Management and Conservation Article

Factors Affecting Golden-Cheeked Warbler Nest Survival in Urban and Rural Landscapes

JENNIFER L. REIDY,[1] *Department of Fisheries and Wildlife Sciences, 302 Anheuser-Busch Natural Resources Building, University of Missouri, Columbia, MO 65211-7240, USA*

FRANK R. THOMPSON, III, *United States Department of Agriculture Forest Service, Northern Research Station, 202 Anheuser-Busch Natural Resources Building, University of Missouri, Columbia, MO 65211-7240, USA*

REBECCA G. PEAK, *The Nature Conservancy, P.O. Box 5190, Fort Hood, TX 76544-0190, USA*

ABSTRACT We evaluated hypotheses concerning temporal, landscape, and habitat effects on nest survival of golden-cheeked warblers (*Dendroica chrysoparia*) in an urban and a rural landscape during the breeding seasons of 2005 and 2006 in central Texas, USA. We found support for temporal effects of year and cubic effect of date and included them in candidate models that evaluated habitat and landscape effects. Nest survival was lower in 2006 than in 2005 and decreased nonlinearly as the breeding season progressed. We found support for edge effects with decreased nest survival nearer edges and in areas with increased open edge density (wooded habitat abutting open habitat) or decreased trail density. However, confidence intervals for the model-averaged odds ratios overlapped 1.0 for all edge variables. Overall daily survival rate was 0.964 (95% CI = 0.949–0.975), resulting in a 25-day period survival of 0.398 (95% CI = 0.269–0.524). Period survival in Austin's urban landscape (0.399, 95% CI = 0.270–0.526) was similar to survival in Fort Hood's rural landscape (0.396, 95% CI = 0.261–0.528). Both landscapes likely support self-sustaining populations based on reasonable assumptions for adult survival and number of nesting attempts. We suggest that some large urban preserves can provide breeding habitat of comparable quality to rural locations and recommend protecting large parcels (>100 ha) of breeding habitat with limited fragmentation and reducing the amount of wooded edge abutting open habitat to ensure nest survival regardless of their landscape context. (JOURNAL OF WILDLIFE MANAGEMENT 73(3):407–413; 2009)

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Factors affecting nest survival of migrant songbirds may act in a hierarchical top-down manner where large-scale effects such as fragmentation constrain or provide context for small-scale effects (Thompson et al. 2002, Stephens et al. 2003), likely resulting from patterns in nest predator diversity, abundance, and behavior (Chalfoun et al. 2002*b*). Recent studies of avian communities (Knutson et al. 2004, Peak et al. 2004) and single species or populations (Driscoll et al. 2005, Bakermans and Rodewald 2006) support the idea that multiple scales affect nest survival. However, only a few studies have incorporated factors associated with human development into their analysis (Bakermans and Rodewald 2006, Burhans and Thompson 2006). As human development continues to fragment, alter, and destroy native habitats, it is increasingly important to assess and understand how urbanization impacts avian populations (Marzluff et al. 2001). Knowledge of which scale and which factors affect nest success can aid in prioritizing management decisions (Thompson et al. 2002, Driscoll et al. 2005) and is critical for effective management of endangered species (Dearborn and Sanchez 2001).

The golden-cheeked warbler (*Dendroica chrysoparia*) is a federally endangered Neotropical migrant songbird whose current breeding range is restricted to ≤25 counties in central and south-central Texas, USA (Ladd and Gass 1999). Because females construct their nests from the peeling bark of mature Ashe juniper (*Juniperus ashei*), golden-cheeked warbler nesting habitat is restricted to mature Ashe juniper–oak (*Quercus* sp.) forests (Ladd and Gass 1999). Habitat loss and fragmentation resulting from urbanization and agricultural clearing (including ranching) are considered the main threats to the golden-cheeked warbler's population viability (U.S. Fish and Wildlife Service 1992). Urban and suburban growth is particularly high in their central breeding range in and around Travis County (Wahl et al. 1990, U.S. Fish and Wildlife Service 1992).

