

AMOUNT AND TYPE OF FOREST COVER AND EDGE ARE IMPORTANT PREDICTORS OF GOLDEN-CHEEKED WARBLER DENSITY

REBECCA G. PEAK^{1,3} AND FRANK R. THOMPSON III²

¹U. S. Army Garrison-Fort Hood, Directorate of Public Works, 4612 Engineer Drive, Room 76, Fort Hood, TX 76544

²U.S. Department of Agriculture Forest Service, Northern Research Station, 202 Anheuser-Busch Natural Resources Building, University of Missouri, Columbia, MO 65211–7260

Abstract. Considered endangered by the U.S. Fish and Wildlife Service, the Golden-cheeked Warbler (*Setophaga chrysoparia*) breeds exclusively in the juniper–oak (*Juniperus ashei*–*Quercus* spp.) woodlands of central Texas. Large-scale, spatially explicit models that predict population density as a function of habitat and landscape variables can provide important insight for its management and recovery. We used distance sampling to model detection probability and to estimate the density and abundance of singing male Golden-cheeked Warblers on Fort Hood Military Reservation. We used an information-theoretic approach to evaluate hypotheses concerning the effects of proportion of forest type and forest cover, forest-edge density, and patch size on density. We fitted generalized linear models with detection probability as an offset term to predict density as a function of the habitat and landscape variables, calculate a model-based density and abundance estimate, and map density across the area sampled. The design-based estimates were 0.39 males ha⁻¹ and 7557 singing males. The most supported model contained proportion of forest type and forest cover, both of which had a positive effect on density, as well as forest-edge density, which had a negative effect. The model-based estimates of 0.39 males ha⁻¹ and 7571 singing males were greater than estimates extrapolated from intensive territory monitoring. Knowledge of factors affecting Golden-cheeked Warbler density can be used to inform recovery efforts, and our density model can be used to assess the effects of various activities proposed for military training and of environmental disturbance on warbler densities.

Key words: abundance, density, detection probability, distance sampling, habitat variables, landscape variables, *Setophaga chrysoparia*.

La Cantidad y el Tipo de Cobertura y de Borde de Bosque son Predictores Importantes de la Densidad de *Setophaga chrysoparia*

Resumen. La especie *Setophaga chrysoparia*, considerada en peligro por el Servicio de Vida Silvestre y Pesca de EUA, cría exclusivamente en los bosques de enebro y roble (*Juniperus ashei*–*Quercus* spp.) del centro de Texas. Modelos espacialmente explícitos de gran escala que predicen la densidad poblacional como una función de las variables del hábitat y del paisaje pueden brindar información importante para su manejo y recuperación. Usamos muestreos de distancia para modelar la probabilidad de detección y para estimar la densidad y abundancia de individuos machos canoros de *S. chrysoparia* en la Reserva Militar Fuerte Hood. Usamos un enfoque de la teoría de la información para evaluar las hipótesis concernientes sobre los efectos de la proporción del tipo de bosque y de la cobertura del bosque, de la densidad de borde de bosque y del tamaño del parche sobre la densidad. Ajustamos modelos lineales generalizados con la probabilidad de detección como un término de compensación para predecir la densidad como función de las variables del hábitat y del paisaje, calcular la densidad y abundancia estimada basada en el modelo y mapear la densidad a lo largo del área muestreada. Las estimaciones basadas en el diseño fueron 0.39 machos ha⁻¹ y 7557 machos canoros. El modelo con mejor soporte contuvo una proporción de tipo de bosque y de cobertura de bosque, ambos de los cuales tuvieron un efecto positivo sobre la densidad, lo mismo que la densidad de borde del bosque, la cual tuvo un efecto negativo. Las estimaciones basadas en los modelos de 0.39 machos ha⁻¹ y 7571 machos canoros fueron más grandes que las estimaciones extrapoladas de monitoreos territoriales intensivos. El conocimiento de los factores que afectan la densidad de *S. chrysoparia* puede ser usado para optimizar los esfuerzos de recuperación, y nuestro modelo de densidad puede ser usado para evaluar los efectos de varias actividades propuestas de entrenamiento militar y de los disturbios ambientales en la densidad de *S. chrysoparia*.

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³E-mail: rpeak1969@gmail.com

INTRODUCTION

Knowledge of relationships between birds and their habitat is the foundation of avian conservation planning and management. Advances in our understanding of how the surrounding landscape affects the distribution and abundance of breeding songbirds that migrate to the neotropics (Forman and Godron 1986, Flather and Sauer 1996, Freemerk et al. 1995, Bolger et al. 1997) demonstrate the importance of developing avian conservation plans that use spatially explicit models over large areas (Millspaugh and Thompson 2009). The availability of geographic information systems (GIS) and remotely sensed data has facilitated modeling the effects of the surrounding landscape on songbird populations. Additionally, GIS-based habitat models that assess the effects of landscape metrics on avian populations offer natural-resource professionals the advantage of delineating habitat without time- and labor-intensive ground-based surveys.

