THE CONDOR
Ornithological Applications
www.cooper.org

Volume 116, 2014, pp. 546–559
DOI: 10.1650/CONDOR-14-51.1

RESEARCH ARTICLE

Seasonal productivity and nest survival of Golden-cheeked Warblers vary with forest type and edge density

Rebecca G. Peak[1]* and Frank R. Thompson III[2]

[1] U.S. Army Garrison–Fort Hood, Directorate of Public Works, Fort Hood, Texas, USA
[2] U.S.D.A. Forest Service, Northern Research Station, University of Missouri, Columbia, Missouri, USA
* Corresponding author: rpeak1969@gmail.com

Submitted March 17, 2014; Accepted July 25, 2014; Published October 1, 2014

ABSTRACT

Knowledge of the demography and habitat requirements of the endangered Golden-cheeked Warbler (*Setophaga chrysoparia*) is needed for its recovery, including measures of productivity instead of reproductive indices. We report on breeding phenology and demography, calculate model-based estimates of nest survival and seasonal productivity and evaluate support for relationships with forest type, forest edge density, day of year, and year, and determine correspondence in these 2 measures of reproductive success. Males arrived in early March. Females laid the first egg of the first clutch in early April, made up to 5 nesting attempts, and completed nesting by mid-June. The most-supported nest survival model included day of year, proportion of juniper and juniper–oak forest within a 100-m radius of each nest, and the interactive effect of year and forest edge density. The most-supported seasonal productivity model included proportion of each forest type and the interactive effect of year and forest edge density. Seasonal productivity increased from 1.38 to 3.96 fledglings per territory and from 1.38 to 2.40 fledglings per territory across 0.00 to 0.87 and 0.00 to 1.00 proportion of juniper and proportion of juniper–oak forest, respectively. Seasonal productivity ranged from 1.86 to 3.12 fledglings per territory in 2010 and 2004, respectively (mean $\pm$ SD = 2.36 $\pm$ 0.37). Correlations between nest survival and seasonal productivity were strong when we controlled for the effect of year indicating demographic parameters other than nest survival, particularly renesting, double brooding, and polygyny, made an important contribution to actual seasonal productivity. The similarity in relationships of both measures of reproductive success with forest type and edge density and parallel findings for density with these habitat metrics reported in other studies provide strong rationale for protecting sites with high proportions of juniper and juniper–oak forest and less forest edge to further recovery efforts for the Golden-cheeked Warbler.

Keywords: breeding demography, breeding phenology, forest edge density, forest type, nest survival, seasonal productivity, temporal factors, *Setophaga chrysoparia*

La productividad estacional y la supervivencia del nido de *Setophaga chrysoparia* varían con el tipo de bosque y la densidad de borde

RESUMEN

Se necesitan conocer la demografía y los requerimientos de hábitat de la especie en peligro *Setophaga chrysoparia* para su recuperación, incluyendo mediciones de productividad en lugar de índices reproductivos. Brindamos resultados de fenología reproductiva y de demografía, calculamos estimaciones de supervivencia del nido y productividad estacional basadas en modelos y evaluamos las relaciones con el tipo de bosque, la densidad de borde de bosque, el día del año y el año, y determinamos la correspondencia en estas dos medidas de éxito reproductivo. Los machos llegaron a principios de marzo. Las hembras pusieron el primer huevo de la primera nidada a principios de abril, realizaron hasta cinco intentos de nidificación y completaron la nidificación hasta mediados de junio. El modelo de supervivencia del nido con mayor soporte incluyó el día del año, la proporción de bosque de enebro y enebro-roble dentro de un radio de 100 m desde cada nido, y el efecto interactivo del año y la densidad de borde de bosque. El modelo de productividad estacional con mayor soporte incluyó la proporción de cada tipo de bosque y el efecto interactivo del año y la densidad de borde de bosque. La productividad estacional aumentó de 1.38 a 3.96 volantones por territorio y de 1.38 a 2.40 volantones por territorio a través de 0.00 a 0.87 y de 0.00 a 1.00 de proporción de enebro y de proporción de bosque de enebro-roble, respectivamente. La productividad estacional varió entre 1.86 y 3.12 volantones por territorio en 2010 y 2004, respectivamente (media $\pm$ DE = 2.36 $\pm$ 0.37). Las correlaciones entre supervivencia del nido y productividad estacional fueron fuertes cuando controlamos por el efecto del año, indicando que los parámetros demográficos distintos de la supervivencia del nido, particularmente la nidificación repetida, la nidada doble y la poliginia contribuyeron de modo importante a la productividad estacional. La similitud en las relaciones de ambas medidas de éxito reproductivo con el tipo de bosque y la densidad de borde, y los hallazgos

paralelos de densidad usando estas métricas de hábitat presentados en otros estudios, brindan un fuerte argumento para proteger los sitios con alta proporción de bosque de enebro y enebro-roble y menos borde de bosque, permitiendo impulsar los esfuerzos de recuperación de *S. chrysoparia*.

Palabras clave: demografía reproductiva, densidad de borde de bosque, factores temporales, fenología reproductiva, productividad estacional, *Setophaga chrysoparia*, supervivencia del nido, tipo de bosque

INTRODUCTION

Despite ongoing advances in our understanding of migratory birds' year-round ecology, there are still relatively few bird species for which we have accurate estimates of habitat-specific demographic parameters (Faaborg et al. 2010). Accurate estimation of parameters such as survival and productivity requires intensive field studies of individually marked birds, which by necessity are conducted at a local scale (Sherry and Holmes 1999, Anders and Marshall 2005, Faaborg et al. 2010). Reproductive indices do not always correlate well with productivity because many factors other than nest survival influence total number of fledglings per territory produced in a season (Fauth 2001, Thompson et al. 2001). Researchers have developed models that incorporate nest survival and aspects of breeding demography to predict productivity (Ricklefs 1970, Pease and Grzybowski 1995, Powell et al. 1999, Farnsworth and Simons 2001), but these models may produce biased estimates of productivity by assuming a fixed number of renesting attempts, constant nest survival throughout the season, or the same number of fledglings from every nest. Furthermore, some of these models do not provide an associated measure of variation in productivity among individuals within a population. Accurate estimates of productivity and its variation are critical for modeling population growth rate (Conroy et al. 1995).

The Golden-cheeked Warbler (*Setophaga chrysoparia*; Figure 1) is a federally endangered Neotropical migratory songbird with a restricted breeding range of 27 counties in central Texas (Groce et al. 2010). Its breeding habitat is old-growth and mature second-growth juniper–oak (*Juniperus ashei–Quercus* spp.) woodlands (Ladd and Gass 1999). Ashe juniper is often the dominant tree species found in breeding habitat (Pulich 1976, Dearborn and Sanchez 2001, Emrick et al. 2010), and strips of its peeling bark are important components of Golden-cheeked Warbler nests (Pulich 1976). Spanish oak (*Quercus buckleyi*) and plateau live oak (*Quercus fusiformis*) are the most common broadleaf species found in breeding habitat, although a variety of other oak and deciduous tree species also occur across the breeding range (Ladd and Gass 1999). Both Ashe juniper and oak species provide important foraging and nesting substrate for Golden-cheeked Warblers (Kroll 1980, Ladd 1985, Beardmore 1994).

