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Research Article

Density and Nest Survival of Golden-Cheeked Warblers: Spatial Scale Matters

JENNIFER L. REIDY,[1] *School of Natural Resources, University of Missouri, 302 Natural Resources Building, Columbia, MO 65211, USA*
FRANK R. THOMPSON, III, *U.S. Forest Service Northern Research Station, 202 Natural Resources Building, Columbia, MO 65211, USA*
LISA O'DONNELL, *City of Austin, Austin Water, Wildland Conservation Division, Balcones Canyonlands Preserve, Austin, TX 78738, USA*

ABSTRACT Conservation and management plans often rely on indicators such as species occupancy or density to define habitat quality, ignoring factors that influence reproductive success, and potentially limiting conservation achievements. We examined relationships between predicted density and nest survival with environmental features at multiple spatial scales for the golden-cheeked warbler (*Setophaga chrysoparia*) in a large preserve within an urbanizing landscape. Larger-scale features of the forest and landscape composition best predicted density, whereas small-scale vegetation features best predicted nest success. Predicted warbler density was more influenced by vegetation structure at the forest (100-m) and landscape (1-km) scales than at the plot (5–11.3-m) scale. Predicted warbler density increased with greater woodland cover (100-m), average canopy height (100-m), and mixed woodland cover (1-km). Average predicted density derived from distance sampling models fit to count data across 1,506 points surveyed during 2011–2014 was 0.21 males/ha (95% CI = 0.20–0.22). Nest survival ($n = 610$ nests) was strongly correlated with vegetation and terrain characteristics at the plot scale. Period nest survival decreased 28% and increased 36% and 21% across the range of slope, woody understory, and juniper basal area, respectively. Daily nest survival averaged 0.97 (0.96–0.98) but declined throughout the breeding season and varied annually (2011–2015). We recommend management for a high percentage of closed-canopy, tall mixed juniper (*Juniperus ashei*)-oak (*Quercus* spp.) woodland at the forest and landscape scales to support high densities of warblers. We also recommend protecting upland woodlands with a well-developed woody understory and greater basal area of junipers because these characteristics were associated with greater nest success.

KEY WORDS basal area, canopy height, habitat quality, mixed woodland, *Setophaga chrysoparia*, slope, understory, woodland cover.

Conservation and management planning for species of conservation concern requires a thorough understanding of how vegetation and landscape characteristics affect individual or population persistence, typically referred to as habitat quality (Hall et al. 1997, Johnson 2007). Habitat quality has generally been assessed by relating attributes of the environment to density of the species, but density may not adequately capture relationships between habitat and individual fitness if density and fitness are not highly correlated (Van Horne 1983). Van Horne (1983) posited that habitat quality should be viewed in terms of density, survival, and productivity. Although Bock and Jones (2004) reported fairly high congruency between density and fitness parameters (e.g., productivity) their review included studies that compared 2 general habitat types or landscapes. Such study designs may not elucidate habitat use or selection patterns in density and productivity for species that favor a narrow range of vegetation conditions or reveal patterns along a habitat gradient. Factors influencing abundance or population density may differ from those affecting productivity or individual fitness (Franklin et al. 2000, Winter et al. 2005); these patterns may result from processes operating at multiple or different spatial scales (Winter et al. 2006, Chalfoun and Martin 2007, Johnson 2007). For migratory songbirds, density reflects individual settlement patterns and a series of hierarchical, multi-scale habitat selection decisions by individuals as they arrive on the breeding grounds (Hilden 1965). Habitat should provide ample foraging and nesting opportunities, and preferably maximize the individual's probability of successfully rearing young. Ideally, environmental conditions that influence density would also influence reproductive success because measuring abundance is less time-consuming than measuring reproductive success. However, selective pressures for food availability and for safe nesting sites may operate at different spatial scales (Chalfoun and Martin 2007). Nest predation is often the limiting factor for songbird productivity and nest predators

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[1]*Corresponding author e-mail address: jennifer.reidy@gmail.com*

may prefer or select the same habitat features as their prey, particularly if bird nest contents are a primary source of food during the nesting season (Sperry and Weatherhead 2009). Despite the need for information on habitat relationships operating at the population and individual scale, there remains a dearth of studies in the ornithological literature evaluating consequences of habitat use on density and nest survival (Johnson 2007).

We conducted a multi-scale analysis to identify spatial scales that may influence density and nest survival of golden-cheeked warblers (*Setophaga chrysoparia*; warbler), an endangered songbird that breeds only in mature Ashe juniper (*Juniperus ashei*)-oak (*Quercus* spp.) woodlands and forests within central Texas. Warbler habitat is generically described as juniper-oak woodland, but there is substantial variation within woodland vegetation structure and composition that may affect perceived or realized habitat quality as measured by density or nest (or territory) success (Peak and Thompson 2013, 2014; Stewart et al. 2014; Reidy et al. 2016; Sesnie et al. 2016). Previous studies focused separately on relationships between vegetation structure or woodland characteristics on warbler occupancy (Magness et al. 2006, Farrell et al. 2013), density (Peak and Thompson 2013, Reidy et al. 2016, Sesnie et al. 2016), and productivity (Peak and Thompson 2014), and only one investigated multiple spatial scales with fine-scale and coarse-scale vegetation, and terrain data (DeBoer and Diamond 2006). Collectively these studies highlight the conservation value of contiguous mature woodland to occupancy, density, and nest success, but they do not provide the level of inference that can be gained by simultaneously considering both density and nest survival at multiple spatial scales.

Our objective was to identify environmental attributes at multiple spatial scales important for predicting warbler density and nest survival at a large preserve embedded in an urbanizing landscape. We first evaluated the effects of explanatory variables on density at the plot (5–11.3-m radius around the survey point), forest (100-m radius), and landscape (1-km radius) scales. We hypothesized warbler density was best predicted by the forest scale than the landscape or plot scale because the forest scale best represented the scale of a territory. Within that scale, we predicted density would be positively related to woodland cover or woodland type and canopy height, and negatively related to woodland edge. We examined the effects of similar explanatory variables on nest survival at the nest-site, plot (5–11.3-m radius around the nest site), forest, and landscape scales and predicted nest survival rates based on supported relationships. We opted to include previously examined and novel covariates because we monitored a large number of nests that covered a wide range of local vegetation and landscape conditions we expected warblers experience across the breeding range. We predicted nest-site variables would be less important than those at the plot or forest scales because the nest predator assemblage is likely constrained by vegetation associations at a larger scale, but at the landscape scale, predators may be ubiquitous (Thompson et al. 2002). However, it is difficult to predict overall relationships because the dominant nest predators in this study area, Texas rat snakes (*Elaphe obsoleta lindheimerii*) and Woodhouse's scrub-jay (*Aphelocoma woodhouseii*; Reidy et al. 2008), prefer different elements of these woodlands and therefore, nests in some areas may be more subject to predation by one predator and less subject to predation by another (Reidy and Thompson 2012).

