E. Burhans. 1999. Video identification of predators at songbird nests in old fields. *Auk* 116:259-264.
- _____, and D. E. Burhans. 2003. Predation of songbird nests differs by predator and between field and forest habitats. *Journal of Wildlife Management* 67:408-416.
- U. S. Fish and Wildlife Service. 1992. Golden-cheeked Warbler (*Dendroica chrysoparia*) recovery plan. Albuquerque, New Mexico.
- Verhulst, S., K. Oosterbeek, and B. J. Ens. 2001. Experimental evidence of effects of human disturbance on foraging and parental care in oystercatchers. *Biological Conservation* 101:375-380.
- Wahl, R., D. D. Diamond, and D. Shaw. 1990. The Golden-cheeked Warbler: a status review. U. S. Fish and Wildlife Service, Fort Worth, Texas.
- Wetterer, J. K., and J. A. Moore. 2005. Red imported fire ants (Hymenoptera: Formicidae) at gopher tortoise (Testudines: Testudinidae) burrows. *Florida Entomologist* 88:349-354.
- Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211-1214.
- Williams, G. E., and P. B. Wood. 2002. Are traditional methods of determining nest predators and nest fates reliable? An experiment with Wood Thrushes (*Hylocichla mustelina*) using miniature video cameras. *Auk* 119:1126-1132.

Table 1. Support for models with and without video camera monitoring predicting Golden-cheeked Warbler nest survival in Austin, Texas from 2005-2006 based on 537 camera monitored and 384 non-camera monitored intervals. Models are ranked based on Akaike's information criteria (AIC_c), ΔAIC_c , and Akaike weights (w_i). AIC_c is based on the $-2 \times \log$ -likelihood ($-2L$) and the number of parameters (K).

Model	-2L	K	AIC_c	ΔAIC_c	w_i
Null	-145.930	7	305.952	0.000	0.712
Camera	-145.821	8	307.760	1.807	0.288

Table 2. Cause-specific daily and period mortality rates and 95% confidence intervals (CI) for Golden-cheeked Warblers nests in Austin, Texas during 2005-2006 (537 intervals) and Fort Hood, Texas during 1997-2002 and 2005 (736 intervals).

Source	Austin				Fort Hood			
	# of events	Daily rate	Period rate	CI	# of events	Daily rate	Period rate	CI
Mortality	21	0.0391	0.631	0.437-0.760	28	0.0380	0.6208	0.458-0.736
Abandon	2	0.0037	0.060	0.000-0.141	1	0.0014	0.0222	0.000-0.065
Weather	1	0.0019	0.030	0.000-0.088	0			
Predation	18	0.0335	0.541	0.376-0.706	27	0.0367	0.5986	0.461-0.737
<i>Texas rat snake</i>	8	0.0149	0.255	0.104-0.406	12	0.0163	0.2737	0.143-0.405
<i>Great Plains rat snake</i>	0				1	0.0014	0.0228	0.000-0.067
<i>Western Scrub-Jay</i>	4	0.0074	0.1275	0.011-0.244	1	0.0015	0.0228	0.000-0.067
<i>American Crow</i>	0				4	0.0054	0.0912	0.006-0.176
<i>Cooper's Hawk</i>	2	0.0037	0.0637	0.000-0.149	1	0.0014	0.0228	0.000-0.067
<i>Brown-headed Cowbird</i>	0				2	0.0027	0.0456	0.000-0.107
<i>Fox Squirrel</i>	3	0.0056	0.0956	0.000-0.198	4	0.0054	0.0912	0.006-0.176
<i>Fire ants</i>	1	0.0019	0.0319	0.000-0.093	1	0.0014	0.0228	0.000-0.067