Little information exists on how processes operating at any scale impact nest success or productivity of golden-cheeked warblers. Paired males had higher inferred success (based on evidence of adults feeding young) in territories closer to residential development than agriculture or residual grassland and in large patches (>100 ha) in Travis County (Coldren 1998). In a rural landscape, on Fort Hood Military Reservation, nest survival declined with increasing forest edge density (Peak 2007), and there was only marginal support for nest-site and territory factors affecting nest survival when nest predator groups were analyzed separately (Stake 2003).

In addition to habitat features, temporal factors such as year, nest stage, and date have been shown to affect nest success of songbirds (Grant et al. 2005). These often represent effects that could be related to predator behavior or other environmental factors not otherwise captured by models (Grant et al. 2005, Shaffer and Thompson 2007). On Fort Hood, Stake (2003) did not find support that temporal factors affected nest survival, whereas Peak (2007) found marginal support that nest stage and day of year affected nest survival.

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[1] *E-mail: jennifer.reidy@gmail.com*

Our objective was to determine which factors affect golden-cheeked warbler nest survival. We evaluated hypotheses concerning temporal, landscape, and habitat effects on nest survival in an urban and a rural landscape in central Texas. We predicted that nest survival would decrease through the season (Stake 2003, Peak 2007), be lower for the nestling stage than the incubation stage (Stake 2003), and would not vary by year (Stake 2003, Peak 2007). We predicted that small-scale effects such as nest-site and territory factors would affect nest survival less than large-scale effects such as edge and landscape factors (Thompson et al. 2002). Because Stake (2003) found percent canopy cover, stem count, average canopy height, and substrate species had little effect on nest success, we chose to evaluate different nest-site variables (nest ht and nest cover). We predicted that nest survival would be higher for nests located on slopes (>10°) and in areas of low trail density (Stake 2003). We predicted that nest survival would decrease with increasing open edge density (Peak 2007) because of greater predator activity or abundance near edges (Chalfoun et al. 2002*a*). We predicted that nest survival would decrease with increases in open and developed habitats in the landscape (Rodewald 2002) because of increased abundance of predators (Bakermans and Rodewald 2006) and brown-headed cowbirds (*Molothrus ater*; Robinson et al. 1995, Burhans and Thompson 2006).

STUDY AREA

We conducted our study during 2005 and 2006 at 2 locations separated by approximately 112 km in central Texas: Austin, an urban location in Travis County, and Fort Hood Military Reservation, a rural location within Bell and Coryell counties. Study sites in Austin were Emma Long Metropolitan Park (30°20′N, 97°50′W; 385 ha), Forest Ridge Preserve (30°23′N, 97°47′W; 294 ha), and Jester Preserve (30°23′N, 97°47′W; 119 ha), all owned and managed by the city of Austin. Golden-cheeked warbler habitat on these sites was composed of mature juniper–oak woods along steep limestone canyons and densely wooded plateaus, dissected by a network of closed-canopy and ≥1 open-canopy (>10 m wide) trail. Sites were mostly contiguous forest of Ashe juniper, Texas red oak (*Quercus buckleyi*), plateau live oak (*Q. fusiformis*), shin oak (*Q. sinuata*), and elms (*Ulmus* spp.) surrounded by residential neighborhoods and major roadways (Reidy 2007, appendix A). Although mostly designated as a breeding preserve, there was limited public access to trails, including a motorized biking trail on Emma Long, during the golden-cheeked warbler breeding season. A cowbird trap was maintained by the city of Austin at Emma Long to reduce numbers of cowbirds, but no cowbird control was practiced at the other Austin sites.

