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*Population Ecology*

# Estimating Breeding Season Abundance of Golden-Cheeked Warblers in Texas, USA

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**ABSTRACT** Population abundance estimates using predictive models are important for describing habitat use and responses to population-level impacts, evaluating conservation status of a species, and for establishing monitoring programs. The golden-cheeked warbler (*Setophaga chrysoparia*) is a neotropical migratory bird that was listed as federally endangered in 1990 because of threats related to loss and fragmentation of its woodland habitat. Since listing, abundance estimates for the species have mainly relied on localized population studies on public lands and qualitative-based methods. Our goal was to estimate breeding population size of male warblers using a predictive model based on metrics for patches of woodland habitat throughout the species' breeding range. We first conducted occupancy surveys to determine range-wide distribution. We then conducted standard point-count surveys on a subset of the initial sampling locations to estimate density of males. Mean observed patch-specific density was 0.23 males/ha (95% CI = 0.197–0.252, $n = 301$). We modeled the relationship between patch-specific density of males and woodland patch characteristics (size and landscape composition) and predicted patch occupancy. The probability of patch occupancy, derived from a model that used patch size and landscape composition as predictor variables while addressing effects of spatial relatedness, best predicted patch-specific density. We predicted patch-specific densities as a function of occupancy probability and estimated abundance of male warblers across 63,616 woodland patches accounting for 1.678 million ha of potential warbler habitat. Using a Monte Carlo simulation, our approach yielded a range-wide male warbler population estimate of 263,339 (95% CI: 223,927–302,620). Our results provide the first abundance estimate using habitat and count data from a sampling design focused on range-wide inference. Managers can use the resulting model as a tool to support conservation planning and guide recovery efforts. 

**KEY WORDS** abundance, density, endangered species, golden-cheeked warbler, point count, population estimate, *Setophaga chrysoparia*, Texas.

Abundance estimates are of particular importance for evaluating conservation status and determining recovery goals, establishing monitoring programs, describing habitat use patterns, and assessing population-level impacts driven by anthropogenic and natural factors (Campbell et al. 2002, Scott et al. 2005, Fitzgerald et al. 2009, Sirami et al. 2010). Population size estimation is a challenge for most species, but approaches integrating remotely sensed data with predictive models can assist in predicting abundance at large spatial scales (Thompson 2002*a*, Fitzgerald et al. 2009). The golden-cheeked warbler (*Setophaga chrysoparia*) is a neotropical migratory songbird that breeds only in central Texas and winters in the highlands of southern Mexico and Central America (Pulich 1976, Groce et al. 2010). In 1990, the United States Fish and Wildlife Service (USFWS) listed the golden-cheeked warbler (hereafter warbler) as endangered and cited habitat loss and fragmentation as primary threats (USFWS 1990, 1992). Warbler occurrence, density, and recruitment rates appear to decrease as the size of habitat patches and the amount of habitat in the surrounding

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landscape decline (DeBoer and Diamond 2006, Magness et al. 2006, Peak 2007, Butcher et al. 2010, Collier et al. 2010).

Previously, approximations of golden-cheeked warbler abundance within the breeding range were based on estimates of warbler density collected at a few (<20) study sites and extrapolated based on projected extents of breeding habitat (Pulich 1976, Wahl et al. 1990, Rowell et al. 1995, Rappole et al. 2003; Table 1). Population estimates have ranged between 9,644 and 32,032 individuals (Pulich 1976, Wahl et al. 1990), whereas estimates of carrying capacity have ranged from 64,520 to 228,426 individuals (Rowell et al. 1995, Rappole et al. 2003). Variation in population estimates results from the methods used to estimate the extent of habitat, and assumptions regarding what characteristics are representative of warbler habitat (Table 1).

Our objective was to develop a range-wide estimate of abundance for male warblers. We relied on a range-wide model predicting patch level occupancy (Collier et al. 2012) to serve as our sampling frame. We then used point count surveys to estimate patch-specific density of male warblers. We evaluated predictive relationships between patch-specific density and remotely sensed metrics of habitat patches. Using these relationships, we combined our density estimates with the range-wide occupancy model to yield estimates of male warbler abundance across the species' breeding range.

## STUDY AREA

The golden-cheeked warbler breeding range is confined to central Texas, USA, on the eastern half of the Edwards Plateau and the southern half of the Cross Timbers ecoregions (Hatch et al. 1990). We conducted our research across the breeding range on public and private properties in 35 counties (USFWS 1992; Fig. 1). Our sampling units were patches of potential warbler habitat, characterized as oak-juniper woodlands (Collier et al. 2010, 2012), and we defined a patch as a relatively homogenous unit of vegetation distinct from its surroundings (Kotliar and Wiens 1990). To guide us in determining survey locations in 2008, we used a habitat classification developed by SWCA Environmental Consultants (SWCA 2007) that delineated potential warbler habitat as those patches having >50% canopy closure by a mixture of mature or second-growth Ashe juniper (*Juniperus ashei*) and deciduous hardwood trees based on 2004 National Agricultural Imagery Program color infrared digital imagery (1-m resolution). SWCA (2007) excluded patches <4 ha unless immediately adjacent (unspecified distance) to other patches of potential habitat. SWCA's restricted definition of habitat yielded 7,865 patches (approx. 552,000 ha) of potential habitat across the breeding range. Based on our field surveys during 2008, as well as previous work within this system (Butcher et al. 2010, Collier et al. 2010), we found the SWCA (2007) classification narrowly defined warbler habitat; thus, we developed a broader classification of warbler habitat patches for selecting survey sites in 2009 and for evaluating relationships between patch-specific densities and patch metrics.

