



Original Article

Habitat Effects on Golden-cheeked Warbler Productivity in an Urban Landscape

DIANNE H. ROBINSON,^{1,2} *Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA*

HEATHER A. MATHEWSON,³ *Texas A&M Institute of Renewable Natural Resources, Texas A&M University, College Station, TX 77843, USA*

MICHAEL L. MORRISON, *Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA*

R. NEAL WILKINS,⁴ *Texas A&M Institute of Renewable Natural Resources, Texas A&M University, College Station, TX 77843, USA*

ABSTRACT Habitat fragmentation and isolation can result in decreased occupancy and reproductive success within songbirds, particularly for species inhabiting urban environments where available habitat may be limited. The golden-cheeked warbler (*Setophaga chrysoparia*) is a federally endangered songbird that inhabits oak–juniper (*Quercus* spp.–*Juniperus* spp.) woodlands across central Texas, USA. Past research has indicated decreased patch occupancy and productivity near urban areas. We monitored patch occupancy, territory establishment, pairing success, and fledging success of warblers in an urban environment. Warblers occupied 24% ($n = 63$) of patches surveyed; 10% ($n = 63$) of habitat patches had ≥ 1 established territory. Warblers successfully paired in 4 patches and fledged young in 3 patches. We found an increasing probability of occupancy at approximately 65–70% canopy cover, and an added effect of distance to the nearest habitat patch. We found that distance to and size of the nearest habitat patch best predicted territory establishment. Patch size and size of the nearest habitat patch best predicted pairing success. Although our results were inconclusive for fledging success, a review of available data suggests patch size, size of, and distance to the nearest habitat patch all affect warbler reproductive activity. We recommend to manage for oak–juniper woodland patches with $>70\%$ canopy cover that are >26 ha in size, in close proximity to other oak–juniper woodland patches with equal or greater canopy cover and patch size when managing for golden-cheeked warblers within an urban matrix. © 2018 The Wildlife Society.

KEY WORDS golden-cheeked warbler, habitat characteristics, occupancy, productivity, *Setophaga chrysoparia*, urban matrix.

Ecologists have been exploring wildlife–habitat relationships for decades (Grinnell 1917, Leopold 1970, Wiens et al. 1986, Morrison et al. 2008). In particular, researchers have noted negative effects on wildlife from habitat loss through fragmentation and isolation, represented by decreasing habitat patch size and increasing habitat isolation (van Dorp and Opdam 1987, Temple and Cary 1988, Radford and Bennett 2004), all of which can be compounded within an urban environment (Andr n 1994). Geographic expansion of urbanization and an increase in density are expected over the next 50 years, a result of increasing land prices (Alig et al. 2004, Grimm et al. 2008, USEPA 2009).

With the expected increase in urbanization, understanding habitat requirements and effects of habitat fragmentation can result in added information available for improved management decisions to conserve songbirds that utilize urban environments. Smaller habitat-patch fragments result in lower reproductive success for some species (Robinson et al. 1995, Burke and Nol 2000). Occupancy and abundance decrease closer to the edge of the habitat patch (Rich et al. 1994). These results often compound within urban areas, with species richness, occupancy, and reproductive success decreasing with distance to urban areas (Friesen et al. 1995, Kluza et al. 2000, Donnelly and Marzluff 2004). Birds also adjust territory sizes based on resource availability, which may be limited in an urban system (Smith and Shugart 1987). The ability to improve upon management decisions is particularly important for endangered or threatened species.

The golden-cheeked warbler (*Setophaga chrysoparia*; hereafter, warbler), a songbird that is federally endangered as a result of threats of habitat destruction and fragmentation (USFWS 1990, Beardmore et al. 1996, Groce et al. 2010, Duarte et al. 2013), breeds in mature stands of ashe juniper (*Juniperus ashei*) and oak (*Quercus* spp.) across the Edwards

Received: 31 May 2015; Accepted: 3 October 2017

¹E-mail: Diannehd@gmail.com

²Present address: Wisconsin Department of Natural Resources, Waukesha, WI 53188, USA

³Present address: Department of Wildlife, Sustainability, and Ecosystem Sciences, Tarleton State University, Stephenville, TX 76402, USA

⁴Present address: East Foundation, 200 Concord Plaza Drive, Suite 410, San Antonio, TX 78216, USA

Plateau of central Texas, USA (USFWS 1990). The decision to list this warbler was partially due to the assumption that the majority of the breeding population occurred in counties on the eastern Edwards Plateau, where large amounts of urban development exists (Gaines 2008, Bierwagen et al. 2010, Groce et al. 2010). Numerous researchers have conducted studies on the warbler across both urban and rural landscapes (Benson 1990, Jette et al. 1998, Reidy et al. 2007, Cooksey and Edwards 2008, Collier et al. 2012). Previous research on this warbler has indicated lower occupancy in habitat patches near urban areas and a decrease in warbler reproductive success with increased habitat fragmentation (Coldren 1998, Maas 1998, Sperry 2007). Warbler use and reproductive success within different habitat patches can vary based on canopy cover (Dearborn and Sanchez 2001, Klassen et al. 2012) and patch size (Arnold et al. 1996, Butcher et al. 2010). Differences in the surrounding landscape affects productivity of golden-cheeked warblers and other songbirds, especially in relation to habitat fragmentation (van Dorp and Opdam 1987, Bayne and Hobson 2001, Magness et al. 2006, Peak 2007, Sperry 2007).

Thompson et al. (2002) suggested that effects of forest fragmentation provide a “top down” approach, with landscape- and local-level effects providing different impacts on songbird productivity at different spatial scales. Our objective was to determine these different levels of effect on warbler reproduction in relation to site- and landscape-scale habitat characteristics within an urban area. Site- and landscape-scale habitat characteristics can influence patch occupancy as songbirds are first arriving and selecting habitat patches for use. After a male songbird has selected a patch, presence of other males (Farrell et al. 2012), females, food, and space can influence territory establishment, all affected primarily by site-scale habitat characteristics but also by landscape-scale habitat characteristics. Site-scale habitat characteristics are likely the primary influencers on pairing and fledging success in songbirds. We tested hypotheses relating to the effects of various site-scale (patch size, canopy cover, woodland composition) and landscape-scale (distance to and size of the nearest patch) habitat characteristics on patch occupancy, territory establishment, pairing success, and fledging success of warblers within an urban area.