The Fort Hood sites included Belton Lake Outdoor Recreation Area (31°08′N, 97°34′W; 175 ha) and training areas 32 (31°09′N, 97°35′W; 213 ha), 51 (31°16′N, 97°47′W; 250 ha), and 70 (31°04′N, 97°51′W; 196 ha), all owned by the Department of Defense and managed by The Nature Conservancy. Golden-cheeked warbler habitat consisted of steep slopes with flat mesas composed of scrubby woods dominated by Ashe juniper, plateau live oak, post oak (*Q. stellata*), hackberry (*Celtis* sp.), Texas ash (*Fraxinus texensis*), and Texas persimmon (*Diospyros texana*), broken by numerous trails and openings, particularly along mesa tops (Stake 2003), and separated by open grasslands leased for cattle grazing. Trails on training areas were not open to the public, but those on Belton Lake Outdoor Recreation Area were open to hiking and mountain biking. Cowbird control was practiced at Fort Hood and was more intense than at Austin; control included multiple cowbird traps and targeted shooting on and near study sites. Cowbirds did not pose a serious threat to golden-cheeked warbler nest survival in either landscape (Stake et al. 2004, Reidy et al. 2008), so differences in trapping effort should not have affected nest survival.

METHODS

We located golden-cheeked warbler nests from mid-March through mid-June using adult behavioral clues. We monitored nests from >3 m away every 1–3 days until we determined the nest fledged young or failed. We continuously monitored a subset of nests using miniature infrared light-emitting video cameras (Fuhrman Diversified, Inc., Seabrook, TX). We used parental behavior to determine nest stage for nests not monitored with cameras. We considered nests to be successful if we documented fledging by video surveillance or located fledglings at or near the nest within 2 days of the expected fledge day. We considered nests to have failed if we documented no nest activity during monitoring and there was no evidence of fledging. We attempted to find renests following all nest failures.

We measured nest height, nest cover, percent slope, and proximity to edge in late May or early June. We measured nest height in meters from the ground to the rim of the nest with a clinometer. We visually estimated nest cover from the ground as the mean of 6 estimates of percent concealment from 1 m away: above, below, and from the side in each cardinal direction. We measured percent slope with a clinometer and categorized territories as slopes if slope was >10° (to make it comparable to Stake 2003). We measured proximity to edge (nearest open-canopy trail, road, or clearing) using a 30-m measuring tape (we did not measure nests >50 m from an edge). We considered nests within 30 m of an edge (proximity to edge = 1) proximate to an edge.

We used ArcGIS 9 to calculate edge and landscape measurements using a 2-km buffer around nest locations. We digitized habitat patches into 4 habitat classes using a minimum mapping unit of 30 m: wooded (mature juniper–oak forest; probable golden-cheeked warbler habitat); developed (e.g., buildings, parking lots, roads); open (any open, undeveloped land including grazing land); and water (rivers and ponds large enough to show up in imagery). We digitized and classified paved roads, trails, and dirt roads dissecting wooded habitat, and buildings. For each nest, we calculated 1) percentage of open and developed habitat

Table 1. Support for candidate models predicting golden-cheeked warbler nest survival in Austin and Fort Hood, Texas, USA, 2005–2006. Models are ranked from most to least supported based on Akaike's Information Criterion (AIC_c), ΔAIC_c, and Akaike weights (w_i). Akaike's Information Criterion is based on $-2 \times$ log-likelihood (L) and number of parameters in the model (K). Our top model had AIC_c of 552.25.

Model	$-2(L)$	K	ΔAIC_c	w_i
Temporal[a] + open edge density	−270.104	6	0.000	0.402
Temporal + edge[b]	−268.878	8	1.576	0.183
Temporal	−272.798	5	3.378	0.074
Temporal + slope	−271.885	6	3.562	0.068
Temporal + trail density	−271.917	6	3.626	0.066
Temporal + proximity to edge	−272.266	6	4.324	0.046
Temporal + road density	−272.601	6	4.994	0.033
Temporal + building density	−272.679	6	5.150	0.031
Temporal + percent developed habitat	−272.693	6	5.178	0.030
Temporal + location[c]	−272.791	6	5.374	0.027
Temporal + percent open habitat	−272.794	6	5.380	0.027
Temporal + nest-site[d]	−272.612	7	7.029	0.012
Global (all variables listed above)	−266.309	16	12.616	0.001

[a] Includes cubic effect of date and yr.