We delineated potential habitat using an unsupervised classification of woodlands from 2007 and 2008 cloud-free Landsat 5 imagery collected during late spring (Morrison et al. 2010). Using the ISODATA clustering algorithm in Leica ERDAS Imagine 9.3 (Intergraph Corporation, Norcross, GA), we grouped imagery spectral response patterns into 20 statistically different clusters. Using high resolution aerial photography from the National Agriculture Imagery Program (NAIP; 2004 and 2006) and data collected in the field, we identified those clusters that corresponded to woodland land cover, grouping all other land cover types as non-habitat (e.g., wetlands, cropland, urban areas, water, barren, impervious surfaces, grassland). Several woodland clusters were based on characteristics such as slope, aspect, shadows, and composition (e.g., evergreen or deciduous); however, because classification accuracy of these woodlands was low and our intent was to sample woodland cover, we aggregated these clusters into 1 class. To further refine our woodland classification, we used the 2001 National Land Cover Data set (NLCD; Homer et al. 2007) to eliminate any misclassified non-woodland land cover types from our initial classification. We also removed those pixels classified as woodland but with canopy cover <30% using the 2001 NLCD canopy cover layer. Using road data from the Texas Strategic Mapping Program (STRATMAP), we defined breaks between patches by removing pixels that intersected paved or public roads. We thus delineated 63,616 patches (mean patch size = 26.39 ha, range = 2.8–26,967 ha) or approximately 1.678 million ha of potential warbler habitat (Fig. 1). We used ArcGIS 9.3.1 (Environmental Systems Research Institute, Inc., Redlands, CA) and calculated patch size (ha), landscape composition (% woodland within a 400-m radius of a given pixel; Magness et al. 2006), patch core area, and edge-to-area ratio for each of the 63,616 patches of mixed woodland identified within the study area. We calculated the landscape composition value for patches as the mean value for all pixels within the patch. We calculated patch core habitat area as the internal portion of the patch after buffering the exterior edge of the patch internally by 30 m. The distribution of patches used to determine 2008 survey points was biased toward large, contiguous patches, but combined with survey points from 2009 the distribution of surveyed patches included a wider range of patch sizes, shapes, and amount of edge habitat. Thus, we re-projected point count survey locations from 2008 sampling to those patches identified in our habitat delineation for analysis.

## METHODS

### Occupancy Surveys

We used a 2-phase sampling approach (Conroy et al. 2008) whereby we first conducted occupancy (i.e., detection or non-detection) surveys at the patch scale to determine areas that likely supported warblers (Collier et al. 2012). For occupancy surveys, we used a double-observer, removal approach (MacKenzie et al. 2006) in which 2 observers simultaneously yet independently surveyed a habitat patch up to a maximum

**Table 1.** Previous estimates and methods used for total golden-cheeked warbler breeding habitat, density, and projected population size.

| Refs. | Total potential habitat (ha) | Method (habitat delineation) | Density estimate | Method (density) | Total population size | Method (project to population size) |
|---|---|---|---|---|---|---|
| Pulich (1976) | 129,904 | Used Soil Conservation Service definition of "virgin Ashe Juniper" (stands 6–12 m high, trees >75 years old), reduced by author; no imagery used; 31 counties | "Good" = 0.125 pair/ha; "average" = 0.05 pair/ha; "marginal" = 0.03 pairs/ha | Spot-mapping with marked population; Dallas, Bosque, Kendall counties; surveys conducted in 1962 and 1974 | 1962: 18,486 pairs; 1974: 14,750 pairs | Calculated proportion of total habitat for each of 3 habitat quality ranks (23%, 31%, and 46%, respectively), multiplied by respective density estimates |
| Wahl et al. (1990) | 32,149–106,776, 1974–1981; 338,035, 1989: 237,163[a] | Corrected values for habitat loss and patch size[a]; 1974, 1976, and 1981 Landsat imagery, unsupervised and supervised classification from known breeding locations (see Shaw 1989); 1989 value is corrected for estimated habitat loss; 43 counties | 0.149 pair/ha[b] | Median estimate for 16 sites[c] in 11 counties determined primarily by 1-mile transect method (Emlen 1971); surveys conducted in 1987, 1988 | 4,822–16,016 pairs | Median density estimate projected to total potential habitat estimates after corrections |
| USFWS (1992) | Not specified | Used Wahl et al. (1990) habitat total estimate for 1989 adjusted for estimated habitat loss; included the assumption that 34% of patches <50 ha are occupied [d] | Estimates from Pulich (1976) for good, average, and marginal | Estimates for each of 3 habitat ranks from Pulich (1976) | 13,800 territories | Followed Pulich (1976) proportions of habitat quality assuming same proportions apply to habitat delineated by Wahl et al. (1990); not corrected for patch size |
| Rowell et al. (1995) | Method 2: 215,066 (including patches <50 ha: 545,948); Method 1: 1,116,665 | 1990–1992 Landsat, Ashe juniper-deciduous woodlands with >75% canopy cover and patches >50 ha; Method 1: unsupervised classification of polygons; Method 2: supervised classification from point locations; 35 counties | 0.30 individuals/ha | Estimates from Wahl et al. (1990) | 64,520 individuals | Projected density to total habitat from Method 2 for patches >50 ha because less variation in spectral reflectance compared to Method 1 |
| Diamond and True (1998) [e] | 1986: 1,652,035 1996–1997: 1,676,140 | 1986 and 1996–1997 Landsat; land cover classified as Ashe juniper, or mixed juniper-oak forest/woodland, or mixed or primarily deciduous forest | NA | NA | NA | NA |
| Rappole et al. (2003) | 643,454 | Used Diamond and True (1998) classification but removed patches <5 ha[f]; 29 counties | 0.188 territorial males/ha; 89% pairing success[g] | Estimates from 167 males from monitored population on Fort Hood, Coryell and Bell counties from 1992 to 1996 (Jette et al. 1998) | 228,426 individuals | Adjusted mean density of males by 89% pairing success to estimate number of females |
| SWCA (2007) | 552,195 | 2004 digital imagery; >50% canopy closure composed of large Ashe juniper and deciduous trees; patches >4 ha; 43 counties | "High" = 0.22 pair/ha; "low" = 0.025 pair/ha | "High" estimate from long-term monitoring study on Fort Hood, Bell and Coryell counties (Peak 2003); "low" estimate from surveys Government Canyon SNA, Bexar Co. (USFWS 2004) | 13,931–116,565 pairs; adjusted estimate: 20,445–26,978 pairs | Adjusted estimate based on assumptions of density with goal of deriving a "satisfactory minimum population estimate" |

[a] Range of habitat corrected for counties ranked as urban or rural (subjective classification), and their respective estimated habitat loss during interval between imagery and surveys and proportion of habitat patches >50 ha.
[b] Originally 17 sites but authors eliminated 1 site because they considered the density of warblers too high.
[c] Authors selected sites based on known warbler occurrence; 15 public property sites and 2 private.
[d] USFWS included patches <50 ha citing research by Benson (1990).
[e] Did not estimate warbler population size but others have used their habitat delineation to project estimates of population.
[f] Total habitat before adjusting for patch size not specified by authors.
[g] Authors used pairing success to estimate size of female population.