The U.S. Fish and Wildlife Service (1992) listed the Golden-cheeked Warbler as endangered in 1990 on an emergency basis because of concerns over habitat loss and fragmentation of breeding habitat attributed to urban development, agriculture, and construction of flood-control impoundments. The Golden-cheeked Warbler recovery plan lists the need to "determine habitat requirements and selection patterns in the breeding range" as a task necessary to attain the recovery objective of delisting (U.S. Fish and Wildlife Service 1992: Task 1.31). Models developed to predict occupancy as a function of remotely sensed habitat metrics have found that occurrence is positively associated with percent juniper–oak woodland (Magness et al. 2006), patch size (DeBoer and Diamond 2006, Magness et al. 2006, Collier et al. 2010, Mathewson et al. 2012), and vegetation height and canopy cover (Farrell et al. 2013). These models are useful tools for determining the spatial distribution of habitat where 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 of habitat quality. Often it is not practical to assess habitat quality directly, so habitat-specific demographic measures are used as indicators of habitat quality for purposes of avian conservation and habitat management (reviewed in Johnson 2007). Peak and Thompson (2013) examined density of singing male Golden-cheeked Warblers on Fort Hood Military Installation as a function of remotely sensed habitat metrics and found density was positively associated with proportion of juniper and juniper–oak forest within a 100-m radius of each point and with proportion of forest cover within a 1-km radius, but negatively associated with forest edge density within a 100-m radius. Because density is not always positively correlated with habitat quality (Van Horne 1983, Vickery et al. 1992, Bock and Jones 2004), other demographic measures such as productivity and survival should be used in addition to density when assessing habitat quality. In addition to determining habitat requirements in the breeding range, the Golden-cheeked Warbler recovery plan identifies studying the relationship of predators to reproductive success and the effects of habitat fragmentation on reproductive success as tasks necessary to attain the recovery objective of delisting (U.S. Fish and Wildlife Service 1992: Tasks 1.24 and 1.32). Studies using video surveillance have identified Texas rat snakes (*Pantherophis obsoletus*) as the most frequent

FIGURE 1. Golden-cheeked Warbler (*Setophaga chrysoparia*) pair feeding 10-day-old nestlings.

predator of Golden-cheeked Warbler nests (Stake et al. 2004, Reidy et al. 2008). Studies have examined the relationship between Golden-cheeked Warbler reproductive success and a variety of edge-related metrics including forest edge density (Peak 2007), open edge density, proximity to edge, percent open habitat, and percent developed habitat (Reidy et al. 2009), patch size (Coldren 1998, Maas-Burleigh 1998, Butcher et al. 2009), and edge-to-area ratio of a patch (Campomizzi et al. 2012). No one has examined the relationship between nest survival or seasonal productivity and proportion of juniper–oak woodland at the habitat-patch scale; as these measures approach one, the amount of available habitat is maximized, habitat is less fragmented, and there is less edge. Understanding the relationship between reproductive success and proportion of juniper–oak woodland at the habitat-patch scale will enable managers to parameterize habitat-based population models that can be used to assess the status of the species and prioritize sites for recovery.

We report on aspects of Golden-cheeked Warbler breeding phenology and demography, calculate model-based estimates of nest survival and seasonal productivity and evaluate support for relationships with forest type, forest edge density, day of year, and year, and determine correspondence in these two measures of reproductive success. We predicted: (1) forest edge density should be negatively related to nest survival and seasonal productivity because Texas rat snakes preferentially use forest edges (Sperry et al. 2009); (2) proportion of juniper–oak and juniper forest should be positively related to nest survival and seasonal productivity because it is inversely related to edge and both Ashe juniper and oaks provide important foraging substrate for Golden-cheeked Warblers (Kroll 1980, Ladd 1985, Beardmore 1994); (3) day of year should be negatively related to nest survival because snake predation is positively correlated with day of year (Stake 2003); and (4) nest survival and seasonal productivity should vary among years reflecting annual changes in prey or predator abundance patterns (Sherry and Holmes 1992, Holmes et al. 1996, Ostfeld and Keesing 2000).

METHODS

Study Area

Fort Hood Military Installation is an 87,890-ha active U.S. Army military installation located in Bell and Coryell Counties, Texas (31°12′N, 97°44′W). The installation spans the Crosstimbers and Southern Tallgrass Prairie and Edwards Plateau ecoregions (The Nature Conservancy 1997). Fort Hood contains an estimated 24,650 ha of potential Golden-cheeked Warbler habitat (Peak and Thompson 2013) and supports the largest known population under a single management agency (Ladd and Gass 1999). Researchers have studied the demography of Golden-cheeked Warblers on the installation since 1991 (U.S. Fish and Wildlife Service 1993).

Field Methods

Capturing and marking individuals. We collected phenological and demographic data from 5 study sites ranging in size from 164 to 250 ha during the 2003–2013 breeding seasons. Researchers established the study sites as part of a long-term intensive demographic monitoring study implemented in accordance with the terms and conditions outlined in the Biological Opinion (U.S. Fish and Wildlife Service 1993). We used recorded vocalizations of Golden-cheeked Warblers to capture at least one individual from each territory on the study sites. We banded all Golden-cheeked Warblers we captured, regardless of age or sex, with a U.S. Geological Survey aluminum band and a unique combination of plastic-colored leg bands. At the banding location, we recorded coordinates with a GPS. We aged and sexed birds using characteristics described in Pyle (1997) and Peak and Lusk (2009, 2011).

Nest searching and monitoring. We observed warblers once every 5 d for $\geq$2 h from the beginning of March to mid-June to collect data about their behavior, movement patterns, and reproductive activities. Using a GPS unit, we recorded locations to delineate territories and to identify areas between territories to search for undetected males. We used adult behavioral cues to locate nests. Once a nest was located, we monitored it from a distance of $\geq$10 m at least every other day to determine the date the female laid the first egg of the first clutch, number of nesting attempts per territory, number of days between renesting attempts, and date the last nesting attempts were completed. We conducted 25-minute observations of nests daily as the

estimated hatching date approached and made multiple daily nest checks as the estimated fledging date approached to ensure we recorded the correct stage and status of the nest, including number of fledglings. Heights and locations of nests often precluded us from seeing nest contents, so we used parental activity (laying, incubation, or feeding) to assess status as successful or failed.

In the late 1980s, managers initiated Brown-headed Cowbird (*Molothrus ater*) control programs (i.e. trapping and shooting) on Fort Hood and in other parts of the Golden-cheeked Warbler breeding range (Eckrich et al. 1999, Texas Parks and Wildlife Department 2014). The programs were developed in response to high rates of brood parasitism of Black-capped Vireo (*Vireo atricapillus*) nests across their breeding range (U.S. Fish and Wildlife Service 1991). These programs continued over the duration of this study. Video surveillance studies have found that Brown-headed Cowbirds do not pose a serious threat to Golden-cheeked Warbler nest survival (Stake et al. 2004, Reidy et al. 2008), so we did not consider the effects of parasitism on nest survival or seasonal productivity.

We considered a nesting attempt complete when all nestlings fledged or the adults abandoned the nest prior to the fledging date. We confirmed fledging by observing nestlings leaving the nest or by observing color banded adults carrying food either to fledglings or repeatedly to an area near the nest from which we heard begging calls. If no fledglings were located, we considered the nest to have failed and began searching for a renesting attempt. We included data for all nests monitored during the 2003–2013 breeding seasons in the nest survival analysis. We used a subset of territories for which we monitored every nesting attempt to examine seasonal productivity, measured as total number of fledglings per territory produced in a season. Hence, we believe our observed seasonal productivity provides an accurate estimate of actual seasonal productivity because we accounted for renesting attempts, double brooding, and polygyny (Fauth 2001, Thompson et al. 2001).

Habitat metrics. We calculated the proportion of juniper and juniper–oak forest within a 100-m radius of each nest because they represent breeding habitat and are important predictors of density of singing male Golden-cheeked Warblers on Fort Hood (Peak and Thompson 2013). We mapped the distribution of coniferous evergreen forest and woodland ("juniper forest") and mixed cold-deciduous forest and woodland ("juniper–oak forest") from the Texas Ecological Systems Classification (Missouri Resources Assessment Partnership 2009, Peak and Thompson 2013). We calculated forest edge density (m ha^{-1}) using a vegetation map derived from Digital Orthophotography Quarter Quadrangles as the base data layer and Landsat Thematic Mapper 30 m resolution imagery, abiotic data derived from a 10-m digital elevation model, and field data as ancillary data (Pacific Meridian Resources, Atlanta, Georgia, USA 1998). We used this map to calculate forest edge density instead of the Texas Ecological Systems Classification map because it mapped patches at a higher resolution which more accurately depicted boundaries between land-cover classes (i.e. forest edge).

We used FRAGSTATS version 3.3 (McGarigal et al. 2002) to calculate forest edge density and proportion of juniper and juniper–oak forest within a 100-m radius of each nest. We defined edge as the boundary between forest and any other land-cover class, which most often was bare ground or grassland. We chose a 100-m radius around each nest to determine proportion of juniper and juniper–oak forest and forest edge density because this was the finest level possible from our land-cover maps. This scale also corresponds to the appropriate spatial scale for ecology of rat snakes (Weatherhead and Hoysack 1989, Durner and Gates 1993, Sperry et al. 2008). For the seasonal productivity analysis, we related the number of fledglings per territory produced in a season to the averaged proportion of juniper and juniper–oak forest and forest edge density for all nests in a territory.