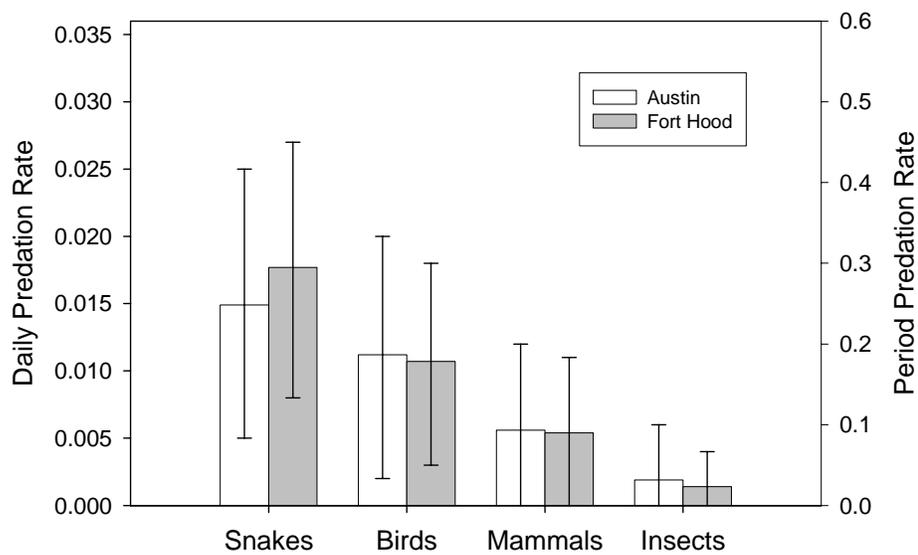


Fig. 1. Daily (left axis) and period (right axis) predation rates and 95% confidence intervals by snakes, birds, mammals, and ants at Golden-cheeked Warbler nests in Austin, Texas (white bars) during 2005-2006 and on Fort Hood, Texas (gray bars) during 1997-2002 and 2005.

CHAPTER 3
SNAKE PREDATION ON NESTING ADULT
GOLDEN-CHEEKED WARBLERS

ABSTRACT

We monitored 116 females and 128 nests with video cameras to identify nest predators of Golden-cheeked Warblers (*Dendroica chrysoparia*) on Fort Hood, Texas from 1997-2002 and in Austin, Texas from 2005-2006. Six female Golden-cheeked Warblers were depredated during 892 camera-monitored intervals during the portion of the nesting cycle when females were sitting on the nest through the night, resulting in a daily predation rate of 0.007. Females attending the nest were captured 67% of the times they were present during a snake predation and 75% of times they were present during nocturnal snake predations. Assuming a daily nest survival of 0.962 and that the female would attempt a second nest if the first nest failed, annual mortality for adult females due to predation on the nest was 12.2%. Snake predation represents an important source of adult mortality for nesting Golden-cheeked Warblers.

Survival of migrant songbirds is generally thought to be high during the breeding season (Sillett and Holmes 2002); however, there is little direct evidence of the level or sources of adult mortality during this period. One potentially important source of adult mortality during the breeding season is predation on adults attending the nests. However, documenting any predation at the nest has been difficult (Pettingill 1976) and predation

on songbirds at or near the nest has rarely been documented (Carter 1992, Pietz and Granfors 2000, Stake 2001, Stake et al. 2004). We monitored nests of Golden-cheeked Warblers (*Dendroica chrysoparia*) with video cameras on Fort Hood, Texas (30° 10' N, 97° 45' W) from 1997-2002 and 2005 and in Austin, Texas (30° 23' N, 97° 34' W) from 2005-2006 to identify nest predators in different landscapes. We identified rat snakes (*Elaphe* spp.) as the leading predator at both sites, depredating 21 of 128 camera-monitored nests. Additionally, we recorded six females being captured and consumed by snakes, three in each landscape. Five of the predations on females were attributed to Texas rat snakes (*Elaphe obsoleta lindheimeri*) and one to a Great Plains rat snake (*Elaphe guttata emoryi*).

All predations on females were nocturnal, occurring between the hours of 21:03 and 23:52 from 18 April to 9 May in Austin and 0:22 and 4:48 from 23 April to 17 May on Fort Hood (Table 1). In general, all snake predations (n=21) were nocturnal but one, occurring between 20:01 and 23:52 from 18 April to 19 May in Austin and between 20:37 and 4:48 from 23 April to 10 June on Fort Hood. One additional predation on Fort Hood occurred at 10:24. Predations on females (and in general) occurred within the first few hours of dark in Austin, whereas snake activity ranged over the course of the night on Fort Hood.