**Figure 1.** Distribution of mixed woodland patches, and locations of abundance surveys conducted during 2008 and 2009 on private or public lands in the 35 county breeding range of the golden-cheeked warbler in Texas, USA.

of 6 surveys (3 double-observer surveys) to determine warbler presence (Collier et al. 2010). We surveyed 434 patches for warbler presence in 2008 and 2009 and if we detected a warbler during occupancy surveys, we returned to the patch to conduct abundance surveys (see below).

To select patches for occupancy surveys, we stratified patches based on administrative units defined by USFWS (USFWS 1992) and used a probability proportional to size (PPS) sampling design (Thompson 2002*a*), in which we randomly selected habitat patches proportional to the distribution of patch sizes across the range. Because habitat patches often spanned multiple public and private landowners, we attempted to locate and contact all property owners of randomly selected patches. However, our access to the entirety of each patch was sometimes limited because of inability to locate landowners, lack of response, unwillingness to participate by landowners, or other logistical constraints. Because landowners tend to base their participation on multiple factors that are often not associated with land management practices that would influence warbler abundance (Hilty and Merenlender 2003, DeBoer and Diamond 2006, Sorice et al. 2011), we assumed that such access restrictions did not bias our sampling. Furthermore, we assumed that properties for which we were unable to acquire access were missing from our sample completely at random (Stevens and Jensen 2007). We did not stratify by ownership type so we focused considerable effort on acquiring access to private property. Our approach further assumed that variability in habitat conditions was not related consistently to designation as private versus public lands as few public or private properties are managed specifically for warbler habitat in Texas (Groce et al. 2010).

## Abundance Surveys

Within each patch selected for abundance surveys, we buffered each survey patch to reduce the proportion of survey area that would fall outside of a habitat patch, such that point count centers in patches >40 ha were located $\geq$100 m from the edge and points in patches $\leq$40 ha were $\geq$25 m from the edge. Under those constraints, we randomly established the maximum number of point count stations while ensuring a 400-m minimum distance between point count centers using ArcGIS 9.3. Small patches (<10 ha) that were inadvertently skipped because they violated the 400-m spacing constraint were processed a second time without the spacing constraint to ensure adequate coverage of point survey locations within small patches. Given our spacing and random placement, we assumed abundance counts at each point were independent within patches. Because our sampling unit was the patch, we did not incorporate any within-patch habitat variability that could influence local differences in male density. We assumed that our random distribution of point count stations captured any within-patch habitat heterogeneity in local vegetation or densities.

Patches selected for point count surveys were conditional on positive detections of warblers during occupancy surveys, but we conducted point count surveys independent of the occupancy sampling process. As such, a zero patch-level abundance estimate was a recordable result when we detected no warblers during point count surveys. During mid-March to mid-May 2008 and 2009, we conducted abundance surveys for warblers using 100-m fixed-radius point counts following methods detailed by Laake et al. (2011). Surveys began at sunrise and ended no later than 13:00. When surveyors detected a bird during occupancy surveys, they immediately initiated point count surveys at the predetermined point count locations. However, if sufficient time was not available to conduct the surveys within the same day, we returned within a week of the occupancy survey. We used a dependent double-observer sampling approach (Cook and Jacobson 1979, Nichols et al. 2000). At each survey point, we randomly assigned primary or secondary observer status. During the 5-minute survey, the primary observer communicated visual and auditory detections of male warblers to the secondary observer, noting the direction and classifying the approximate distance into a distance bin (0–50 m or 50–100 m). Concurrently, the secondary observer recorded detections of any individuals missed by the primary observer (Laake et al. 2011). The combined data from the primary and secondary observers represents a 2-sample capture history. To maximize the spatial distribution of sample locations, we visited each patch on 1 occasion for abundance surveys (Thompson 2002*b*). We did not conduct point counts during inclement weather or periods of high wind. We followed the standard assumptions for point count surveys: 1) population closure, 2) observers correctly identified birds, 3) no double counting, and 4) observers correctly estimated distances to birds (Buckland 2006, Johnson 2008).

**Analysis**

To model male warbler abundance across the breeding range, we first estimated observed patch-specific density using our point count survey data. Next, using an information-theoretic approach to select the best fitting model given the data (Burnham and Anderson 2002); we regressed patch-specific predictor variables against the observed patch-specific density estimates and developed a predictive equation relating biological metrics to density at the patch scale. Using the predictive equation, we predicted densities (as well as lower and upper 95% CL) for each patch of potential habitat from our delineation across the range and converted those to patch-specific abundance. Finally, we used a Monte Carlo simulation to randomly identify occupied patches based on their predicted occupancy probability (Collier et al. 2012) and summed the resultant abundance estimates for each randomly selected patch to generate a population abundance estimate with lower and upper 95% confidence limits for each 1,000 realizations.

We combined point count data collected during 2008 and 2009 because we independently selected point count locations for each study year and we assumed minimal annual variation of patch-level warbler densities. We examined our assumption using the patches randomly selected for abundance surveys in both study years. We estimated observed patch-specific density using the count of male warblers standardized to the total surveyed area (i.e., 3.14 ha for 100-m fixed-radius sample area) within each patch. We assumed that the effect of 100-m radius point count locations that included non-woodland vegetation based on our patch delineation was minimal. We used counts of abundance uncorrected for detection probability because a preliminary evaluation revealed estimated double observer detection rates for warblers using our survey design were high (probability of detection = 0.97; Laake et al. 2011). Furthermore, our uncorrected density estimates will be comparable to previous research on warbler densities and abundance that have not included detection corrections in their estimates (Table 1). We acknowledge that by implicitly assuming a detection probability of 1.0 we likely underestimated density; thus, our estimates may be conservative (Pollock et al. 2002, Thompson 2002*b*). We assumed that density was constant across patches and that the random distribution of our sampling points captured any within-patch vegetation heterogeneity.