STUDY AREA

We conducted our study from 2011 to 2015 on the Balcones Canyonlands Preserve (BCP), a 12,294-ha preserve in western Travis County, Texas, USA (Fig. 1). Our study area was on the eastern edge of the Edwards Plateau and the topography was rolling uplands and deeply dissected hills. Elevation ranged from 120 m to 300 m above sea level. The climate was subtropical humid–subtropical subhumid, characterized by hot summers and cool winters with average annual precipitation of 85 cm. The spring months were typified by mild, wet conditions with an average temperature of 20.2°C and average precipitation of 25 cm during the period 1971–2000 (Ward 2009). The BCP was created in 1996 to mitigate increasing loss and fragmentation of juniper-oak woodland in western Travis County

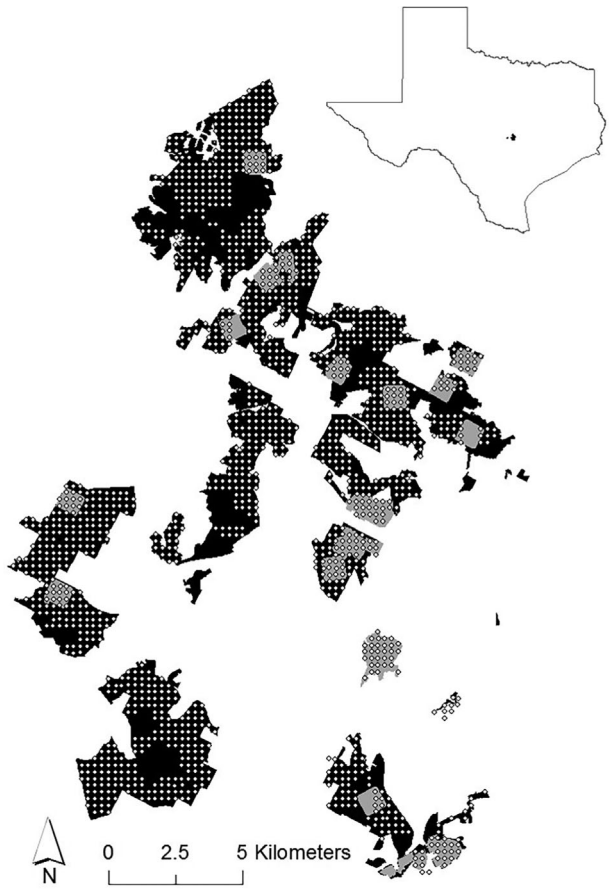

Figure 1. We investigated factors affecting density and nest survival of golden-cheeked warblers on the Balcones Canyonlands Preserve (BCP), Austin, Texas, USA, 2011–2015 (black shading) including 18 intensive monitoring plots (gray shading), and point count locations (white dots).

from increasing urban pressure and represented the largest protected area in warbler recovery region 5 (U.S. Fish and Wildlife Service [USFWS] 1992), a region that historically contained some of the largest and most contiguous patches of juniper-oak woodland (Wahl et al. 1990, Groce et al. 2010, Duarte et al. 2013). Although the majority of the BCP was juniper or mixed juniper-oak woodland (City of Austin et al. 2014), perceived woodland quality varied across the preserve, as measured by warbler density; density was highest in the northeastern portion of the BCP and lowest in the southwest (Reidy et al. 2016). Dominant tree species included Ashe juniper, Texas red oak (*Q. buckleyi*), plateau live oak (*Q. fusiformis*), shin oak (*Q. sinuata* var. *breviloba*), cedar elm (*Ulmus crassifolia*), escarpment black cherry (*Prunus serotina* var. *exima*), and Texas ash (*Fraxinus texensis*). Common understory species included Carolina buckthorn (*Frangula caroliniana*), yaupon holly (*Ilex vomitoria*), red buckeye (*Aesculus pavia* var. *pavia*), Mexican buckeye (*Ungnadia speciosa*), Lindheimer's silktassel (*Garrya ovata* var. *lindheimeri*), and elbow bush (*Forestiera pubescens*; City of Austin et al. 2014).

METHODS

Point Count Surveys and Nest Monitoring

We created a random point grid with 250-m spacing across the BCP in ArcMap 9.3 (ESRI, Redlands, CA, USA). We removed points that were <50 m from major roads because the plot would be partly composed of roadway and road noise would decrease our ability to hear birds, but we did not otherwise remove points based on proximity to edges or property boundaries. We built point transects consisting of 8–15 points that could be efficiently surveyed in a morning. We divided the BCP into 9 areas based on natural watersheds and division from major roadways and surveyed a similar proportion of transects in each area in each year to ensure a balanced sampling effort.

Two observers per year conducted 5-minute, unlimited radius point counts from 10 minutes post-sunrise until approximately 1100 Central Standard Time from mid-April to mid-May 2011–2014. We surveyed each point once (over the course of the study) and observers surveyed transects that were relatively close to each other (for logistical and safety reasons). We conducted surveys in good weather conditions (>10°C, <19 km/hr winds, no or light precipitation). Observers recorded detections of singing male warblers and measured the distance to detected individuals with a laser rangefinder or, when this was not feasible, they estimated the distance. After observers spent 4 weeks practicing, we tested them on species identification and distance estimation prior to conducting point counts.

We established 18 intensive monitoring plots (27–180 ha) spread across the BCP where we color-banded as many territorial males as possible and monitored territorial pairs ≥2 times/week during the breeding season (Bird Banding Lab no. 23615 and University of Missouri Animal Care and Use Committee no. 8383). We searched for warbler nests using behavioral clues from adults and systematic searching from mid-March through mid-June 2011–2015. We monitored nests every 2–4 days post-laying until the nest fledged young or failed; we monitored nests more frequently as the expected fledge date approached. We determined a nest was successful if we observed nestlings leaving the nest, an adult feeding host young, or an adult carrying food to locations other than the nest after the day of expected fledge. If we detected no activity at a nest prior to the expected fledge date and the nest was intact, we made ≥1 subsequent visit to verify no activity and follow the pair for evidence of re-nesting. If we did not confirm fledglings for a nest on the expected fledge date, we continued to monitor the territory for evidence of fledging or re-nesting. Fledglings are often quiet in the days immediately following fledging but are capable of moving large distances; hence, fledglings may not be detected immediately.

Vegetation and Landscape Characteristics

For the plot scale, we measured vegetation structure on plots centered on survey points or nests following a modified BBIRD protocol (Martin et al. 1997). We measured vegetation structure at survey points in early spring and at nest sites in late spring. We measured canopy cover with a concave spherical densiometer and averaged 4 readings taken facing the 4 cardinal directions from the plot center. We calculated small stem density (stems/ha) from the count of live woody stems >10 cm tall that were <2.5 cm diameter at breast height (dbh; we counted stems >2.5 cm dbh as trees) in a 5-m radius around the center. We estimated the percent of bare ground cover (rock and bare ground) in each quadrant in a 5-m radius around the center. We measured the slope with a clinometer facing downhill 10 m in the steepest direction and recorded the direction of the slope (aspect). We calculated the average tree height by measuring a representative juniper and non-juniper (>3 m tall) in each quadrant in an 11.3-m radius using a clinometer. We recorded dbh with a Biltmore stick (Kershaw et al. 2016) of all junipers, live oaks, Texas red oaks, shin oaks, and other trees >2.5 cm dbh in an 11.3-m radius from the center and converted dbh to basal area/ha for junipers, live oaks, all other trees, and total basal area. Additionally, we calculated large stem densities in 3 dbh classes (<10 cm, 10–15 cm, and >15 cm dbh) for 3 tree categories: junipers, live oaks, and all other trees. We chose these categories because juniper is critical for nesting material and nesting sites, live oaks are an evergreen species and are often associated with more xeric and upland woodland than other trees, and other tree species are often used for foraging (Beardmore 1994, Marshall et al. 2013). At nest sites, we also recorded nest tree species, nest height, nest tree height, nest tree dbh, and nest cover ($\bar{x}$ cover estimated 1 m away in each cardinal direction and above and below the nest).