Statistical Analyses

Using data from all years, we calculated mean (minimum, maximum) arrival date of males to breeding sites, initiation date of first clutch of the breeding season, completion date of nesting attempts, and length of breeding season (i.e. date first egg of first clutch was laid to date last nesting attempt was completed). We calculated mean (minimum, maximum, $\pm$ SD) number of renesting attempts, of days between renesting attempts, of days between first and second broods, and of fledglings per territory from the subset of territories for which we monitored every nesting attempt. We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate support for a priori candidate models that represented our hypotheses concerning the relationship between habitat and temporal factors and Golden-cheeked Warbler nest survival and seasonal productivity. Our set of a priori candidate models for nest survival included additive combinations of year, cubic effect of day of year (day of year + day of $year^2$ + day of $year^3$), proportion of juniper forest, proportion of juniper–oak forest, and forest edge density or models with the interactive effect of year and forest edge density (Table 1). We included the cubic effect of day of year in nest survival models because Golden-cheeked Warbler nest survival decreases nonlinearly as the breeding season progresses (Peak 2007, Reidy et al. 2009). We included the interactive effect of year and forest edge density because nest survival generally decreases with increasing forest edge density (Peak 2007, Reidy et al. 2009), but we

TABLE 1. Results of model selection examining the relationship between habitat and temporal factors and nest survival (2003–2013; $n = 9{,}806$) and seasonal productivity (2006–2013; $n = 423$) for Golden-cheeked Warblers on Fort Hood Military Installation, Texas. Forest type is proportion of juniper and juniper–oak forest within a 100-m radius of each nest for the nest survival analysis and for all nests in a territory for the seasonal productivity analysis, 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	K	ΔAIC_c	w_i
Nest survival			
Day of year + day of year^2 + day of year^3 + forest type + year[a]	16	0.00	0.48
Day of year + day of year^2 + day of year^3 + forest type + forest edge density*year	27	0.78	0.32
Day of year + day of year^2 + day of year^3 + forest type + forest edge density + year	17	2.01	0.17
Day of year + day of year^2 + day of year^3 + year	14	7.44	0.01
Day of year + day of year^2 + day of year^3 + forest edge density*year	25	7.48	0.01
Day of year + day of year^2 + day of year^3 + forest edge density + year	15	9.03	0.01
Forest type + year	13	20.33	0.00
Year	11	28.53	0.00
Seasonal productivity			
Forest type + forest edge density * year [b]	18	0.00	0.81
Forest edge density * year	16	4.76	0.08
Forest type + forest edge density + year	11	4.98	0.07
Forest type + year	10	6.15	0.04
Forest edge density + year	9	11.25	0.00
Year	8	1194	0.00

[a] The AIC_c value for the most-supported model was 3065.24.
[b] The AIC_c value for the most-supported model was 1851.30.

hypothesized the relationship between these variables would vary among years reflecting annual changes in predator or prey abundance patterns. Our set of a priori candidate models for seasonal productivity included the same candidate models as for nest survival except we did not consider the cubic effect of day of year because seasonal productivity was calculated for the entire breeding season (Table 1).

We evaluated the goodness-of-fit of the global nest survival model with a Hosmer and Lemeshow (2000) goodness-of-fit test and the global seasonal productivity model using a k-fold cross validation (Boyce et al. 2002). To assess multicollinearity in the global models, we examined tolerance values for the covariates (Allison 1999; PROC REG, SAS Institute, Cary, North Carolina, USA) and checked for overdispersion in the data by examining the Pearson χ^2 test statistic for the global models divided by degrees of freedom (Burnham and Anderson 2002).

We fitted logistic-exposure models (Shaffer 2004, Shaffer and Thompson 2007; proc GENMOD, SAS Institute) to predict nest survival as a function of the covariates and to calculate model-based estimates of nest survival. We fitted generalized linear models with a Poisson distribution to predict seasonal productivity as a function of the covariates (PROC GLIMMIX, SAS Institute). We used Akaike's information criterion for small sample sizes (AIC_c) to rank models from the most to the least supported given the data (Burnham and Anderson 2002). For the nest survival analysis, we used effective sample size (Rotella et al. 2004) to compute AIC_c. We calculated model-averaged nest survival and seasonal productivity estimates based on a confidence set of models with a $\Delta AIC_c < 4$ and that did not include redundant models when we removed uninformative parameters from otherwise competitive models (Burnham and Anderson 2002, Arnold 2010). We calculated daily survival rates as a function of day of year and forest edge density and seasonal productivity as a function of forest edge density based on the confidence set of models by incrementally varying the covariate of interest across its range of observed values while holding the other covariates at their observed means (Shaffer and Thompson 2007). For proportion of juniper and juniper–oak forest, we covaried their proportions within their observed range such that they did not sum to >1. We estimated period nest survival as the daily survival rate expanded for the entire nesting cycle of 25 days (Shaffer and Thompson 2007). We calculated Pearson correlation coefficients between predicted seasonal productivity and period nest survival by year and across the values of the habitat covariates supported in the models to determine the correspondence in these 2 measures of reproductive success. We report values as mean (minimum–maximum) or (± SD).

We created a map of seasonal productivity for Fort Hood by predicting seasonal productivity for each 10-m pixel in potential Golden-cheeked Warbler breeding habitat (Peak and Thompson 2013). To calculate habitat covariate values for each pixel, we used a moving window

TABLE 2. Descriptive statistics for covariates used in models examining the relationship between habitat and temporal factors and nest survival (2003–2013; $n = 9{,}806$) and seasonal productivity (2006–2013; $n = 423$) for Golden-cheeked Warblers on Fort Hood Military Installation, Texas. Day of year is the ordinal date of a given year. Observation interval is the number of days between nest checks. Forest edge density is the length of forest edge in meters divided by the area of the landscape in hectares.

Variable	Mean ± SD	Minimum	Maximum
Nest survival			
Day of year	116.00 ± 15.87	82.00	174.00
Observation interval (days)	1.00 ± 0.56	1.00	6.00
Forest edge density (m ha^{-1})[a]	23.00 ± 11.67	0.00	43.00
Proportion of juniper–oak forest[a]	0.90 ± 0.18	0.00	1.00
Proportion of juniper forest[a]	0.03 ± 0.10	0.00	0.87
Seasonal productivity			
Forest edge density (m ha$^{-1)a}$	21 ± 11.85	0.04	40.45
Proportion of juniper–oak forest[a]	0.90 ± 0.18	0.00	1.00
Proportion of juniper forest[a]	0.03 ± 0.09	0.00	0.87

[a] Within a 100-m radius of each nest.

with the same radius used to calculate habitat covariates for each nest. We used the raster calculator function in ArcGIS version 9.3, the model-averaged coefficients from the most-supported seasonal productivity model, and the habitat covariate values for each pixel to calculate seasonal productivity. Because the most-supported seasonal productivity model included year, we equally weighted the 11 years of the study and used the result to make our predictions.

RESULTS

Mean arrival date for males was 7 March (29 February–15 March, $n = 17$ males). Mean date females laid the first egg of their first clutch was 7 April (22 March–23 April, $n = 255$ nests). Mean date pairs completed nesting was 12 June (4 June–22 June, $n = 11$ years). Mean length of breeding season was 65 days ($n = 11$ years). Females made up to 5 nesting attempts in a breeding season if a previous attempt was not successful (mean = 1.37 nesting attempts, ± 0.65, $n = 423$ territories) with a mean of 6 days between when the previous nest failed and the first egg was laid in the subsequent attempt (3–10 days, ± 1.24, $n = 87$ nests). Mean number of days between first and second broods was 8 days (5–12 days, ± 2.44, $n = 13$ nests). Mean number of fledglings per territory for which we monitored all nesting attempts was 2.36 (0–11 fledglings, ± 0.37, $n = 423$ territories).

We monitored 834 nests from 2003 to 2013 for an effective sample size of 9,806. Values of the covariates varied considerably among nests (Table 2). Tolerance values for all variables in the nest survival models were ≥0.54, indicating multicollinearity was not a problem (Allison 1999). There was no evidence of lack of fit of the global nest survival model based on the Hosmer and Lemeshow (2000) goodness-of-fit test ($\chi^2_8 = 4.93$, $P = 0.77$) and the overdispersion parameter ($\hat{c} = 1.02$).