To evaluate the relationships between observed density of male warblers and our predictor variables, we used generalized linear modeling (GLM) with a negative binomial distribution of the raw count data (McCullagh and Nelder 1989, White and Bennets 1996). We included total area surveyed at the patch scale as an offset term to standardize our count data to a density estimate for comparison across patches. We used a negative binomial distribution of our count data instead of the Poisson distribution commonly used for count data because the negative binomial provides a flexible approach to addressing overdispersion (White and Bennets 1996).

We assembled 8 competing models (Table 2) for predicting male density that were based on patch-specific metrics and probability of patch occupancy derived from the model developed during a concurrent study and described in Collier et al. (2012). We examined correlations among our predictor variables before determining our final set of candidate models. Core area correlated with patch size ($r = 0.997$) and edge-to-area ratio correlated with landscape composition ($r = -0.816$), thus we used patch size and landscape composition as predictors of patch density. We modeled the linear relationship between male patch-specific density and patch size because golden-cheeked warblers are considered to be an area-sensitive species (Butcher et al. 2010) in that demographic parameters are positively associated with patch size (Donovan and Flather 2002). Additionally, we examined a quadratic trend in patch size assuming that once territory density reached a threshold, density remained constant regardless of increases in patch size. We used landscape composition as an alternative predictor because landscape-scale factors might drive mechanisms associated with settlement decisions of territorial males, such as conspecific attraction (Campomizzi et al. 2008, Farrell 2011). We also considered an interaction between patch-size and landscape composition. We did not consider distance between

**Table 2.** Model selection statistics for models using negative binomial regression explaining patch-specific density of golden-cheeked warblers in Texas, in 2008 and 2009.

| Models[a] | $K$[b] | Log likelihood | AIC$_c$[c] | $\Delta$AIC$_c$[d] | $w_i$[e] |
|---|---|---|---|---|---|
| Occ | 2 | −515.78 | 1035.57 | 0 | 0.799 |
| Size + LS | 3 | −516.86 | 1039.71 | 4.20 | 0.098 |
| Size × LS | 4 | −516.10 | 1040.20 | 4.75 | 0.074 |
| Size2 | 3 | −518.47 | 1042.94 | 7.43 | 0.019 |
| logSize | 2 | −520.30 | 1044.60 | 9.04 | 0.009 |
| LS | 2 | −522.87 | 1049.74 | 14.17 | 0.001 |
| Size | 2 | −522.92 | 1049.85 | 14.28 | 0.001 |
| Null | 1 | −535.35 | 1072.71 | 37.10 | 0.000 |

[a] Occ = estimated occupancy from semiparametric model of Collier et al. (2012), Size = size of habitat patch (ha), Size2 = size of habitat patch quadratic trend, LS = landscape composition.
[b] $K$ = no. of parameters.
[c] AIC$_c$ = Akaike's Information Criterion corrected for small sample sizes.
[d] $\Delta$AIC$_c$ = AIC$_c$ relative to the most parsimonious model.
[e] $w_i$ = AIC$_c$ model weight.

patches because our landscape composition metric captured this variability and previous research on warbler occurrence at the point-scale indicated that these variables were not as predictive as is landscape composition (DeBoer and Diamond 2006, Magness et al. 2006).

We also used the patch occupancy prediction from Collier et al. (2012) as a predictor variable of abundance. The geo-additive semiparametric approach detailed in Collier et al. (2012) predicted occupancy probability ($\psi_i$) as a function of covariate data (patch size and landscape composition) and spatial location within the warbler's range expressed as

$$\text{logit}(\psi_i) = \beta_0 + \beta_l X_l + \sum_{k=1}^{20} u_k(\text{Location}_i - \kappa_k) + \varepsilon_i$$

where the $\beta_l\, X_l$ represents a vector of $l$ predictor variables (patch size, landscape composition, patch size-landscape composition interaction, and patch-specific Universal Transverse Mercator [UTM] coordinates) entering the model linearly and (Location $- \kappa_k$) represents the effect of spatial location for each surveyed habitat patch (Gimenez et al. 2009). Collier et al. (2012) used a temporal covariate representing sample survey date for detection modeling because date of survey has been shown to adequately predict detection rates of warblers at the patch scale (Collier et al. 2010).

We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate competing models. We ranked models using Akaike's Information Criterion (AIC$_c$) corrected for small sample sizes. We calculated Akaike weights ($w_i$) to indicate relative likelihood of each model as the best approximating model given the data for our set of candidate models. We considered models $\leq$4 $\Delta$AIC units to be competitive. We judged model adequacy by performing a 10-fold cross-validation. We performed a likelihood ratio test of a saturated model that included occupancy and an interaction between patch size and landscape composition compared to a constant model to examine over-dispersion (Venables and Ripley 2002).

We used the best fitting model given our model set and predicted patch-specific density of male warblers for each habitat patch that we delineated across the range ($n$ = 63,616 patches). We converted predicted density to predicted patch-specific abundance and ran Monte Carlo simulations using the equation

$$\hat{N} = \sum_{i=1}^{n} (y_i \times \text{area} \times k_i)$$

where $y_i$ is the predicted patch-specific density estimate and *area* (ha) is the size of each patch. The covariate $k$ represented a random assignment of occupancy (0 or 1) based on random draws from a Bernoulli distribution using the predicted patch occupancy rates from Collier et al. (2012). We generated a distribution of abundance estimates and associated upper and lower bounds using 1,000 replicates of the above simulation where the summed abundance values for those patches where $k = 1$ represented the predicted population.

