



RESEARCH ARTICLE

Demographic rates of Golden-cheeked Warblers in an urbanizing woodland preserve

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ABSTRACT

Knowledge of demographics is important in conservation planning for endangered species. We monitored the endangered Golden-cheeked Warbler (*Setophaga chrysoparia*) at a large, discontinuous preserve in an urbanizing landscape in central Texas, USA, to estimate survival and productivity. We estimated adult male survival using a spatial Cormack-Jolly-Seber model that separated emigration from mortality by incorporating location data from resightings. Annual male survival varied from 0.45 to 0.67 from 2010 to 2015 (posterior mean $\pm$ SD = 0.57 ± 0.06). Sixty-seven percent of resighted males moved <100 m among years, but a large minority of males moved far enough across years that dispersal should be accounted for in future survival analyses. Mean predicted seasonal productivity varied from 2.32 to 3.18 fledglings territory⁻¹ from 2011 to 2015 (mean $\pm$ SD = 2.46 ± 0.51). Seasonal productivity was best predicted by the proportion of total woodland land cover in a 1 km radius around the annual median location, total edge density in a 1 km radius, and the standard deviation of canopy height in a 100 m radius. Seasonal productivity peaked at high proportions of total woodland cover, and decreased with increasing edge and canopy height standard deviation. Annual trends for survival and productivity were similar; that is, survival and productivity were above or below average in the same years, which could have important implications for population stability. Our estimated demographic rates are within the range of those reported from the best long-term data, from Fort Hood, Texas, and support the need for large patches of nonfragmented, mature woodlands to provide high-quality breeding habitat for this species.

Keywords: breeding phenology, dispersal behavior, seasonal productivity, *Setophaga chrysoparia*, spatial CJS model, survival, urbanizing landscape

Tasas demográficas de *Setophaga chrysoparia* en una reserva urbana de bosque

RESUMEN

El conocimiento de la demografía es importante en la planificación de la conservación de las especies en peligro de extinción. Monitoreamos la especie en peligro *Setophaga chrysoparia* en una gran reserva discontinua en un paisaje en proceso de urbanización en el centro de Texas para estimar su supervivencia y productividad. Estimamos la supervivencia de los adultos macho usando un modelo espacial de Cormack-Jolly-Seber que separó la emigración de la mortalidad mediante la incorporación de la ubicación de los datos a partir de avistamientos repetidos. La supervivencia anual de los machos varió de 0.45 a 0.67 desde 2010 hasta 2015 (media posterior $\pm$ DE = 0.57 ± 0.06). El 67% de los machos avistados más de una vez se movieron menos de 100 m entre años, pero una gran minoría de los machos se movió lo suficiente a lo largo de los años como para que la dispersión sea considerada en los análisis de supervivencia futuros. La productividad estacional promedio predicha varió de 2.32 a 3.18 volantones/territorio desde 2011 hasta 2015 (media $\pm$ DE = 2.46 ± 0.51). La productividad estacional fue mejor predicha por la proporción del total de la cobertura de bosque en un radio de 1 km alrededor de la ubicación mediana anual, la densidad total de borde en un radio de 1 km y el desvío estándar de la altura del dosel en un radio de 100 m. La productividad estacional tuvo un pico a una alta proporción de la cobertura total del bosque y disminuyó con un aumento del desvío estándar de la altura del borde y del dosel. Las tendencias anuales de la supervivencia y la productividad fueron similares, i.e., la supervivencia y la productividad estuvieron por arriba y por debajo del promedio en los mismos años, lo que podría tener implicancias importantes para la estabilidad poblacional. Nuestras tasas demográficas estimadas están dentro del rango de aquellas reportadas para los datos de largo plazo de mejor calidad de Fort Hood, Texas, y apoyan la necesidad de grandes parches de bosque maduro no fragmentado que ofrezcan hábitat reproductivo de alta calidad para esta especie.

Palabras clave: comportamiento de dispersión, fenología reproductiva, modelo CJS espacial, productividad estacional, *Setophaga chrysoparia*, supervivencia, urbanización del paisaje

INTRODUCTION

The Golden-cheeked Warbler (*Setophaga chrysoparia*) is a migratory songbird that breeds exclusively within the woodlands co-dominated by Ashe's juniper (*Juniperus ashei*) that occur in central Texas, USA (Ladd and Gass 1999). The Golden-cheeked Warbler was federally listed as endangered in 1990 because of concern over habitat loss in the breeding and wintering ranges. The U.S. Fish and Wildlife Service (1992) identified the need to "determine survivorship, dispersal, reproductive success, and other population parameters" under the research needs in the recovery plan (Task 1.11). Thus far, knowledge of Golden-cheeked Warbler population biology is mostly restricted to a long-term monitoring program on Fort Hood, Texas, augmented by additional short-term studies conducted on the Balcones Canyonlands National Wildlife Refuge and Balcones Canyonlands Preserve (Groce et al. 2010, O'Donnell et al. 2015, Reidy et al. 2016b). Population parameters, or demographic rates, are the key drivers of population viability analyses (Akçakaya et al. 2004, Bonnot et al. 2011). However, demographic rates are particularly difficult to measure in small, migratory species such as the Golden-cheeked Warbler, and studies are often limited to small areas (Anders and Marshall 2005, Faaborg et al. 2010), which may provide limited inferences across a species' range. Furthermore, key demographic rates remain uncertain for the Golden-cheeked Warbler and either survival or reproductive output has been underestimated (Peak and Thompson 2014, Duarte et al. 2016b). Population-specific demographic rates from many areas are needed to better inform population modeling and conservation planning (Conroy et al. 1995, Johnson 2002, Anders and Marshall 2005).

The majority of capture–mark–resight data for the Golden-cheeked Warbler comes from a single general location, Fort Hood (see Duarte et al. 2014), and the resultant survival rates reflect apparent survival, which confounds mortality and permanent emigration and may not accurately reflect true survival (Gilroy et al. 2012). Several recent advances in spatial modeling have incorporated additional spatial data, such as banding and resighting locations, to estimate true survival by separating the mortality and permanent emigration components (Burnham 1993, Barker 1997, Gilroy et al. 2012, Schaub and Royle 2014). When permanent emigration is accounted for, estimated survival rates increase and should approach true survival (Cilimburg et al. 2002, Marshall et al. 2004, Taylor et al. 2015), thus demonstrating the importance of including information about dispersal behavior in survival analyses.

Information on seasonal productivity of Golden-cheeked Warblers is similarly limited. Other than Fort Hood (Peak and Thompson 2014) and Balcones Canyonlands National Wildlife Refuge (Reidy et al. 2016b), information on reproductive output is limited to nest survival (Reidy et al. 2009b, 2017) or territory success of unbanded populations (Campomizzi et al. 2012). Seasonal productivity may not be well predicted by nest survival, because of influences such as partial nest predation, double brooding, re-nesting, and alternative mating strategies (Thompson et al. 2001, Anders and Marshall 2005, Peak and Thompson 2014). Territory success of Golden-cheeked Warblers has often been reported using a reproductive index (Campomizzi et al. 2012, Long et al. 2017), but this method has been shown to be unreliable for Golden-cheeked Warblers as well as other bird species (Rivers et al. 2003, Morgan et al. 2010, Reidy et al. 2015).