The most-supported nest survival model included cubic effect of day of year, proportion of juniper forest, proportion of juniper–oak forest, and year (Table 1). The second- and third-ranked models included an interactive effect of year and forest edge density and an additive effect of these 2 covariates, respectively. We excluded the third-ranked model from the confidence set because the addition of the additive effect of forest edge density did not overcome the 2 AIC–point penalty associated with an additional parameter (Arnold 2010). We calculated model-averaged predictions of nest survival and unconditional 95% confidence intervals (95% CI) using the 2 most-supported nest survival models.

There was a strong relationship between cubic effect of day of year and period nest survival; period nest survival decreased 100% across the observed range of days for active nests (Figure 2). Overall, the relationship between forest edge density and period nest survival was negative, but the strength of the relationship varied among years. Period nest survival decreased 7% across the observed range of forest edge density within a 100-m radius of nests for all years combined, but decreased as much as 9% in 2003 and 2010 to as little as 4% in 2004 (Figure 3A). The proportion of juniper forest within a 100-m radius had a larger effect size than the proportion of juniper–oak forest. Period nest survival was 0.07 when proportion of juniper and juniper–oak forest within 100-m radius were zero and increased to 0.65 and 0.32 when proportion of juniper and juniper–oak forest was at maximum, 0.87 and 1.0, respectively, and the other forest type was held at zero. This represented an increase in period nest survival of 775% and 418% across the observed range of proportion of juniper and juniper–oak forest, respectively (Figure 4). Period nest survival varied among years from as much as 0.59 in 2004 to as little as 0.24 in 2010 (Figure 5). The mean of the annual daily and period nest survival estimates were 0.96 (± 0.01) and 0.37 (± 0.10), respectively.

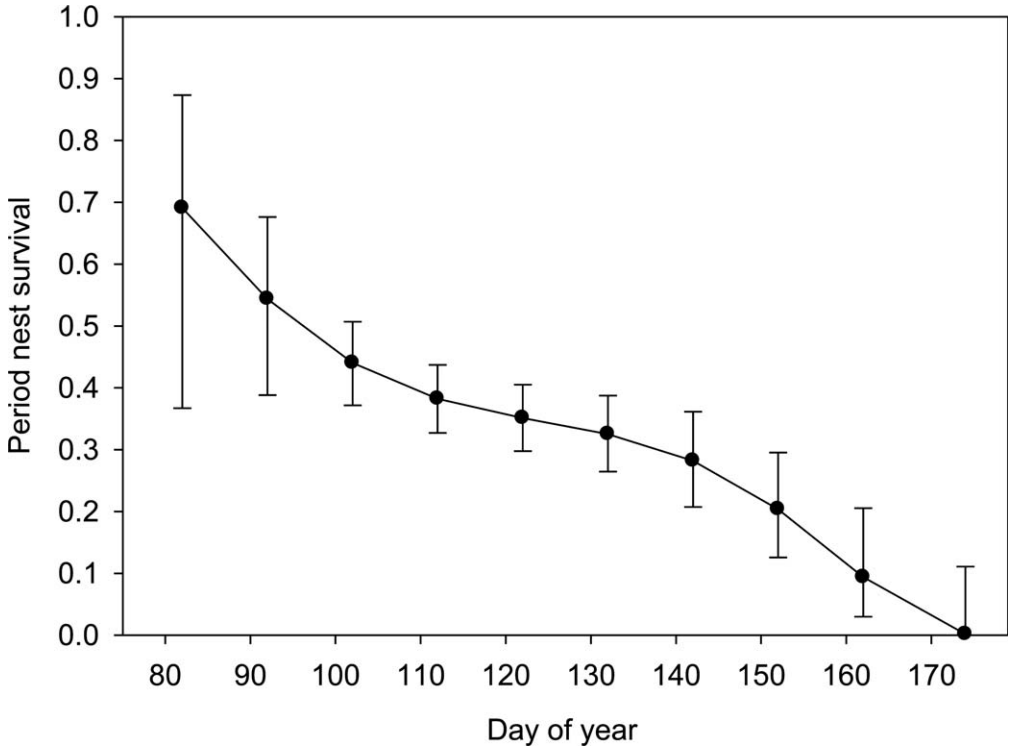

FIGURE 2. Period nest survival (± 95% confidence intervals) decreased nonlinearly as the breeding season progressed for Golden-cheeked Warblers on Fort Hood Military Installation, Texas, 2003–2013.

We monitored every nesting attempt in 423 territories from 2006 to 2013. Values of the covariates varied considerably among territories (Table 2). Tolerance values for all variables in the seasonal productivity models were ≥0.54, indicating multicollinearity was not a problem (Allison 1999). The *k*-fold validation of the global seasonal productivity model indicated a good fit with a positive mean correlation between observed and predicted fledglings per territory ($r = 0.32$, 95% CI = 0.18–0.46) and the overdispersion parameter ($\hat{c}$) equaled 0.85, also indicating no evidence of lack of fit.

The most-supported seasonal productivity model included proportion of juniper forest, proportion of juniper–oak forest, and an interactive effect of year and forest edge density (Table 1). No other models had a $\Delta AIC_c < 4$ (Table 1) so we based all inference on the most-supported model. The relationship between forest edge density and seasonal productivity varied among years (Figure 3B). Seasonal productivity decreased from 3.25 to 1.56 fledglings per territory across the observed range of forest edge density in 2006 but increased from 2.03 to 4.89 fledglings per territory across the observed range of forest edge density in 2012 (Figure 3B). Seasonal productivity ranged from 1.38 to 3.96 fledglings per territory across varying amounts of juniper and juniper–oak forest (Figure 4). Seasonal productivity increased from 1.38 to 3.96 and from 1.38 to 2.40 fledglings per territory across the observed ranges of proportion of juniper and juniper–oak forest, respectively, when the other forest type was held at zero (Figure 4). Seasonal productivity ranged from 1.86 fledglings per territory in 2010 to 3.12 fledglings per territory in 2004, with a mean annual seasonal productivity of 2.36 (± 0.37). Seasonal productivity varied greatly across potential warbler habitat based on variation in the habitat across the sampled areas (Figure 6).

Correlations between period nest survival and seasonal productivity were highly variable. There was a strong, positive correlation between predicted period nest survival and seasonal productivity across the range of observed values for proportion of juniper and juniper–oak forest ($r = 0.98$, $n = 21$, $P = 0.001$). Correlations were weak and nonsignificant across years ($r = 0.40$, $n = 8$, $P = 0.32$) and for the interactive effect of forest edge density and year ($r = 0.19$, $n = 40$, $P = 0.25$).

DISCUSSION

Breeding phenology and demography, evaluations of relationships between reproductive success and habitat and temporal variables, and unbiased estimates of habitat-specific population parameters are necessary components for accurate assessment of population status. We evaluated