We derived measures of composition and structure at a forest (100-m radius) and landscape scale (1-km radius) around each survey point and nest using ArcMap 10.0 (ESRI). We created a finer resolution and more up-to-date map of vegetation cover by intersecting the Texas Ecological Systems phase 1 (TESP1) vegetation classification with a

light detection and ranging (LiDAR)-based map of vegetation height (Reidy et al. 2016). The TESP1 vegetation classification was a 10-m resolution vegetation classification developed for central Texas derived from satellite imagery and slope, aspect, landscape position, hydrology, and soil type data (Elliott et al. 2014). The LiDAR data was a 2-m resolution map of vegetation height derived from LiDAR data gathered in winter 2012. We used the vegetation heights obtained from LiDAR to modify the TESP1 layer to better delineate edges with non-forest. To do this, we evaluated each 10-m pixel in forest and woodland types in the TESP1 layer and if >50% of the 25 2-m resolution pixels from the LiDAR canopy height layer were <3 m tall, we reclassified the pixel as open land cover. We then defined open edge as the boundary between forest-woodland and all other non-urban land covers. At the 100-m forest scale, we calculated the percent of juniper and mixed woodland types, woodland cover (sum of juniper and mixed woodland), total canopy cover, open and urban edge density, mean and standard deviation of canopy height, and distance to any edge (nests only). At the 1-km landscape scale, we calculated the percent of juniper and mixed woodland, total woodland, and urban cover using the TESP1 land cover classification described above.

Density Analysis

We fit hierarchical density models to our point count data in the R package, unmarked. We used the distsamp function to estimate detection probability based on distances to warbler detections and Poisson regression to consider covariate effects on density (Royle et al. 2004, Fiske and Chandler 2011). The assumptions of distance sampling are individuals at distance zero are always detected, individuals are detected at their initial location, and distances to the detected individuals are accurately estimated (Buckland et al. 2001). We truncated observations at 130 m, effectively eliminating the farthest 10% of detections (Buckland et al. 2001), and grouped remaining detections into 4 unequal distance bins with break points at 36 m, 56 m, and 85 m to represent similar numbers of detections in each bin. We standardized all continuous covariates prior to analysis ($\bar{x} = 0$, standard deviation = 1). We first compared support for the hazard-rate, uniform, and half-normal key function by identifying the model with the lowest Akaike's Information Criterion for small sample sizes (AIC_c) to determine which fit the distance data best (Buckland et al. 2001). Because the hazard-rate and half-normal key functions received almost identical support ($\Delta AIC_c = 0.016$), we then compared support for 16 models comprised of all combinations of the variables observer, slope, and total tree basal area, as well as an intercept-only (null) model, using the hazard-rate and half-normal key functions (8 models each). We predicted the observer would affect detection probability because observer is a well-documented source of detection variation (Peak and Thompson 2013, Reidy et al. 2016). We predicted that detection may be inversely related to tree volume and slope steepness because bird song likely carries farther in areas of lower tree volume and across open space. Sesnie et al. (2016) reported support for variables measuring similar qualities (canopy cover and topographic roughness). We then included the most supported detection model while evaluating vegetation and landscape covariates in the density models.

We used an information-theoretic approach to evaluate candidate models representing our *a priori* predictions about factors affecting warbler density. We used a 2-stage approach to develop models. We first considered candidate models within each of the 3 scales: plot, forest, and landscape (Appendix I). We conducted preliminary analyses comparing support for our multiple measures of tree structure (linear and quadratic relationships with basal area, tree density, and the proportion of the basal area that was juniper) and forest structure (mixed and juniper woodland, total woodland, and canopy cover). Basal area (quadratic relationship) and total woodland received the most support, so we built predictive models using these variables in the plot and forest scales, respectively. We compared all single and additive combinations of variables within each scale and ranked models by AIC_c. We created a final set of 9 candidate models consisting of the top model for each scale, all additive combinations of these models, a site model (as a surrogate for uncaptured differences), and a null model (intercept-only; Table 1). Prior to analysis, we calculated tolerance values for all variables in the global model to assess multi-collinearity using PROC REG (SAS Institute, Cary, NC, USA; Allison 1999) and developed predictive models comprised of uncorrelated variables. We evaluated goodness of fit for the most-supported model with the Freeman–Tukey test based on a parametric bootstrap for 100 simulations (Fiske and Chandler 2011, Sillett et al. 2012). We ranked the final candidate set of models based on AIC_c and made inferences from the top model or model-averaged parameters and predictions if model selection

Table 1. Number of parameters (*K*), the difference between the Akaike's Information Criterion for small sample sizes for the top model and the current model (ΔAIC_c), and model support based on Akaike weights (w_i) for distance-based models evaluating effects of vegetation structure and landscape composition at 3 spatial scales on density of golden-cheeked warblers (M/ha) on Balcones Canyonlands Preserve, Texas, USA, April–May 2011–2014.

Model name	*K*	ΔAIC_c[a]	w_i
Forest[b] + landscape[c]	15	0.00	0.81
Plot[d] + forest + landscape	22	2.96	0.19
Forest	13	15.99	0.00
Plot + forest	20	19.48	0.00
Plot + landscape	20	74.78	0.00
Landscape	13	108.95	0.00
Site	19	114.01	0.00
Plot	18	138.48	0.00
Null	11	189.88	0.00

[a] AIC_c of the top model was 3,896.88.
[b] Forest model variables (100 m): total woodland cover, canopy height.
[c] Landscape model variables (1 km): juniper woodland cover, mixed woodland cover.
[d] Plot model variables: tree height and basal area of juniper, live oak, and deciduous trees.

uncertainty existed (we considered models with $\Delta AIC_c < 2$ as competitive [Burnham and Anderson 2002]). We plotted predicted densities as a function of covariates for which 95% confidence intervals did not overlap zero by varying the variable of interest across its observed range while holding other continuous covariates at their mean and categorical covariates at their observed proportion (Shaffer and Thompson 2007). We ran 100 iterations of a parametric bootstrap to incorporate uncertainty in the predicted densities.

Nest Survival Analysis

We estimated daily survival using the logistic exposure method (Shaffer 2004) with a binomial response for each monitoring interval (success = 1, failure = 0). We considered only active nests (nests known to have ≥1 egg or nestling during monitoring) and excluded intervals in the building or pre-laying stage for the analysis. We used an information-theoretic approach to evaluate 16 candidate models representing our *a priori* predictions about factors affecting warbler nest survival. We grouped variables from vegetation surveys and remotely sensed data into 4 scales: nest-site, plot, forest, and landscape. We included year, day of year, and nest stage (egg or nestling) in every model because they affect warbler nest survival (Peak 2007, Reidy et al. 2009, Reidy and Thompson 2012) and we wanted to control for their effect. Our candidate models included a nest-site model with the variables nest tree species (juniper or other), nest cover, nest tree height, nest tree dbh, and canopy cover; a plot model with the variables juniper basal area, non-juniper basal area, slope, aspect, small stem density, average tree height, and percent bare ground; a forest model with the variables total woodland cover, open edge density, urban edge density, mean and standard deviation of canopy height within 100 m of nests, and distance to any edge; a landscape model with the variables total woodland cover and urban cover in a 1-km radius; all additive combinations of the nest-site, plot, forest, and landscape models; and an intercept-only (null) model (Table 2). We assessed multi-collinearity by calculating tolerance values for covariates in the global model (Allison 1999). Because we had several correlated measures representing forest structure, we first compared support for different measures of canopy structure (canopy cover, juniper woodland and mixed woodland, and total woodland cover). Our preliminary analysis showed greater support for a single measure of percent woodland cover, so we proceeded with this variable in subsequent analyses. We evaluated goodness of fit of the global model with a Hosmer and Lemeshow (2000) test and inspected the Pearson χ^2 statistic for the global model for evidence of lack of fit (Burnham and Anderson 2002). We ranked models based on AIC_c and followed the same procedures used for the density models for reporting parameter estimates and predictions. We calculated period nest survival by exponentiating the daily survival rate by 25, which is the average number of days combined for laying, incubation, and nestling stages.

