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Original Article

Population Viability of Golden-cheeked Warblers in an Urbanizing Landscape

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ABSTRACT Population viability analyses can assess species persistence under current or simulated future conditions and guide conservation and management efforts for species of concern. We evaluated population viability of an endangered songbird, the golden-cheeked warbler (*Setophaga chrysoparia*), over a 50-year period using empirically derived population parameters collected from 2009 to 2015 on the Balcones Canyonlands Preserve (BCP), Travis County, Texas, USA. Assuming the extent and quality of habitat within the BCP does not change, the population remained stable with a population size of approximately 1,800 males, adult survival of 0.57, seasonal productivity of 1.32 male fledglings/territory, and assumed juvenile survival of 0.40. Population viability, however, was sensitive to changes in vital rates. The population declined toward local extinction when vital rates were at the low end of rates considered (0.47 adult survival, 1.14 male fledglings/territory, 0.28 juvenile survival), but had little to no probability of local extinction when vital rates were at the upper end (0.67 adult survival, 1.50 male fledglings/territory, 0.44 juvenile survival). Obtaining accurate estimates of juvenile survival remains problematic, but if juvenile survival is as low as previously reported elsewhere (0.28), the stability observed during the years of our study could be due to immigration of individuals displaced by habitat loss in the surrounding landscape. Increased carrying capacity, which served as a proxy for increased habitat quality within the BCP, was insufficient to sustain the population when productivity was low, illustrating the need for adequate seasonal productivity. Consistent with previous studies, our findings underscore the importance of managing for high-quality breeding habitat and maintaining connectivity with other large habitat patches to promote the long-term viability of the species. We suggest monitoring survival and productivity of high-concern species may be justified because assessment of status from abundance alone can be confounded by immigration and other factors.

KEY WORDS adult survival, central Texas, endangered species, golden-cheeked warbler, juniper–oak woodland, juvenile survival, population viability, productivity, PVA, *Setophaga chrysoparia.*

Population viability analysis (PVA) is a widely used modeling approach for predicting extinction risk and exploring outcomes of various conservation and management scenarios for endangered species (Beissinger and Westphal 1998, Akçakaya and Brook 2009). Population viability analysis models consider vital rates, life-history traits, and habitat associations to predict the viability or persistence of a population or a species in a landscape and are often performed for endangered species as part of the recovery plan process to guide conservation and management (Akçakaya and Brook 2009). Population viability analysis models can also elucidate what changes in life-history parameters population growth (λ) is most sensitive, and the consequences of management scenarios (e.g., productivity, adult survival, juvenile survival; Bonnot et al. 2013).

The golden-cheeked warbler (*Setophaga chrysoparia*) is a federally endangered species that breeds exclusively in Ashe juniper–oak (*Juniperus ashei–Quercus* spp.) woodlands and forests located in central Texas, USA (Ladd and Gass 1999). The main threat to this species during the breeding season is habitat loss and fragmentation, mostly due to widespread clearing associated with agriculture and urbanization (USFWS 1990). Despite its endangered status, potential breeding habitat was reduced by 29% between 2000 and 2010, and remaining habitat was increasingly fragmented and isolated, particularly near urbanizing areas,

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thereby reducing potential carrying capacity and productivity of breeding pairs (Duarte et al. 2013). Previous population models have relied on vital rates estimated mostly from monitoring data conducted in Fort Hood, Texas, and are for the most part outdated (USFWS 1996, Alldredge et al. 2004, Vaillant et al. 2004, Horne et al. 2011). A recent PVA was performed for the entire breeding range that incorporated abundance and vital rate information from additional studies and sites. Duarte et al. (2016*a*) concluded a low risk of species extinction (depending on vital rates and dispersal dynamics, which are unknown), but emphasized considerable uncertainty in their models despite using the largest estimate of population size reported for the golden-cheeked warbler.