The Golden-cheeked Warbler (*Setophaga chrysoparia*) is a migratory songbird that breeds exclusively in the juniper-oak (*Juniperus ashei*-*Quercus* spp.) woodlands of central Texas. In 1990, the U.S. Fish and Wildlife Service (1992) listed this species as endangered on an emergency basis because of concerns over habitat loss and fragmentation attributed to urban development, agriculture, and flood-control impoundments. Information on habitat requirements and habitat-selection patterns in the breeding range is needed for recovery (U. S. Fish and Wildlife Service 1992). Three studies have investigated the effects of landscape or habitat on the Golden-cheeked Warbler's occurrence. DeBoer and Diamond (2006) found that occurrence was positively associated with larger patches with less edge. Magness et al. (2006) assessed occurrence at scales of radii of 100, 200, 400, and 800 m and found that percent of woodland in the landscape and patch size were the most important variables in predicting occurrence at all scales. Occurrence was positively associated with density of edges at the 100-m scale but negatively associated with it at the larger scales. Collier et al. (2010) found that probability of patch occupancy was positively associated with patch size and predicted that all patches >160 ha should be occupied. These models are useful tools that managers can use to determine the spatial distribution of habitat where Golden-cheeked Warblers are likely to occur and hence provide important insight for habitat management and recovery.

Assessing the status of a species requires not only knowledge of the spatial distribution of its habitat but also its density. Models that predict density as a function of habitat and landscape variables can be used to predict the response of avian populations to management or environmental disturbance and to estimate population size. However, if the estimate is calculated from count data unadjusted for probability of detection, it will be biased if that probability is less than one (Rosenstock et al. 2002). The probability of a bird being detected during a survey depends on many factors, including habitat type, the

observer's ability, distance from lines or points, and environmental conditions (Shields 1979, Ralph and Scott 1981, Bibby and Buckland 1987, Buckland et al. 2001). Therefore, count data adjusted for detection probability should provide less biased density estimates, which allow for stronger inference about avian-habitat relationships than estimates calculated from count data unadjusted for detection probability (Pollock et al. 2002).

Our objectives were to evaluate hypotheses concerning the effects of habitat and landscape factors on the density of singing male Golden-cheeked Warblers, predict density and abundance as a function of these variables, and map the species' density across the area we sampled. We used an information-theoretic approach (Burnham and Anderson 2002) to compare support for hypotheses regarding the effects of proportion of forest type, density of forest edges, patch size, and proportion of forest cover on density. We predicted: (1) proportion of juniper-oak forest should affect density positively because strips of peeling bark from mature Ashe juniper (*Juniperus ashei*) are an important component of this species' nests (Pulich 1976, Kroll 1980) and both Ashe juniper and oaks provide important foraging substrate for Golden-cheeked Warblers (Kroll 1980, Ladd 1985, Beardmore 1994); (2) forest-edge density should affect the warbler's density negatively because occurrence is negatively correlated with amount of and distance from edge (DeBoer and Diamond 2006, Sperry 2007) and forest edges affect nest survival negatively (Peak 2007, Reidy et al. 2009); (3) patch size should affect density positively because occurrence (DeBoer and Diamond 2006, Magness et al. 2006, Collier et al. 2010) and reproductive success (Fink 1996, Coldren 1998, Butcher et al. 2010) are positively correlated with patch size and; (4) proportion of forest cover should positively affect density because the overall amount of forest in the landscape is an important predictor of occurrence (DeBoer and Diamond 2006, Magness et al. 2006, Collier et al. 2010).

METHODS

STUDY AREA

Our study took place during the breeding season of 2008 on Fort Hood, an 87 890-ha military installation in Bell and Coryell counties, Texas (31° 10' N, 97° 45' W). The installation provides resources and training facilities for active and reserve units in support of the army's mission and has two basic types of training areas (Eckrich et al. 1999, Hayden et al. 2001). Areas where armored divisions and support units train are referred to as maneuver training areas and constitute an estimated 53 300 ha of the installation. Areas of training in firing of weapons are referred to as the live-fire training area and constitute an estimated 24 000 ha of the installation (Fig. 1A). The remaining 10 590 ha, the cantonment area, are where office buildings, housing, motor pools, and barracks are located (Fig. 1A). In addition to its importance to the army, Fort