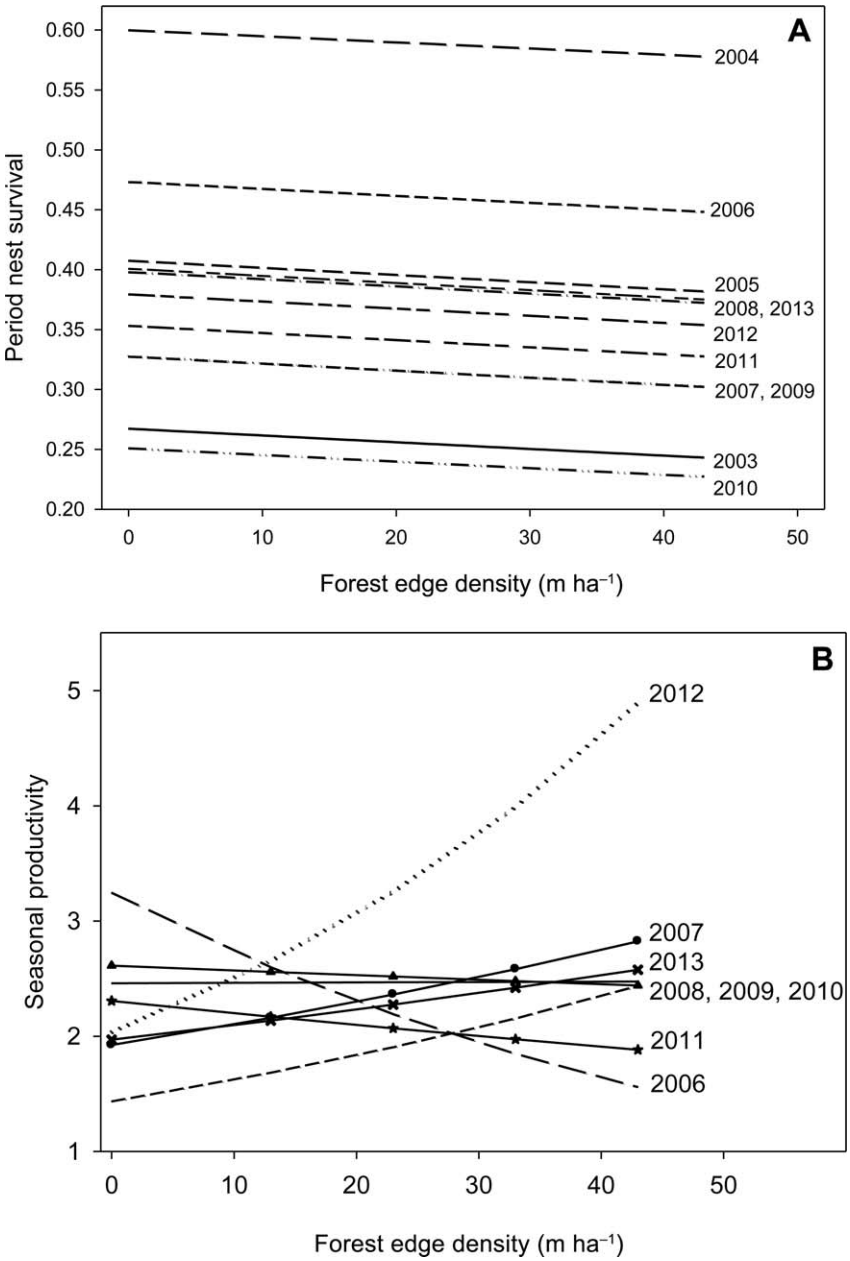

FIGURE 3. Relationship between period nest survival (**A**) (2003–2013) and seasonal productivity (**B**) (2006–2013) with forest edge density (m ha^{-1}) and seasonal productivity.

Golden-cheeked Warbler breeding phenology and demography based on territories defended by color-marked individuals over 11 years. We also examined reproductive success of Golden-cheeked Warblers as a function of proportion of juniper–oak woodland at the habitat-patch scale. Period nest survival was related to day of year, and both period nest survival and seasonal productivity were related to year, proportion of forest type, and forest edge density.

Period nest survival decreased as the breeding season progressed, which is consistent with the results of previous studies examining the relationship between day of year and Golden-cheeked Warbler nest survival (Stake 2003, Peak 2007, Reidy et al. 2009). Texas rat snakes are the most frequent predator of Golden-cheeked Warbler nests (Stake et al. 2004, Reidy et al. 2008). Sperry et al. (2008) found that snake activity on Fort Hood peaks from May through June. Mean date for first clutch initiation is 7 April, so birds may have greater nest survival earlier in the breeding season before temperatures and snake activity increase (Huey 1982, Peterson et al. 1993, Sperry et al. 2008). Although predation is the major cause of nest failure for

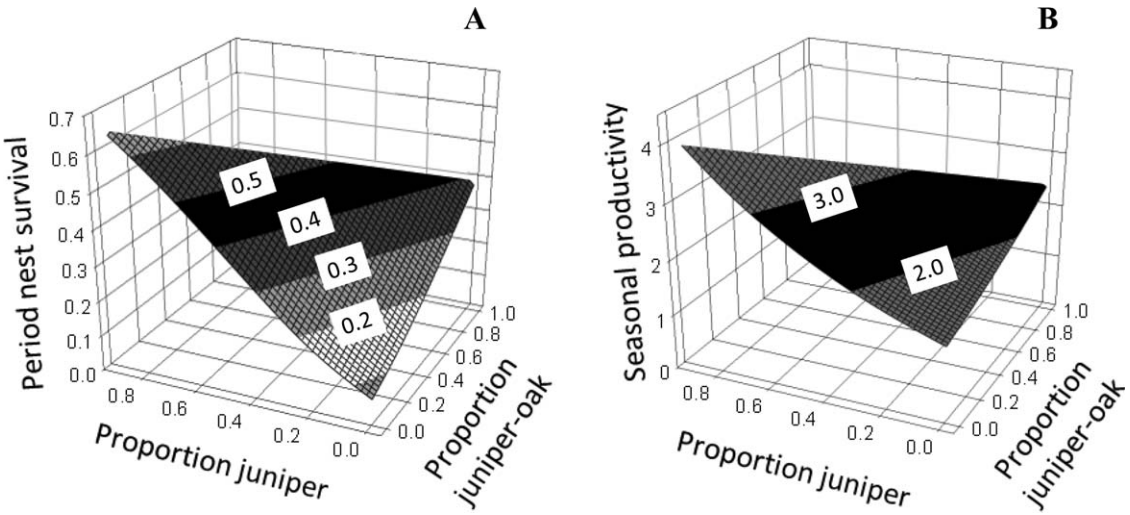

FIGURE 4. Period nest survival (**A**) and seasonal productivity (**B**) of Golden-cheeked Warblers increased with proportion of juniper and juniper–oak forest within a 100-m radius of each nest and for all nests in a given territory, respectively.

Golden-cheeked Warblers, weather events and abandonment also have been documented as causes of nest failure (Reidy and Thompson 2012) and also may have contributed to decreased period nest survival as the breeding season progressed.

As predicted, the relationship between forest edge density and period nest survival was negative, which further supports the general pattern of increased nest predation near forest edges for Golden-cheeked Warblers (Peak 2007, Reidy et al. 2009, Sperry et al. 2009). However, the strength of the relationship varied among years, which could reflect annual changes in prey abundance patterns. Small mammals are the most common prey of Texas rat snakes even during the avian breeding season (Sperry and

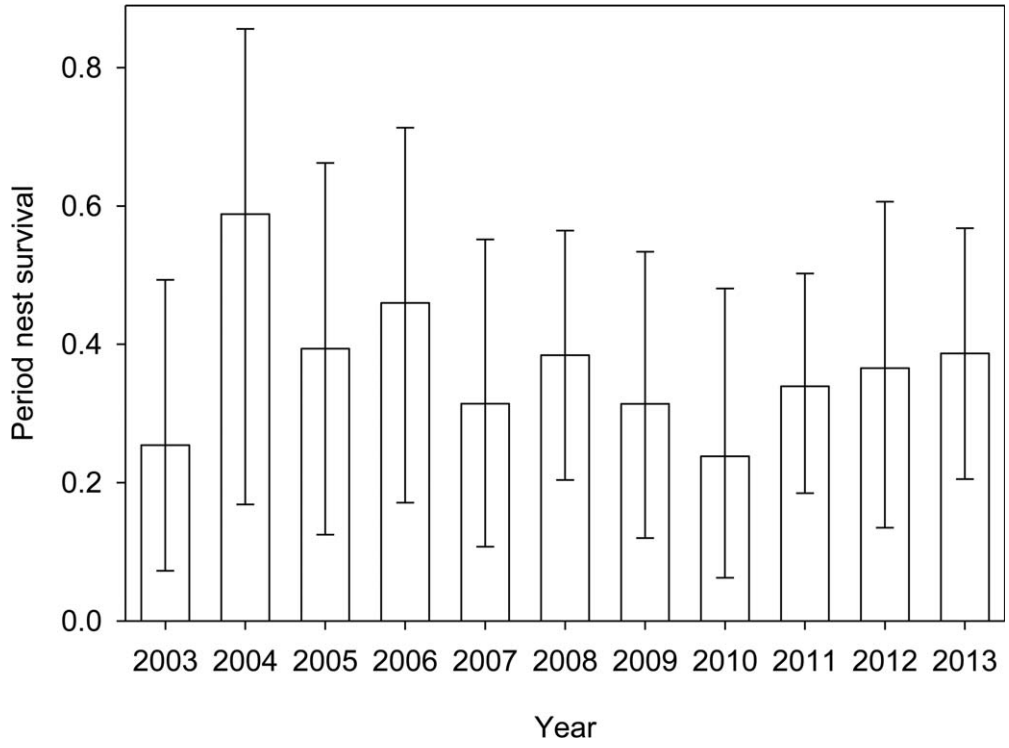

FIGURE 5. Period nest survival (±95% confidence intervals) varied among years for Golden-cheeked Warblers on Fort Hood Military Installation, Texas, 2003–2013.