We studied the population of golden-cheeked warblers breeding in Balcones Canyonlands Preserve (BCP), which is a rapidly urbanizing site in recovery region 5 (USFWS 1992). Recovery region 5 contains the second (BCP) and third (Balcones Canyonlands National Wildlife Refuge) largest protected areas in the entire breeding range (Groce et al. 2010). While recovery region 5 experienced less overall habitat loss (~23%) than most regions between 2000 and 2010, it had the greatest rate of habitat fragmentation, resulting in increased edge and smaller forest patches (Duarte et al. 2013). Such fragmentation has been linked to lower nest survival and seasonal productivity of golden-cheeked warblers (Peak 2007, Reidy et al. 2009, 2018, Peak and Thompson 2014). The BCP was created in 1996 to mitigate increasing habitat loss and represents approximately 60% of the protected woodland in recovery region 5 (USFWS 1996, Groce et al. 2010). However, creation of the BCP allows for the development of approximately 70% of the remaining unprotected habitat in Travis County (USFWS 1996). Additionally, there is increasing pressure to allow more infrastructure and public access, including roads and trails, within the BCP. With these ongoing management challenges, we need to better understand the long-term viability of this increasingly isolated population, especially given its importance to the regional and global population.

We modeled the viability of the golden-cheeked warbler population on the BCP based on site-specific estimates of vital rates and abundance (Reidy et al. 2016*a*, 2018). Our objectives were to 1) predict population size for the golden-cheeked warbler on the BCP over a 50-year time period using site-specific estimates of abundance and vital rates, 2) determine the response of the population (increase or decrease in abundance) to changes in vital rates, and 3) evaluate the population response to changes in habitat quality within the BCP (represented as changes in carrying capacity) at varying productivities. We treated the BCP as a closed population with no net immigration or emigration because we were interested in its viability as a stand-alone population given the urban expansion around the preserves. Additional woodland patches exist near the BCP but support few breeding golden-cheeked warblers (Robinson et al. 2018). With expected additional habitat loss within the region, the BCP will become increasingly isolated from other large woodland patches. We simulated the population response to varying vital rates that represented the range of empirical estimates for key demographics rates. We simulated changes in productivity in conjunction with carrying capacity because we expected those parameters were likely the most responsive to management efforts on the BCP (adult survival within the BCP is likely high [Reidy et al. 2018] and juvenile survival while on the breeding grounds may also be high [JLR, unpublished data; Trumbo 2019]). Our results should aid conservation planners and managers by adding to our knowledge of the population dynamics of the golden-cheeked warbler in an urbanizing area.

STUDY AREA

The BCP was located in western Travis County, Texas (30°20′N, 97°50′W), on the eastern edge of the Edwards Plateau, along the Balcones Escarpment. The area was characterized by steeply dissected, heavily wooded hills and upland plateaus. The BCP was a discontinuous network of separate patches totaling 12,325 ha at the time of our study, ranging in size from 180 to >3,500 ha, and owned and managed by several agencies (Fig. 1; City of Austin and Travis County 2018). During our study, we estimated that 7,323 ha (59%) was juniper-dominated woodland (>70% of the canopy was juniper) and 3,934 ha (32%) was mixed juniper–oak woodland. The dominant habitat types consisted most commonly of Ashe juniper, Texas red oak (*Q. buckleyi*), plateau live oak (*Q. fusiformis*), shin oak (*Q. durandii* var. *breviloba*), cedar elm (*Ulmus crassifolia*), escarpment black cherry (*Prunus serotina* var. *serotina*), and Texas ash (*Fraxinus texensis*). Common understory species included Carolina buckthorn (*Rhamnus caroliniana*), yaupon holly (*Ilex vomitoria*), red buckeye (*Aesculus pavia* var. *pavia*), Mexican buckeye (*Ungnadia speciosa*), Lindheimer silk-tassel (*Garrya ovata* var. *lindheimeri*), and elbowbush (*Forestiera pubescens*; City of Austin et al. 2014). An extreme drought in 2011 resulted in extensive and expanding areas of juniper mortality in upland portions of the BCP. Mean annual temperatures ranged from 15–27° C and the mean precipitation was the area is 863 mm.