To add demographic information from an additional area of the breeding range of Golden-cheeked Warblers, we monitored color-banded populations on the Balcones Canyonlands Preserve (BCP). The BCP is important to monitor because only Fort Hood has more protected property preserving Golden-cheeked Warbler breeding habitat (Groce et al. 2010) and because it is located within the rapidly urbanizing landscape of Austin, Texas. We predicted true survival for adult males using a spatial Cormack-Jolly-Seber ("s-CJS") model that allowed us to separate permanent emigration from mortality. We present information on dispersal and breeding phenology, including arrival dates, breeding season length, and extent of double brooding. We also report the number of fledglings produced per territory based on nest monitoring and fledgling surveys and relate this measure of seasonal productivity to habitat structure around the territory and to landscape composition.

METHODS

Study Area

We conducted this study on the BCP, a 12,294 ha network of preserves in western Travis County, Texas (30°40'N, 97°85'W). The BCP is situated along the eastern edge of the Edwards Plateau ecoregion and at the eastern edge of the Golden-cheeked Warbler's breeding range. The BCP was established to mitigate habitat loss for the Golden-cheeked Warbler and other endangered and rare species (City of Austin and Travis County 1996). The BCP is predominantly mature closed-canopy woodland consisting primarily of Ashe's juniper, plateau live oak (*Quercus fusiformis*), shin oak (*Q. sinuata* var. *breviloba*), Texas red oak (*Q. buckleyi*), and cedar elm (*Ulmus crassifolia*).

Field Data Collection

We initiated color banding on nine 40 ha monitoring plots in 2009 as part of an increased effort to determine territory density and estimate reproductive output. We banded at 3 additional plots in 2010. In 2011, we discontinued banding at 3 plots and added 8 more plots, ranging in size from 40 to 180 ha, that we monitored through 2015. Changes in monitoring plots were made to ensure that we monitored a representative sample of the habitat available on the BCP. The final series of 17 monitoring plots where we focused our territory monitoring during 2011–2015 (Figure 1) is fairly representative of the BCP (see Reidy et al. 2016a: table 1). We also surveyed additional areas around monitoring plots to increase resightings and document dispersal events (described below).

Capturing and marking adults. We banded adult Golden-cheeked Warblers from mid-March through mid-May, 2009–2015, on monitoring plots to establish the number of territorial males, delineate territorial boundaries, and determine pairing and breeding success. We played prerecorded Golden-cheeked Warbler songs beneath the middle of georeferenced mist nets (6 m long) to capture adults, and we banded individuals with a unique combination of 2 or 3 colored leg bands and a federal band. We aged and sexed each individual according to Pyle (1997) and Peak and Lusk (2009, 2011). Playback typically elicits a strong response in males, but much less so in females, so the majority (94%) of our banded individuals were males. We assigned age as second-year (SY), after-second-year (ASY), or, when designation of SY or ASY was not possible, as after-hatch-year (AHY). During 2014 and 2015, we also banded nestling Golden-cheeked Warblers. We did not attempt to capture independent juveniles.

Resighting. We searched for banded adults on and around monitoring plots with active banding, and in additional resighting-only areas to document return rates (for plots where banding was discontinued) and dispersal. This varying level of effort was akin to core banding areas with expanded resighting areas used in Cilimburg et al. (2003) and Marshall et al. (2004). Because the level of effort varied, we categorized resighting areas according to survey intensity (Figure 1). High-intensity resighting areas were the 17 monitoring plots (defined above) that we surveyed 2–3 times wk^{-1} from March 15 to June 15, 2009–2015. Medium-intensity resighting areas consisted of the accessible wooded areas in a 100 m wide buffer around the 17 monitoring plots and 6 additional plots where BCP partners monitored territories without banding; these areas were surveyed at least once a week from March 15 to June 15, 2010–2015. Low-intensity resighting areas were polygons delineated around and between monitoring plots and buffers. These areas were surveyed beginning in 2010. Low-intensity resighting areas also included the 3 monitoring plots where we discontinued banding after 2010 but

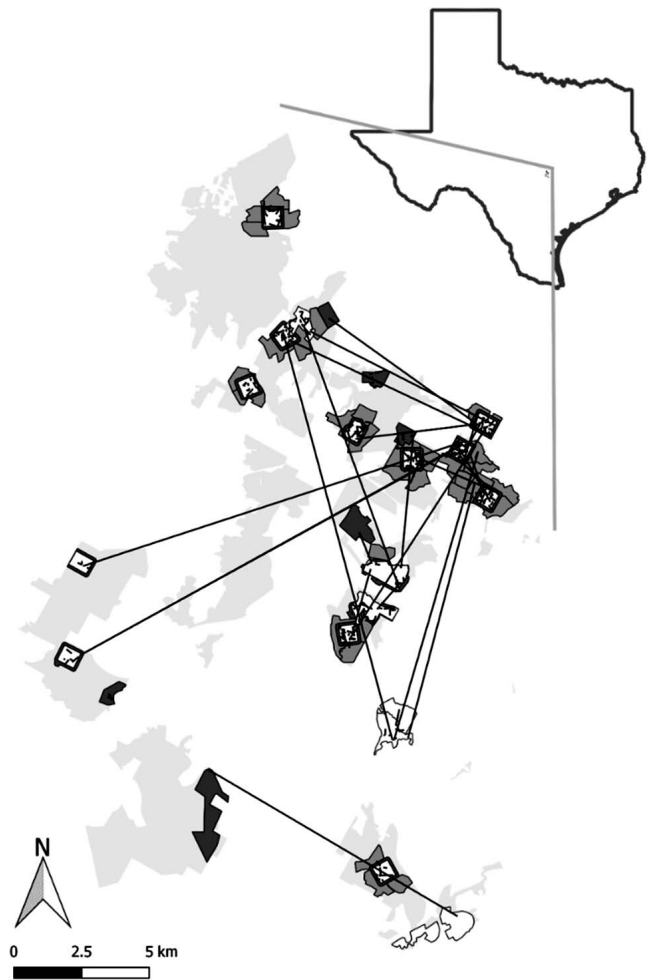


FIGURE 1. Location of 17 high-intensity (white fill, black outline), 23 medium-intensity (dark gray fill, black outline), and 37 low-intensity (medium gray fill, black outline) resighting areas used to monitor Golden-cheeked Warbler populations on Balcones Canyonlands Preserve (light gray), Texas, USA, 2009–2015. Observed inter-year movements within the network of survey plots are indicated by dark lines.

continued to search for banded adults from 2011 through 2015. Low-intensity resighting areas were surveyed 3–5 times during the breeding season, with each visit separated by ≥ 2 wk in order to resight banded birds that had moved off plots and beyond the buffers. Observers attempted to identify all detected individuals but did not use playback to alter the bird's behavior or location. Observers were assigned to specific plots and buffers or search areas and surveyed those throughout the breeding season.

Territory monitoring. Official surveys began on March 15 each year, but we monitored plots for evidence that Golden-cheeked Warblers had arrived beginning on about March 1 of each year. We documented the date on which males and females were first detected on our plots and also consulted e-bird (<http://ebird.org/>) records for any earlier

observations of Golden-cheeked Warblers. Observers surveyed monitoring plots and, to a lesser extent, buffers, to resight color-banded adults, record GPS locations of adults, and document presence of females, nesting behaviors or nests, and fledglings. Two observers were assigned to plots with >5 territories, whereas only one observer was typically assigned to plots with ≤ 5 territories. Additional observers helped on plots as needed with finding nests, counting fledglings, banding, and resighting. We attempted to collect ≥ 5 unique locations for each individual (>30 m apart) during each visit with a goal of accumulating ≥ 33 locations across the breeding season to delineate territories. Previous research has found this number to be adequate for calculating minimum convex polygon territorial boundaries (Davis et al. 2010).