STUDY AREA

We conducted this study within a 40-km² circle in northwest Austin, Texas, that was inclusive of urban areas within Travis and Hays counties and the golden-cheeked warbler breeding range (Robinson 2013). Most habitat patches within this urban framework had multiple landowners, so we contacted >1,000 private and public landowners within the urban landscape, approximately 400 of which allowed us to conduct research on their property. This resulted in monitoring 63 habitat patches during the breeding season (Mar–Jun) in 2011 and 2012. Our study area annual mean temperature and precipitation was 17.4° C and 45.47 cm for 2011 and 20.7° C and 58.29 cm for 2012 (NOAA 2010). Our study area mean temperature and precipitation during the breeding season was 13.6° C and 12.85 cm for 2011 and 22.9° C and 25.5 cm

for 2012 (NOAA 2010). Based on the 2001 National Land-Cover Database (NLCD), approximately 65% of our study area consisted of developed commercial and residential areas, with some cropland and other vegetation types interspersed (Homer et al. 2007). We selected our study sites from the remaining 35% of the landscape, consisting of potential habitat patches using delineations of mature oak–juniper woodlands from Collier et al. (2012).

METHODS

Study Site Selection

We used 6 criteria to select potential study sites (habitat patches): habitat patch delineations, proximity to urban areas, edge:area ratio, habitat patch canopy cover, habitat patch size, and woodland composition of the habitat patch. We used patch delineations of mature oak–juniper woodlands from Collier et al. (2012) and ground-truthed patch boundaries during the field season. Based on past studies in urban areas (Coldren 1998, Sperry 2007), we used the 2001 NLCD and the Buffer tool in ArcGIS 9.3.1 (Environmental Systems Research Institute, Redlands, CA, USA) to select patches where $\geq 25\%$ of the patch edge was within 50 m of urban areas, to ensure all potential habitat patches had a possible effect from urban areas. Other studies have found negative effects for golden-cheeked warblers associated with increased habitat patch edge (Maas 1998, DeBoer and Diamond 2006, Peak 2007, Sperry 2007); therefore, we chose patches with an edge:area ratio < 0.035 . We used 2010 National Agricultural Imagery Program color infrared digital imagery at 1-m resolution and the Zonal Statistics tool in ArcGIS 9.3.1 to determine the mean percent canopy cover for each delineated habitat patch. We then selected habitat patches with $\geq 35\%$ canopy cover, which represents the range of canopy cover used by golden-cheeked warblers within our region (Dearborn and Sanchez 2001, Campbell 2003). We selected patches 2–75 ha in size to encompass previously observed occupancy and reproductive success thresholds for golden-cheeked warblers (Arnold et al. 1996, Butcher et al. 2010). We used the landscape composition metric (defined as the mean percentage of woodlands within a 400-m-radius circle around a given pixel) from Collier et al. (2012) to determine oak–juniper woodland composition within and surrounding habitat patches and only surveyed patches with $> 40\%$ oak–juniper woodland composition (Magness et al. 2006). We ground-truthed habitat patches during the field season, modifying or removing any patch or patch boundary found to be inaccurate or outside our criteria through ground-truthing. All remaining habitat patches that fell within our criteria and not removed after ground-truthing were used in our study, for 63 total habitat patches—30 unique habitat patches in 2011 and 33 unique habitat patches in 2012. We did not visit any habitat patches in both years.

Habitat Characteristics

We measured site- and landscape-scale habitat characteristics that were most likely to influence occupancy and productivity of golden-cheeked warblers: patch size, woodland composition,

Table 1. Models developed to test habitat-based covariates against productivity response variables for golden-cheeked warblers within urban areas of Travis and Hays counties, Texas, USA, 2011–2012.

Model type	Covariates ^a			Response variables		
	1	2	3	Occupancy	Territory establishment	Pairing success
Additive	CanCov	DistNear		X		
Additive	CanCov	SizeNear		X		
Additive	CanCov	SizeNear	DistNear	X		
Additive	Size	SizeNear	DistNear	X	X	
Additive	Size	SizeNear		X	X	X
Additive	Size	DistNear		X	X	X
Additive	Size	WoodComp		X	X	X
Additive	SizeNear	DistNear		X	X	X
Multiplicative	Size	CanCov		X	X	X

^a CanCov signifies canopy cover of the patch of interest; DistNear signifies distance to the next nearest habitat patch; Size signifies size of the habitat patch of interest; SizeNear signifies size of the next nearest habitat patch; WoodComp signifies woodland composition of the habitat patch of interest.

patch canopy cover, and size of and distance to the nearest habitat patch. We determined patch size, woodland composition, and canopy cover of each habitat patch as described above. We determined size of and distance to the nearest habitat patch in ArcGIS 9.3.1 using patch delineations from Collier et al. (2012) after all patches <2.01 ha were removed. Collier et al. (2012) considered a gap of 10 m a sufficient split between habitat patches. Although warblers could easily travel between patches ≥ 10 m apart, we found this was rare within our study and these gaps often served as territory boundaries. Other studies of the golden-cheeked warbler have used these same criteria for delineating patch boundaries (e.g., Butcher et al. 2010, Farrell et al. 2012).