[b] Includes open edge density, trail density, and proximity to edge.

[c] Includes Austin and Fort Hood.

[d] Includes nest ht and nest cover.

within 1 km, 2) edge density (m/ha) of wooded habitat abutting open habitat within 100 m (open edge), 3) road density (m/ha) and building density (no. of buildings/ha) within 500 m, and 4) trail density (m/ha) within 25 m. We chose these scales because we believed they were representative of the biologically relevant scale for the respective attribute for this species and they captured variability in the attribute among sites and nests.

Analysis

We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate support for candidate models that represented a priori hypotheses concerning factors affecting nest survival of golden-cheeked warblers. First, we determined support for the temporal variables year (2005 or 2006), nest stage (laying, incubation, nestling), and day of year (linear = date, quadratic = date + date^2, cubic = date + date^2 + date^3) and additive combinations of these. We then included the most supported (defined below) temporal variables in all candidate models representing hypothesized habitat and landscape effects. We included these temporal variables in all models because we considered them to be nuisance parameters that we wanted to control for while investigating support for other effects (Grant et al. 2006). Candidate models (Table 1) included a nest-site model with the variables nest cover and nest height; a territory model with the variable slope; 4 edge models with the variables proximity to edge, trail density, and open edge density examined separately and together in an additive model; 2 landscape models with the variable percent open habitat in one and the variable percent developed habitat in the other; 2 urban models evaluating the variables road and building density separately; a location model with the variable location (Austin or Fort Hood); a global model with all covariates; and a null model that included only temporal effects.

We calculated tolerance values for covariates in the global model to detect multi-collinearity before proceeding with model selection (Allison 1999) and examined the over-dispersion parameter for evidence of lack of fit (Burnham and Anderson 2002). Because several variables represented hypothesized effects of landscape factors at radii up to 1 km, it was possible that fates of nests were not independent and had significant spatial autocorrelation. To assess this, we examined the global model with and without an exponential and a spherical spatial autocorrelation factor (PROC GLIMMIX, SAS Version 9.1; SAS Institute, Cary, NC) based on geographic coordinates for each nest. All 3 models had similar fit, parameter estimates, and standard errors, so we proceeded without further consideration of spatial autocorrelation.

We evaluated support for 13 candidate models (Table 1) using Akaike's Information Criterion for small sample sizes (AIC_c). We report the likelihood values AIC_c, ΔAIC_c, and Akaike weights (w_i) for the models (Burnham and Anderson 2002). Because no single model had a majority of support, we report model-averaged parameter estimates, standard errors, odds ratios, and their associated 95% confidence intervals based on models with $\Delta AIC_c < 2$ (models considered to have most support; Burnham and Anderson 2002).

We used the logistic exposure method (Shaffer 2004) to model factors hypothesized to affect nest survival and to estimate nest survival rates. The logistic exposure 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. We classified nest losses due to all sources as failures because we could not always assign the source of failure. We included only nests with confirmed activity (eggs or nestlings) in analyses. We fit models with PROC GENMOD (SAS version 9.1; SAS Institute) by using a binomial response distribution (success = 1, failure = 0) and the logit link function defined by Shaffer (2004).

We estimated model-averaged daily and period survival rates as a function of explanatory variables of interest. To compute period rates, we used a 25-day nesting cycle. 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 (Shaffer and Thompson 2007). We held categorical variables constant at levels representing the proportions of observations at each category level (Shaffer and Thompson 2007). We estimated nest survival for Austin and Fort Hood using the median values of habitat and landscape variables associated with each location (Table 2) rather than the pooled median values.

RESULTS

We monitored 195 active nests resulting in 1,568 monitoring intervals used for analyses. Of these nests, 100 were in

Table 2. Descriptive statistics for continuous and categorical covariates used in logistic exposure models examining golden-cheeked warbler nest survival in Austin ($n = 100$) and Fort Hood ($n = 95$), Texas, USA, 2005–2006.