Table 2. Number of parameters (K), the difference between the Akaike's Information Criterion for small sample sizes for the top model and the current model (ΔAIC_c), and model support based on Akaike weights (w_i) for models evaluating effects of nest-site, plot, forest, and landscape variables on daily survival of golden-cheeked warbler nests ($n = 610$) on Balcones Canyonlands Preserve, Texas, USA, spring 2011–2015.

Model name	K	ΔAIC_c[a]	w_i
Plot[b]	16	0.00	0.77
Null	9	3.96	0.11
Plot + landscape[c]	18	5.40	0.05
Landscape	11	6.18	0.04
Nest site[d] + plot	21	7.83	0.02
Nest site	14	9.61	0.01
Forest[e]	15	10.04	0.00
Plot + forest	22	10.47	0.00
Nest site + plot + landscape	23	11.66	0.00
Nest site + landscape	16	11.66	0.00
Plot + forest + landscape	24	12.47	0.01
Forest + landscape	17	13.01	0.00
Nest site + forest	20	13.25	0.00
Nest site + plot + forest	27	15.90	0.00
Nest site + forest + landscape	22	19.45	0.00
Nest site + plot + forest + landscape	29	20.81	0.00

[a] AIC_c of top model was 1,498.77.
[b] Plot variables: juniper basal area, non-juniper basal area, slope, aspect, small stem density, canopy height, bare ground cover .
[c] Landscape variables (1 km): percent total woodland cover, percent urban land cover.
[d] Nest-site variables: nest tree substrate (juniper or other), nest cover, tree height, canopy cover, nest tree dbh.
[e] Forest variables (100 m): percent total woodland, mean canopy height, canopy height standard deviation, open edge density, urban edge density, distance to any edge.

RESULTS

Density

We surveyed 1,506 points (Fig. 1) and detected 642 singing male warblers within 130 m of the survey location. There was substantial variation in the vegetation measurements across points; for example, woodland cover ranged from 4% to 100% and mean canopy height ranged from 0 m to 9 m (Table 3). The hazard-rate key function with the covariates observer and total tree basal area received the most support for the detection model ($w_i = 0.72$). The effective detection radius varied by observer (range = 49–88 m) and detection probability increased with increasing basal area ($\beta = 0.07$, 95 CI = 0.03–0.11). The overall detection probability was 0.56.

At the plot scale, basal area and tree height were in the top 7 density models and accounted for 88% of the model weight; additional variables were uninformative because their contribution did not overcome the 2 AIC_c penalty for each additional parameter (Arnold 2010; Appendix I). At the forest scale, total woodland cover and canopy height were in the top model and these covariates were also in the remaining 7 models that together with the top model accounted for 100% of model weight (Appendix I). At the landscape scale, the top model consisted of juniper woodland and mixed woodland, and there were no additional informative parameters (Appendix I). When we considered combinations of the best plot, forest, and

Table 3. Descriptive statistics for habitat covariates used to estimate density (M/ha) and nest survival of golden-cheeked warblers on Balcones Canyonlands Preserve, Texas, USA, 2011–2015. The scale of measurement (100 m or 1 km) for remotely sensed variables is included.

	Points ($n = 1{,}506$)				Nests ($n = 610$)			
Variable	$\bar{x}$	**SD**	**Min.**	**Max.**	$\bar{x}$	**SD**	**Min.**	**Max.**
Slope (°)	10.0	8.2	0	47	11.3	9.0	0	47
Aspect (°)	170.3	105.4	0	359	175.7	101.4	0	359
Tree height (m)	6.4	2.1	0	21	7.6	2.0	4	35
Bare ground cover (%)	27.0	18.7	0	99	20.5	13.2	0	87
Total small stem density (stems/ha)	3,910.1	4,680.7	0	53,594	5,540.7	7,282.7	0	74,930
Ashe juniper basal area (m^2/ha)	15.2	9.2	0	61	18.7	9.0	0	53
Live oak basal area (m^2/ha)	2.3	4.0	0	33				
Deciduous basal area (m^2/ha)	2.3	4.2	0	59				
Non-juniper basal area (m^2/ha)					5.9	5.8	0	83
Total tree basal area (m^2/ha)	19.9	11.4	0	187				
Proportion of juniper basal area	0.76	0.24	0	1				
Large juniper density (trees/ha)	208.6	178.8	0	975	314.1	173.0	0	800
Medium juniper density (trees/ha)	356.4	238.7	0	1,525	332.4	221.8	0	1,150
Small juniper density (trees/ha)	1,203.7	906.0	0	5,125	744.9	649.5	0	6,250
Large live oak density (trees/ha)	38.0	67.6	0	500	48.9	73.6	0	425
Medium live oak density (trees/ha)	25.0	56.8	0	700	21.4	45.6	0	325
Small live oak density (trees/ha)	28.8	70.7	0	750	19.9	53.6	0	525
Large deciduous tree density (trees/ha)	38.4	66.6	0	475	55.1	77.6	0	525
Medium deciduous tree density (trees/ha)	27.6	51.9	0	375	36.9	55.5	0	400
Small deciduous tree density (trees/ha)	107.3	200.1	0	2,100	176.1	242.7	0	1,500
Nest tree species (juniper)					0.66	0.47	0	1
Nest cover (%)					53.5	19.0	5	100
Nest height (m)					6.6	2.0	2	23
Nest tree height (m)					8.3	2.3	4	25
Canopy cover (%)					88.8	10.3	21	100
Nest tree dbh (cm)					23.2	10.6	6.5	85
Total woodland cover (%)—100 m	68.8	20.0	4	100	96.8	8.5	35	100
Open edge density (m/ha)—100 m	109.4	59.4	0	267	22.2	41.9	0	233
Urban edge density (m/ha)—100 m	14.8	19.7	0	104	2.4	15.9	0	221
Canopy height (m)—100 m	4.8	1.8	0	9	6.3	1.2	3	10
Canopy height standard deviation—100 m	2.1	0.9	0	16	1.8	0.4	1	3
Distance to any edge (m)					148.7	109.9	0	670
Juniper woodland cover (%)—1 km	26.6	7.3	4	48				
Mixed woodland cover (%)—1 km	18.7	9.6	5	46				
Total woodland cover (%)—1 km					83.4	8.4	52	100
Urban land cover (%)—1 km	29.7	12.0	7	77	8.5	7.8	0	45

landscape model, the forest + landscape model had the greatest support ($w_i = 0.81$; Table 1). Warbler density was strongly positively associated with total woodland cover ($\beta = 0.33$, 95% CI = 0.20–0.46) and canopy height ($\beta = 0.28$, 95% CI = 0.16–0.39) at the forest scale, and with the amount of mixed woodland at the landscape scale ($\beta = 0.18$, 95% CI = 0.10–0.26). Density estimates were 0.07–0.29, 0.09–0.29, and 0.13–0.27 males/ha across the range of total woodland cover (100-m), canopy height (100-m), and mixed woodland cover (1-km), respectively (Fig. 2). Average predicted density across the 1,506 points was 0.21 males/ha (95% CI = 0.20–0.22) based on this model. The second most supported model based on all 3 scales was plot + forest + landscape ($\Delta AIC_c = 2.96$; Table 1). Although this model had less support, we nevertheless interpreted the plot-scale effects in it,