METHODS

Model Description

We used a Lefkovitch stage-matrix model that incorporated stochasticity to project the golden-cheeked warbler population on the BCP over 50 years, which we implemented in RAMAS GIS (Version 6.0, Applied Biomathematics, Setauket, NY, USA). We used a male-based model that incorporated estimates of adult male survival and productivity from Reidy et al. (2018). We used a male-based projection model because obtaining rigorous survival and abundance estimates for female songbirds is difficult. Baseline abundance and vital rates were based on estimates from Reidy et al. (2016*a*, 2018), who linked abundance and vital rates to habitat characteristics on the BCP. We simulated the BCP population as a single population, even though it consists of discontinuous patches of woodland, because 10% of males were estimated to move >1 km and

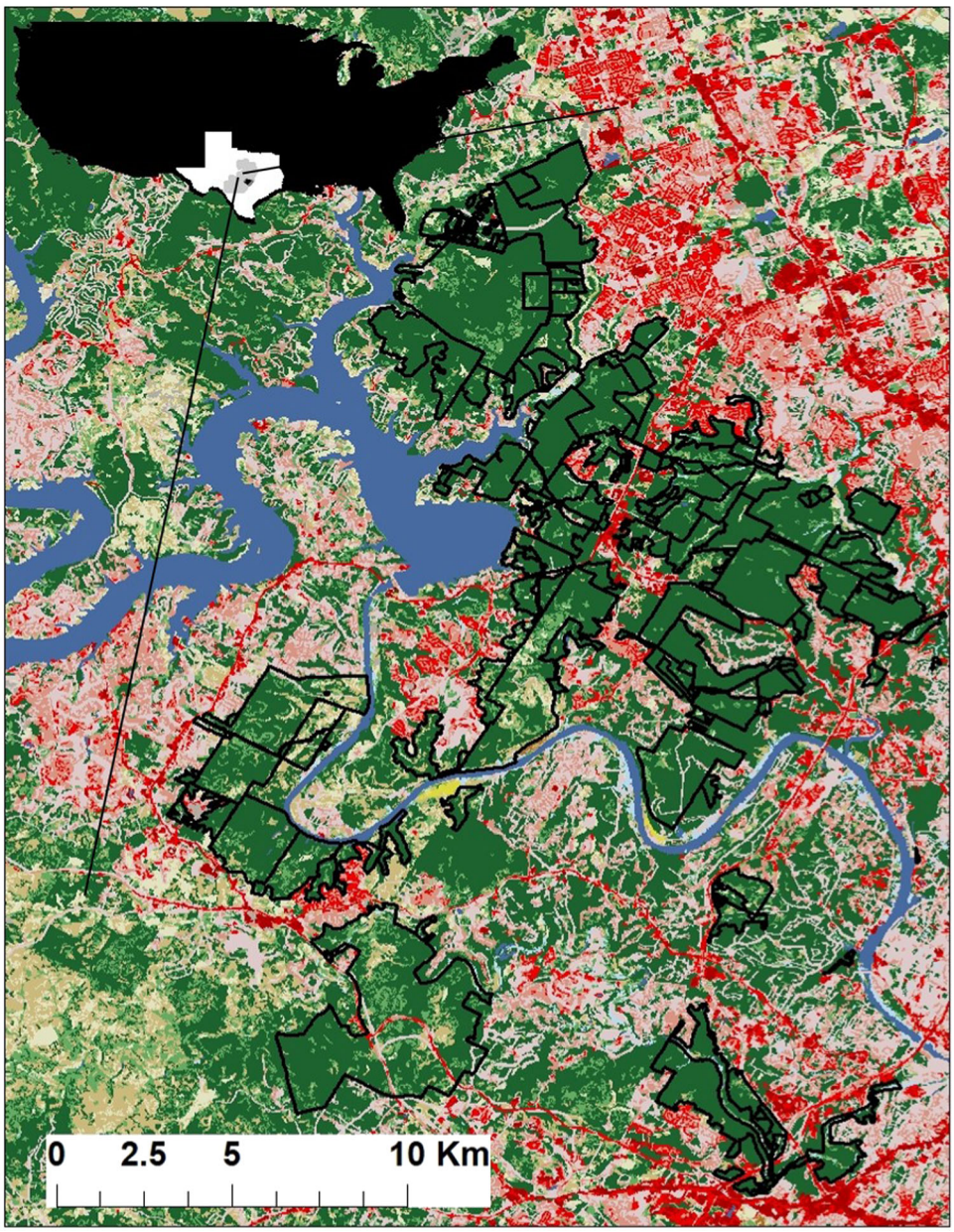

Figure 1. We evaluated population viability of golden-cheeked warblers (males/ha) over a 50-year period using empirically derived population parameters collected from 2009 to 2015 on Balcones Canyonlands Preserve (BCP), Austin, Texas, USA (black outline). The BCP was mostly wooded–forested (dark green) and surrounded by urban land uses (pink and red). The inset shows Texas (white) within the United States (black), with the 8 recovery regions defined by the U.S. Fish and Wildlife Service (gray); recovery region 5 includes Travis County (dark gray), and within that is the BCP.

banded males have been documented moving among study plots at distances up to 16 km (Reidy et al. 2018).