Patch Occupancy

We determined occupancy for 63 potential habitat patches—30 during the 2011 breeding season and 33 during the 2012 breeding season. These habitat patches consisted of >400 private and public properties. We defined patch occupancy as ≥ 1 warbler detected in the habitat patch at any point during occupancy surveys. This occupancy definition incorporated any golden-cheeked warblers detected within a habitat patch, regardless of length of stay. Observers visited each patch 6 times starting mid-March (MacKenzie and Royle 2005, Collier et al. 2012) with 7 days between each visit over a 6-week time period, concluded in late April and well into the warbler breeding season (Campbell 2003). This survey length allowed for a greater potential of warbler detections across the breeding season (Collier et al. 2012). If we did not detect a warbler after 6 visits, we assumed warbler movement between patches had stopped and considered the surveyed patch unoccupied; we did not visit unoccupied patches again that season for additional monitoring surveys. To determine initial locations of warblers for subsequent monitoring, observers surveyed along parallel transects systematically established approximately 150 m apart. Number of transects per study site and length of transect varied by patch size and structure. Observers walked along each transect, stopping for 2–3 min at points located every 100 m to listen for warblers, and recorded the GPS coordinates of any warblers seen or heard at any point during these initial surveys (Morrison et al. 2008).

Patch Reproductive Activity

We monitored warbler territories weekly during the breeding season to determine territory establishment and productivity for all occupied patches of the original 63. We defined territory establishment as a habitat patch containing ≥ 1 active territory, which we determined if we observed a male actively defending a territory for >4 weeks. We defined pairing success as a habitat patch containing ≥ 1 warbler pair, which we determined if we observed a male detected with a female during ≥ 2 separate visits. Golden-cheeked warbler fledglings generally do not move out of their natal area within the first 7 days of fledging (D. H. Robinson, personal communication); therefore, we defined fledging success as ≥ 1 observation of a male or female within the patch caring for ≥ 1 fledgling that was ≤ 7 days old. Our primary interest was to determine productivity on a patch basis, not on a territory basis; therefore, locating ≥ 1 fledgling within the habitat patch within the first 7 days of fledging was sufficient for the purpose of our study. It was not necessary to assign a fledgling to a specific territory, as long as that fledgling was ≤ 7 days old prior to movement out of the patch. We determined pairing and fledging success for all established territories using a method based on Vickery et al. (1992). This is a reliable system used successfully in studies on territorial songbirds (Christoferson and Morrison 2001), and applied previously to golden-cheeked warbler studies (Butcher et al. 2010, Lackey et al. 2011, Klassen et al. 2012). The Vickery method assigns a rank to male or female behavior according to the observed reproductive activity for each monitoring visit to a territory. This ranking system helped us to determine reproductive success for the territory while not disrupting nests of an endangered species.

Table 2. Multivariate covariance correlation for habitat patch characteristics (patch size, woodland composition, canopy cover, distance to and size of nearest habitat patch) for golden-cheeked warblers within urban areas of Travis and Hays counties, Texas, USA, 2011–2012.

	Size	WoodComp	CanCov	DistNear	SizeNear
Size	1.00	0.22	0.27	0.01	0.16
WoodComp	0.22	1.00	0.22	-0.36	0.31
CanCov	0.27	0.22	1.00	-0.11	0.18
DistNear	0.01	-0.36	-0.11	1.00	-0.13
SizeNear	0.16	0.31	0.18	-0.13	1.00

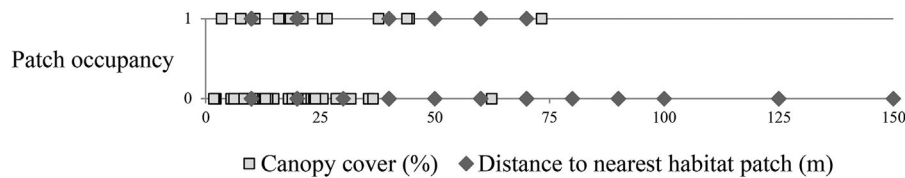


Figure 1. Habitat patch occupancy relative to canopy cover and distance to the nearest habitat patch for golden-cheeked warblers within Hays and Travis counties, Texas, USA, 2011–2012. Patch occupancy of zero signifies no warbler detected in the habitat patch at any point during occupancy surveys. Patch occupancy of one signifies ≥ 1 warbler detected in the habitat patch at any point during occupancy surveys.

Analysis

We used a multivariate covariance correlation (Ott and Longnecker 2001) in Program R 2.15.1 (R 2.15.1, www.r-project.org, accessed 13 Sep 2012) to test for correlation between covariates and used a chi-square goodness of fit test (Ott and Longnecker 2001) to test for interannual variation within our covariates of each habitat patch. We used Presence 11.0 to determine detectability within our habitat patches (MacKenzie et al. 2006). We used logistic regression models to determine which habitat variables best predicted the binary response variables of patch occupancy, territory establishment, pairing success, and fledgling success (Ott and Longnecker 2001). We tested the effect of each covariate individually on warbler reproductive potential, and developed models that tested specific *a priori* hypotheses representing combinations of covariates that we thought would influence warbler reproductive potential (Table 1). We predicted that increasing canopy cover, patch size, size of the nearest habitat patch, and woodland composition would result in increasing probability of reproductive success, regardless of the response variable measured. We predicted decreasing distance to the nearest patch would result in an increase in the probability of reproductive success, regardless of the response variable measured.

Occupancy is the selection of a habitat patch by the male, and thus a combination of site- and landscape-scale habitat characteristics likely affects warbler occupancy. We evaluated models that considered several additive combinations of variables for warbler occupancy. For territory establishment and pairing success, we did not consider additive models that included canopy cover because other research has shown little effect of canopy cover on territory productivity (Klassen et al. 2012, Marshall et al. 2013). We evaluated the interactive effect of patch size and canopy cover on all response variables because the influence of one covariate on warbler responses might vary depending upon the level of the other covariate.