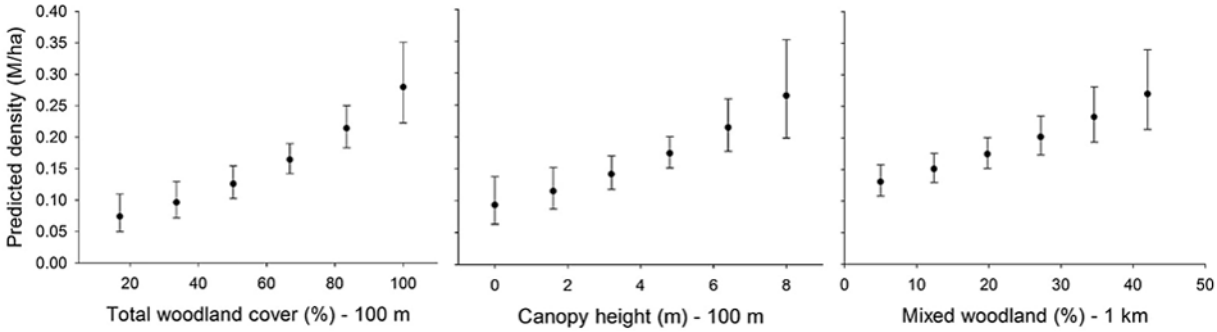

Figure 2. Predicted density of golden-cheeked warblers (M/ha) as a function of forest and landscape variables on Balcones Canyonlands Preserve, Texas, USA, April–May 2011–2014. The *x*-axis includes the scale of measurement for the variable. Error bars represent 95% confidence intervals.

conditional on this model, because plot-scale attributes can be affected by local woodland management. Warbler density increased with tree height and juniper basal area and peaked at low to intermediate levels of live oak and deciduous basal area; however, confidence intervals overlapped zero (Appendix II).

Nest Survival

We monitored 610 active nests for 3,009 intervals between nest checks during 2011–2015. We confirmed ≥1 fledgling from 388 nests (64%). Vegetation characteristics varied greatly across this sample of nests; for example, woodland cover ranged from 35% to 100% and mean canopy height in a 100-m radius ranged from 3 to 10 m (Table 3). Most nests (66%) were placed in junipers, followed by live oaks (21%), cedar elms (8%), and shin oaks (4%). We fit logistic exposure models to predict nest success and the goodness-of-fit test ($\chi^2_8 = 3.02$, $P = 0.93$) and overdispersion parameter ($\hat{c} = 1.08$) for the global model indicated there was no evidence of lack of fit. Tolerance values were ≥0.4, indicating no substantial multicollinearity among covariates.

The plot model received 77% of model support and included the variables juniper and non-juniper basal area, slope, aspect, total small stem density, bare ground, and tree height (Table 2). Because this model received substantial support and the null model received the second most support ($\Delta AIC_c = 3.96$), we chose to base predictions on the top model. The odds of nest survival were 2% lower for every 1% increase in slope, 3% greater for every 1,000 stems/ha increase in small stem density, and 2% greater for every m^2/ha increase in juniper basal area. Nest survival decreased 26% and increased 32% and 22% across our range of slope, small stem density, and juniper basal area (Fig. 3). The other covariates in the nest patch model were uninformative. Nest survival varied by year and day of year (Fig. 4) but did not differ between the egg stage (0.97, 95% CI = 0.96–0.98) and the nestling stage (0.97, 95% CI = 0.97–0.98). Average daily nest survival rate was 0.97 (95% CI = 0.97–0.98) and period survival for the 25-day nesting cycle was 0.51 (95% CI = 0.44–0.57).

DISCUSSION

Understanding what environmental conditions are important at different spatial scales is essential to planning and implementing management. In our study, warbler density and nest survival were most influenced by vegetation and landscape characteristics operating at different spatial scales. Density was mostly related to characteristics at the forest and landscape scale, whereas nest survival was most influenced by structure at the plot scale. We did not directly investigate habitat selection, but by relating warbler density and nest survival to specific features of the vegetation structure and terrain, we can better define woodlands we expect to be high quality. Our results indicate land managers need to consider multiple spatial scales when designing management strategies to optimize density and nest success. This is the first multi-scale analysis of this nature for warblers, but previous research on Fort Hood, Texas, reveals hints of different relationships between density and nest survival within the same spatial scale. Density was more strongly related to increasing mixed woodland than juniper woodland and showed a significant decline related to increasing edge (Peak and Thompson 2013), whereas nest survival was more strongly related to increasing juniper woodland than mixed woodland and edge was less associated with nest survival (Peak and Thompson 2014). Although we found no support for large-scale effects on nest survival, we conducted a *post hoc* analysis to provide context for our research compared to their study. We evaluated the same models as Peak and Thompson (2014) and found 48% of model support for the temporal model (year and cubic effect of day of year), and 27% model support for temporal variables plus edge, which had a marginally positive effect on nest survival. These important differences underscore the need to obtain empirical data at multiple locations and landscapes across a study species' range before making broad recommendations about habitat quality.

We found strong support for relationships between warbler density and forest- and landscape-scale features. The amount of total woodland cover and canopy height at the forest scale and the amount of mixed woodland at the landscape scale were significantly positively related to warbler density.

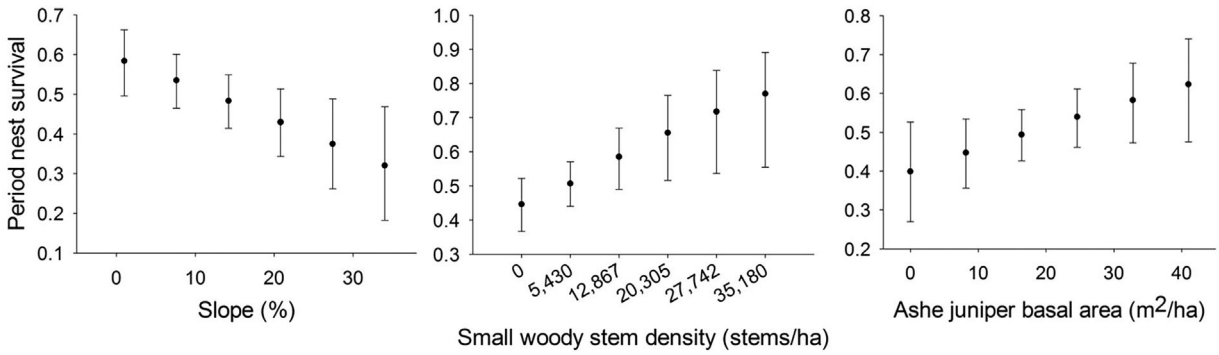

Figure 3. Predicted golden-cheeked warbler nest survival (25-day period) as a function of slope, small stem density, and juniper basal area across Balcones Canyonlands Preserve, Texas, USA, 2011–2015. Error bars represent 95% confidence intervals.

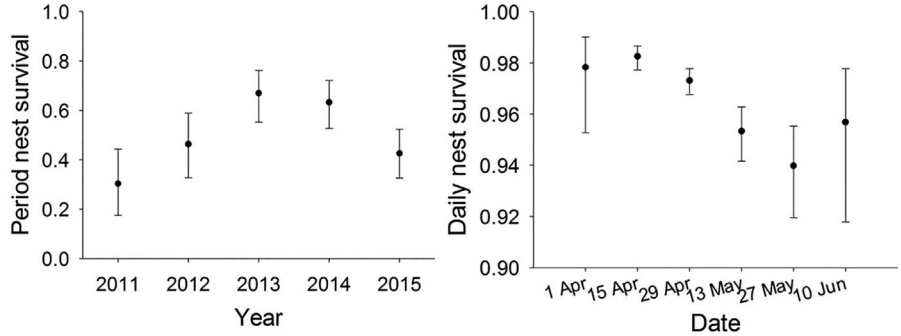

Figure 4. Temporal patterns of golden-cheeked warbler nest survival as a function of year (presented for period survival) and day of year (presented for daily survival) across Balcones Canyonlands Preserve, Texas, USA, 2011–2015. Error bars represent 95% confidence intervals.