We estimated the starting population size for the BCP based on the spatially explicit density model reported in Reidy et al. (2016*a*). They estimated density of males for all 180 × 180-m pixels (which approximated the area surveyed by a point count and average size of a territory) on the BCP based on a hierarchical Bayesian model fit to 1,507 point counts systematically distributed across the BCP and surveyed during April and May, 2011–2014. Reidy et al. (2016*a*) estimated density from a model that accounted for detectability and availability of singing males, and compared the estimated densities with actual densities from 18 monitoring plots for which the majority of territories had uniquely banded males. The best-fitting model tended to overpredict density, particularly on low-density plots (Reidy et al. 2016*a*). Therefore, we used the principle of double-sampling to adjust the model-based predictions to more closely match observed territory densities (Bart and Earnst 2002). We fit a polynomial regression relating the estimated densities to observed densities:

$$D_t = \beta_1 D_m + \beta_2 D_m^2 + \beta_3 D_m^3$$

where D_t was the mean observed density on an intensive monitoring plot for 2011–2014 and D_m was the mean model-based prediction for the pixels within an intensive

monitoring plot. We chose a third-order polynomial because it fit better than a linear or first- or second-order polynomial. We converted the density estimates for each pixel to abundance and then summed these to derive an estimate of male abundance across the BCP.

We assumed ceiling-type density dependence, which is appropriate for territorial songbirds for which breeding is relatively unaffected by density at abundances below carrying capacity (K; Akçakaya 2002). Our habitat-based estimate of the starting population represented an estimate of the current population but we do not know how current population size relates to K without additional information on what is currently constraining the size of this population. Therefore, we arbitrarily set K as 125% of the estimated starting population. Population projections are unaffected by K until the population size approaches the ceiling, and this estimate of K was large enough for us to detect whether the population would increase in a scenario. We treated the BCP as a closed population because we were interested in the ability of the BCP to sustain a golden-cheeked warbler population without depending on the surrounding, urbanizing landscape.

We based the Lefkovitch stage-matrix model on annual time steps with an annual census immediately before breeding. Age class 0 was juveniles <1 year old, age class 1 was individuals 1 year old, and age class 2 was individuals ≥2 years old. This resulted in the following matrix:

$$\begin{bmatrix} S_0 m_1 & S_0 m_2 \\ S_1 & S_2 \end{bmatrix}$$

where m_1 and m_2 were the productivity of age class 1 and 2, respectively, expressed as male fledglings per male per year, and S_0, S_1, and S_2 were survival of age class 0, 1, and 2, respectively (Caswell 2001, Akçakaya 2002). We assumed no age-related variability in productivity ($m_1 = m_2$) and constant adult survival with no obligate mortality ($S_1 = S_2$), which is a suitable model for small, short-lived birds (Noon and Sauer 2001). Age-specific productivity and survival may be incorporated into population models of migratory songbirds, but we relied on vital rate estimates from Reidy et al. (2018), and they did not provide age specific productivity or survival. Nevertheless, their estimates are from a large sample of territories during years the population appeared stable, which should serve as representative mean productivity and survival for our model. We parameterized the model with a range of values for productivity and survival based on estimates from the BCP and other studies (described below). We included environmental and demographic stochasticity in each model. We incorporated environmental stochasticity by selecting vital rates from an appropriate distribution defined by a mean and standard deviation (SD). We selected productivities ($S_0 m$) from a log-normal distribution and selected survivals (S_1, S_2) from a log-normal distribution if the mean was <0.5 and from a mirrored log-normal distribution if the mean was >0.5. Annual survival was between 0.47–0.67 and SDs modest (Table 1), which avoided the need for truncation of survivals <0 or >1 and resulted in a suitable distribution of random values around the desired mean. We used a SD of 0.19 for productivities and 0.14 for survival based on estimated seasonal productivities and estimated process variation for survival (Akçakaya 2002, Reidy et al. 2018). The number of survivors and the number of fledglings produced in each stage each year were drawn from binomial and Poisson distributions, respectively, to obtain integer values for the numbers of individuals (Akçakaya 2002).