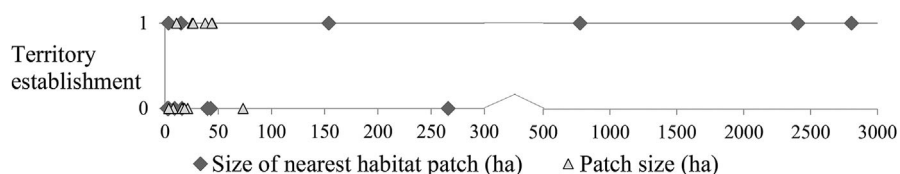


Figure 2. Territory establishment relative to patch size and size of the nearest habitat patch for golden-cheeked warblers within Hays and Travis counties, Texas, USA, 2011–2012. Territory establishment of zero signifies no male actively defending a territory for >4 weeks. Territory establishment of one signifies a male actively defending a territory for >4 weeks.

We fit models using Akaike's Information Criterion (AIC). We ranked relative model support using ΔAIC_c , and considered models with $\Delta AIC_c \leq 2.0$ equally likely models (Burnham and Anderson 2002). We calculated the 95% confidence intervals around the regression coefficient to determine the direction of the effect of a variable. To examine effects of the habitat variables on warbler reproduction, we graphed the predictive values from the best fit model.

RESULTS

We surveyed 63 unique habitat patches—30 patches in 2011 and 33 in 2012—ranging in size from 1.8 to 73 ha. Canopy cover across all surveyed patches ranged from 46% to 83%, and woodland composition ranged from 39% to 70%. Surveyed patches ranged from 10 to 225 m from the nearest neighboring patch, with the neighboring patch ranging in size from 2 to 2,800 ha. There was no correlation found among habitat patch covariates (Table 2). There was no difference between years in the distribution of sampled patches for patch size, woodland composition, canopy cover, distance to nearest patch, or size of nearest patch ($\chi^2_5 = 9.24$, $P = 0.10$); thus, we did not include year effect in our model analyses. Our mean detection probability was 0.26 for all habitat patches (95% CI = 0.16–0.38). Warblers occupied 25% of the patches surveyed, with occupancy occurring only when patches had $>62\%$ canopy cover and were within 80 m of another habitat patch ($n = 63$; Fig. 1). We found 10% of all habitat patches had ≥ 1 established territory ($n = 63$). Within occupied patches, warblers consistently established territories in habitat patches ≥ 22 ha in size and with the nearest habitat patch ≥ 300 ha in size (Fig. 2). Four of the 63 patches had warblers that successfully paired, with 3 of the 63 patches supporting warbler pairs that successfully fledged (Table 3).

Patch Occupancy

Two occupancy models had $\Delta AIC_c \leq 2.0$ (Table 4). The top-ranked model included an additive effect of canopy cover

Table 3. Landscape information for each habitat patch where pairing occurred and with nests that successfully fledged golden-cheeked warblers within urban areas of Travis and Hays counties, Texas, USA. All patches where pairing occurred and that had fledglings were from 2011.

Pairing success	Fledging success	Patch size (ha)	Percent canopy cover (%)	Size of nearest patch (ha)	Distance to nearest patch (m)	Woodland composition (%)
Yes	Yes	26	80	2,806	20	64
Yes	Yes	38	80	777	20	62
Yes	No	44	81	2,405	10	50
Yes	Yes	44	66	154	10	40

($\beta = 0.12$, $SE = 0.04$, 95% $CI = 0.04-0.21$) and distance to the nearest habitat patch ($\beta = -0.02$, $SE = 0.01$, 95% $CI = -0.0002$ to -0.05) on occupancy. The main effects model for canopy cover had a positive effect on probability of occupancy ($\beta = 0.12$, $SE = 0.04$, 95% $CI = 0.05-0.21$). We used the additive model, holding distance to the nearest habitat patch constant, and found the probability of occupancy increased at approximately 65–70% canopy cover (Fig. 3). In the additive model, the effect of distance to the nearest habitat patch was negative and a review of these data showed all occupied patches were within 70 m of the nearest habitat patch (Fig. 1).

Patch Reproductive Activity

Two additive models had $\Delta AIC_c \leq 2.0$ for territory establishment; both models contained effects of distance to and size of the nearest habitat patch on territory establishment within a patch (Table 5). In the top model, distance to the nearest habitat patch ($\beta = -0.13$, $SE = 0.08$, 95% $CI = -0.34$ to -0.02) negatively influenced territory establishment, while size of the nearest habitat patch ($\beta = 0.001$, $SE < 0.001$, 95% $CI = 0.00009-0.002$) had a positive effect. We did not consider the additional variable in

the second model, patch size, to be influential because the confidence interval around the coefficient included zero (patch size: $\beta = 0.03$, $SE = 0.03$, 95% $CI = -0.03-0.09$).

We found the additive model for patch size ($\beta = 0.08$, $SE = 0.04$, 95% $CI = 0.007-0.17$) and size of the nearest habitat patch ($\beta = 0.002$, $SE < 0.001$, 95% $CI = 0.0005-0.002$) best predicted pairing success (Table 6). There was a positive linear relationship between patch size and probability of pairing success (Fig. 4).

We were unable to use maximum likelihood estimation on fledging success because only 3 habitat patches had warblers that successfully fledged. These 3 patches were all >26 ha in size and within 20 m of a habitat patch that was >150 ha in size. There were no obvious patterns among these 3 habitat patches in woodland composition or canopy cover (Table 3).

DISCUSSION

As we hypothesized, a combination of site- and landscape-scale habitat characteristics influences breeding in golden-cheeked warblers. Historically, researchers considered golden-cheeked warblers to be a closed-canopy species because of their feeding and nesting requirements (Pulich 1976, Campbell

Table 4. Model selection results for probability of habitat patch occupancy of golden-cheeked warblers within urban areas of Travis and Hays counties, Texas, USA, 2011–2012.