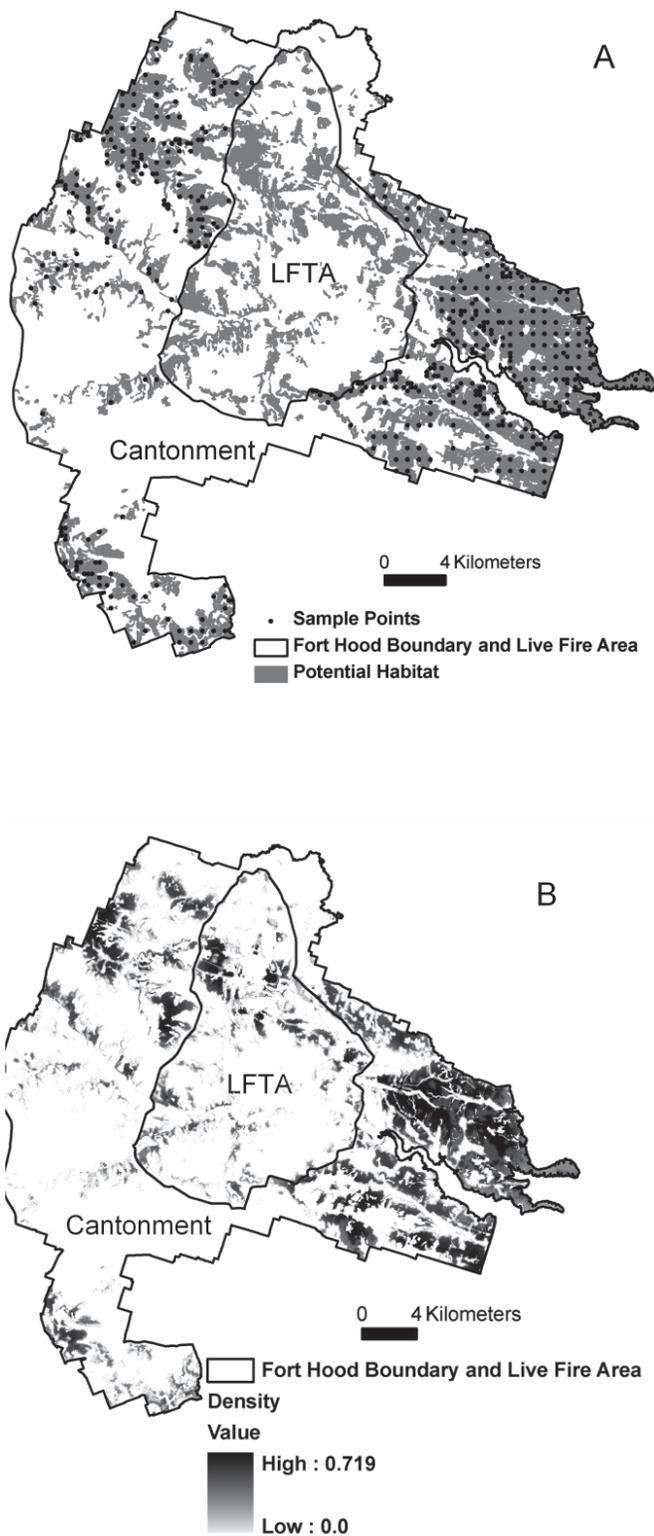


FIGURE 1. (A) Distribution of potential Golden-cheeked Warbler habitat and survey points ($n = 489$) sampled for singing male Golden-cheeked Warblers on Fort Hood Military Installation, Texas, 2008. Observers did not sample potential habitat located in the live-fire training area (LFTA). (B) Map of predicted Golden-cheeked Warbler density (males ha^{-1}) on Fort Hood Military Installation, Texas, 2008.

Hood manages the largest breeding population of the Golden-cheeked Warbler under a single management agency (Ladd and Gass 1999). The installation contains some of the largest remaining contiguous patches of Golden-cheeked Warbler habitat in the Lampasas Cut Plain region of its breeding range (Wahl et al. 1990). Estimates of survival of Golden-cheeked Warbler nests on the installation demonstrate that Fort Hood functions as high-quality breeding habitat and thus plays a critical role in maintaining this endangered species' long-term viability (Peak 2007).

STUDY DESIGN

We used a map of potential Golden-cheeked Warbler habitat (Reemts and Teague 2007) to define our sampling frame. Using 2004 leaf-off (nongrowing season) color infrared digital imagery from the National Agricultural Imagery Program (resolution 1 m), vegetation data from previous studies, additional sampling focused on gaps in spatial and thematic data, existing vegetation and habitat maps, and ancillary GIS data, Reemts and Teague (2007) identified 35 vegetation associations at Fort Hood. They used a spatially balanced randomized design to collect additional vegetation data to validate the map. Using ArcGIS (Environmental Systems Research Institute, Redlands, CA), they delineated polygons that represented the vegetation associations and created a data layer of potential habitat by combining 15 associations that contained Ashe juniper as a codominant tree. For the last 19 years observers have detected Golden-cheeked Warblers in these vegetation associations during point counts on Fort Hood (Peak 2011a). The combination of those associations yielded an estimate of 24 650 ha of potential habitat, but because of access restrictions observers did not survey 5196 ha located in the live-fire training area and our sampling was limited to 19 454 ha of potential habitat (Fig. 1A).

On the basis of data from Peak (2011b), we concluded that observers needed to survey approximately 500 points to obtain a number of detections adequate for reliable modeling of the detection function (Buckland et al. 2001). Using ArcView (Environmental Systems Research Institute, Redlands, CA), we selected a random starting point on Fort Hood and from it systematically placed survey points at 300-m intervals to develop a 300×300 -m grid of points across the entire installation. Of those points, 489 were located in our sampling frame (Fig. 1A).