	Austin					Fort Hood				
Variable	Mean or frequency	SE	Median	Min.	Max.	Mean or frequency	SE	Median	Min.	Max.
Date	114.2	0.4	113	88	159	118.7	0.58	117	89	163
Nest ht	6.3	0.06	6.1	2.9	15.4	5.0	0.60	4.6	2.5	9.9
Nest cover	45.8	0.52	45	13.3	82.5	50.4	0.72	45.8	15	95
Trail density	85.2	4.50	0	0	463	68.0	4.18	0	0	320.4
Open edge density	6.1	0.60	0	0	46.6	14.6	1.41	0	0	187
Road density	16.7	0.37	15.4	0	41.4	3.1	0.21	0	0	20.5
Building density	0.1	0.01	0	0	1.9	0.0	0.00	0	0	0
% open	3.3	0.13	1.2	0	18.4	31.6	0.34	30.4	18.1	53.4
% developed	10.3	0.28	8.1	0.2	37	0.3	0.05	0	0	8.1
Slope[a]	59.5					71.4				
Proximity to edge[a]	46.3					31.1				

[a] Reported as % frequency of category 0 (slope <10%, edge >30 m).

Austin (32 in 2005 and 68 in 2006) and 95 on Fort Hood (23 in 2005 and 72 in 2006). Mean interval length between nest checks was 1.47 days (SE: ±0.02). We determined 125 nests (64%) successfully fledged ≥1 host young.

When we examined support for temporal variables, we found the most support for a cubic effect of date ($w_i = 0.24$), followed closely by a model that included a cubic effect of date and year ($w_i = 0.21$). Therefore, we included the cubic effect of date and year in the landscape and habitat models.

The overdispersion parameter for the global model containing temporal, landscape, and habitat effects ($\hat{c} = 0.97$) indicated no evidence of lack of fit. Tolerance values for all variables in the global model were ≥0.6, so we concluded multi-collinearity was not a problem. We found the most support for our hypothesis that edge effects affected nest survival; the top model included open edge density and the second model included all edge variables (Table 1). All other models had a $\Delta \mathrm{AIC}_c > 3.3$ and $w_i < 0.075$, so we model averaged parameter estimates and predictions from the top 2 models.

Overall daily survival was 0.964 (95% CI = 0.949–0.975) and overall period survival was 0.398 (95% CI = 0.269–0.524). Period survival in Austin (0.399, 95% CI = 0.270–0.526) was similar to survival on Fort Hood (0.396, 95% CI = 0.261–0.528). Model-averaged survival rates and odds ratios indicated only temporal and edge variables had meaningful effects (Table 3). Survival declined nonlinearly from 99% at the beginning of the season to 85% at the end (Fig. 1), but confidence intervals were large and mostly overlapping, particularly toward the end of the nesting season when few nests were monitored. Period survival was higher in 2005 (0.489; 95% CI = 0.281–0.669) than in 2006 (0.361; 95% CI = 0.224–0.502), with nests in 2005 having 39% greater odds of surviving than nests in 2006, although confidence intervals were wide and overlapped (Table 3).

Table 3. Predictor variables, model-averaged parameter estimates, unconditional standard errors, odds ratios (OR), and 95% confidence intervals for the top 2 models hypothesized to affect golden-cheeked warbler nest survival in Austin and Fort Hood, Texas, USA, 2005–2006.

Variable	Estimate	SE	OR	95% CI
Date	−2.6785	1.2796	0.069	0.006–0.888
Date + date^2	0.0207	0.0102	1.021	1.000–1.042
Date + date^2 + date^3	−0.0001	0.0000	1.000	1.000–1.000
Yr (2005 vs. 2006)	0.3311	0.3082	1.393	0.752–2.579
Trail density	0.0005	0.0009	1.001	0.999–1.002
Proximity to edge[a]	0.1077	0.1904	1.114	0.761–1.630
Open edge density	−0.0077	0.0033	0.992	0.986–0.999

[a] Categorical variable; 0 = >30 m, 1 = ≤30.