Models ^a	K^b	AIC_c^c	ΔAIC_c^d	ModelLik ^e	$AIC_c \text{ wt}^f$	LL ^g	Cum.Wt ^h
CanCov + DistNear	3	62.330	0.000	1.000	0.470	-27.962	0.470
CanCov	2	64.064	1.734	0.420	0.197	-29.932	0.667
CanCov + DistNear + SizeNear	4	64.556	2.226	0.329	0.154	-27.933	0.822
CanCov + SizeNear	3	65.916	3.586	0.166	0.078	-29.754	0.900
Size \times CanCov	4	67.243	4.913	0.086	0.040	-29.277	0.940
WoodComp	2	68.821	6.491	0.039	0.018	-32.310	0.958
Size + WoodComp	3	69.564	7.234	0.027	0.013	-31.578	0.971
Size + DistNear	3	70.266	7.936	0.019	0.009	-31.930	0.980
DistNear	2	70.761	8.431	0.015	0.007	-33.280	0.987
SizeNear + DistNear	3	72.010	9.680	0.008	0.004	-32.802	0.990
Size + DistNear + SizeNear	4	72.075	9.745	0.008	0.004	-31.693	0.994
Size	2	72.449	10.119	0.006	0.003	-34.124	0.997
Size + SizeNear	3	73.658	11.329	0.003	0.002	-33.626	0.999
SizeNear	2	74.009	11.679	0.003	0.001	-34.905	1.000

^a CanCov signifies canopy cover of the patch of interest; DistNear signifies distance to the next nearest habitat patch; Size signifies size of the habitat patch of interest; SizeNear signifies size of the next nearest habitat patch; WoodComp signifies woodland composition of the habitat patch of interest.

^b K signifies the number of estimated parameters for each model.

^c AIC_c signifies the corrected Akaike's Information Criterion.

^d ΔAIC_c signifies the appropriate change in AIC_c .

^e ModelLik signifies the relative likelihood of the model given the data.

^f $AIC_c \text{ Wt}$ signifies the model probabilities.

^g LL signifies log-likelihood of each model.

^h Cum.Wt signifies the cumulative Akaike weights.

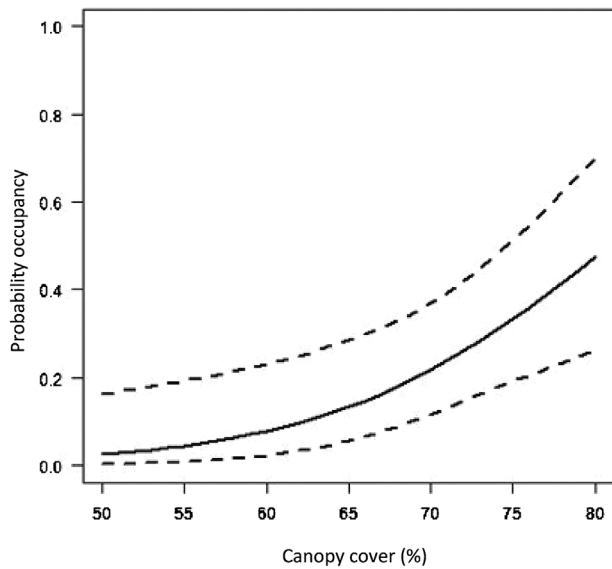


Figure 3. Probability of habitat patch occupancy for golden-cheeked warblers by percent canopy cover, holding distance to nearest patch (m) constant at the mean value (43 m), in urban areas within Hays and Travis counties, Texas, USA, 2011–2012.

2003). As such, male golden-cheeked warblers selecting to occupy habitat patches with greater canopy cover may be the result of less food available within an urban site, or fewer nesting sites available within a predominantly urban landscape. Our results demonstrate that golden-cheeked warblers may require canopy cover 2–3 times greater within an urban matrix than in rural areas (Dearborn and Sanchez 2001, Campbell 2003, Klassen et al. 2012). However, recent research has shown canopy cover requirements vary across the range because of habitat availability; thus, our results may represent a regional variation not currently well-understood (Klassen et al. 2012). Future research should study the potential for regional

variation within golden-cheeked warbler habitat characteristics to determine the specific canopy cover needs for warblers across the range (Campomizzi et al. 2012).

Across reproductive measures, we found that, consistent with our hypotheses, a combination of site- and landscape-scale habitat characteristics affected potential for reproductive success in golden-cheeked warblers within an urban matrix. Habitat characteristics for neighboring patches (distance to and size of the nearest habitat patch) affected patch occupancy and had a significant effect on territory establishment. Similar to Farrell et al. (2012), we found no effects on reproductive activity from canopy cover. Farrell et al. (2012) found pairing and fledging success increased with increasing territory density, but reported no correlation with canopy cover and that habitat selection by golden-cheeked warblers was a factor of conspecific cues, not just habitat characteristics. We did find that a combination of site- and landscape-scale habitat characteristics (patch size, size of the nearest habitat patch) influenced potential for pairing success, suggesting that golden-cheeked warblers successfully paired in large habitat patches near other large habitat patches.

We saw a wide confidence interval as probability of pairing success increased; this is likely a combined effect of relatively few habitat patches with pairing success (4 of 63 habitat patches), and no pairing success occurring in habitat patches >45 ha. These results suggest that golden-cheeked warblers may not persist over the long term within an urban matrix. However, we only surveyed 2 habitat patches between 45 and 75 ha. Additional surveys in habitat patches within that patch size realm could better explain golden-cheeked warbler pairing success as it relates to patch size within an urban matrix, and help managers understand if golden-cheeked warblers have a high chance of success in habitat patches that they manage within the urban matrix.

Table 5. Model selection results for probability of territory establishment of golden-cheeked warblers within urban areas of Travis and Hays counties, Texas, USA, 2011–2012.