When surveying avian species, counting a single bird multiple times is possible, which would bias point survey data (Buckland 2006). Given our short point count period (5 min), we concluded that double counting was unlikely; however, we were interested in exploring the potential impacts of being wrong in reaching such a conclusion. Thus, we estimated minimum density and population size based on 2 possible scenarios of double counting. First, given that double counting could not occur if observers detected 0 or 1 warbler at a point during a survey, and that the likelihood of observers having over counted when reporting 2 birds is unlikely given our survey design, we re-examined our data by limiting total counts at a point to a maximum of 2 (Table 3). Second, to exclude potential bias of double counting warblers between the 2 observers, we used the number of birds counted only by the primary observer, representing the minimum count that would be obtained from a single-visit standard point count (Nichols et al. 2000).

# RESULTS

### Abundance Counts and Density Estimation

We conducted 1,057 point count surveys in 301 mixed woodland patches (2008: $n$ = 151 patches; 2009: $n$ = 150) across the warbler's breeding range (Fig. 1). Survey points per

**Table 3.** Number of survey points and total number of singing male golden-cheeked warblers counted during point-count surveys in central Texas in 2008 and 2009.

| Total count | No. of points | % of points |
|---|---|---|
| 0 | 551 | 52.1 |
| 1 | 302 | 28.6 |
| 2 | 133 | 12.6 |
| 3 | 58 | 5.5 |
| 4 | 11 | 1.0 |
| 5 | 2 | 0.2 |

patch ranged from 1 to 35 (mean = 3.5, SD = 4.11). We detected 796 warblers during both years of our surveys. For patches surveyed for abundance estimation, patch size ranged from 2.8 to 26,967 ha (mean = 743.7, 95% CI = 497.2–990.2, median = 141.2, $n = 301$). Mean patch size for patches primarily in private ownership ranged from 3.2 to 26,970 ha (mean = 740.1, 95% CI = 388.3–1,093.5, median = 147.3, $n = 178$) and for public properties ranged from 2.8 to 11,880 ha (mean = 747.8, 95% CI = 420.3–1,075, median = 119.2, $n = 123$). Mean landscape composition (% woodland vegetation within 400-m radius) ranged from 15% to 92% (mean = 65.4, 95% CI = 63.7–67.0, median = 67.1, $n = 301$). Mean landscape composition for patches primarily in private ownership ranged from 15% to 91% (mean = 64, 95% CI = 62–66, median = 65.7, $n = 178$) and for public properties ranged from 26% to 92% (mean = 67.2, 95% CI = 64.3–70.1, median = 72.8, $n = 123$). For the sub-sample of patches surveyed in both years ($n = 34$), density estimates were similar (2008: 0.25 males/ha, 95% CI = 0.18–0.32; 2009: 0.23 males/ha, 95% CI = 0.15–0.29), supporting our assumption of minimal annual variation between our survey years.

Thirty-four percent ($n = 301$) of patches in which we conducted abundance point counts had no warbler detections. Mean observed patch-specific density of male warblers for both years, was 0.23 males/ha (95% CI = 0.197–0.252, $n = 301$ patches). Density varied between USFWS recovery regions (USFWS 1992); mean observed density in the north region was 0.15 males/ha (95% CI = 0.10–0.17, $n = 86$ patches), the central region equaled 0.19 males/ha (95% CI = 0.15–23, $n = 106$), and the south region equaled 0.32 males/ha (95% CI = 0.26–37, $n = 109$).

### Model Results and Abundance Estimation

The goodness-of-fit test indicated that the saturated model fit the data ($\chi^2_4 = 52.1$, $P < 0.001$). Based on our model selection results, patch-specific occupancy probability best predicted male warbler density (Table 2). The standardized model parameter estimates for the fitted model indicated that for every 0.25 increase in predicted patch occupancy probability (i.e., 1-unit increase for scaled data), the density of males increased by 61% ($\beta = 0.478$, 95% CI: 0.326–0.636).

Using our predicted patch-specific density estimates as a function of predicted patch occupancy probability and based on 1,000 simulated realizations of population distribution, we estimated median singing male warbler abundance across the range as 262,013 singing males (95% CI: 223,164–301,081; Fig. 2). Under the assumption that the maximum number of male warblers detected was 2, predicted density and estimated population size declined 10.9% (Table 4). Removal of the secondary observer's data resulted in a 13.4% decrease in density and population size estimates (Table 4). Cross-validation indicated a predictive error of 15% but upon removal of 1 extreme outlier the error dropped to 5%. We summarized estimates of golden-cheeked warbler habitat area and abundance from the literature (Table 1). Methods used to estimate the amount of habitat varied but generally used Landsat imagery. In all cases, however, authors gathered data at only a few locations and then extrapolated across the estimated habitat range.

## DISCUSSION

We estimated male golden-cheeked warbler population size across the breeding range in central Texas, USA using a relationship that accounts for predicted occupancy of a habitat patch, which in turn reflects the geographic spatial location, patch size, and landscape composition (Collier et al. 2012). The relationship with occupancy suggests that abundance decreased from south to north, and with decreasing patch size and woodland cover. We did not find a relationship between abundance and these environmental covariates per se, but instead the relationship relied on spatial location within the warbler range. Indeed, estimates from our raw count data (observed patch-specific density), when grouped by USFWS Recovery Regions, indicated that density was greater for regions in the south than in the north. This pattern was not unexpected because the southern portion of the range contains the greatest percentage of available warbler habitat (Groce et al. 2010), and the habitat typically occurs in less fragmented, larger patches that are considered more suitable habitat for warblers (DeBoer and Diamond 2006, Baccus et al. 2007; Fig. 3). Our study suggested that more warblers exist than previously estimated (Table 1), or that the carrying capacity of available habitat is greater, and below we discuss how differences in study design, analysis, and assumptions contributed to discrepancies in population size estimates.