The most strongly supported habitat or landscape effect was open edge density, which occurred in both top models, and the confidence interval for its odds ratio did not overlap 1.0. Period survival declined from 0.405 (95% CI = 0.273–0.533) to 0.019 (95% CI = 0.000–0.303) over the observed range of edge density (Fig. 2), and there was an 0.8% decrease in nest survival for every 1 m/ha increase in open edge density (Table 3). Proximity to edge and trail density were in the second best model. Based on model averaging, nests ≥30 m from edges had >11% greater odds of surviving than did nests <30 m from an edge, but confidence intervals overlapped 1.0 (Table 3), and period survival for nests farther from an edge (0.428; 95% CI = 0.290–0.560) was similar to that of nests closer to an edge (0.389, 95% CI = 0.233–0.544). Period survival increased from 0.405 (95% CI = 0.273–0.533) to 0.490 (95% CI = 0.213–0.722) over the observed range of trail density, but the confidence interval for the odds ratio overlapped 1.0 (Table 3).

DISCUSSION

Ours is the first study to evaluate golden-cheeked warbler nest survival at several scales in urban and rural landscapes. We found support for temporal and edge effects but did not find support for small-scale nest or habitat effects or a negative effect of urban environments. Our estimate of golden-cheeked warbler nest success was similar to previous estimates from Fort Hood (39% [Stake et al. 2004], 34% [Peak 2007]) and higher than the success estimate (27%) from a small nest sample monitored in the western portion of the warbler's range (Pulich 1976).

Lack of support for effects of nesting stage suggest that the temporal decrease in nest survival was due to changes in

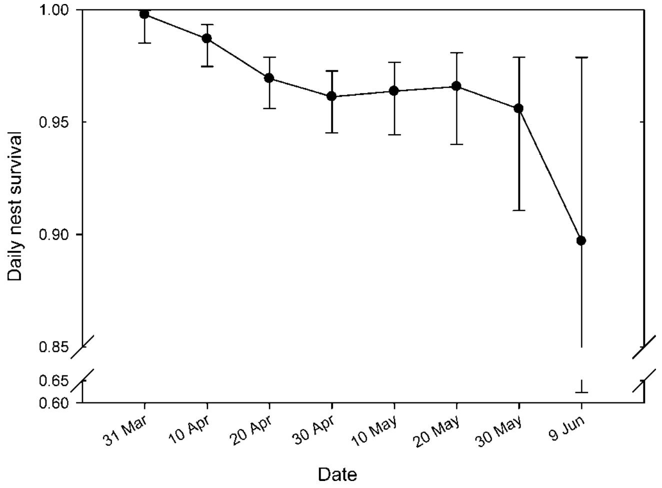

Figure 1. Predicted daily survival rates and 95% confidence intervals for golden-cheeked warbler nests as a function of date in Austin and Fort Hood, Texas, USA, 2005–2006.

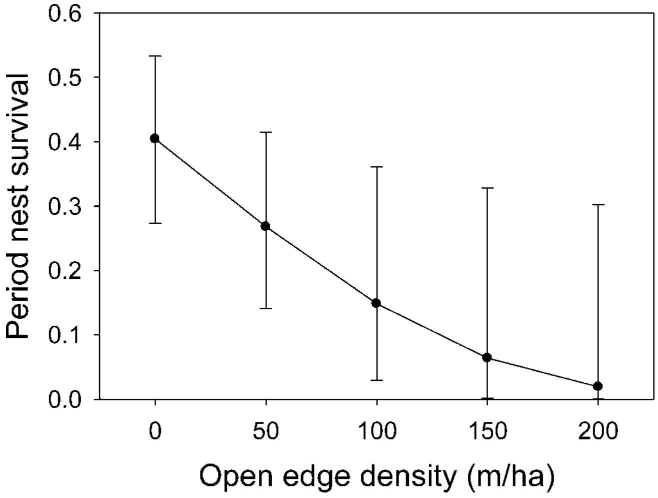

Figure 2. Predicted 25-day period nest survival rates and 95% confidence intervals for golden-cheeked warbler nests as a function of open edge density (m/ha) within a 100-m radius of the nest in Austin and Fort Hood, Texas, USA, 2005–2006.