Peak (2011b) field-tested the distance-sampling method with the Golden-cheeked Warbler and reported that abundance estimated by point-transect sampling was greater than actual abundance determined by intensive territory monitoring because observers did not satisfy the assumptions associated with distance-sampling theory. To minimize the effects of violating this method's assumptions on the accuracy of our estimates, we implemented the following recommendations of Peak (2011b): (1) conducted a 4-week training session for observers to learn the protocol, Golden-cheeked Warbler behavior and song, and

the theory and assumptions of distance sampling; (2) used either a laser range finder (accuracy ± 1 m; Bushnell, Overland Park, KS) or a Garmin global positioning system (GPS) MAP 76 unit (3D differential location; Garmin International, Olathe, KS) to measure all distances; (3) checked distance measurements by comparing the accuracy of the laser range finder and GPS unit to known distances every other week; (4) recorded the distance from the point to where the bird was first detected if the bird moved prior to the observer reaching the point; and (5) limited the duration of the count to 2 min.

Three observers worked separately to survey each point once from 5 April to 24 May 2008. We randomly assigned approximately one-third of the points on the east side of the installation and one-third on the west side to each observer. Surveys started 30 min after sunrise and continued until 4 hr after sunrise, when temperatures were ≥ 10 °C, wind speeds were ≤ 18 km hr⁻¹, and there was no precipitation. Observers recorded only detections of singing male Golden-cheeked Warblers, and if more than one male was detected at a point, they focused first on measuring the distance to the nearest bird. If observers could not determine a bird's location with reasonable certainty, they did not record the distance of detection.

HABITAT AND LANDSCAPE METRICS

We used the land-cover and land-use map based on the Texas Ecological Systems Classification (Missouri Resources Assessment Partnership 2009) to calculate proportion of forest type, forest-edge density, patch size, and proportion of forest cover. We used this map to fit models and make predictions instead of the map of potential habitat developed by Reemts and Teague (2007) because the Texas Ecological Systems Classification map is available statewide and thus more broadly applicable than their map. A visual comparison of these two maps revealed their correspondence in vegetation types is high.

Land-cover classes used in the Texas Ecological Systems Classification map were derived directly from decision-tree classification based on three dates of Landsat Thematic Mapper satellite imagery at a resolution of 30 m and environmental data derived from a digital elevation model. The map included four forest and woodland types: (1) coniferous evergreen forest and woodland ("juniper forest") where $>75\%$ of the relative tree cover was Ashe juniper; (2) mixed cold-deciduous forest and woodland of Texas red oak (*Q. buckleyi*), plateau live oak (*Q. fusiformis*), cedar elm (*Ulmus crassifolia*), post oak (*Q. stellata*), and Ashe juniper ("juniper-oak forest") where $\leq 50\%$ of the relative tree cover was Ashe juniper; (3) broadleaf evergreen (*Q. fusiformis*) forest and woodland ("broadleaf-evergreen forest") where $>75\%$ of the relative tree cover was plateau live oak; and (4) cold-deciduous forest and woodland of Texas red oak, cedar elm, sugar hackberry (*Celtis laevigata*), and post oak ("cold-deciduous forest") where $>75\%$ of the relative tree cover was cold-deciduous trees.

We used FRAGSTATS (McGarigal and Marks 1994) to calculate forest-edge density (m ha⁻¹) and proportion of forest type within a 100-m radius of each survey point, the area of the forest patch where the survey point was located, and proportion of forest cover within a 1-km radius of each survey point. To calculate forest-edge density and proportion of forest cover, we reclassified the original 15 land-cover classes as either forest (Ashe juniper, juniper-oak, broadleaf-evergreen, and cold-deciduous forest) or nonforest (barren/impervious, cold-deciduous shrub, crops, coniferous evergreen shrub, grass farm, grassland, open water, high-intensity urban, low-intensity urban, marsh, and swamp) cover and defined edge as the boundary between forest and nonforest. Forest-edge density was the length of forest edge in meters divided by the area of the landscape in hectares. We chose a 100-m radius for proportion of forest type and forest-edge density because the map of land cover and land use was not precise enough to support a more detailed analysis, and we truncated detections at 89 m to model detection probability as a function of distance. We chose a 1-km radius for proportion of forest cover as a compromise between the need to capture landscape effects and to minimize overlap of landscapes around survey points. To prevent the model's coefficient for forest-edge density from being too small, we divided values of forest-edge density by 100, so the coefficient for that variable represents a change in bird density for each 100 m ha⁻¹ change in forest-edge density rather than for each 1 m ha⁻¹ change.