Nest searching and monitoring. We searched for nests for all territorial pairs on monitoring plots during 2011–2015 using adult behavioral clues and systematic searches. We monitored nests every 2–4 days postlaying until the nest fledged young or failed; monitoring occurred more frequently as the expected fledge date approached. We recorded adult behavior to determine nest stage or approximate nestling age and considered a nest successful if we observed nestlings leaving the nest, an adult feeding host fledglings, or an adult carrying food to locations other than the nest after the day of expected fledge. If we detected no activity at a nest prior to the expected fledge date and the nest was intact, we made at least one more subsequent visit to verify no activity and follow the pair for evidence of renesting. If we did not confirm fledglings for a nest on the expected fledge date, we continued to monitor the territory for evidence of fledging or renesting. We attempted to document all nesting attempts for every territorial pair.

Fledgling surveys. We searched for and attempted to count all fledglings in association with every territory on monitoring plots. In our experience, fledgling Golden-cheeked Warblers are often easiest to count immediately postfledging, when both adults and all young are usually near the nest and adults elicit high-pitched chips. Fledglings may scatter and are often split between adults within days of fledging, making complete counts more difficult and time-intensive. Fledglings again become easier to count as they become a little older and mobile but still dependent on adults. We have documented only 2 broods of 5 nestlings since 2005, so we considered a count of 4 fledglings adequate. If <4 fledglings were found during initial visits, we continued monitoring in the territory until we were certain of a final count or recorded a minimum count, which we distinguished in our records as complete or minimum counts. We continued to monitor successful territories for evidence of double brooding. We searched for evidence of fledglings for every territorial pair regardless of whether an active nest was found.

Landscape and patch metrics. We calculated attributes of the landscape and territory in ArcMap 10 (ESRI, Redlands, California, USA) using the Texas Ecological Systems Classification (TESP; Texas Parks and Wildlife Department 2012) and a LiDAR-based map of vegetation height (Reidy et al. 2016a, 2017). We chose the TESP land-cover map because it has fairly high resolution (10 m); uses ancillary data such as slope, soil, and roads layers to refine broad land-cover categories; and spans the entire breeding range of Golden-cheeked Warblers. We included the LiDAR layer because it has greater resolution (2 m), is more current (collected in 2012 as opposed to TESP, which was based on imagery collected in 2005 and 2006), and can be used to calculate canopy height as well as to identify areas where land-cover classifications may need to be updated because of changes in the land use that occurred between 2006 and 2012 (we considered this a necessary update to our land-cover map because our study area is located in a rapidly urbanizing landscape). For example, by intersecting the TESP land-cover map and LiDAR-based canopy height map, we were able to reclassify woodland pixels as open–non-woodland if canopy height was <3 m tall as indicated by LiDAR (see Reidy et al. 2016a, 2017). We assessed potential habitat attributes within a 1 km radius of the median territory location to capture characteristics of the landscape composition within and around the territory and the greater woodland patch (landscape scale), and within a 100 m radius of the median territory location because it approximates the average Golden-cheeked Warbler territory size (territory scale). These scales have also been supported in previous research at this site (Reidy et al. 2016a, 2017). We used the median location of all male resightings rather than the mean to minimize the influence of outlier observations (e.g., a silent male following a female in a neighboring territory).

We summed all juniper ($>75\%$ of canopy is juniper) and mixed juniper–hardwood (neither tree group is $>75\%$ of the canopy) forest and woodland classes into a single woodland class and calculated the proportion of area in woodland in the landscape. We defined edge as the border between woodland and open or urban land-cover types and calculated edge density (m ha^{-1}) for each radius. We also calculated proportion of canopy cover, canopy height, and the standard deviation of canopy height in the 100-m-radius territory scale.

Statistical Analyses

Adult survival. We used encounter histories and spatial location data from banded adult males to estimate survival probability and dispersal parameters. We estimated true survival using an s-CJS model developed by Schaub and Royle (2014). This model links the spatial locations of resighted individuals with individual capture histories to jointly model survival and dispersal behavior. The detec-

tion process is spatially explicit and assumes that resightings are possible only within the boundary of a defined study area. True survival may then be estimated by accounting for the fraction of dispersal movements that results in permanent emigration from the study area. Furthermore, by modeling nondetectable dispersal movements away from study areas, this analysis estimates the shape of the true dispersal distribution and does not show the same overrepresentation of near-zero dispersal distances present in the raw movement data.

The survival component of Schaub and Royle's (2014) s-CJS model describes the true live or dead state of each individual i in each year t as the outcome of a Bernoulli process, defined by survival probability s . This survival outcome also conditions on the previous state of each individual, such that only individuals that were alive at time $t - 1$ may be alive at time t . In our study, we fitted the survival component of the s-CJS model of Schaub and Royle (2014) with annual survival treated as a random effect. Specifically, we assumed that year-specific survival probabilities s_t arise from a normal distribution on the logistic scale with overall mean μ and precision τ . We report mean annual survival on the probability scale and used the delta method (Seber 1982) to calculate the probability-scale variance in annual survival based on the logistic-scale process variance.

The dispersal component of the s-CJS model treats movement as a random-walk process, whereby a symmetric probability distribution describes the potential x and y positions of an individual in relation to its previous location (Schaub and Royle 2014). In the present study, we fitted 3 separate s-CJS models that differed in the symmetric probability distribution describing dispersal: (1) a T distribution defined by mean, precision, and degrees of freedom parameters; (2) a normal distribution defined by mean and precision parameters; and (3) a double-exponential distribution defined by mean and scale parameters. For each model, the mean of the dispersal distribution is taken to be the location of the individual at time $t - 1$, while the additional parameter(s) defining the shape of the distribution are estimated. Because dispersal movements are assumed to be random in space, emigration from a study plot may be either permanent or temporary, and the probability that an individual leaves or returns to a study area depends on the individual's actual location in relation to the study area's boundaries (Schaub and Royle 2014).

The observation process of the s-CJS model provides the link between individual-level encounter histories and the corresponding spatial location data. To be encountered, an individual must be alive and present within a study area. Individual spatial locations (easting, northing) are provided as data with missing observations for years in which a given individual was not encountered. Individual spatial

locations are then treated as a partially observed latent variable and are used to calculate an indicator ($r_{i,t}$) that represents whether individual i is inside a study area at time t . Here, we let this indicator denote whether the location of an individual is outside all study areas and not observable ($r_{i,t} = 0$) or is within a resighting area that was surveyed with low ($r_{i,t} = 1$), medium ($r_{i,t} = 2$), or high intensity ($r_{i,t} = 3$). We performed this assessment using a point-in-polygon test based on the "ray-crossing algorithm" (Shimrat 1962), which we coded in the BUGS/JAGS language to evaluate whether the estimated spatial coordinates of unobserved individuals fell within each category of study sites and were detectable with probability $p_{r_{i,t}}$. The encounter-history data, which were provided as a 1/0 detection/nondetection matrix, were then treated as a Bernoulli random variable with success probability equal to $p_{r_{i,t}}$ and conditional on the individual being alive at time t .

We fitted the s-CJS model to 7 yr of encounter-history data for male Golden-cheeked Warblers on the BCP. Because Duarte et al. (2014) reported that apparent survival of adult male Golden-cheeked Warblers did not vary spatially for a large sample across Fort Hood, we treated survival as spatially uniform across the BCP in our study. We used the median of all banding and resighting locations within the year (easting, northing) to represent each individual's spatial location, which was intended to reflect the location of an individual's territory with limited influence of outlier locations. This differed from Schaub and Royle (2014), who used nest locations to represent an individual's spatial position in each year, because not all individuals in our study had known nest locations.