Four of 21 (19%) nest predations by snakes were on nests in the egg stage and 17 (81%) in the nestling stage. Two of the four (50%) snake predations on eggs resulted in adult predation. Of the remaining two, the female was present at one and left the nest 3 mins prior to the snake appearing at the nest (this was the one diurnal snake predation) and at the other nest, the female left the nest just after sunset, several hours prior to the

snake predation. A Mourning Dove (*Zenaida macroura*) nest located just below the Golden-cheeked Warbler's nest was depredated the same night suggesting the female was possibly scared from the nest by the presence of a predator below her nest depredating the dove nest. Four of 17 (23%) snake predations on nestlings resulted in adult predation and occurred while the nestlings were young (≤ 4 days old), necessitating brooding. Females were present and escaped two (12%) snake predations. Both nests contained 5- or 6-day old nestlings. At one nest, the female was brooding and left the nest as the snake appeared in view. This predation occurred about 30 mins after sunset when the female was still alert. She peered below the nest 3 mins prior to the snake appearing on camera and flew off as the snake approached. At the other nest, the female was sleeping on the rim of the nest and was actually pushed off the rim by the snake as it investigated and began consuming the nestlings. Eleven (65%) snake predations occurred late in the nestling stage when females were no longer brooding. Females were preyed upon 29% (6/21) of the total snake predations, 67% (6/9) of the times they were present during the predation, and 75% (6/8) of the nocturnal predations for which the female was at the nest.

We estimated the daily predation rate on nesting females using program Micromort 1.2 (Heisey and Fuller 1985). Micromort is a maximum-likelihood approach that is a generalization of the Mayfield method (1961, 1975) and uses the Taylor series approximation to compute 95% confidence intervals, similar to Johnson (1979). We observed 6 predations on females during the 892 observation days when females were sitting on the nest (days 3-19 of the nest cycle, assuming the female begins incubation on the penultimate egg; Pulich 1976), producing a daily predation rate of 0.007 (0.001-0.012). We estimated the possible contribution this source of mortality could have on

breeding season or annual adult female mortality. We assumed a daily nest survival rate of 0.962 over the entire 25-day nest cycle and used this to estimate the proportion of nests surviving each day. We applied the daily female predation rate (assuming a constant predation rate) to the nests available on days 3-19 to determine the female mortality rate occurring on each day of the nest cycle. We used the period nest survival (38%) to determine the number of females that were likely to re-nest (62%) minus the number of female mortalities from the first nest attempt and we repeated the above procedure to estimate the mortality rate during the second attempt. We estimated that 7.9% and 4.3% of females were depredated during the first and second nesting attempts, respectively, resulting in a loss of 12.2% of nesting females to predation.

Predation on the nest was an important source of mortality during the breeding season for female Golden-cheeked Warblers. Almost all snake predations in this system were nocturnal (Stake et al. 2004, this study), so female Golden-cheeked Warblers may be especially vulnerable since they sleep on the nest for so many nights. It is not clear whether snakes find nests during the day and return at night to depredate the nest or use cues other than visual stimuli to locate nests. Since the likelihood of the female Golden-cheeked Warbler being depredated by a snake is high while she is attending the nest at night, it is probably beneficial to the population that the majority of snake predations occur late in the nestling stage after the female has stopped brooding (Stake et al., this study).

Songbirds nesting in climates hospitable to snakes, particularly those exhibiting nocturnal foraging patterns or well-known nest predators such as rat snakes, may be particularly vulnerable to such predation. While open-cup nesters have more opportunity

to escape than cavity nesters, species who nest on sturdy substrates, such as Golden-cheeked Warblers, or on the ground, may not detect a predator in time to escape, especially during the night. We suspect more nest studies using time-lapse video surveillance in regions with nocturnal snakes will reveal additional predation on incubating and brooding adult songbirds.