STATISTICAL ANALYSES

We used a variation of the two-stage modeling approach presented by Buckland et al. (2009) to evaluate the effects of habitat and landscape variables on density while accounting for uncertainty in detection probability. First, we calculated detection probability from point-transect data recorded by distance sampling (Table 1) and a design-based estimate of density and abundance for the sampling frame. Second, we

TABLE 1. Number of points surveyed (n) and singing male Golden-cheeked Warblers detected (K) by observer on point-transect surveys on Fort Hood Military Installation, Texas, 2008. Detection probabilities (P), effective detection radius (EDR) in meters (m), and density (males ha⁻¹) adjusted for effective detection radius (D) are based on the most supported distance-sampling model for estimating detection probability and density of singing male Golden-cheeked Warblers and given by observer. Overall estimates of P , EDR, and D are for the entire sampling frame and account for observer-specific detection probabilities.

Observer	n	K	P	EDR (m)	D
1	168	53	0.33	51.50	0.38
2	158	54	0.26	45.00	0.54
3	163	47	0.46	60.17	0.25
Overall	489	154	0.36	52.22	0.39

fitted generalized linear models to predict density as a function of habitat and landscape variables (“density models”) and to calculate a model-based estimate of density and abundance for the sampling frame. We included the log of detection probability calculated during the first stage of the approach as an offset term so the model estimated density directly instead of detections per point (Buckland et al. 2009).

We used the program DISTANCE 6.0 (Thomas et al. 2010) to estimate density for the sampling frame on the basis of detection probabilities calculated from ungrouped point-transect survey data. We checked for violation of the assumptions associated with distance-sampling theory by plotting a frequency histogram of the raw detection data. To improve the model’s fit, we right-truncated data at 89 m, eliminating 10% of the detections (Buckland et al. 2001). We compared hazard-rate, half-normal, and uniform key functions without series-expansion terms and included all additive combinations of observer, day of year, and time of day, expressed as minutes after sunrise, as potential covariates with the most appropriate key function (Table 2). We specified observer as a factor covariate in the model and day of year and time of day as nonfactor covariates. We selected the most appropriate model for estimating detection probability and density by comparing detection-probability histograms, goodness-of-fit test statistics, and Akaike’s information criterion (AIC) values for each model.

We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate our hypotheses concerning the effects of proportion of forest type (juniper, juniper-oak, and broadleaf-evergreen forest), forest-edge density, patch size (log transformed), and proportion of forest cover

TABLE 2. Model-selection results for estimating probability of detection and density of singing male Golden-cheeked Warblers from ungrouped point-transect survey data on Fort Hood Military Installation, Texas, 2008. Key functions are half normal, hazard rate, or uniform. Covariates in the models include observer as a factor and time of day, expressed as minutes after sunrise, and day of year as continuous variables. The number of parameters (*K*) in each model includes the intercept. Models are ordered by increasing ΔAIC , and *P* values are from chi-squared goodness-of-fit tests.

Model	<i>K</i>	ΔAIC	<i>P</i>
Half normal + observer ^a	3	0.00	0.98
Half normal + observer + time of day + day of year	5	1.38	0.95
Half normal	1	1.79	0.69
Half normal + observer + day of year	4	1.92	0.96
Hazard rate	2	2.39	0.97
Half normal + day of year	2	2.49	0.59
Half normal + time of day	2	3.63	0.98
Hazard rate + observer	4	3.91	0.98
Half normal + observer + time of day	4	4.18	0.98
Half normal + time of day + day of year	3	4.21	0.98
Uniform	0	83.92	0.00

^aThe AIC_c value for the most supported model was 1354.71.

on density and to select the most appropriate model for calculating a model-based density estimate. Our set of a priori candidate models for density included a null model with only an intercept, a model with proportion of forest type, models with proportion of forest type and all possible two- and three-way combinations of forest-edge density, patch size, and proportion of forest cover, and a global model with all variables (Table 3). We log-transformed values of patch size because we hypothesized the effect of patch size should decrease as patch size increased and preliminary analyses indicated the log-transformed variable had more support than the nontransformed variable.

To assess multicollinearity, we calculated tolerance values for variables in the global density model (Allison 1999; PROC REG, SAS Institute, Cary, North Carolina) and checked for overdispersion in the data with the Pearson χ^2 test statistic for this model divided by degrees of freedom (Burnham and Anderson 2002). We fitted density models (proc GLIMMIX, SAS Institute, Cary, NC) with a Poisson response distribution, count as the response variable, and the log of detection probability from the most supported distance-sampling model (Table 2) as an offset term so it predicted density. We used Akaike’s information criterion for small sample sizes (AIC_c) to rank density models from the most to the least supported, given the data (Burnham and Anderson 2002). We calculated ΔAIC_c and Akaike weights (*w_i*) as measures of support for the density models.

We used the most supported density model to interpret effects and make predictions because it received strong support. Because generalized linear models make no allowance for error associated with estimation of detection probability, we used a parametric bootstrap procedure to estimate the model’s parameters and make predictions (Efron and Tibshirani 1993). We randomly selected values of detection probability from a normal

TABLE 3. Results of model selection examining habitat and landscape factors affecting density of singing male Golden-cheeked Warblers on Fort Hood Military Installation, Texas, 2008 (*n* = 489). *K* is the number of parameters in the model, AIC_c is Akaike’s information criterion for small sample sizes, ΔAIC_c is the scaled value of AIC_c, and *w_i* is the Akaike weight, which represents support for each model.