All models were fitted in a Bayesian framework using the program JAGS (Plummer 2003), executed in R (R Core Team 2014) using the package "jagsUI" (Kellner 2015). We selected vague prior distributions for all parameters to reflect a lack of prior knowledge about model parameters. We assigned independent uniform (0, 1) prior distributions for detection probability in high-, medium-, and low-intensity survey areas. We also chose a uniform (0, 1) distribution for mean annual survival probability and a uniform (0, 100) distribution for the logistic-scale variance parameter describing interannual variation in survival. Similarly, all dispersal parameters were assigned non-informative uniform prior distributions. We simulated posterior distributions for all model parameters based on 3 parallel Markov chains. We ran each chain for a total of 50,000 iterations, discarded the first 30,000 iterations as burn-in, and thinned the remaining samples at a rate of 1:25. The Gelman-Rubin statistic indicated adequate convergence for all model parameters ($\hat{R} < 1.1$; Gelman and Rubin 1992).

We used posterior predictive checks to compare model fit among our 3 s-CJS models, which were structurally

identical apart from their assumed dispersal distributions. This assessment method is based on the idea that a model providing a good fit will generate predicted data with similar properties to the observed data (Chambert et al. 2014). For each model, we selected random draws from the joint posterior distribution and used the parameter values obtained to simulate 1,000 replicate datasets that shared the same overall structure as our observed mark–resight dataset. Thus, each simulated dataset was initialized with the same number of individuals, number of study years, individual banding years, and individual banding locations as the original dataset. Individual capture histories and spatial locations were then stochastically simulated through time according to the given model structure and parameter values. We calculated 4 summary metrics from each simulated dataset to compare with the observed data: (1) the mean number of sighting years per individual, (2) the proportion of individuals observed in >2 yr, (3) the 50th percentile of observed displacements between years (m), and (4) the 90th percentile of observed displacements between years (m). The discrepancy between model predictions and the observed data for these 4 metrics indicates whether the observed return rates, typical observed movement distances, and observed incidences of extreme movement could plausibly be generated by each fitted model. R scripts for the survival analysis and posterior predictive checks are available in [Supplemental Material Appendices A and B](#).

Breeding phenology and seasonal productivity. We calculated the mean and range of the earliest arrival date of males and females, the earliest date nest building and incubation was observed, and the latest date that a nest fledged for each year. We calculated the 1st and 99th percentiles of active nest dates (laying through fledging) to calculate the length of the breeding season. We calculated the mean and range of the number of nesting attempts and the number of days between nesting attempts for failed nests and double brood attempts. We calculated the percentage of males that were paired (pairing success) and the percentage of territories that produced fledglings (breeding success). Despite a majority of our females being unbanded, we are confident that we accurately recorded instances of successful double brooding and alternative mating strategies such as polygyny because we intensively monitored all territories throughout the season. We expect that we missed some unknown proportion of failed double-brooding attempts. Instances of polygyny were documented when we observed a banded male attending to 2 active nests simultaneously, when a banded male was attending an active nest and feeding fledglings that could not have been produced by the female attending the nest, or when a banded male was feeding 2 sets of fledglings that could not have been produced by the same female (based on age). Instances of polyandry were documented when we

recorded different males feeding at a nest or feeding the same fledglings.

We defined seasonal productivity as the total number of fledglings observed in a territory each season. We monitored 1,114 territories, and 754 had one or more fledglings across all years; however, observers indicated potentially incomplete counts for 330 of the 754 successful territories. We reasoned that the primary sources of variation affecting incomplete counts were related to plots and observers, who were assigned to plots. Therefore, we added a plot-level adjustment to potentially incomplete counts so that estimates would be less biased. We calculated the mean fledgling counts for successful territories (≥ 1 fledgling) for complete and potentially incomplete counts by plot, calculated the difference, and added this mean difference to incomplete fledgling counts by plot. This preserved the variation in the original counts but served as a plot-specific bias adjustment, which we concluded was preferable to ignoring the bias or deleting 30% of the data.

We calculated mean fledglings territory⁻¹ season⁻¹ (hereafter “fledglings territory⁻¹”) from the raw and bias-adjusted counts but also produced model predictions based on supported relationships between bias-adjusted fledgling counts and territory and landscape attributes evaluated using an information-theoretic approach. We constructed 12 candidate models consisting of single or additive combinations of territory or landscape variables that were based on our assumption that nest predation was the primary habitat-based factor affecting productivity (Stake et al. 2004, Reidy et al. 2008, Sperry et al. 2009) and that these variables captured much of the variation in habitat and landscape composition, structure, and successional state developed from remotely sensed data layers (for additional details, see Reidy et al. 2016a, 2017, Sennie et al. 2016). We included year in every model because seasonal productivity varied annually at Fort Hood (Peak and Thompson 2014). We included total woodland cover in the landscape and canopy cover in the territory because we hypothesized that lower woodland or canopy cover could represent greater fragmentation, edge, and interspersed and potentially lower productivity (Peak and Thompson 2014). We included landscape edge density because we hypothesized that it was negatively related to productivity (Peak 2007, Reidy et al. 2008, Peak and Thompson 2014). We considered linear and quadratic forms of landscape woodland cover and landscape edge density because we hypothesized that both linear and nonlinear threshold effects were possible for these variables. We included mean and standard deviation of canopy height because we hypothesized that greater canopy height represented more mature woodland with potential greater productivity; and greater standard deviation in canopy height could represent greater

interspersed openings and edge and potentially greater predation from edge-adapted nest predators (Reidy et al. 2008, Sperry et al. 2009).

We fitted generalized linear mixed models with a Poisson distribution to predict seasonal productivity based on hypothesized fixed effects (PROC GLIMMIX; SAS Institute, Cary, North Carolina, USA). Mean overlap across all 100 m and 1 km territory buffers was only 0.3% and 7.0%, respectively, but was certainly greater for those within a study plot, possibly resulting in correlated responses for territories within a year on a plot. Therefore, we included a random effect in all models specifying the subject as plot nested within year to account for these potential correlations. We evaluated multicollinearity in all candidate models and reformulated any models with tolerance values for any variables <0.4 (PROC REG; SAS Institute; Allison 1999). We evaluated goodness-of-fit by examining whether the Pearson chi-square test statistic divided by degrees of freedom for the global model was close to 1 (Burnham and Anderson 2002) and used a tenfold cross-validation to compare correlations between predicted and observed values (Boyce et al. 2002). We also compared mean predicted seasonal productivity based on the most supported model to mean observed seasonal productivity on monitoring plots. We evaluated model support by ranking models with Akaike's Information Criterion.

We predicted seasonal productivity as a function of variables in the most supported model by varying covariate values across their observed range while holding other variables at their median and for a balanced sample across years (Shaffer and Thompson 2007). We created a spatially explicit map of seasonal productivity across the BCP based on the covariates in the most supported model. We report means $\pm$ SD unless otherwise noted.

RESULTS

Adult survival. We banded 794 adult males and 56 adult females during 2009–2015. We also banded 91 nestlings during 2014–2015. Among males, 332 (42%), 438 (55%), and 24 (3%) were aged as ASY, SY, and AHY, respectively, at the time they were banded. Forty-five males (~6%) were not resighted after they were banded, which suggests that some small portion of the population was transient or nonterritorial. We resighted 149, 155, and 13 returning males aged ASY, SY, and AHY at the time of banding in subsequent years. Mean return rate was 44% for SY males, compared to 50% for ASY males, where return rates were calculated from males resighted in any year after the year in which they were banded. Males banded in 2015 were excluded from return-rate calculations. We resighted 15 returning females and 4 returning individuals (1 female and 3 males) that were banded as nestlings; because of

these low returns or detections, we restricted our survival analyses to males.