A positive relationship between occupancy probability and local abundance is well formulated in biology (Gaston et al. 2000, He and Gaston 2003). Indeed, some degree of this relationship is inevitable at the extreme limits of population size: local abundance necessarily increases when habitat is saturated, and at low levels of abundance, occurrence patterns are not maintained (Gaston 1999). Density-dependent habitat selection is one mechanism that might explain the abundance–occupancy relationship in golden-cheeked warblers since the species demonstrates conspecific attraction (Campomizzi et al. 2008, Farrell 2011) but other mechanisms also may contribute (see review Gaston et al. 2000). Given that the occupancy estimates are a function of patch size and landscape composition (Collier et al. 2012), the abundance–occupancy relationship is likely a response to variations in habitat conditions if these metrics predict habitat quality (i.e., survival or reproductive success). Similarly, lower predicted occupancy and abundance in the northern

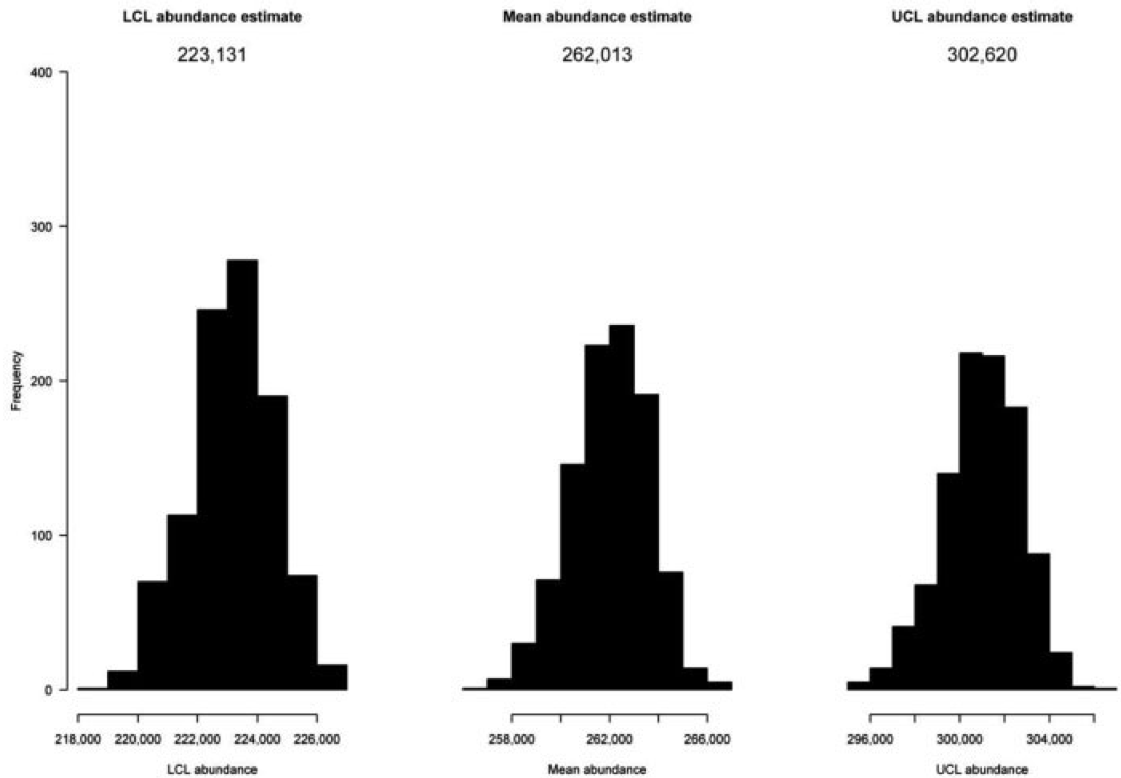


**Figure 2.** Predicted distribution for the range-wide population abundance of male golden-cheeked warbler estimates and associated 95% lower (LCL) and upper (UCL) confidence limits in Texas, USA, 2008–2009, based on predicted patch-specific density estimates as a function of predicted patch occupancy probability.

portion of the warbler's range might be a consequence of interrupted dispersal dynamics because of landscapes with smaller or isolated habitat patches (Donovan and Flather 2002).

The relationship between warbler density and patch-scale metrics that we used to predict abundance across the species' range was consistent with patch-scale metrics previously shown to affect warbler density at local scales (Magness et al. 2006, Baccus et al. 2007). Species–habitat relationships are complex and studies of this broad-scale application necessarily rely on assumptions concerning the validity of selected habitat metrics to define the relationship (Boyce and McDonald 1999, Fitzgerald et al. 2009). Warbler densities are likely to vary within patches in response to habitat characteristics such as tree species composition, density of junipers or oaks, and relative age of woodland (see review in Groce et al. 2010), variables that are important to define habitat at finer scales (Fitzgerald et al. 2009). We did not attempt to incorporate these relatively fine-scale variables, because our intent was to analyze patch-scale relationships across a broad geographic range. We depended upon random sampling to account for the within-patch variation in warbler densities, including any variation that might result from within-patch differences in habitat. With future use of more advanced remote sensing technologies, our model could incorporate additional landscape-scale and local-scale metrics. As with any large-scale study, precision and accuracy at finer scales are inherently reduced and further refinement of our model is needed for application at local scales.

## Patch-Specific Density

Our study differs from previous approaches that estimated population size of this species in that we estimated density from random samples across the species' breeding range and we based our method of inference to potential habitat on a predictive species–habitat relationship at the patch-scale (Table 1). Our density estimates of males were from randomly sampled point count locations across the 35-county breeding range, spanning a range of public and private properties. Even though inferential expansion to a broad geographic extent assumes that sampling is representative of the conditions across that area (Gutzwiller and Barrow

**Table 4.** Estimates and 95% confidence intervals of golden-cheeked warbler density and predicted warbler population size in central Texas in 2008 and 2009 based on 3 data analysis options: observed estimates with no correction for detection probability, limiting individual counts to a maximum of 2 detections, and estimates for data from observer 1 only.

| Method | Patch-specific density (95% CI) | Predicted population size (95% CI) |
|---|---|---|
| Uncorrected | 0.224 (0.197–0.252) | 262,013 (223,164–301,081) |
| Maximum 2 count | 0.205 (0.182–0.228) | 234,862 (202,031–267,601) |
| Observer 1, not corrected for detection | 0.194 (0.169–0.219) | 226,871 (191,658–262,091) |