Increased predation pressure on adults attending nests likely explains the lower survival rates for female Wood Thrushes (*Hylocichla mustelina*) than males during the breeding season (Powell et al. 2000, Coulter 2005). It may also explain lower female Black-throated Blue Warbler (*Dendroica caerulescens*) survival during the breeding season (Sillett and Holmes 2002) and lower annual survival estimates for female Ovenbirds (*Seiurus aurocapillus*; Bayne and Hobson 2002) compared to male survival. Breeding season female mortality is a possible explanation for the skewed sex ratios observed in some migrant songbirds during the breeding season (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1995). Migrant songbird populations are considered to be more sensitive to changes in adult survival than nest success (Noon and Sauer 1992, Donovan and Thompson 2001), so the loss of substantial numbers of breeding females to predators simultaneous to nest failure may be calamitous, especially for an endangered bird. We believe the extent of adult mortality during the breeding season warrants further investigation in other species and ecosystems.

LITERATURE CITED

- Bayne, E. M., and K. A. Hobson. 2002. Annual survival of adult American Redstarts and Ovenbirds in the southern boreal forest. *Wilson Bulletin* 114:358-367.
- Carter, W. A. 1992. Black-and-white Warbler nest failure in Pontotoc County, Oklahoma. *Bulletin of the Oklahoma Ornithological Society* 25:22-23.
- Coulter, S. C. 2005. Effects of forest fragmentation on Wood Thrushes in the Atchafalaya Basin, Louisiana. M.S. Thesis, University of Arkansas, Fayetteville, Arkansas.
- Donovan, T. M., and F. R. Thompson III. 2001. Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. *Ecological Applications* 11:871-882.
- Gibbs, J. P., and J. Faaborg. 1990. Estimating the viability of Ovenbirds and Kentucky Warbler populations in forest fragments. *Conservation Biology* 4:193-196.
- Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. *Journal of Wildlife Management* 49:668-674.
- Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651-661.
- Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255-261.
- _____. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456-466.
- Noon, B. R., and J. R. Sauer. 1992. Population models for passerine birds: structure, parameterization, and analysis, p. 441-464. *In* D. R. McCullough and R. H. Barret, [eds.], *Wildlife 2001: Populations*. Elsevier Applied Science, New York.
- Pettingill, O. S., Jr. 1976. Observed acts of predation on birds in northern lower Michigan. *Living Bird* 15:33-41.
- Pietz, P. J., and D. A. Granfors. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. *Journal of Wildlife Management* 64:71-87.
- Powell, L. A., J. D. Lang, M. J. Conroy, and D. G. Krementz. 2000. Effects of forest management on density, survival, and population growth of Wood Thrushes. *Journal of Wildlife Management* 64:11-23.

- Pulich, W. M. 1976. The Golden-cheeked Warbler: a bioecological study. Texas Parks and Wildlife Department, Austin, Texas.
- Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296-308.
- Stake, M. M. 2001. Predation by a Great Plains Rat Snake on an adult female Golden-cheeked Warbler. *Wilson Bulletin* 113: 460-461.
- Stake, M. M., J. Faaborg, and F. R. Thompson III. 2004. Video identification of predators at Golden-cheeked Warblers nests. *Journal of Field Ornithology* 75:337-344.
- Van Horn, M. A., R. M. Gentry, and J. Faaborg. 1995. Patterns of Ovenbird (*Seiurus aurocapillus*) pairing success in Missouri forest tracts. *Auk* 112:98-106.
- Villard, M.-A., P. R. Martin, and C. G. Drummond. 1993. Habitat fragmentation and pairing success in the Ovenbird (*Seiurus aurocapillus*). *Auk* 110:759-768.

Table 1. Temporal features of rat snake predation on female Golden-cheeked Warblers at the nest in Austin, Texas during 2005-2006 and Fort Hood, Texas during 1997-2002.

Predator	Site	Date	Time	Stage
Great Plains rat snake	Fort Hood	4/23/00	00:22	Egg
Texas rat snake	Fort Hood	5/7/02	04:48	Egg
Texas rat snake	Fort Hood	5/17/02	01:49	Nestling
Texas rat snake	Austin	5/9/05	23:52	Nestling
Texas rat snake	Austin	4/18/06	22:12	Nestling
Texas rat snake	Austin	4/21/06	21:03	Nestling