Posterior predictive checks indicated that the s-CJS model with a T distribution describing dispersal in both the x direction and the y direction best fit the data; we used this model for further inference about dispersal, survival, and detection processes (Table 1). Data simulated according to this model closely predicted the mean number of sighting years per individual and the proportion of birds observed in multiple years but overestimated the median inter-year displacement by 22% and the 90th percentile of inter-year displacements by 18%. The s-CJS models treating dispersal as a double-exponential or normal distribution considerably overestimated actual movement distances. This resulted in the under-prediction of observed return-rate metrics, both the mean number of sighting years per individual and the proportion of individuals seen in multiple years.

The estimated probability of resighting banded males was 0.99 ± 0.01 (posterior mean $\pm$ SD) on high-intensity resighting areas, 0.92 ± 0.06 on medium-intensity resighting areas, and 0.42 ± 0.10 on low-intensity resighting areas. The observed median inter-year movement distance was 64 m (range: 2–15,964 m; median 56 m for ASY and 82 m for SY males; $n = 472$ movements) and did not vary substantially among years (range: 53–73 m); moreover, 39% and 67% of 472 observed male movements were <50 m and <100 m among years (annual change in median location), respectively. We recorded 158 (33%) movements >100 m and 42 (9%) movements >300 m. We documented 17 movements between study plots (up to ~16 km) and resighted birds that had moved off monitoring plots (Figure 1). The fitted T distribution describing the estimated “true” dispersal distribution based on the s-CJS model was fat-tailed, indicating a high probability of near-zero dispersal distances as well as a nontrivial probability of considerably larger dispersal movements (Figure 2). For example, although 27% of males were predicted to move <50 m among subsequent years, 10% of males were predicted to disperse >1 km. Mean annual survival was estimated at 0.57 ± 0.06 (posterior mean $\pm$ SD), with a process variance of 0.019 representing variability in survival among years (Figure 3). Point estimates for annual survival probabilities ranged from 0.67 ± 0.04 for 2011–2012 to 0.45 ± 0.04 for 2014–2015 (Figure 3).

Breeding phenology and seasonal productivity. Mean earliest arrival date for males and females on the BCP plots was March 6 and March 13, respectively (range: March 2–12 for males and March 8–15 for females; $n = 5$ yr). Mean earliest date that males were reported for the BCP area in the e-Bird database was March 7 (range: March 6–14, 2011–2015). Mean nest initiation (building) was first detected on March 19 (range: March 16–23; $n = 5$ yr),

TABLE 1. Posterior predictive checks of model fit for adult male Golden-cheeked Warbler survival on the Balcones Canyonlands Preserve, Austin, Texas, USA. Four test statistics were calculated from the observed data and from data simulated according to each dispersal model. Expectations based on each model are presented as the mean (with 95% credible intervals in parentheses) of simulated datasets. Percent difference (%Diff) was calculated as the difference in the mean simulated value in relation to the observed value.

Test statistic	Observed	T distribution		Double-exponential distribution		Normal distribution	
		Expected	%Diff	Expected	%Diff	Expected	%Diff
Mean number of years sighted	1.59	1.56 (1.39–1.74)	–2.1%	1.43 (1.23–1.59)	–10.0%	1.20 (1.07–1.31)	–25.0%
Proportion resighted >2 times	0.39	0.36 (0.29–0.44)	–6.2%	0.31 (0.19–0.39)	–20.4%	0.17 (0.07–0.25)	–57.5%
Median inter-year displacement (m)	64	78 (67–91)	+22.2%	325 (285–359)	+403.8%	1,085 (756–1,392)	+1,594.2%
90th percentile inter-year displacement (m)	271	316 (259–389)	+17.5%	785 (660–938)	+189.7%	3,013 (2,235–3,775)	+1,011.8%

mean incubation was first detected on March 30 (range: March 25–April 4; $n = 5$ yr), and mean last fledge date was June 12 (range: June 4–21; $n = 5$ yr). The average length of the breeding season was 76.6 days $\pm$ 6.3 ($n = 5$ yr). We documented ≤ 4 nesting attempts in a territory within a given season (mean = 1.24 nesting attempts, SD = 0.50; $n = 601$ territories), with a mean of 6 days between nest failure and laying in a subsequent nest (range: 3–12 days; $n = 22$ nesting attempts). We found few instances of initiation of a double-brood during the building stage, so we calculated the number of days between fledging a first nest and laying in a second nest by subtracting the number of days in the nesting cycle (25) from the number of days between

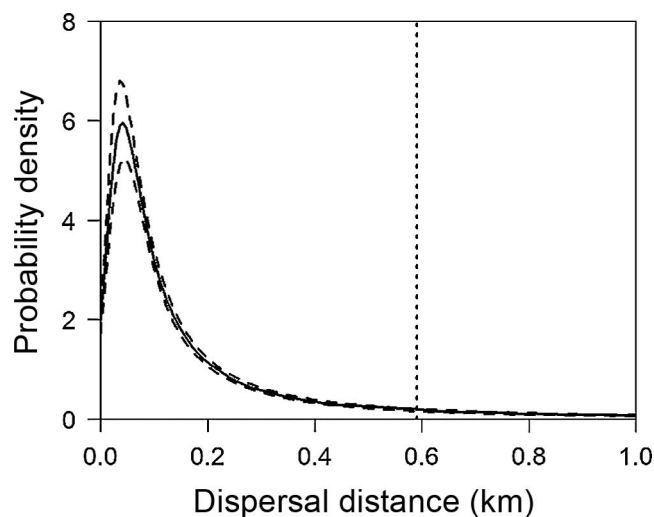


FIGURE 2. Predicted distribution of inter-year movements for adult male Golden-cheeked Warblers within the Balcones Canyonlands Preserve, Austin, Texas, USA, based on the best-fitting spatial Cormack-Jolly-Seber model. The probability density (y axis) indicates the relative likelihood that a movement between adjacent years will be of a given distance. The dotted vertical line indicates the estimated 90th percentile for inter-year movements.

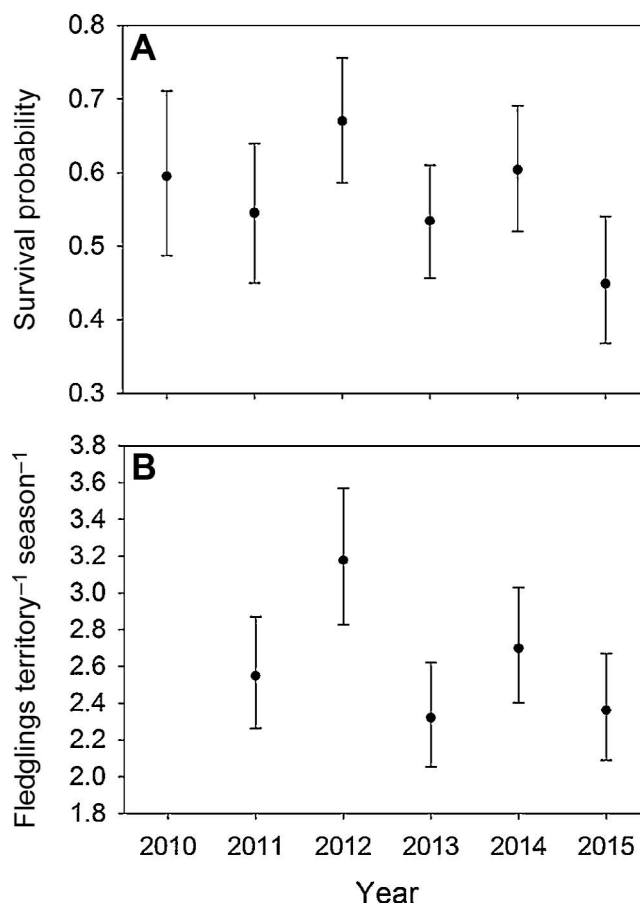


FIGURE 3. Annual survival (posterior means $\pm$ 95% credible intervals) of male Golden-cheeked Warblers within the Balcones Canyonlands Preserve, Austin, Texas, USA, based on the best-fitting spatial Cormack-Jolly-Seber model (**A**) and annual seasonal productivity (means $\pm$ 95% confidence intervals) of Golden-cheeked Warblers based on the most-supported productivity model (**B**). Survival probability represents the annual survival from the preceding year (e.g., 2010 is survival from 2009 to 2010). Note that productivity was not estimated in 2010.