Similar density relationships were observed on Fort Hood, Texas (Peak and Thompson 2013) and Balcones Canyonlands National Wildlife Refuge, Texas (Sesnie et al. 2016). Collectively, these studies show mature, closed-canopy mixed woodlands support the highest densities of breeding males. However, all of these studies were in protected areas and it is unknown if these patterns extend across the entire breeding range. No studies have investigated relationships between density and woodland structure in the southwestern or northern portions of the breeding range, which may or may not be similar to the general association with closed-canopy woodland in the central and eastern portion of the range. Limited data from the southwestern and northern portions of the breeding range suggest warblers use less mature and more open-canopy woodland, but these areas also support low numbers of territories (Kroll 1980, USFWS 1992, Klassen et al. 2012).

We consider the influence of canopy height an important and underappreciated feature of preferred warbler breeding habitat. Most studies that classify warbler breeding habitat rely on land cover classifications based on aerial imagery; however, this imagery cannot distinguish canopy height, and therefore, may overestimate important predictors such as canopy cover (Farrell et al. 2013, Jensen et al. 2013), and consequently, the amount of breeding habitat for warblers. Additionally, reliance on imagery not adjusted for canopy height can lead to inaccurate estimates of size, abundance, distribution, and fragmentation of woodland patches. We found compelling support that taller, more mature woodland supports greater densities of warblers, suggesting this attribute should be included in future studies defining or characterizing warbler breeding habitat.

Although the plot scale was less supported than forest or landscape scales, there was some support for relationships between warbler density and basal area, and tree height. Warblers reached peak densities at high basal area of junipers and low or moderate basal area of live oaks and deciduous trees. Although these relationships were not significant in the plot + forest + landscape model, they were significant in the plot model from Stage 1. Warblers showed especially strong relationships with deciduous trees, where areas with a low basal area of approximately 4 m^2/ha maximized density, but areas with greater basal areas (>10 m^2/ha) had very low warbler densities. Warbler densities also peaked in areas with taller trees. Measuring these attributes in the field is time-consuming and therefore limited to small scales; however, continuing advancements in remote sensing will likely allow for measurement of increasingly fine-scale vegetation attributes, such as tree structure, in the future (Lee et al. 2016, Sesnie et al. 2016). Our results are consistent with previous studies that showed warblers prefer areas with a high juniper component but also some oaks (not pure juniper stands; Kroll 1980, Marshall et al. 2013, Sesnie et al. 2016) and areas with taller canopy height (DeBoer and Diamond 2006, Farrell et al. 2013). Although juniper is clearly a necessary component of warbler habitat, our results demonstrate that oaks are also essential to provide optimal habitat; however, oaks should only make up a minor component of the overall tree composition.

Our mean density estimate (0.21 M/ha) for the 1,506 survey points is slightly lower than the Bayesian hierarchical model estimate from the same count data (0.24 M/ha) and slightly higher than the area-weighted mean density derived from the intensive territory monitoring plots on BCP (0.17 M/ha; Reidy et al. 2016). Furthermore, our model performed nearly identically to the model in Reidy et al. (2016) when used to estimate densities on the 18 intensive territory monitoring plots and compare them to observed territory densities ($R^2 = 0.75$). Therefore, we are confident our model captured important density relationships. Our mean density estimate is substantially lower than 0.39 male warblers/ha reported on Fort Hood. Although we expect woodlands within Fort Hood to support higher warbler densities because it has a greater percentage of mixed juniper-oak woodland versus juniper woodland, the sampling frame for that study only included probable breeding habitat and their model also over-predicted when compared to territory counts (Peak and Thompson 2014).

Even though density estimates were similar, there are several important distinctions between our study and Reidy et al. (2016). The Reidy et al. (2016) model was based solely on remotely sensed variables, whereas our current analysis evaluated fine-scale vegetation structure measured at the point and remotely sensed data at the 100-m and 1-km

scales. Although remotely sensed data are readily updated and span the breeding range, they may not provide inferences at the scale that most land managers operate at or that is most influential for warblers. Hence, we opted to use remotely sensed data and point-level measurements to determine the relative importance of explanatory variables measured at multiple scales. Additionally, Reidy et al. (2016) used a Bayesian hierarchical model that considered occupancy and density, whereas, we used a maximum likelihood approach that modeled only density and allowed us to easily compare support for a large number of models. Reidy et al. (2016) also estimated availability (the probability that a bird that is present within the survey area sings) in addition to detectability (the probability that the observer detects the bird given that it sings), but availability was high (0.90) and fairly stable across sampling conditions, and apparently had minimal effect on estimates.

Whereas warbler density was best predicted at the forest scale, nest survival was more influenced by environmental conditions at the plot scale, specifically the variables slope, small stem density, and basal area of junipers. Because nest predation is the primary source of nest failure for warblers (Stake et al. 2004, Reidy et al. 2008), we expect these relationships are influenced by predator activity or search patterns. The positive effects of small woody stems (or understory) and increased woodland structure are likely because greater habitat structure around the nest provides more cover for predators to search and may also make adult activity near the nest less noticeable to visually oriented predators (Mullin and Cooper 1998, 2000). Texas rat snakes, the dominant nest predator (Stake et al. 2004, Reidy et al. 2008), preferred areas with greater structure, such as areas closer to large trees and understory trees (Sperry et al. 2009), suggesting that warblers nesting in areas preferred by snakes may not suffer higher predation even though rat snakes may be close to warbler nests. Texas rat snakes preferred slopes in winter but used all vegetation and terrain types in proportion to their availability during the warbler breeding season, even though slopes supported greater abundance of small mammals (Sperry and Weatherhead 2009). Little published information exists on habitat associations for Woodhouse's scrub-jay, another dominant nest predator in this landscape, but they were more common on steeper slopes, and in areas of less understory and lower basal area of junipers on the BCP (J. L. Reidy, University of Missouri, unpublished data) suggesting that jay predation may be partially responsible for observed relationships. The negative effect of slope on nest survival is contrary to results with other measures of habitat quality, such as occupancy (DeBoer and Diamond 2006). Our results suggest nest predators are less likely to locate nests that are in dense upland woodland with a well-developed understory layer.

Thompson et al. (2002) suggested that landscape factors can have an overriding influence on nest success and constrain local effects; however, we did not find support for landscape-scale effects such as proportion of woodland or edge density on nest survival. Nest predators within this landscape may be ubiquitous or otherwise not constrained by the large-scale landscape features we examined and therefore nest predation was influenced more by predator activity and search patterns in close proximity to the nest rather than overall abundance within the broader area (Thompson et al. 2002, Thompson 2007). We searched for and monitored nests across a range of local conditions (Table 3), but our study still essentially occurred in a common landscape consisting of a refuge in an urbanizing matrix. Ninety percent of nests were surrounded by $\geq$90% woodland cover within 100 m and >70% woodland cover within 1 km; however, much beyond this the landscape was highly urban. Arguably we did not monitor nests across a wide enough range of landscapes to observe the strong fragmentation or edge effects observed for songbirds elsewhere in the Midwest (Robinson et al. 1995, Thompson et al. 2002). Our intensive monitoring plots were generally representative of the BCP, with the only noticeable differences being that plots had slightly more canopy cover and taller canopy height at the local forest scale, and more urban land cover in the surrounding landscape (Reidy et al. 2016; Table 1). Interestingly, within these monitoring plots, warbler nests tended to be in taller trees, in areas of more mixed and juniper woodland at the 100-m and 1-km scale, and in areas of less open edge and urban land cover compared to plot means (Reidy et al. 2016). Urban land cover around nest monitoring plots averaged 37% versus 8% around nests. Our data suggest warblers on the BCP are likely selecting nest sites in taller trees and in less fragmented patches away from urban land cover compared to what is available.