Model	<i>K</i>	ΔAIC_c	<i>w_i</i>
Forest type + edge density + forest cover ^a	6	0.00	0.43
Forest type + edge density + forest cover + patch size	7	1.79	0.18
Forest type + forest cover	5	2.28	0.14
Forest type + edge density	5	2.28	0.14
Forest type + forest cover + patch size	6	4.25	0.05
Forest type + edge density + patch size	6	4.26	0.05
Forest type	4	7.03	0.01
Forest type + patch size	5	8.56	0.01
Null	1	35.42	0.00

^aThe AIC_c value for the most supported model was 710.02.

distribution defined by the point estimate of detection probability and its standard error from the distance-sampling model and refit the density model with the generated values of detection probability as an offset term. We repeated this procedure 10 000 times, then calculated the mean and 95% confidence interval (CI) for parameters and predictions. Our estimates were conditional on both the most supported distance-sampling and density model identified by AIC and AIC_c , respectively, prior to the bootstrap. Except where otherwise noted, we interpret only coefficients with 95% CI that do not include zero. We generated predictions of the mean values of the covariates in the density model and over the range of each covariate while holding other covariates at their mean and generated a density map by predicting density for each pixel in the sampling frame.

We validated the density model by comparing its predictions to independent density estimates derived from intensive territory monitoring at two sites, of 213 and 250 ha. The protocol used for this monitoring was described by Peak (2011b). We predicted density for each pixel in the intensively monitored sites and compared it to observed density (number of territories ha^{-1}).

RESULTS

Observers recorded 154 detections of singing male Golden-cheeked Warblers during the 2-min counts (Table 1). The half-normal key function with no series-expansion term and observer as a covariate had the smallest AIC value, and results of the goodness-of-fit test indicated that it provided a good fit to the data (Table 2). The design-based density estimate for the sampling frame was 0.39 males ha^{-1} (95% CI = 0.34–0.45), corresponding to an estimated 7557 singing males (95% CI = 6581–8678).

Values of the explanatory variables varied considerably by survey point (Table 4). Initially, in the global density

model, multicollinearity of the variables representing proportion of each forest type was high, as indicated by tolerance values of 0.12–0.36. After we removed cold-deciduous forest as an explanatory variable, tolerance values ranged from 0.30 to 0.94 with only one value <0.40 , which we considered acceptable. The overdispersion parameter for the global model equaled 0.95, indicating the fit was adequate.

The most supported density model included proportion of forest type and forest-edge density within a 100-m radius of each survey point and proportion of forest cover within a 1-km radius of each survey point (Table 3). Comparison of ΔAIC_c values of this model and the next most supported model demonstrated the addition of patch size did not improve the model (Arnold 2010) and no other model had a $\Delta AIC_c < 2.00$, so we did not further consider the effect of patch size on density and did not average models. The proportions of juniper–oak forest within a 100-m radius and of forest within a 1-km radius had a positive effect on density, while forest-edge density within a 100-m radius had a negative effect (Table 5). The coefficient for proportion of juniper forest within a 100-m radius also was positive, but its 95% CI overlapped zero (Table 5). Density increased 190%, 119%, and 147% across the range of values for proportion of juniper–oak forest, juniper forest, and forest cover, respectively (Fig. 2). Density decreased 71% across the range of values for forest-edge density (Fig. 2).

Observers monitored 73 territories in the 213-ha site and 84 territories in the 250-ha site, resulting in density estimates of 0.343 and 0.338 males ha^{-1} , respectively (R. Peak, unpubl. data). Predicted densities from our model were 0.486 and 0.493 males ha^{-1} , representing 104 and 123 singing males, respectively. The mean predicted density for the intensively monitored sites (0.49 males ha^{-1}) was 44% greater than the mean observed density (0.34 males ha^{-1}). Extrapolation of mean observed density to our sampling frame resulted in an abundance estimate of 6597 singing male Golden-cheeked Warblers, which is 15% less than the estimate derived from

TABLE 4. Descriptive statistics for explanatory variables used in models examining density of singing male Golden-cheeked Warblers on Fort Hood Military Installation, Texas, 2008 ($n = 489$).

Variable	Median \pm SD	Minimum	Maximum
Proportion of juniper–oak forest ^a	0.68 \pm 0.36	0.00	1.00
Proportion of juniper forest ^a	0.16 \pm 0.29	0.00	1.00
Proportion of broadleaf–evergreen forest ^a	0.01 \pm 0.05	0.00	0.95
Forest edge density (m ha^{-1})	38.60 \pm 66.40	0.00	324.90
Patch size (ha)	893.20 \pm 1284.20	0.50	3515.70
Proportion of forest cover ^b	0.73 \pm 0.18	0.16	1.00

^aWithin a 100-m radius of each survey point.