TABLE 2. Descriptive statistics of covariates used to evaluate the relationships between seasonal productivity (fledglings territory⁻¹ season⁻¹) of Golden-cheeked Warblers and landscape-scale (1 km) and territory-scale (100 m) covariates on the Balcones Canyonlands Preserve, Austin, Texas, USA.

Variable	Label	Mean	SD	Minimum	Maximum
Landscape woodland cover: 1 km	Landsc woods	0.88	0.08	0.42	0.99
Landscape edge density (m ha ⁻¹): 1 km	Landsc edge	70.99	24.87	21.88	152.62
Standard deviation of canopy height (m): 100 m	Can ht SD	2.11	0.75	0.84	6.84
Mean canopy height (m): 100 m	Can ht	8.72	1.12	5.37	12.38
Territory edge density (m): 100 m	Territory edge	13.18	30.69	0.00	247.71
Canopy cover: 100 m	Can cover	0.89	0.09	0.43	0.99

fledgling the first and second nest. A mean of 33.6 ± 3.2 days elapsed between the first and second broods fledgling (range: 27–37 days; $n = 16$ successful double-brooding attempts), so we estimated 8.6 days as the average interval between double-brooding nesting attempts.

We determined pairing and breeding success for 1,114 territories wholly or partially within our intensive monitoring plots during 2011–2015, finding that 1,019 males (91%) were paired and 754 territories (68%) produced at least one fledgling. We documented successful double brooding for 5% of territories (54 of 1,114 territories) and never observed >2 successful nesting attempts. We documented 11 cases of polygyny (2 in 2011, 4 in 2012, 1 in 2014, and 4 in 2015), 2 cases of polyandry, and one instance of female mate-switching (i.e. banded female switched banded males within season). We determined complete fledgling counts (confidence = 1) for 784 territories (70%; $n = 1,114$ territories), of which 360 territories were confirmed to produce zero fledglings.

The mean number of observed fledglings for our sample was 2.10 ± 1.78 (range: 0–8; $n = 1,114$ territories). However, the mean number of observed fledglings for successful territories (≥ 1 fledgling) was 3.65 ± 1.08

(range: 1–8; $n = 424$ territories) and 2.39 ± 1.11 (range: 1–7; $n = 330$ territories) for complete and potentially incomplete counts, respectively. After adjusting for bias in incomplete counts, the mean number of fledglings per territory was 2.46 ± 1.93 (range: 0–8; $n = 1,114$ territories).

Landscape and territory attributes varied across our sample of territories (Table 2). We found no evidence of lack of fit for the global model ($\hat{c} = 1.29$), and there was a significant positive correlation between predicted and observed values based on a tenfold validation procedure ($r = 0.44$, 95% CI: 0.30–0.58). We fitted 12 candidate models predicting seasonal productivity. The global model was the most supported model (Table 3). This model included the quadratic form of landscape woodland cover, landscape edge density, and standard deviation of canopy height ($w_i = 0.58$; Table 3). Two additional models had $\Delta AIC_c < 4$, but both were reduced versions of the most supported model or varied by a linear vs. quadratic term and had less than half the support of the most supported model; therefore, we based further inference and predictions on the most supported model. Parameter estimates for the most supported model (β , SE) were as follows:

TABLE 3. Support for candidate models predicting seasonal productivity (fledglings territory⁻¹ season⁻¹) of 1,114 Golden-cheeked Warbler territories during 2011–2015 on the Balcones Canyonlands Preserve, Austin, Texas, USA. AIC_c (Akaike's Information Criterion corrected for small sample size) of the most supported model was 4,655.26, K is the number of parameters in the model, ΔAIC_c is the difference between the model of interest and the most-supported model, and w_i is the Akaike weight, which represents model support.

Model ^a	K	ΔAIC_c	w_i
Year + Landsc woods + Landsc woods ² + Landsc edge + Can ht SD	10	0.00	0.58
Year + Landsc woods + Landsc woods ² + Landsc edge	9	1.63	0.25
Year + Landsc woods + Landsc woods ² + Landsc edge + Landsc edge ²	10	3.47	0.10
Year + Landsc woods + Landsc woods ²	8	4.23	0.07
Year + Can ht + Can ht SD + Territory edge	9	24.72	0.00
Year + Can cover + Can ht + Can ht SD	9	36.70	0.00
Year + Can ht SD	7	37.97	0.00
Year + Can cover + Territory edge	8	38.52	0.00
Year + Territory edge	7	38.71	0.00
Year	6	42.90	0.00
Year + Can ht	7	44.12	0.00
Year + Can cover	7	44.37	0.00

^a See Table 2 for variable descriptions.

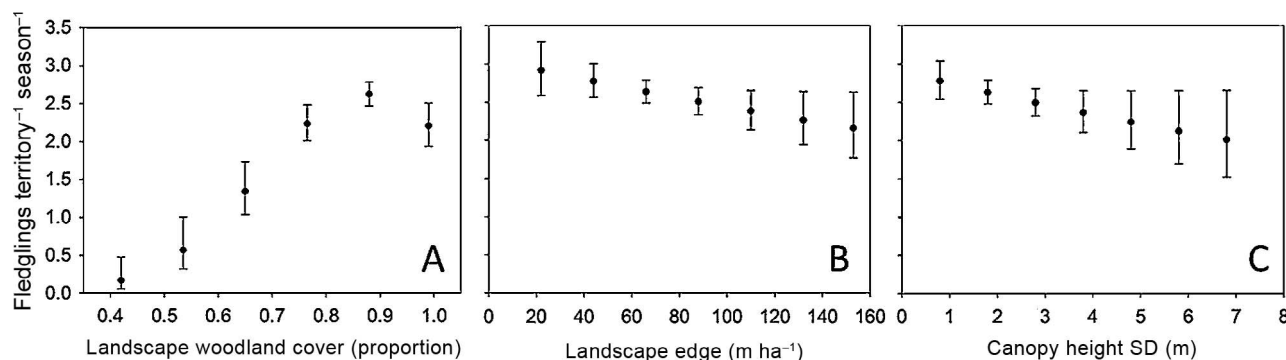


FIGURE 4. Predicted seasonal productivity of Golden-cheeked Warblers as a function of (A) landscape woodland cover, (B) landscape edge density, and (C) standard deviation of canopy height around the territory on the Balcones Canyonlands Preserve, Austin, Texas, USA, 2011–2015.

intercept (−8.984, 2.025), year 2011 (0.076, 0.084), year 2012 (0.297, 0.083), year 2013 (−0.018, 0.085), year 2014 (0.134, 0.082), landscape woodland cover (23.131, 4.767), landscape woodland cover² (−13.213, 2.818), landscape edge density (−0.002, 0.001), and standard deviation of canopy height (−0.075, 0.029). Average predicted seasonal productivity based on our sample of territories was 2.46 ± 0.51 fledglings territory⁻¹. Predicted mean seasonal productivity ranged from 2.32 fledglings territory⁻¹ for 2013 to 3.18 fledglings territory⁻¹ for 2012 (Figure 3).