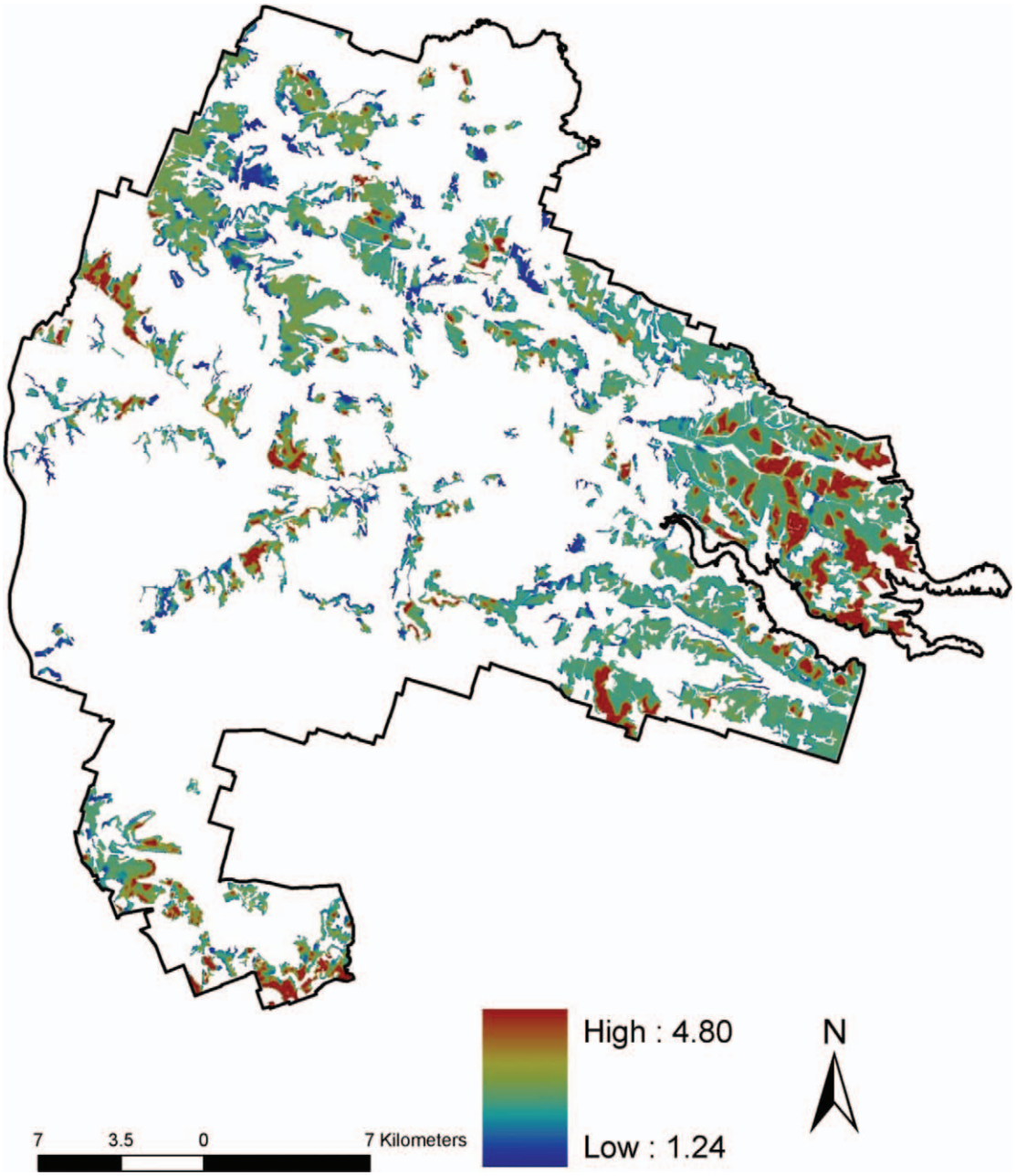

FIGURE 6. Map of predicted Golden-cheeked Warbler seasonal productivity (total number of fledglings per territory produced in a season) on Fort Hood Military Installation, Texas 2006–2013.

Weatherhead 2008), so in years when small mammals are abundant snakes may be more likely to prey on them instead of the contents of Golden-cheeked Warbler nests. Annual variation in the relationship between period nest survival and forest edge density also could reflect annual changes in the abundance and activity patterns of nest predators. Sperry and Weatherhead (2008) documented body condition of Texas rat snakes before, during, and after a drought and found a drop in body condition during the drought indicative of decreased food consumption.

Period nest survival increased as proportion of juniper–oak and juniper forest within a 100-m radius of each nest increased, which emphasizes the overall importance of juniper–oak woodlands on nest survival regardless of cover of Ashe juniper. It also emphasizes the importance of juniper–oak woodlands relative to other forest and non-forest types; as the proportion of these 2 forest types increased, proportion of other forest types (e.g., broadleaf evergreen forest, cold-deciduous forest) and non-forest types (e.g., grassland, bare ground, hardscapes, and roads)

decreased. The relationship between proportion of juniper forest and period nest survival was stronger than the relationship between juniper–oak forest and period nest survival, which could reflect differences in habitat quality between the 2 forest types. Food availability is an important attribute of breeding habitat (Blake 1983, Burke and Nol 1998, Rodenhouse et al. 2003). Golden-cheeked Warbler foraging substrate changes throughout the breeding season with oak species providing foraging substrate early in the breeding season and Ashe juniper providing it later in the breeding season (Pulich 1976, Beardmore 1994, Marshall et al. 2013). Avoidance of nest predators is another important attribute of breeding habitat (Thompson 2007). Texas rat snakes are more frequently located in deciduous trees than Ashe juniper because deciduous trees provide retreat sites such as tree cavities where snakes can safely digest prey (J. H. Sperry personal communication). Increased use of deciduous trees for retreat sites rather than Ashe juniper could increase the likelihood of nests in juniper–oak woodlands being located by rat snakes. Variation in the relationship between period nest survival and proportion of forest type also could reflect differences in settlement patterns between the 2 forest types (Fretwell and Lucas 1970), but we do not have data to examine this aspect of habitat quality.

We found similar relationships between seasonal productivity and proportion of forest type and edge density as we did for period nest survival, with the exception of greater annual variation in the relationship of seasonal productivity with forest edge density. The relationship between seasonal productivity and forest edge density varied from negative to positive depending on the year. Variation in seasonal productivity and the interactive effect of year and forest edge density could reflect the propensity of Golden-cheeked Warblers to renest after a failed nesting attempt, double brood, and utilize alternate mating strategies (Thompson et al. 2001, Fauth 2001). Golden-cheeked Warblers made up to 5 nesting attempts in a breeding season following nest failure. Renesting after failed attempts produced 42% ($n = 179$) of the broods we monitored during the study. While double brooding has been documented for Golden-cheeked Warblers, it is infrequent for this species (Ladd and Gass 1999, Peak and Grigsby 2012). Consequently, we do not have data to examine how ecological factors such as age of adults, food availability, timing of breeding, and number young produced during the first nesting attempt affect the probability that a female will attempt a second brood. Polygyny also has been documented for this species (Peak et al. 2010), but we do not have data to examine the selective pressures that favor this alternative mating strategy.

To put our observed mean annual seasonal productivity estimate of 2.36 in context, we used a simple 2-stage projection model (Pulliam 1988) to determine that an apparent adult and juvenile survival probability estimate of 0.63 and 0.315, respectively (among other possibilities), would maintain a stable Golden-cheeked Warbler population ($\lambda = 1$) on Fort Hood. Alldredge et al. (2002) reported an apparent adult survival probability estimate of 0.57 for Golden-cheeked Warblers on Fort Hood. Apparent adult survival of Neotropical migratory songbirds ranges from 0.41 to 0.83 (Faaborg et al. 2010). However, these estimates likely underestimate true adult survival probability because they do not account for dispersal of adults between breeding seasons (Brawn and Robinson 1996, Cilimburg et al. 2002). We believe an evaluation of Golden-cheeked Warbler population viability using models that incorporate spatial and temporal variation in empirical estimates of survival and productivity is needed.