abundance or behavior of the predator community or alternative prey during the season, rather than a response to changes in the adults' behavior (e.g., increased visitation rates during the nestling stage). Peak (2007) found nest survival on Fort Hood was affected by date, but not year, and had mixed results for stage effects. Stake (2003) found more support for temporal variables (date, yr, stage) affecting nest predation when he examined snakes, the most frequent nest predators of golden-cheeked warblers (Stake et al. 2004, Reidy et al. 2008), separately from other predator groups. Snake activity increased throughout the golden-cheeked warbler breeding season (Sperry et al. 2008). Birds, mostly corvids, were the next most frequently observed nest predator group (Stake et al. 2004, Reidy et al. 2008). Some corvids are known to shift their foraging strategy in response to their own nesting cycle (Sieving and Willson 1999). We clearly need more information on predator activity and foraging patterns throughout the golden-cheeked warbler's breeding season if we are to further understand temporal patterns of nest survival.

Aside from temporal effects, we found the most support for our hypothesis that edge factors affected nest survival. Open edge density was in the top 2 models, and nest survival declined substantially with increasing amounts of open edge. Forest edge density negatively affected golden-cheeked warbler nest survival on Fort Hood (Peak 2007). Maas-Burleigh (1998) similarly concluded inferred reproductive success was higher in unfragmented patches than in fragmented patches on Fort Hood. Proximity to edge also impacted nest survival negatively. Because of sample size limitations, we were unable to examine the effect of each edge type separately, making it difficult to interpret the true impact of each. However, this result does suggest increasing fragmentation associated with soft edges within breeding patches has negative consequences. Soft edges such as trails create small canopy gaps and receive some human visitation. Human presence may deter or attract some predators from using trails as travel lanes (Miller and Hobbs 2000). It is unknown how major nest predators of golden-cheeked warblers respond to different types of soft edge.

We believe higher abundance of predators in fragmented landscapes and higher predator activity near edges contributed to lower nest survival near edges. Snakes and corvids are the main predators of golden-cheeked warblers (Stake et al. 2004, Reidy et al. 2008) and both groups respond positively to increased edge and fragmentation. Black rat snakes (*Elaphe obsoleta*) are known to prefer edge and fragmented habitats and although this may be for thermoregulatory reasons, it nonetheless increases their chances of locating birds' nests along edges (Blouin-Demers and Weatherhead 2001). Although habitat preferences of Texas rat snakes and Great Plains rat snakes (*E. guttata*) are unknown, both are common in woods, pastures, and suburban areas throughout the golden-cheeked warbler's breeding range (Tennant 1998). Abundance of corvids such as blue jays (*Cyanocitta cristata*) and western scrub-jays (*Aphelocoma californica*) is positively associated with increased development in the golden-cheeked warbler's breeding range (Sexton 1987, Engels and Sexton 1994), whereas abundance of American crows (*Corvus brachyrhynchos*) is positively associated with increased open edge (Verbeek and Caffrey 2002, Smith 2004). Edge effects associated with open habitats and fragmentation were most evident at a local scale ($\leq$100 m from nest) and did not extend to the landscape scale.

MANAGEMENT IMPLICATIONS

Based on our observed nest survival rates and other commonly assumed demographic rates for warblers, nest survival was sufficient in both Austin and Fort Hood to sustain populations of golden-cheeked warblers (Donovan and Thompson 2001). We therefore suggest that habitat patches like those we studied can provide important breeding habitat in both urban and rural landscapes. Nest survival was influenced by temporal and edge factors, both of which may be related to predator activity or abundance throughout the golden-cheeked warbler's breeding season and habitat patches. We suggest management to reduce the amount of forest open edge and ensure the presence of large (>100 ha) blocks of contiguous mature juniper–oak woodlands where there is a desire to increase nest survival of golden-cheeked warblers. Further research investigating predator behavior and life-history and predator-specific patterns in nest predation is needed to more fully understand observed spatial and temporal patterns in nest survival.

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