^bWithin a 1-km radius of each survey point.

TABLE 5. Coefficients and 95% confidence intervals (CI) for explanatory variables based on the most supported model for predicting density of singing male Golden-cheeked Warblers on Fort Hood Military Installation, Texas, 2008. Confidence intervals incorporate error in estimation of detection probability from the most supported distance-sampling model through 10 000 iterations of a parametric bootstrap procedure.

Variable	Coefficient	95% CI
Intercept	–2.71	–3.98, –1.42
Proportion of juniper–oak forest	1.24	0.07, 2.36
Proportion of juniper forest	0.92	–0.29, 2.12
Proportion of broadleaf–evergreen forest	–4.20	–0.29, 2.12
Forest edge density (m ha^{-1}) ^a	–0.45	–0.91, –0.01
Proportion of forest cover	1.13	0.02, 2.21

^aForest-edge density was rescaled so the coefficient represents change in bird density for every 100 m ha^{-1} change in forest-edge density.

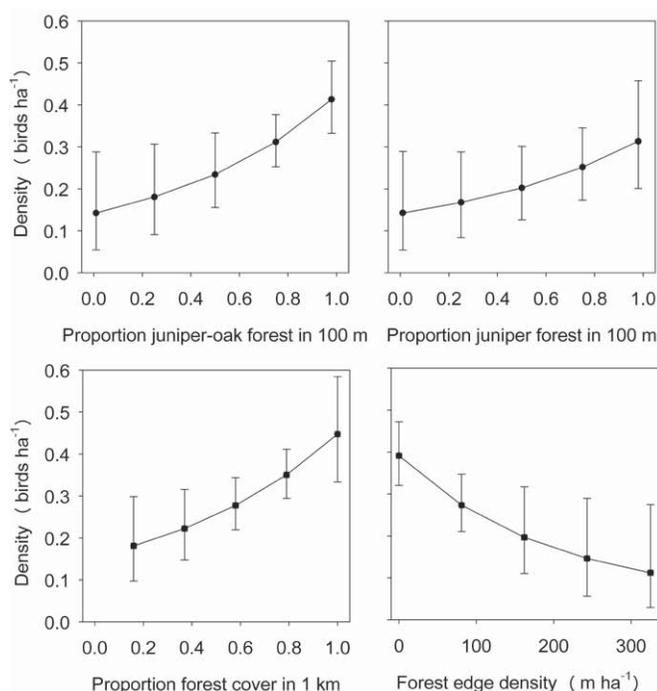


FIGURE 2. Effects of proportion of juniper–oak forest, juniper forest, and forest-edge density (m ha^{-1}) within a 100-m radius of each survey point, and proportion of forest cover within a 1-km radius of each survey point on density ($\text{birds ha}^{-1} \pm 95\%$ confidence intervals) of singing male Golden-cheeked Warblers on Fort Hood Military Installation, Texas, 2008.

distance sampling but within the 95% CI. The mean predicted density for all pixels in the sampling frame was 0.39 singing males ha^{-1} (range 0.00–0.72; Fig. 1B), which when multiplied by the area of the sampling frame yields 7571 singing males, 14 greater than the design-based estimate derived from distance sampling.

DISCUSSION

To evaluate the effect of habitat and landscape factors on density of singing male Golden-cheeked Warblers, we included detection probability calculated from point-transect survey data as an offset term in generalized linear models. Density was positively affected by proportion of juniper–oak forest, which is consistent with our prediction and results of previous studies (Kroll 1980, Ladd 1985, DeBoer and Diamond 2006, Emrick et al. 2010). Furthermore, Dearborn and Sanchez (2001) found that patches in which Golden-cheeked Warblers nest were characterized by a dense cover of Ashe juniper above a height of 2 m. We believe the positive relationship between density and proportion of juniper–oak forest reflects strips of peeling bark from mature Ashe juniper trees being an important component of this species' nests (Pulich 1976), and

both Ashe juniper and oak trees are important substrate for its foraging (Kroll 1980, Ladd 1985, Beardmore 1994).

Density also was positively affected by proportion of juniper forest, but the magnitude of this effect was less than that of juniper–oak forest, and its 95% CI included zero. The Texas Ecological Systems Classification map from which we calculated proportion of forest type classified juniper forest as areas where >75% of the relative tree cover was Ashe juniper and juniper–oak forest as areas where $\leq 50\%$ of the relative tree cover was Ashe juniper. Hence variation in density between forest types could reflect variation in habitat quality as a result of differences in percentages of Ashe juniper. Further investigation of the effects of forest type on Golden-cheeked Warbler density and other demographic variables is needed.