We found varying levels of correlation between period nest survival and seasonal productivity. Some correlations were strong when we controlled for the effect of year, as indicated by the predictions across the range of proportion of juniper and juniper–oak forest. However, correlations across years were not significant, probably reflecting changes in productivity among years due to varying levels of double brooding and polygyny. Whether or not a female produced either one or two broods in a breeding season was likely influenced by arrival date and length of breeding season. These patterns of correlation indicate that demographic parameters other than nest survival, particularly renesting, double brooding, and polygyny, made an important contribution to actual seasonal productivity (Thompson et al. 2001). However, we also demonstrated that period nest survival did capture important relationships between habitat factors and productivity within years.

The relationship we found between habitat and period nest survival and seasonal productivity is generally consistent with the relationship between habitat and Golden-cheeked Warbler density. Density of singing male Golden-cheeked Warblers is positively related to proportion of these forest types within a 100-m radius of each survey point, but negatively related to forest edge density within 100 m (Peak and Thompson 2013). The relationship between density and proportion of juniper–oak forest within a 100-m radius was stronger than the relationship between density and proportion of juniper forest, which is the reverse of what we found for period nest survival and seasonal productivity. We think it is worth noting that the relationship between proportion of juniper and juniper–oak forest was positive for period nest survival, seasonal productivity, and density, but negative (most years) for forest edge density. The fact that the strength of the relationship differed between productivity and density and

the 2 forest types could indicate there are non-habitat factors affecting territory selection or productivity, or different selective pressures affecting these aspects of habitat quality (e.g., nest predation, food availability). However, we caution against over-interpreting these slight differences in proportion of each forest type because these variables are moderately correlated and coefficient values could vary among different datasets because of difficulties in separating these relationships statistically when fitting models.

Our intensive, long-term study of marked individuals provided less-biased estimates of population productivity than would a study that uses indices of productivity, because renesting, double brooding, and polygyny affect productivity in ways that indices are not able to capture. Even though our study sites represented only 5% of potential warbler breeding habitat on Fort Hood, similarities between our estimates of nest survival and other estimates using indices calculated from studies conducted in others parts of the breeding range (Butcher et al. 2009, Reidy et al. 2009, Campomizzi et al. 2012, Klassen et al. 2012) provide some confidence that our results have broader inference. Nonetheless, we call for implementation of more long-term studies of marked Golden-cheeked Warblers across the breeding range to obtain better estimates of productivity and its variation. We believe our analysis of the relationship between nest survival and productivity and these habitat factors, in conjunction with previous studies, provides strong evidence of the importance of landscapes with high proportions of juniper and juniper–oak forest and a low amount of forest edge to sustain populations of Golden-cheeked Warblers. Therefore, protecting sites that contain large contiguous patches of juniper–oak forest with less edge between forest and non-forest cover, as well as implementing measures to reduce forest edge density, such as controlling populations of browsing animals and promoting reforestation of cleared areas into mature second-growth juniper–oak woodlands, should further recovery efforts for Golden-cheeked Warblers.

ACKNOWLEDGMENTS

We thank C. D. True and D. D. Diamond with the Missouri Resource Assessment Partnership for calculating habitat and landscape metrics; W. D. Dijak with the USDA Forest Service Northern Research Station for statistical and geographic information systems assistance; editors and reviewers for constructive comments; and numerous seasonal field biologists for field assistance. This project was sponsored by the Department of the Army with The Nature Conservancy through Cooperative Agreement Nos. DPW-ENV 97-A-0001 and DPW-ENV 02-A-0001.

LITERATURE CITED

Alldredge, M. W., J. S. Hatfield, D. D. Diamond, and C. D. True (2002). Population Viability Analysis of the Golden-cheeked Warbler. Final report submitted to U.S. Fish and Wildlife Service, Albuquerque, NM, USA.

Allison, P. D. (1999). Logistic Regression Using the SAS System: Theory and Application. SAS Institute, Cary, NC, USA.

Anders, A. D., and M. R. Marshall (2005). Increasing the accuracy of productivity and survival estimates in assessing landbird population status. Conservation Biology 19:66–74.

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

Beardmore, C. J. (1994). Habitat use of Golden-cheeked Warblers in Travis County, Texas. M.S. thesis, Texas A&M University, College Station, TX, USA.

Blake, J. G. (1983). Trophic structure of bird communities in forest patches in east-central Illinois. The Wilson Bulletin 95: 416–430.

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

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow (2002). Evaluating resource selection functions. Ecological Modeling 157:281–300.

Brawn, J. D., and S. K. Robinson (1996). Source-sink population dynamics may complicate the interpretation of long-term census data. Ecology 77:3–12.

Burke, D. M., and E. Nol (1998). Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. The Auk 115:96–104.

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

Butcher, J. A., M. L. Morrison, D. Ransom Jr., R. D. Slack, and R. N. Wilkins (2009). Evidence of minimum patch size threshold of reproductive success in an endangered songbird. The Journal of Wildlife Management 7:133–139.

Campomizzi, A. J., S. L. Farrell, T. M. McFarland, 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.

Cilimburg, A. B., M. S. Lindberg, J. J. Tewksbury, and S. J. Hejl (2002). Effects of dispersal on survival probability of adult Yellow Warblers (*Dendroica petechia*). The Auk 119:778–789.

Coldren, C. L. (1998). The effects of habitat fragmentation on the Golden-cheeked Warbler. Ph.D. dissertation, Texas A&M University, College Station, TX, USA.

Collier, B. A., M. L. Morrison, S. L. Farrell, A. J. Campomizzi, J. A. Butcher, D. I. Mackenzie, and R. N. Wilkins (2010). Monitoring Golden-cheeked Warblers on private lands in Texas. The Journal of Wildlife Management 74:140–147.

Conroy, M. J., Y. Cohen, F. C. James, Y. G. Matsinos, and B. A. Maurer (1995). Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. Ecological Applications 5:17–19.

Dearborn, D. C., and L. L. Sanchez (2001). Do Golden-cheeked Warblers select nest locations on the basis of patch vegetation? The Auk 118:1052–1057.

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

Durner, G. M., and J. E. Gates (1993). Spatial ecology of black rat snakes on Remington Farms, Maryland. The Journal of Wildlife Management 57:812–826.

Eckrich, G. H., T. E. Koloszar, and M. D. Goering (1999). Effective landscape management of Brown-Headed Cowbirds at Fort Hood, Texas. Studies in Avian Biology 18:267–274.

Emrick, V. R., S. Tweddale, and M. St. German (2010). Characterization of Golden-cheeked Warbler (*Dendroica chrysoparia*) habitat at Fort Hood, Texas, USA. Endangered Species Research 11:215–220.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux Jr., P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, et al. (2010). Recent advances in understanding migration systems of New World land birds. Ecological Monographs 80:3–48.

Farnsworth, G. L., and T. R. Simons (2001). How many baskets? Clutch sizes that maximize annual fecundity of multiple-brooded birds. The Auk 118:973–982.

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

Fauth, P. T. (2001). Wood Thrush populations are not all sinks in the agricultural Midwestern United States. Conservation Biology 15:523–527.

Fretwell, S. D., and H. L. Lucas, Jr. (1970). On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

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

Holmes, R. T., P. P. Marra, and W. T. Sherry (1996). Habitat specific demography of breeding Black-throated Blue Warblers (*Dendroica caerulescens*): Implications for population dynamics. Journal of Animal Ecology 65:183–195.

Hosmer, D. W., Jr., and S. Lemeshow (2000). Applied Logistic Regression. John Wiley and Sons, New York, NY, USA.

Huey, R. B. (1982). Temperature, physiology, and the ecology of reptiles. In Biology of the Reptilian Vol. 12 (C. Gans and F. H. Pough, Editors). Academic Press, London, UK. pp. 15–92.

Johnson, M. D. (2007). Measuring habitat quality: A review. The Condor 109:489–504.

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

Kroll, J. C. (1980). Habitat requirements of the Golden-cheeked Warbler: Management implications. Journal of Range Management 33:60–65.