Models ^a	K^b	AIC_c^c	ΔAIC_c^d	ModelLik ^e	$AIC_c Wt^f$	LL ^g	Cum.Wt ^h
SizeNear + DistNear	3	31.780	0.000	1.000	0.389	-12.686	0.389
Size + SizeNear + DistNear	4	32.773	0.993	0.609	0.237	-12.042	0.625
Size + DistNear	3	33.984	2.204	0.332	0.129	-13.789	0.754
DistNear	2	34.211	2.431	0.297	0.115	-15.005	0.870
Size + SizeNear	3	36.457	4.677	0.096	0.038	-15.025	0.907
CanCov	2	36.637	4.858	0.088	0.034	-16.219	0.941
SizeNear	2	37.104	5.325	0.070	0.027	-16.452	0.969
Size × CanCov	4	37.941	6.161	0.046	0.018	-14.625	0.986
Size	2	39.696	7.916	0.019	0.007	-17.748	0.994
Size + WoodComp	3	41.179	9.399	0.009	0.004	-17.386	0.997
WoodComp	2	41.827	10.048	0.007	0.003	-18.814	1.000

^a CanCov signifies canopy cover of the patch of interest; DistNear signifies distance to the next nearest habitat patch; Size signifies size of the habitat patch of interest; SizeNear signifies size of the next nearest habitat patch; WoodComp signifies woodland composition of the habitat patch of interest.

^b K signifies the number of estimated parameters for each model.

^c AIC_c signifies the corrected Akaike's Information Criterion.

^d ΔAIC_c signifies the appropriate change in AIC_c .

^e ModelLik signifies the relative likelihood of the model given the data.

^f $AIC_c Wt$ signifies the model probabilities.

^g LL signifies log-likelihood of each model.

^h Cum.Wt signifies the cumulative Akaike weights.

Table 6. Model selection results for probability of pairing success of golden-cheeked warblers within urban areas of Travis and Hays counties, Texas, USA, 2011–2012.

Models ^a	K^b	AIC_c^c	ΔAIC_c^d	ModelLik ^e	AIC_cWt^f	LL ^g	Cum.Wt ^h
Size +							
SizeNear	3	21.960	0.000	1.000	0.529	-7.777	0.529
SizeNear +							
DistNear	3	23.998	2.038	0.361	0.191	-8.795	0.721
SizeNear	2	24.295	2.336	0.311	0.165	-10.048	0.885
Size +							
DistNear	3	27.397	5.437	0.066	0.035	-10.495	0.920
Size	2	28.238	6.278	0.043	0.023	-12.019	0.943
Size × CanCov	4	28.421	6.461	0.040	0.021	-9.866	0.964
DistNear	2	29.130	7.170	0.028	0.015	-12.465	0.979
CanCov	2	29.682	7.722	0.021	0.011	-12.741	0.990
Size +							
WoodComp	3	30.386	8.426	0.015	0.008	-11.990	0.998
WoodComp	2	32.847	10.887	0.004	0.002	-14.323	1.000

^aCanCov signifies canopy cover of the patch of interest; DistNear signifies distance to the next nearest habitat patch; Size signifies size of the habitat patch of interest; SizeNear signifies size of the next nearest habitat patch; WoodComp signifies woodland composition of the habitat patch of interest.

^b K signifies the number of estimated parameters for each model.

^c AIC_c signifies the corrected Akaike's Information Criterion.

^d ΔAIC_c signifies the appropriate change in AIC_c .

^eModelLik signifies the relative likelihood of the model given the data.

^f AIC_cWt signifies the model probabilities.

^gLL signifies log-likelihood of each model.

^hCum.Wt signifies the cumulative Akaike weights.

Smaller habitat patch sizes and increased habitat isolation negatively influence reproductive activity in other songbird species. Songbirds often select habitat patches in close proximity to other habitat to increase the potential for more food resources available, nesting habitat opportunities, and pairing potential (van Dorp and Opdam 1987, Andrén 1994, Bayne and Hobson 2001, Radford and Bennett 2004). This was consistent with our study results, where all occupied habitat patches were within 80 m of another habitat patch, and this distance decreased in habitat patches with paired warblers. Habitat-patch isolation

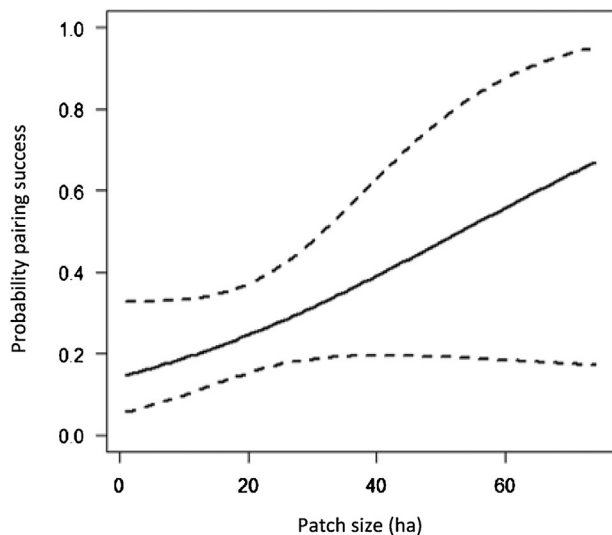


Figure 4. Probability of pairing success for golden-cheeked warblers by habitat patch size (ha), holding size of the nearest habitat patch (ha) constant at the mean value (233 ha), in urban areas within Hays and Travis counties, Texas, USA, 2011–2012.

has strong implications for the reproductive status of the golden-cheeked warbler within a highly fragmented urban matrix, where patch isolation may be more common with increased developed acreage within city limits. Within a rural matrix, scientists have seen positive effects from habitat-patch size on territory establishment, pairing success, and fledging success, but in habitat patches nearly half the size of those we saw in our urban study (Butcher et al. 2010). Size of the habitat patch may have a stronger effect on the successful production of fledglings within an urban matrix than a rural matrix. This could be a result of increased predator movement and activity along edges, decreased food availability with decreased overall habitat, and masking of communication signals used in breeding and survival from louder background noises associated with highways and human activity (Kluza et al. 2000, Patricelli and Blickley 2006, Peak 2007, Halfwerk et al. 2011).