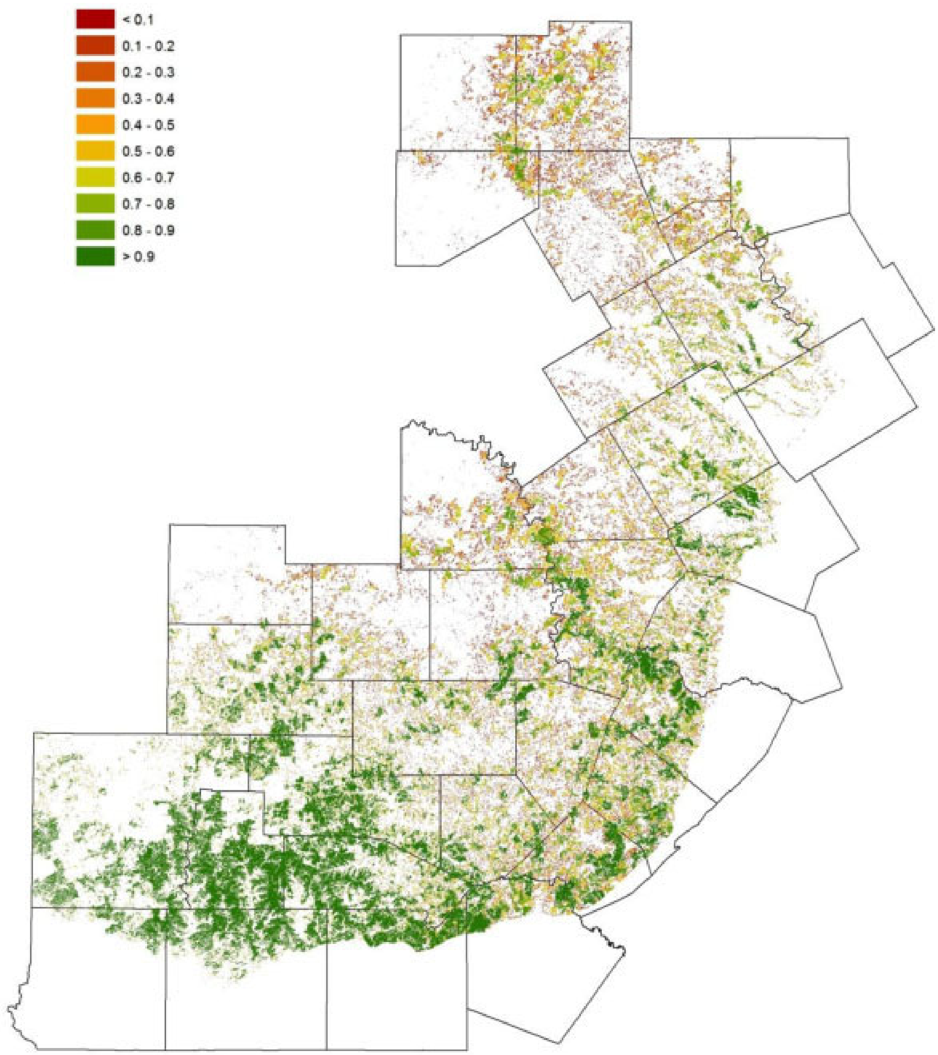


**Figure 3.** Predicted patch-specific occupancy probability for male golden-cheeked warblers in Texas, USA, 2008–2009. Figure from Collier et al. (2012).

2001) no previous study reporting population sizes of golden-cheeked warblers has used density estimates from randomly located study sites. Previous calculations of warbler abundance used density estimates primarily from study sites in the north or central portions of the breeding range (e.g., Pulich 1976, Rappole et al. 2003). Furthermore, some population size estimates were based on a mean or median density estimate from a few locations (Wahl et al. 1990, Rowell et al. 1995, Rappole et al. 2003), implying a constant density and thus failing to address variation in densities among habitat patches and across the range (Royle and Nichols 2003). Although Wahl et al. (1990) estimated site-specific densities at 17 sites in 11 counties, they did not incorporate variation in abundance in their population size estimate because they used the median density estimate, assuming constant density across the range. Pulich (1976) addressed regional variation in density by deriving estimates from 3 study sites across the range; however, for projection to potential habitat he assumed a constant density within 3 habitat assessment ranks (Table 1). We addressed regional and among-patch heterogeneity in density by defining habitat patches as our sampling unit and projecting patch-specific densities to our potential habitat delineation. Although our approach requires the assumption of constant density within patches, we suggest that this is an improvement from previous estimates of golden-cheeked warbler abundance.

We used standard methods for avian point count surveys and we assumed a detection probability of 1.0. It is widely recognized that assuming a constant detection probability results in biased estimates because failing to account for detection typically produces underestimates of abundance (Pollock et al. 2002, Thompson 2002*b*, Johnson 2008). We accepted the potential for a negative bias because evidence that the use of a dependent double-observer close capture model resulted in a high probability (>0.97) of detecting a male warbler by at least 1 of the 2 observers (Laake et al. 2011). Multiple factors influence detectability, including skills of observers, habitat, ambient noise, weather, distance, and temporal effects (Johnson 2008). Correcting for detectability requires additional assumptions concerning these sources of heterogeneity in detection.

Johnson (2008) warned against making additional assumptions concerning detection heterogeneity until further investigations identify these sources because it could result in the application of an inadequate correction factor and, subsequently, a false confidence in accuracy. Several factors in combination likely affected detectability of warblers differently across the range in this study and by not systematically correcting for detection we eliminated any concerns regarding which sources of variability should be controlled statistically (Diefenbach et al. 2007, Johnson 2008). However, we collected our data in a manner conducive to future evaluation of some these effects on detection heterogeneity. For example, the assumption of constant detection could be relaxed by applying a distance-based or double-observer approach to our data (Nichols et al. 2000, Laake et al. 2011). We further accepted the potential for negative bias from our uncorrected density estimates to produce more conservative estimates given the endangered status of the warbler.