Seasonal productivity peaked at 2.62 fledglings territory⁻¹ when landscape woodland cover was 0.88 but decreased to 0.57 fledglings territory⁻¹ when landscape woodland cover was 0.42 (Figure 4A). Seasonal productivity decreased with increasing landscape edge density and standard deviation of canopy height, declining from 2.92 to 2.16 fledglings territory⁻¹ across the observed range of landscape edge density (Figure 4B) and 2.78 to 2.01

fledglings territory⁻¹ across the observed range of standard deviation of canopy height (Figure 4C). Predicted seasonal productivity was similar to observed seasonal productivity for 15 of 17 monitoring plots and was greater for the remaining 2 plots (Figure 5). Predicted seasonal productivity was greater in interior portions of the BCP and averaged 1.96 ± 0.70 fledglings territory⁻¹ (range: 0.00–3.04 fledglings territory⁻¹) across the BCP based on a balanced sample across 2011 to 2015 (Figure 6). The map-based prediction reflects predicted mean productivity over the entire BCP but does not account for breeding density.

DISCUSSION

Survival and productivity drive population dynamics, and knowledge of these demographic rates is critical for endangered species management and conservation. Previous population modeling efforts for Golden-cheeked Warblers have relied on data from a few study areas within Fort Hood (e.g., Alldredge et al. 2004, Horne et al. 2011). We present the first estimates of adult male survival and seasonal productivity from a relatively long-term dataset for Golden-cheeked Warblers breeding at sites other than Fort Hood. While our estimates generally correspond with demographic rates estimated on Fort Hood (Peak and Thompson 2014), we caution that additional research on Golden-cheeked Warblers breeding in more fragmented woodlands and in other portions of the breeding range are still necessary because both Fort Hood and the BCP are considered high-quality habitat composed of protected areas of mostly mature, closed-canopy woodlands.

Survival and dispersal. Our mean survival estimate for the BCP was greater than the recent apparent survival estimate for Fort Hood (0.57 vs. 0.47) provided by Duarte et al. (2014). This difference should at least partly reflect the fact that traditional mark–recapture analyses underestimate survival whenever there is a nonzero probability

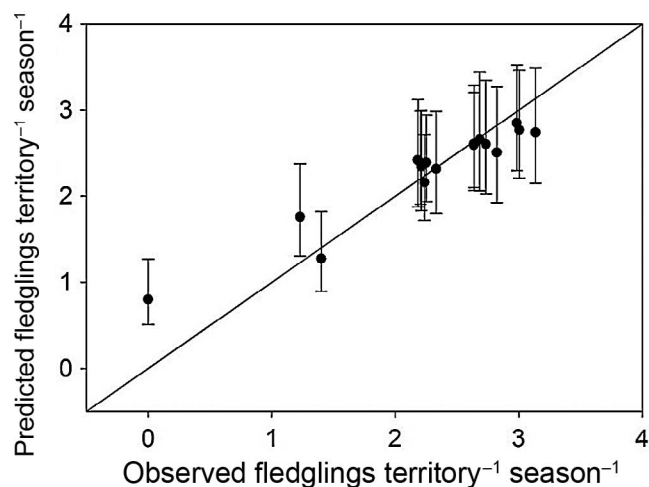


FIGURE 5. Predicted vs. observed seasonal productivity of Golden-cheeked Warblers on 17 monitoring plots within the Balcones Canyonlands Preserve, Austin, Texas, USA.



FIGURE 6. Predicted seasonal productivity (fledglings territory⁻¹ season⁻¹) of Golden-cheeked Warblers across the Balcones Canyonlands Preserve, Austin, Texas, USA.

of birds dispersing away from the study area. By incorporating a dispersal-process model, our s-CJS analysis accounted for the loss of some individuals from the study population due to permanent emigration rather than mortality. Survival varied considerably across years in our study, but annual survival estimates fell within the reported range of annual apparent survival estimates for the long-term study at Fort Hood (Duarte et al. 2014). The process variance, which describes the expected interannual variation in survival, was greater in our study (0.019) than at Fort Hood (0.012; Duarte et al. 2014). Both results indicate that there is considerable variability in survival among years that could lead to large temporal fluctuations in population sizes. Because long-term (e.g., multi-decade) studies may be required to adequately characterize the variability in interannual survival (Altwegg et al. 2006),

additional monitoring would be required to determine whether survival is consistently more variable on the BCP. Persistently low return rates and annual survival estimates for Golden-cheeked Warblers on the BCP, similar to those seen in 2015 (present study) and 2016 (City of Austin personal communication), could also have considerable negative effects on this population and provide justification for continued monitoring. We were unable to account for annual variation in dispersal probability because of the relative infrequency of dispersal movements in any individual year, especially for longer distance classes. Instead, movement data from all years were used to fit a single dispersal curve. As a result, estimated process variance describing interannual variation in survival is confounded with variation in dispersal behavior among years. Differences among annual point estimates for survival should therefore reflect a combination of annual variation in survival and bias due to above- or below-average levels of dispersal (McKellar et al. 2015).

Our study provides the first documentation of movement and dispersal behavior for adult male Golden-cheeked Warblers outside of Fort Hood. Our return rates were in the range reported on Fort Hood but our dispersal patterns were different (Jetté et al. 1998). The majority of resighted males (67%) on the BCP settled in the same general area (median movement <100 m), indicating high site fidelity for a large portion of territorial males, whereas the median distance at which adult males settled in subsequent years on Fort Hood was 141 m (Jetté et al. 1998). However, a large minority (33%) moved far enough between years that they may not have been resighted within monitoring plots or buffers. Our survey design involving multiple closely spaced monitoring plots, plus additional resighting areas between monitoring plots, maximized our ability to resight dispersing males. The long-distance dispersal events we documented are much larger than the range reported on Fort Hood, which was ≤ 3.5 km (Jetté et al. 1998). We also observed within-season dispersal events, which typically occurred late in the season for unpaired or unsuccessful males. These between- and within-year movements suggest that Golden-cheeked Warblers move more than previously thought and that dispersal patterns should be considered in future survival analyses. Interestingly, and perhaps importantly, despite detected movement within the BCP, we never resighted a banded Golden-cheeked Warbler that had been banded elsewhere, such as on the nearby Balcones Canyonlands National Wildlife Refuge or Fort Hood, despite several years and dozens of observers searching across the BCP, and only once has a banded Golden-cheeked Warbler from the BCP been resighted elsewhere (an SY male banded on BCP in 2016 was resighted in 2017 on Balcones Canyonlands National Wildlife Refuge, ~ 12 km away). Therefore, the ability (or lack thereof) of this species to disperse has

important implications for population dynamics and needs to be explored further (Duarte et al. 2016a, 2016b). Continued development around the BCP will further reduce and fragment available breeding habitat immediately outside the BCP and could result in isolating this population from other suitable woodland patches.