We also did not find support for effects at our smallest scale, the nest-site. Warblers may be able to safely nest in a variety of nest-site conditions, given they are in a relatively safe nest plot, such as areas with relatively flatter slopes and well-developed understory and canopy structure. We caution against extending our results to other areas of the breeding range where nest predators may be different or less ubiquitous within the landscape. Stake et al. (2004) reported a slightly different nest predator assemblage at Fort Hood, Texas, than that on the BCP (Reidy et al. 2008) and no information exists for the rest of the breeding range.

Temporal trends of nest survival were consistent with previous studies on the BCP and Fort Hood (Peak 2007, Reidy et al. 2009, Peak and Thompson 2014), with nest survival declining throughout the breeding season and varying by year. Our results re-enforce the importance of monitoring populations over time and not inferring nest success or reproductive output based on limited sampling or reproductive indices (Reidy et al. 2015). These temporal patterns may result from changes in predator activity patterns or abundance. One factor that may cause annual variation in predator behavior is weather (Sperry and Weatherhead 2008, Cox et al. 2013, Sherry et al. 2015). Rat snakes increase activity as temperatures warm during the spring and early summer and this increased activity may be correlated with changes in seasonal nest success (Sperry et al. 2008). Snake and bird predation on songbirds, including warblers, in Texas and Missouri increased as daily temperatures increased (Cox et al. 2013). Although little is known about other dominant

nest predators in relation to seasonal activity patterns, it is possible other nest predators fluctuate seasonally and annually in their dietary preferences or food availability.

Our overall daily nest survival estimate (0.97) was slightly higher than a previous sample from the BCP and from Fort Hood but was within the range reported for both study areas (Reidy et al. 2009, Peak and Thompson 2014). The generally high reproductive success means the BCP offers high-quality nesting habitat, at least in some years. Warblers are typically single-brooded and as such, nest survival and seasonal productivity are highly correlated, at least within years (Peak and Thompson 2014). Thus, understanding what affects nest survival is important to understanding relative seasonal productivity, although more rigorous study is needed to confirm this.

MANAGEMENT IMPLICATIONS

Conservation for warblers that focuses on protecting or managing for mixed juniper-oak woodland (as defined by the TESP1 layer) should benefit warbler abundance and nest success. Management of juniper-dominated woodland to increase oak recruitment, and management of oak-dominated woodlands for juniper recruitment, should improve habitat for warblers. Woodlands with abundant canopy juniper ($>30\,m^2$/ha basal area) and a well-developed shrub and understory layer (>25,000 stems/ha) result in structural complexity that benefits nest success. Additionally, woodland habitat on more level uplands (i.e., $<10^{\circ}$) may be better quality habitat for nesting, at least in uplands that support closed-canopy woodlands. Our study area was within a large protected preserve system within an urbanizing landscape and at the plot and forest level had generally high woodland cover and low overall fragmentation. We recommend future research on factors affecting abundance and productivity in the more fragmented woodlands in the northern and western portions of the breeding range and the less urban landscapes of the southwestern portion of the breeding range.

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LITERATURE CITED

Allison, P. D. 1999. Logistic regression using the SAS system: theory and application. SAS Institute, Cary, North Carolina, USA.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Beardmore, C. J. 1994. Habitat use of golden-cheeked warblers in Travis County, Texas. Thesis, Texas A&M University, College Station, USA.

Bock, C. E., and Z. F. Jones. 2004. Avian habitat evaluation: should counting birds count? Frontiers in Ecology and the Environment 2:403–410.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling. Oxford University Press, New York, New York, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Chalfoun, A. D., and T. E. Martin. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. Journal of Applied Ecology 44:983–992.

City of Austin, Travis County, U.S. Forest Service, and University of Missouri. 2014. Golden-cheeked warbler (*Setophaga chrysoparia*) monitoring program. Balcones Canyonlands Preserve Annual Report 2014. <https://www.traviscountytx.gov/images/tnr/Docs/2014/appendix_f.pdf>. Accessed 26 Sep 2016.

Cox, W. A., F. R. Thompson III, and J. L. Reidy. 2013. The effects of temperature on nest predation by mammals, birds, and snakes. Auk 130:784–790.

DeBoer, T. S., and D. D. Diamond. 2006. Predicting presence-absence of the endangered golden-cheeked warbler (*Dendroica chrysoparia*). Southwestern Naturalist 51:181–190.

Duarte, A., J. L. R. Jensen, J. S. Hatfield, and F. W. Weckerly. 2013. Spatiotemporal variation in range-wide golden-cheeked warbler breeding habitat. Ecosphere 5:152.

Elliott, L. F., D. D. Diamond, C. D. True, C. F. Blodgett, D. Pursell, D. German, and A. Treuer-Kuehn. 2014. Ecological mapping systems of Texas: summary report. Texas Parks and Wildlife Department, Austin, Texas, USA. <http://tpwd.texas.gov/gis/programs/landscape-ecology/supporting-documents/final-summary-report/view>. Accessed 1 Feb 2017.

Farrell, S. L., B. A. Collier, K. L. Skow, A. M. Long, A. J. Campomizzi, M. L. Morrison, K. B. Hays, and R. N. Wilkins. 2013. Using LiDAR-derived vegetation metrics for high-resolution, species distribution models for conservation planning. Ecosphere 4:1–18.

Fiske, I., and R. B. Chandler. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in Northern spotted owl populations in northwestern California. Ecological Monographs 70:539–590.

Groce, J. E., H. A. Mathewson, M. L. Morrison, and R. N. Wilkins. 2010. Scientific evaluation for the 5-year status review of the golden-cheeked warbler. Final report submitted to the Texas Parks and Wildlife Department, Austin, Texas, USA, and to the U.S. Fish and Wildlife Service, Region 2, Albuquerque, New Mexico, USA.

Hall, L. S., P. R. Krausman, and M. L. Morrison. 1997. The habitat concept and a plea for standard terminology. Wildlife Society Bulletin 25:173–182.

Hilden, O. 1965. Habitat selection in birds. Annales Zoologici Fennici 2:53–75.

Hosmer, D. W. Jr., and S. Lemeshow. 2000. Applied logistic regression. John Wiley and Sons, New York, New York, USA.

Jensen, J. L. R., S. Irvin, and A. Duarte. 2013. Lidar-based detection of shrubland and forest land cover to improve identification of golden-cheeked warbler habitat. Papers in Applied Geography 36:74–82.

Johnson, M. D. 2007. Measuring habitat quality: a review. Condor 109: 489–504.

Kershaw, J. A., M. J. Ducey, T. W. Beers, and B. Husch. 2016. Forest mensuration. John Wiley and Sons, Chichester, United Kingdom.

Klassen, J. A., M. L. Morrison, H. A. Mathewson, G. G. Rosenthal, and R. N. Wilkins. 2012. Canopy characteristics affect reproductive success of golden-cheeked warblers. Wildlife Society Bulletin 36:54–60.

Kroll, J. C. 1980. Habitat requirements of the golden-cheeked warbler: management implications. Journal of Range Management 33:60–65.

Lee, J.-H., Y. Ko, and E. G. McPherson. 2016. The feasibility of remotely sensed data to estimate urban tree dimensions and biomass. Urban Forestry and Urban Greening 16:208–220.

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.