Farrell et al. (2012) found that golden-cheeked warblers selected habitat patches of lower quality based on conspecific cues. Although we did not specifically test this hypothesis, all patches where pairing occurred had >1 male territory within the patch and were within 20 m of another habitat patch >150 ha in size. Anecdotally, we generally heard golden-cheeked warblers singing within these adjacent habitat patches (D. H. Robinson, personal communication). This information suggests that although site- and landscape-scale habitat characteristics are certainly strong contributors to golden-cheeked warbler occupancy and productivity within an urban matrix, conspecific cues and proximity to other golden-cheeked warblers also may play a strong role in their decision-making process when selecting a habitat patch to occupy and breed.

MANAGEMENT IMPLICATIONS

We suggest considering site- and landscape-scale habitat characteristics when managing for golden-cheeked warbler occupancy and productivity, in particular within an urban matrix. Not all oak-juniper woodlands will support nesting golden-cheeked warblers, and within an urban matrix landscape-scale habitat alterations may be necessary to improve the potential for warblers, which are likely to be financially and time-draining endeavors. When managing for golden-cheeked warblers within an urban matrix, we recommend to manage for oak-juniper woodland patches with >70% canopy cover that are >26 ha in size, in close proximity to other oak-juniper woodland patches of equal or greater configuration. It also may be necessary to consider proximity to other golden-cheeked warblers and effects from conspecific cues when managing for warblers within an urban matrix, although additional research could contribute to better understanding of the relationships among conspecifics and habitat characteristics.

ACKNOWLEDGMENTS

We thank the Texas Department of Transportation for the funding that facilitated this research. The Department of Wildlife & Fisheries Sciences and Institute of Renewable Natural Resources at Texas A&M University provided technical, logistic, and administrative support; we would especially like to thank B. Collier, V. McCallister, T. McFarland, and T. Snellgrove for their support. Thanks goes to the >400 private and public landowners who allowed us access to their property and made this research possible, and the many field technicians for their hard work in data collection. We thank M. Donaghy-Cannon and anonymous reviewers for constructive comments provided on earlier drafts of this manuscript. Finally, we would like to thank the graduate students in Dr. Morrison's lab for feedback throughout the course of this research.

LITERATURE CITED

- Alig, R. J., J. D. Kline, and M. Lichtenstein. 2004. Urbanization on the US landscape: looking ahead in the 21st century. *Landscape and Urban Planning* 69:219–234.
- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71:355–366.
- Arnold, K. A., C. L. Coldren, and M. L. Fink. 1996. The interactions between avian predators and golden-cheeked warblers in Travis County, Texas. Texas Transportation Institute. Texas A&M University, College Station, USA.
- Bayne, E. M., and K. A. Hobson. 2001. Effects of habitat fragmentation on pairing success of ovenbirds: importance of male age and floater behavior. *Auk* 118:380–388.
- Beardmore, C. J., J. Hatfield, and J. Lewis, editors. 1996. Golden-cheeked warbler population and habitat viability assessment report. U. S. Fish and Wildlife Service, Austin, Texas, USA.
- Benson, R. H. 1990. Habitat area requirements of the golden-cheeked warbler on the Edwards Plateau. Texas Parks and Wildlife Department, Austin, USA.
- Bierwagen, B. G., D. M. Theobald, C. R. Pyke, A. Choate, P. Groth, J. V. Thomas, and P. Morefield. 2010. National housing and impervious surface scenarios for integrated climate impact assessments. *Proceedings of the National Academy of Sciences* 107:20887–20892.
- Burke, D. M., and E. Nol. 2000. Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario. *Ecological Applications* 10:1749–1761.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference. Springer-Verlag, New York, New York, USA.
- Butcher, J. A., M. L. Morrison, D. Ransom Jr., R. D. Slack, and R. N. Wilkins. 2010. Evidence of a minimum patch size threshold of reproductive success in an endangered songbird. *Journal of Wildlife Management* 74:133–139.
- Campbell, L. 2003. Endangered and threatened animals of Texas: their life history and management. Texas Parks and Wildlife Department, Austin, USA.
- Campomizzi, A. J., S. L. Farrel, H. A. Mathewson, M. L. Morrison, and R. N. Wilkins. 2012. Species conservation at a broad spatial scale: reproductive success of golden-cheeked warblers across their breeding range. *Wildlife Society Bulletin* 36:440–449.
- Christoferson, L. L., and M. L. Morrison. 2001. Integrating methods to determine breeding and nesting status of 3 western songbirds. *Wildlife Society Bulletin* 29:688–696.
- Coldren, C. L. 1998. The effects of habitat fragmentation on the golden-cheeked warbler. Dissertation, Texas A&M University, College Station, USA.
- Collier, B. A., J. E. Groce, M. L. Morrison, J. C. Newnam, A. J. Campomizzi, S. L. Farrell, H. A. Mathewson, R. T. Snellgrove, R. J. Carroll, and R. N. Wilkins. 2012. Predicting patch occupancy in fragmented landscapes at the rangewide scale for an endangered species: an example of an American warbler. *Diversity and Distributions* 18:158–167.
- Cooksey, M. L., and S. M. Edwards. 2008. Monitoring of the golden-cheeked warbler and the black-capped vireo on Camp Bullis, Texas: 2008 field season report. Fort Sam Houston, San Antonio, Texas, USA.
- Dearborn, D. C., and L. L. Sanchez. 2001. Do golden-cheeked warblers select nest locations on the basis of patch vegetation? *Auk* 118:1052–1057.
- DeBoer, T. S., and D. D. Diamond. 2006. Predicting presence-absence of the endangered golden-cheeked warbler (*Dendroica chrysoparia*). *Southwestern Naturalist* 51:181–190.
- Donnelly, R., and J. M. Marzluff. 2004. Importance of reserve size and landscape context to urban bird conservation. *Conservation Biology* 18:733–745.
- Duarte, A., J. L. Jensen, J. S. Hatfield, and F. W. Weckerly. 2013. Spatiotemporal variation in range-wide golden-cheeked warbler breeding habitat. *Ecosphere* 4(12):152.
- Farrell, S. L., M. L. Morrison, A. J. Campomizzi, and R. N. Wilkins. 2012. Conspecific cues and breeding habitat selection in an endangered woodland warbler. *Journal of Animal Ecology* 81:1056–1064.
- Friesen, L. E., P. F. J. Eagles, and R. J. Mackay. 1995. Effects of residential development on forest-dwelling Neotropical migrant songbirds. *Conservation Biology* 9:1408–1414.
- Gaines, J. P. 2008. Looming boom: Texas through 2030. *Tierra Grande* 1841:1–6.
- Grimm, N. B., S. H. Faeth, N. E. Golubiewski, C. L. Redman, J. Wu., X. Bai, and J. M. Briggs. 2008. Global change and the ecology of cities. *Science* 319:756–760.
- Grinnell, J. 1917. The niche-relationships of the California thrasher. *Auk* 34:427–433.
- 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. Texas A&M Institute of Renewable Natural Resources, College Station, USA.
- Halfwerk, W., L. J. M. Holleman, C. M. Lessells, and H. Slabbekoorn. 2011. Negative impact of traffic noise on avian reproductive success. *Journal of Applied Ecology* 48:210–219.
- Homer, C., J. Dewitz, J. Fry, M. Coan, N. Hossain, C. Larson, N. Harold, A. McKerrow, J. N. VanDriel, and J. Wickham. 2007. Completion of the 2001 National Land Cover Database for the conterminous United States. *Photogrammetric Engineering and Remote Sensing* 73:337–341.
- Jette, L. A., T. J. Hayden, and J. D. Cornelius. 1998. Demographics of the golden-cheeked warbler (*Dendroica chrysoparia*) on Fort Hood, Texas. U.S. Army Corps of Engineers Technical Report 98/52, Fort Hood, Texas, USA.
- 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.
- Kluza, D. A., C. R. Griffin, and R. M. DeGraaf. 2000. Housing developments in rural New England: effects on forest birds. *Animal Conservation* 3:15–26.