As predicted, forest-edge density affected Golden-cheeked Warbler density negatively. Reports of the effect of edge on Golden-cheeked Warbler occurrence have been mixed, with a negative relationship found in some cases (DeBoer and Diamond 2006, Sperry 2007) but not others (Kroll 1980, Magness et al. 2006). Density of other passerines nesting in forest also is lower near habitat edges (Kroodsma 1982, Van Horn et al. 1995). A decrease in density with increasing density of forest edges could be a behavioral or demographic response to nest predation and brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) near forest edges. A general pattern of increased nest predation near habitat edges has been documented for many forest passerines (Paton 1994, Andr n 1995, Hartley and Hunter 1998, Sisk and Battin 2002; but see Lahti 2001), including the Golden-cheeked Warbler (Peak 2007, Reidy et al. 2009).

We also found strong support for our prediction that proportion of forest cover affected density positively, which is consistent with patterns in Golden-cheeked Warbler occurrence (DeBoer and Diamond 2006, Magness et al. 2006, Collier et al. 2010), as well as with abundance of other migratory passerines nesting in forest (Flather and Sauer 1996, Howell et al. 2000, Thompson et al. 2012). A positive relationship between density and proportion of forest cover could be a bird's response to increased quantity of suitable habitat (Whitcomb et al. 1981, Temple and Cary 1988) or to factors that affect habitat quality, such as microhabitat characteristics (Lynch and Whigham 1984), food availability (Blake 1983, Burke and Nol 1998), or changes in levels of nest predation associated with proportion of forest cover (Donovan et al. 1995, Robinson et al. 1995, Tewksbury et al. 1998) and its effect on the abundance and activity patterns of nest predators (Donovan et al. 1997, Chalfoun et al. 2002, Thompson et al. 2002). Texas rat snakes (*Elaphe obsoleta lindheimeri*) are the most frequent predator of Golden-cheeked Warbler nests (Stake et al. 2004) and they use forest edges preferentially (Sperry et al. 2009).

At the intensively monitored sites, mean predicted density was 44% greater than mean observed density. Mean predicted density may have been greater because the

intensive territory monitoring failed to count all territorial males present. However, given the high proportion of color-banded individuals and intensity of the effort, the potential for undercounting was small. The density model's performance at the intensively monitored sites also could reflect a positive bias. Field evaluations of the distance-sampling method have reported positive biases equal to or greater than those we observed and attributed them to location error (Allredge et al. 2008) and the species' behavior and movement patterns (Buckland 2006, Cimprich 2009, Peak 2011b). Alternatively, the model's performance at the intensively monitored sites may not be representative of its performance across the sampling frame because of sampling error; the two sites represent only 2% of the sampling frame. Furthermore, mean predicted density for the intensively monitored sites (0.49 males ha⁻¹) was greater than that for the sampling frame (0.39 males ha⁻¹), suggesting densities in the study sites are positively biased. We believe estimates may be positively biased for a combination of these reasons. Nonetheless, we believe our approach has merit because it allowed us to account for factors known to affect detection probability, such as distance (Bibby and Buckland 1987, Buckland et al. 2001) and interobserver variability (Ralph and Scott 1981, Balph and Romesburg 1986, Norvell et al. 2003) and to examine the effects of habitat and landscape factors on density, both of which allow for more robust spatial and temporal comparisons regarding the effect of management or environmental disturbance on densities.

We studied the effects of remotely sensed habitat and landscape factors on the density of singing male Golden-cheeked Warblers, which allowed us to predict density as a function of these variables and map the result over a large area. Use of large-scale models for conservation planning is essential because landscape patterns, such as edge effects and area sensitivity, affect wildlife populations (Paton 1994, Robinson et al. 1995). Nevertheless, smaller-scale vegetation characteristics, such as canopy cover, tree species composition, and density and age of a forest stand also affect Golden-cheeked Warbler density (Kroll 1980, Ladd 1985, Wahl et al. 1990, Dearborn and Sanchez 2001). Consequently, further investigation of these factors is needed for the potential effects of succession, environmental disturbance, and management on density of this species to be understood.

We found strong support for the positive effects of proportion of juniper–oak forest at the habitat scale and forest cover at the landscape scale and for the negative effect of forest-edge density at the habitat scale on Golden-cheeked Warbler density. Consequently, management that protects large contiguous patches of juniper–oak forest and reduces edge between forest and nonforest cover should benefit Golden-cheeked Warblers. This could include management such as controlling populations of browsing animals, controlling oak wilt, and promoting reforestation of cleared areas such as fence rows, trails, grazed areas, pastures, and logged areas. Additionally, our density model can

be used to assess the effects of proposed military training and environmental disturbance on warbler densities.

Even though our density model was developed from count data recorded in 2008 only, we believe broader inferences from it are possible because abundance estimates that breeding season are within the range of those observed at Fort Hood over the last 10 years (Peak 2011a). However, point-transect surveys in additional years would allow for stronger inference than is possible from one year and permit assessments of trends in abundance in a spatially explicit way. Finally, because density is not always positively correlated with other measures of demography (Van Horne 1983, Vickery et al. 1992, Bock and Jones 2004), fitness-related metrics such as survival and productivity in addition to density should be used to assess habitat quality and prioritize sites for recovery.

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