We attempted to reduce variation in detectability and to minimize bias associated with standard avian point counts through our study design (Pollock et al. 2002, Johnson 2008). We used 5-minute point count periods to minimize double counting of birds within the survey area or by counting birds that have moved through the area (Buckland 2006). We used a dependent double-observer method because it is robust to violations of the closure assumption (Moore et al. 2004). Although we consistently use well-trained observers, another benefit of the double-observer approach is that it reduces the prospect of species misidentification (Moore et al. 2004). We assumed a closed population because we conducted single-occasion point counts in each patch. Given the distribution of our survey patches, individuals did not likely move among our survey patches. By conducting single-occasion point counts, we were unable to detect and control for any temporal variation, but this was a trade-off to increase our survey efforts across a greater spatial extent (Thompson et al. 2002). To minimize temporal variation, we limited our surveys to the peak of the warbler breeding season, but we recognize that detection probability decreases across this period and we likely negative biased counts as the season progressed (Collier et al. 2010).

We report an estimate of the population size of male warblers during the breeding season, making no assumptions regarding breeding status of males. In other words, our counts included males that were territorial and paired, territorial and unpaired, or non-territorial floaters. Previous studies have reported population sizes of total breeding individuals that required assumptions associated with population-level pairing success to obtain an estimate of female population size (Table 1). The bias associated with assumptions of male breeding status, and consequently pairing success, depends on the study design, survey or monitoring effort, or adjustments to male-based detections. Because many songbird populations, including the golden-cheeked warbler, consist of territorial but unpaired males (Newton 1992), assuming that each male detected during a survey represents a breeding pair overestimates the female proportion of the population. Nevertheless, even with information garnered from monitoring protocols concerning pairing success, these studies tend to overlook non-territorial males that can constitute a substantial proportion of a population. For many songbirds, particularly those in fragmented habitats, male breeding status varies with habitat condition and demographic factors, such as densities or age structure (Newton 1992, Jette et al. 1998, Bayne and Hobson 2001). Although studies that monitor territories can capture variability in male breeding status at a local scale, these methods are impractical for broad-scale application (Buckland 2006). Until further assessment of how male breeding success varies across the range, we are unable to determine the degree of precision and bias in reported population sizes adjusted by pairing success estimates from a few locations. In our study, we eliminated the need for uninformed adjustments to calculate female population size and instead we present an approach that can incorporate future consideration of male breeding status across the range.

### Other Habitat Delineations

Population size estimates necessarily depend on the habitat delineation used to project a local density estimate to the range of potential habitat. Thus, the underlying question of all attempts to estimate population size is how habitat is defined and what habitat characteristics can be estimated using remotely sensed techniques. Much of the variation in estimated population sizes for the golden-cheeked warbler are created because of differences in data sources used to identify potential habitat (e.g., Landsat imagery, NLCD), each having differing resolutions and classification accuracies (Table 1). In addition, studies use different characterizations of the landscape to define habitat, oftentimes assuming a minimum threshold for warbler occurrence or other restrictions based on evaluations of habitat quality (Table 1). These approaches are inherently conservative, producing negatively biased habitat and population size estimates. Given the uncertainties in identifying warbler habitat in terms of habitat quality, we made no assumption regarding habitat quality in our broadly defined habitat delineation and provided an estimate of available potential habitat. Indeed, our total habitat estimate is similar to other recent studies when assumptions regarding habitat quality are removed (Diamond and True 1998, Diamond 2007). There may be concern that overestimating habitat would inflate our population size estimates, but the additional woodland included in our liberal estimation of habitat was primarily small patches and edge habitat (Fig. 3; Morrison et al. 2010, Collier et al. 2012). Occupancy probability was $\leq$0.10 for 59% of the patches in our habitat delineation (Collier et al. 2012) resulting in low predicted density estimates for a large portion of the habitat; thus, including habitat often assumed as lower quality contributed little to our total population size estimates.

Previous population size estimates are from data acquired on primarily public properties, whereas over half of the habitat patches in our study were private properties across the warbler's range. Given the differences in land uses observed on our private properties and that there was no significant difference in our habitat metrics between private and public lands, we assumed that warbler density and habitat conditions did not vary from properties for which we did not acquire access. Similarly, habitat patches within which landowners actively managed for golden-cheeked warblers did not bias our sample of public properties. Of public lands, TPWD state parks dominated our sample and few of these implement management plans for warblers (Groce et al. 2010). Only 5% of our survey patches were on properties managed specifically for warblers (e.g., Balcones Canyonland Preserve, Travis County).

Our study is an example of how researchers and land managers can use predictive models to estimate population abundance. Application of this model is at the range-wide scale but implementation of our approach at the regional scale is possible by incorporating additional information to refine abundance relationships. As remote-sensing technology evolves, we can examine additional habitat variables that might inform within-patch heterogeneity. Furthermore, our framework provides the opportunity to include detection probability to move beyond an index of warbler abundance (Johnson 2008).

# MANAGEMENT IMPLICATIONS

Our results indicate that warblers were more abundant in larger woodland patches of which most occur in the southern portion of the breeding range. Having this knowledge will help direct limited resources to the most effective areas for conservation of the species and will help guide management decisions (Fitzgerald et al. 2009). The population abundance estimate we generated can also inform recovery planning for the warbler. A better understanding of the influence of patch size and landscape composition on the occupancy and abundance of golden-cheeked warblers will provide a tool for recovery planning. If recovery planning is to involve the designation of focal areas for prioritizing conservation efforts, then the model developed here could provide a valuable planning aid in the process. As future habitat conservation plans and biological assessments are developed, the results of this work could inform impact assessments for estimating incidental take as well as supporting the development of more accurate metrics for crediting and mitigation programs. By providing a framework for more reliably predicting abundance and changes in abundance, our results provide the basis for assessment of this species' status. With further refinement of the model to account for differences in within-patch habitat quality, our results form the basis for advancing a system for monitoring of the warbler's abundance patterns, ultimately supporting decisions leading to recovery.

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