Ladd, C. G. (1985). Nesting habitat requirements of the Golden-cheeked Warbler. M.S. thesis, Southwest Texas State University, San Marcos, TX, USA.

Ladd, C., and L. Gass (1999). Golden-cheeked Warbler (*Dendroica chrysoparia*). In The Birds of North America 420 (A. Poole, Editor.). Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bna.420

Maas-Burleigh, D. S. (1998). Factors influencing demographics of Golden-cheeked Warblers (*Dendroica chrysoparia*) at Fort Hood Military Reservation, Texas. M.S. thesis, University of Oklahoma, Norman, OK, 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., M. L. Morrison, and R. N. Wilkins (2013). Tree species composition and food availability affect productivity of an endangered species: The Golden-cheeked Warbler. The Condor 115:882–892.

Mathewson, H. A., J. E. Groce, T. M. McFarland, M. L. Morrison, J. C. Newman, R. T. Snelgrove, B. A. Collier, and R. N. Wilkins (2012). Estimating breeding season abundance of Golden-cheeked Warblers in Texas, USA. The Journal of Wildlife Management 76:1117–1128.

McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene (2002). FRAGSTATS v3: Spatial Pattern Analysis Program for Categorical Maps. University of Massachusetts, Amherst, MA, USA. http://www.umass.edu/landeco/research/fragstats/fragstats.html

Missouri Resources Assessment Partnership (2009). Texas Vegetation Classification Project. University of Missouri, Columbia, MO, USA. http://morap.missouri.edu/index.php/texas-ecological-systems-classification/

Ostfeld, R. S., and R. Keesing (2000). Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology and Evolution 15:232–236.

Peak, R. G. (2007). Forest edges negatively affect Golden-cheeked Warbler nest survival. The Condor 109:628–637.

Peak, R. G., and N. A. Grigsby (2012). Monitoring Golden-cheeked Warbler survival and productivity on Fort Hood, Texas. In Endangered Species Monitoring and Management at Fort Hood, Texas: 2012 Annual Report. U.S. Army Garrison-Fort Hood, TX, USA.

Peak, R. G., and D. J. Lusk (2009). Alula characteristics as indicators of Golden-cheeked Warbler age. North American Bird Bander 34:106–108.

Peak, R. G., and D. J. Lusk (2011). Test of the plumage criteria used to sex the Golden-cheeked Warbler in the first basic plumage. North American Bird Bander 36:110–112.

Peak, R. G., D. J. Lusk, and J. D. Peppers (2010). Polygyny in the Golden-cheeked Warbler. Bulletin of the Texas Ornithological Society 43:44–47.

Peak, R. G., and F. R. Thompson III (2013). Amount and type of forest cover and edge are important predictors of Golden-cheeked Warbler density. The Condor 115:659–668.

Pease, C. M., and J. A. Grzybowski (1995). Assessing the consequences of brood parasitism and nest predation on seasonal fecundity in passerine birds. The Auk 112:343–363.

Peterson, C. R., A. R. Gibson, and M. E. Dorcas (1993). Snake thermal ecology: The causes and consequences of body-temperature variation. In Snakes: Ecology and Behavior (R. A. Seigel and J. T. Collins, Editors). McGraw-Hill New York, NY, USA. pp. 241–314.

Powell, L. A., M. J. Conroy, D. G. Krementz, and J. D. Lang (1999). A model to predict breeding-season productivity for multi-brooded songbirds. The Auk 116:1001–1008.

Pulich, W. M. (1976). The golden-cheeked warbler: A bioecological study. Texas Parks and Wildlife Department, Austin, TX, USA.

Pulliam, H. (1988). Sources, sinks, and population regulation. American Naturalist 132:550–566.

Pyle, P. (1997). Identification Guide to North American Birds, Part I. Slate Creek Press, Bolinas, CA, USA.

Reidy, J. L., M. M. Stake, and F. R. Thompson III (2008). Golden-cheeked Warbler nest mortality and predators in urban and rural landscapes. The Condor 110:458–466.

Reidy, J. L., F. R. Thompson III, and R. G. Peak (2009). Factors affecting Golden-cheeked Warbler nest survival in urban and rural landscapes. The Journal of Wildlife Management 73: 407–413.

Reidy, J. L., and F. R. Thompson III. (2012). Predator identity can explain nest predation patterns. Studies in Avian Biology 43: 135–148.

Ricklefs, R. E. (1970). The estimation of a time function of ecological use. Ecology 51:508–513.

Rodenhouse, N. L., T. S. Sillett, P. J. Doran, and R. T. Holmes (2003). Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season. Proceedings of the Royal Society of London, Series B 270: 2105–2110.

Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer (2004). Modeling nest-survival data: A comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation 27:187–205.

Shaffer, T. L. (2004). A unified approach to analyzing nest success. The Auk 121:526–540.

Shaffer, T. L., and F. R. Thompson III (2007). Making meaningful estimates of nest survival with model-based methods. Studies in Avian Biology 34:84–95.

Sherry, T. W., and R. T. Holmes (1992). Population fluctuations in a long-distance Neotropical migrant: Demographic evidence for the importance of breeding season events in the American Redstart. In Ecology and Conservation of Neotropical Migrant Landbirds (J. M. Hagan III and D. W. Johnston, Editors). Smithsonian Institution Press, Washington, DC, USA. pp. 431–442.

Sherry, T. W., and R. T. Holmes (1999). Demographic monitoring of migratory bird populations: The importance of parameter estimation using marked individuals. In Strategies for Bird Conservation: The Partners in Flight Planning Process (R. Bonney, D. N. Pashley, R. J. Cooper, and L. Niles, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. http://birds.cornell.edu/pifcapemay

Sperry, J. H., R. G. Peak, D. A. Cimprich, and P. J. Weatherhead (2008). Snake activity affects seasonal variation in nest predation risk for birds. Journal of Avian Biology 39:379–383.

Sperry, J. H., and P. J. Weatherhead (2008). Prey-mediated effects of drought on condition and survival of a terrestrial snake. Ecology 89:2770–2776.

Sperry, J. H., D. A. Cimprich, R. G. Peak, and P. J. Weatherhead (2009). Is nest predation on two endangered bird species higher in habitats preferred by snakes? Ecoscience 16:111–118.

Stake, M. M. (2003). Golden-cheeked Warbler nest predators and factors affecting nest predation. M.S. thesis, University of Missouri, Columbia, MO, USA.

Stake, M. M., J. Faaborg, and F. R. Thompson III (2004). Video identification of predators at Golden-cheeked Warbler nests. Journal of Field Ornithology 75:337–344.

Texas Parks and Wildlife Department (2014). Cowbird trapping program. Texas Parks and Wildlife, Austin, TX, USA. http://www.tpwd.texas.gov/huntwild/wild/nuisance/cowbirds/trapping_program/index.phtml

The Nature Conservancy (1997). Designing a Geography of Hope: Guidelines for Ecoregion-Based Conservation in The Nature Conservancy. The Nature Conservancy Ecoregional Working Group, Arlington, VA, USA.

Thompson, B. C., G. E. Knadle, D. L. Brubaker, and K. S. Brubaker (2001). Nest success is not an adequate comparative estimate of avian reproduction. Journal of Field Ornithology 72:527–536.

Thompson, F. R., III (2007). Factors affecting nest predation on forest songbirds in North America. Ibis 149:98–109.

U.S. Fish and Wildlife Service (1991). Black-capped Vireo (*Vireo atricapillus*) Recovery Plan. U.S. Fish and Wildlife Service, Austin, TX, USA.

U.S. Fish and Wildlife Service (1992). Golden-cheeked Warbler (*Dendroica chrysoparia*) Recovery Plan. U.S. Fish and Wildlife Service, Albuquerque, NM, USA.

U.S. Fish and Wildlife Service (1993). Biological opinion. U.S. Fish and Wildlife Service, Arlington, TX, USA.

Van Horne, B. (1983). Density as a misleading indicator of habitat quality. The Journal of Wildlife Management 47:893–901.

Vickery, P. D., M. L. Hunter, and J. V. Wells (1992). Is density an indicator of breeding success? The Auk 109:706–710.

Weatherhead, P. J., and D. J. Hoysack (1989). Spatial and activity patterns of black rat snakes (*Elaphe obsoleta*) from radiotelemetry and recapture data. Canadian Journal of Zoology 67: 463–468.