Breeding-season mortality likely represents a minor component of annual population losses for migratory songbirds (Silleet and Holmes 2002). Although we have no a priori reason to believe that mortality differs spatially for Golden-cheeked Warblers (Duarte et al. 2014), there are potentially more sources of mortality related to the urbanizing landscape than in a more rural landscape. For example, 2 of 3 documented mortalities were human related—one bird was killed by a vehicle while crossing a road and one bird was killed after striking a window of a commercial building (the third was killed during a fight with another male). We also documented cases of injury or disease that may result in death during the breeding season or shortly thereafter. We suspect that dispersal varies spatially because males that fail to breed or arrive late and settle in less favored habitat may be more likely to disperse the following year (Haas 1998, Hoover 2003, Joos et al. 2014). Although we considered preliminary models with separate survival and dispersal parameters for males that successfully bred and those that did not, this analysis required a sub-model to predict the breeding success of individuals for years in which it was not observed. Having an inadequate model for breeding success, we were unable to successfully resolve differences in dispersal behavior among successful and unsuccessful breeders. However, on the basis of our observations of late-season movements of unpaired or unsuccessful paired males, we consider this a promising area for future research.

A final limitation of our survival analysis was our inability to estimate survival and dispersal parameters for females and juveniles because of our limited number of resightings. We do not know whether there is differential survival for females annually or during the breeding season. Reidy et al. (2009a) estimated that ~15% of females experience predation by snakes while attending nests. There is no comparable estimate of male mortality during the breeding season. Juvenile survival is an especially difficult parameter to estimate for songbirds such as Golden-cheeked Warblers because of their high natal dispersal probability (Jetté et al. 1998, Anders and Marshall 2005).

Productivity. Overall, nesting phenology was fairly similar to that reported on Fort Hood, and with comparable low rates of successful double brooding and alternative mating strategies (Peak and Thompson 2014). Because our seasonal productivity for successful territories (3.65 fledglings territory⁻¹) was very similar to the number of young produced by successful nests on the BCP (3.8

fledglings nest⁻¹; Reidy et al. 2008) and we documented few successful double broods, we consider our estimate of seasonal productivity to be very reasonable for this population. Seasonal productivity was slightly greater on BCP (2.46 fledglings territory⁻¹) than on Fort Hood (2.36 fledglings territory⁻¹; Peak and Thompson 2014) and burned plots on Balcones Canyonlands National Wildlife Refuge (2.22 fledglings territory⁻¹; Reidy et al. 2016b) but similar to unburned plots on Balcones Canyonlands National Wildlife Refuge (2.51 fledglings territory⁻¹; Reidy et al. 2016b). Mean observed and predicted seasonal productivity estimates were the same (2.46 fledglings territory⁻¹), and observed seasonal productivity was well predicted for 15 of 17 plots (Figure 5). For the remaining 2 plots, we surmise that the predicted seasonal productivity was greater than the observed seasonal productivity because the small number of territories on these plots precluded high predictive power of our model. In addition, the land-cover map we used may not adequately capture the effects of extremely low-density residential development on these small and isolated patches of protected woodland. Both plots are on the urban–exurban interface and support 2 species of known nest predators, Woodhouse's Scrub-Jay (*Aphelocoma woodhouseii*) and Blue Jay (*Cyanocitta cristata*), whereas most larger woodland patches on the BCP support only Woodhouse's Scrub-Jay.

Our map-based estimate of 1.96 fledglings territory⁻¹ is the average across all habitat within the BCP and is not restricted to expected Golden-cheeked Warbler habitat within the BCP. It is based on all the pixels within the BCP and includes areas that Golden-cheeked Warblers may not currently use; therefore, the map-based mean seasonal productivity was lower than the sample-based mean seasonal productivity, which was based on the population of territories we monitored. Our sample-based estimate of 2.46 fledglings territory⁻¹ best reflects the expected productivity for this population because it is based on territories within breeding habitat. However, our predictions across the entire BCP enable land managers to identify or protect areas of already high productivity, or to make comparisons to evaluate management efforts.

Seasonal productivity was best predicted by features at the landscape and territory scales. Seasonal productivity peaked at high values of landscape woodland cover and was significantly lower at the lowest proportion. We also found strong support that seasonal productivity was greater in landscapes with less edge and in territories with more homogeneous canopy height, both of which are characteristics of more mature, closed-canopy woodlands that likely have less predator activity. Cumulatively, these habitat conditions resulted in greater predicted productivity within the interior portions of the BCP (Figure 6). Predicted productivity was greater in the northeastern patches and followed similar spatial patterns as predicted

density (Reidy et al. 2016a). These results, taken together with previous occupancy, density, and nest survival results from the BCP, Fort Hood, and elsewhere (Magness et al. 2006, Collier et al. 2012, Peak and Thompson 2013, 2014, Reidy et al. 2016a, 2017), provide strong evidence that Golden-cheeked Warblers need large patches of non-fragmented mature juniper–oak woodland for optimal breeding conditions (high density and productivity). Land managers can promote high-quality breeding habitat for Golden-cheeked Warblers by protecting large woodland patches and implementing measures to reduce forest edge density.

We know of no comprehensive assessments of seasonal productivity beyond our study and Peak and Thompson (2014), so it is unclear whether the relationships observed on the BCP and Fort Hood extend to other portions of the breeding range, such as the southern extent where woodland patches are largest, or the western and northern extent where woodland patches are mostly small and fragmented (Collier et al. 2012). Campomizzi et al. (2012) reported that territory success varied regionally across the breeding range but did not vary consistently by woodland patch size, patch edge, or canopy cover. Because of differences in sampling methods, we cannot compare our results to the results in that study. Additional demographic data need to be collected in other areas of the breeding range for a comprehensive understanding of warbler population dynamics and habitat relationships.

It is not yet clear what the implications of our estimated demographic rates are for this population. Peak and Thompson (2014) conducted a simple exploratory population projection model using their observed seasonal productivity of $2.36 \text{ fledglings territory}^{-1}$ and reported that apparent survival of 0.63 and 0.315 for adults and juveniles, respectively, was needed to maintain a stable population on Fort Hood. Our average estimate of seasonal productivity is slightly greater than this, but adult survival is slightly lower and juvenile survival is unknown. Population growth rates are likely dynamic, changing annually with varying demographic rates. Interestingly, annual trends in survival and productivity were similar (Figure 3), with above-average survival and productivity in 2012 and 2014 and below-average survival and productivity in 2011, 2013, and 2015, which suggests that the population may only be stable or growing in some years. Our estimates of adult survival and productivity are between the vital-rate points used by Duarte et al. (2016a) in their scenarios 2 and 3 to project the Golden-cheeked Warbler's range-wide viability under simulated conditions. Under either scenario, the population on the BCP may be expected to sustain itself under current conditions (Duarte et al. 2016a). Despite this optimistic outlook, the BCP will increasingly become an archipelago of woodland within an urban matrix, and connectivity to neighboring high-quality woodland patches

is likely to decrease as surrounding woodlands are cleared and splintered for development. Information on dispersal for adults and juveniles is necessary to validate survival estimates and determine the species' ability to move between patches. We recommend continued monitoring of demographic rates in this urbanizing landscape.

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Ethics statement: The University of Missouri's Animal Care and Use Committee approved all field procedures (ACUC protocol no. 8383). Banding was conducted under USGS Bird Banding Laboratory permit no. 23615. J.L.R. held appropriate state, federal, and banding permits to conduct field activities.

Author contributions: J.L.R., F.R.T., and L.O. conceived the study design and developed the methods. J.L.R. and L.O. led the data collection effort. J.L.R., F.R.T., and G.M.C. analyzed the data. All authors contributed to the writing of the manuscript. F.R.T. and L.O. facilitated funding.

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