- Lackey, M. A., Z. G. Loman, N. Fisher, S. F. Farrell, B. A. Collier, and R. N. Wilkins. 2011. Effects of road construction noise on the endangered golden-cheeked warbler. *Wildlife Society Bulletin* 35:15–19.
- Leopold, A. 1970. *A Sand County almanac: with essays on conservation from Round River*. Ballantine, New York, New York, USA.
- Maas, D. S. 1998. Factors influencing demographics of golden-cheeked warblers (*Dendroica chrysoparia*) at Fort Hood Military Reservation, Texas. Thesis, University of Oklahoma, Norman, USA.
- MacKenzie, D. I., and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology* 42:1105–1114.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Academic Press, San Diego, California, USA.
- 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. E., 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* 114:882–892.
- Morrison, M. L., W. M. Block, M. D. Strickland, B. A. Collier, and M. J. Peterson. 2008. *Wildlife study design*. Second edition. Springer, New York, New York, USA.
- National Oceanic and Atmospheric Administration [NOAA]. 2010. U.S. Department of Commerce, Washington D.C., USA. <http://www.ncdc.noaa.gov/land-based-station-data/quality-controlled-local-climatological-data-qclcd>. Accessed 18 Apr 2013.
- Ott, R. L., and M. Longnecker. 2001. *An introduction to statistical methods and data analysis*. Sixth edition. Cengage Learning, Belmont, California, USA.
- Patricelli, G. L., and J. L. Blickley. 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. *Auk* 123:639–649.
- Peak, R. G. 2007. Forest edges negatively affect golden-cheeked warbler nest survival. *Condor* 109:628–637.
- Pulich, W. M. 1976. *The golden-cheeked warbler*. Texas Parks and Wildlife Department, Austin, Texas, USA.
- Radford J. Q., and A. F. Bennett. 2004. Thresholds in landscape parameters: occurrence of the white-browed treecreeper *Climacteris affinis* in Victoria, Australia. *Biological Conservation* 117:375–391.
- Reidy, J. L., F. R. Thompson III, and R. G. Peak. 2007. Factors affecting golden-cheeked warbler nest survival in urban and rural landscapes. *Journal of Wildlife Management* 73:407–413.
- Rich, A. C., D. S. Dobkin, and L. J. Niles. 1994. Defining forest fragmentation by corridor width: the influence of narrow forest-dividing corridors on forest-nesting birds in southern New Jersey. *Conservation Biology* 8:1109–1121.
- Robinson, D. H. 2013. Effects of habitat characteristics on occupancy and productivity of a forest-dependent songbird in an urban landscape. Thesis, Texas A&M University, College Station, USA.
- 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.
- Smith, T. M., and H. H. Shugart. 1987. Territory size variation in the ovenbird: the role of habitat structure. *Ecology* 68:695–704.
- Sperry, C. 2007. Influences of borders on golden-cheeked warbler habitat in the Balcones Canyonlands Preserve, Travis County, Texas. Thesis, Texas State University, San Marcos, USA.
- Temple, S. A., and J. R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conservation Biology* 2:340–347.
- Thompson III, F. R., 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. Environmental Protection Agency [USEPA]. 2009. Land-use scenarios: national-scale housing-density scenarios consistent with climate change storylines (final report). EPA/600/R-08/076F. Global Change Research Program, National Center for Environmental Assessment, Washington, D.C., USA.
- U.S. Fish and Wildlife Service [USFWS]. 1990. Endangered and threatened wildlife and plants; emergency rule to list the golden-cheeked warbler as endangered. *Federal Register* 55:18844–18845.
- van Dorp, D., and P. F. M. Opdam. 1987. Effects of patch size, isolation and regional abundance on forest bird communities. *Landscape Ecology* 1:59–73.
- Vickery, P. D., M. L. Hunter Jr., and J. V. Wells. 1992. Use of reproductive index to evaluate relationships between habitat quality and breeding success. *Auk* 109:697–705.
- Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1986. A lesson in the limitations of field experiments: shrubsteppe birds and habitat alteration. *Journal of Animal Ecology* 49:523–536.

Associate Editor: Donaghy Cannon.