Marshall, M., M. L. Morrison, and R. N. Wilkins. 2013. Tree species composition and food availability affect productivity of an endangered species: the golden-cheeked warbler. Condor 115:882–892.
Martin, T. E., C. R. Paine, C. J. Conway, W. M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD field protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, USA.
Mullin, S. J., and R. J. Cooper. 1998. The foraging ecology of the gray rat snake (*Elaphe obsolete spiloides*) —visual stimuli facilitate location of arboreal prey. American Midland Naturalist 140:397–401.
Mullin, S. J., and R. J. Cooper. 2000. The foraging ecology of the gray rat snake (*Elaphe obsolete spiloides*). II. Influence of habitat structural complexity when searching for arboreal avian prey. Amphibia-Reptilia 21:211–222.
Peak, R. G. 2007. Forest edges negatively affect golden-cheeked warbler nest survival. Condor 109:628–637.
Peak, R. G., and F. R. Thompson III. 2013. Amount and type of forest cover and edge are important predictors of golden-cheeked warbler density. Condor 115:659–668.
Peak, R. G., and F. R. Thompson III. 2014. Seasonal productivity and nest survival of golden-cheeked warblers vary with forest type and edge density. Condor 116:546–559.
Reidy, J. L., L. O'Donnell, and F. R. Thompson III. 2015. Evaluation of a reproductive index for estimating songbird productivity: case study of the golden-cheeked warbler. Wildlife Society Bulletin 39:721–731.
Reidy, J. L., M. M. Stake, and F. R. Thompson III. 2008. Golden-cheeked warbler nest mortality and predators in urban and rural landscapes. Condor 110:458–466.
Reidy, J. L., and F. R. Thompson III. 2012. Predatory identity can explain nest predation patterns. Pages 135–148 *in* C. A. Ribic, F. R. Thompson, III, and P. J. Pietz, editors. Video surveillance of nesting birds. Studies in Avian Biology (no. 43), University of California Press, Berkeley, USA.
Reidy, J. L., F. R. Thompson III, C. Amundson, and L. O'Donnell. 2016. Landscape and local effects on occupancy and densities of an endangered wood-warbler in an urbanizing landscape. Landscape Ecology 31: 365–382.
Reidy, J. L., F. R. Thompson III, and R. G. Peak. 2009. Factors affecting golden-cheeked warbler nest survival in urban and rural landscapes. Journal of Wildlife Management 73:407–413.
Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987–1990.
Royle, J. A., D. K. Dawson, and S. Bates. 2004. Modeling abundance effects in distance sampling. Ecology 85:1591–1597.
Sesnie, S. E., J. M. Mueller, S. E. Lehnen, S. M. Rowin, J. L. Reidy, and F. R. Thompson III. 2016. Airborne laser altimetry and multispectral imagery for modeling golden-cheeked warbler (*Setophaga chrysoparia*) density. Ecosphere 7:e01220.
Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526–540.
Shaffer, T. L., and F. R. Thompson III. 2007. Making meaningful estimates of nest survival with model-based methods. Studies in Avian Biology 34:84–95.
Sherry, T. W., S. Wilson, S. Hunter, and R. T. Holmes. 2015. Impacts of nest predators and weather on reproductive success and population limitation in a long-distance migratory songbird. Journal of Avian Biology 46:559–569.
Sillett, T. S., R. B. Chandler, J. A. Royle, M. Kéry, and S. A. Morrison. 2012. Hierarchical distance-sampling models to estimate population size and habitat-specific abundance of an island endemic. Ecological Applications 22:1997–2006.
Sperry, J. H., D. A. Cimprich, R. G. Peak, and P. J. Weatherhead. 2009. Is nest predation on two endangered bird species higher in habitats preferred by snakes? Ecoscience 16:111–118.
Sperry, J. H., R. G. Peak, D. A. Cimprich, and P. J. Weatherhead. 2008. Snake activity affects seasonal variation in nest predation risk for birds. Journal of Avian Biology 39:379–383.
Sperry, J. H., and P. J. Weatherhead. 2009. Does prey availability determine seasonal patterns of habitat selection in Texas ratsnakes? Journal of Herpetology 43:55–64.
Stake, M. M., J. Faaborg, and F. R. Thompson III. 2004. Video identification of predators at golden-cheeked warbler nests. Journal of Field Ornithology 75:337–344.
Stewart, L. R., M. L. Morrison, M. R. Hutchinson, D. N. Appel, and R. N. Wilkins. 2014. Effects of a forest pathogen on habitat selection and quality for the endangered golden-cheeked warbler. Wildlife Society Bulletin 38:279–287.
Thompson, F. R. III. 2007. Factors affecting nest predation on forest songbirds in North America. Ibis 149:98–109.
Thompson, F. R. III, T. M. Donovan, R. M. DeGraaf, 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 [USFWS]. 1992. Golden-cheeked warbler (*Dendroica chrysoparia*) recovery plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.
Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.
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, USA.
Ward, N. 2009. Austin climate data. University of Texas, Austin, Texas, USA.
Winter, M., D. H. Johnson, and J. A. Shaffer. 2005. Variability in vegetation effects on density and nesting success of grassland birds. Journal of Wildlife Management 69:185–197.
Winter, M., D. H. Johnson, J. A. Shaffer, T. M. Donovan, and W. D. Svedarsky. 2006. Patch size and landscape effects on density and nesting success of grassland birds. Journal of Wildlife Management 70: 158–172.

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Appendix I

Number of parameters (K), the difference between the Akaike's Information Criterion for small sample sizes for the top model and the current model (ΔAIC_c), and model support based on Akaike weights (w_i) for models evaluating effects of plot, forest, and landscape variables on density of golden-cheeked warbler males (M/ha) on Balcones Canyonlands Preserve, Texas, USA, spring 2011–2014. Only models with >0.00 w_i are shown.

Model name	K	ΔAIC_c	w_i
Plot models[a]			
Basal area + tree height	18	0.00	0.33
Basal area + slope + tree height	19	1.68	0.14
Basal area + tree height + bare ground cover	19	2.00	0.12
Basal area + woody stems + tree height	19	2.00	0.12
Basal area + slope + tree height + bare ground cover	20	3.67	0.05
Basal area + slope + woody stems + tree height	20	3.67	0.05
Basal area + woody stems + tree height + bare ground cover	20	4.00	0.05
Basal area	17	4.38	0.04
Basal area + slope + woody stems + tree height + bare ground	21	5.67	0.02
Basal area + slope	18	5.99	0.02
Basal area + bare ground	18	6.33	0.01
Basal area + woody stems	18	6.38	0.01
Basal area + slope + bare ground	19	7.89	0.01
Basal area + slope + woody stems	19	7.99	0.01
Basal area + woody stems + bare ground	19	8.33	0.01
Forest models			
Woodland cover + canopy height	13	0.00	0.30
Woodland cover + canopy height + open edge density	14	1.20	0.17
Woodland cover + canopy height + canopy height variation	14	1.45	0.15
Woodland cover + canopy height + urban edge density	14	1.50	0.14
Woodland cover + canopy height + canopy height variation + open edge density	15	2.86	0.07
Woodland cover + canopy height + canopy height variation + urban edge density	15	2.96	0.07
Woodland cover + canopy height + open edge density + urban edge density	15	3.07	0.07
Woodland cover + canopy height + canopy height variation + open edge density + urban edge density	16	4.70	0.03
Landscape models			
Juniper cover + mixed woodland cover	13	0.00	0.49
Juniper cover + mixed woodland cover + urban cover	14	1.90	0.19
Mixed woodland cover	12	2.02	0.18
Mixed woodland cover + urban cover	13	2.55	0.14

[a]The AIC_c for the most supported model was 4,035.36 for plot, 3,912.86 for forest, and 4,005.83 for landscape.

Appendix II

Predicted density of golden-cheeked warblers (M/ha) as a function of plot variables from the plot + forest + landscape model on Balcones Canyonlands Preserve, Texas, USA, April–May 2011–2014. Error bars represent 95% confidence intervals.