We used empirically derived estimates of productivity and adult survival from data collected on the BCP in our baseline scenario (Table 1). Reidy et al. (2018) estimated seasonal productivity from a sample of 1,114 territories monitored on 18 plots across the BCP during March through June, 2011–2015. They estimated seasonal productivity as the total number of fledglings assigned to a

Table 1. Model parameters[a] and resulting population size, growth, and viability[a] after 50 simulated years for a starting population of 1,779 male golden-cheeked warblers on the Balcones Canyonlands Preserve, Austin, Texas, USA, based on 1,000 simulations. Scenarios were named for the parameter that varied from the baseline model.

Scenario	K	m_1, m_2	$S_{1,2}$	S_0	Median N	Asymptotic λ	Realized λ	P 50% decline	P extinct
baseline	2,224	1.32	0.57	0.40	2,050	1.098	1.003	0.062	0.000
$m = 1.14$	2,224	1.14	0.57	0.40	786	1.026	0.984	0.534	0.081
$m = 1.50$	2,224	1.50	0.57	0.40	2,225	1.170	1.004	0.000	0.000
$S_1 = 0.47$	2,224	1.32	0.47	0.40	297	0.998	0.965	0.981	0.253
$S_1 = 0.67$	2,224	1.32	0.67	0.40	2,225	1.198	1.004	0.000	0.000
$S_0 = 0.28$	2,224	1.32	0.57	0.28	16	0.940	0.910	0.991	0.842
$S_0 = 0.32$	2,224	1.32	0.57	0.32	229	0.992	0.960	0.857	0.330
$S_0 = 0.36$	2,224	1.32	0.57	0.36	1,259	1.045	0.993	0.332	0.025
$S_0 = 0.44$	2,224	1.32	0.57	0.44	2,225	1.150	1.004	0.000	0.000
K = 1,668, $m = 1.14$	1,668	1.14	0.57	0.40	718	1.026	0.974	0.625	0.099
K = 1,668, $m = 1.32$	1,668	1.32	0.57	0.40	1,539	1.098	0.997	0.116	0.002
K = 1,668, $m = 1.50$	1,668	1.50	0.57	0.40	1,555	1.170	0.997	0.000	0.000
K = 2,780, $m = 1.14$	2,780	1.14	0.57	0.40	1,117	1.026	0.982	0.491	0.068
K = 2,780, $m = 1.32$	2,780	1.32	0.57	0.40	2,600	1.098	1.007	0.000	0.000
K = 2,780, $m = 1.50$	2,780	1.50	0.57	0.40	2,781	1.170	1.009	0.000	0.000

[a] K = carrying capacity; m_1 and m_2 = productivity of 1- and ≥2-yr-old males (male fledglings/territory), and $m_1 = m_2$; S_0, S_1, and S_2 = survival of age class 0, 1, and 2, respectively, and $S_1 = S_2$; median N = no. of males at year 50; asymptotic λ = the growth rate calculated from the stage matrix without effects of demographic and environmental stochasticity and density dependence; realized λ = mean annual change in the projected population size over the 50-yr simulation; P 50% decline = probability of a 50% population decline; P extinct = probability of extinction with an extinction threshold of 100 males.

territory each year, which accounted for the contribution of partial nest success and double-brooding. We calculated m_1 and m_2 for our baseline scenario using the most supported productivity model reported by Reidy et al. (2018) for a balanced sample across years, using mean values for all habitat covariates in the model, which resulted in an estimate of 1.32 (SE = 0.046) male fledglings/territory, assuming a 50:50 sex ratio. Reidy et al. (2018) estimated adult survival from a sample of 794 color-banded males monitored on the same 18 plots used for productivity monitoring during March through June, 2009–2015. Reidy et al. (2018) searched for color-banded adults on monitoring plots 2–3 times/week during March through May and once per week through June, and to a lesser extent on adjacent wooded areas for dispersed adults. Reidy et al. (2018) used a spatial Cormack–Jolly–Seber capture–recapture model that separated emigration from mortality and estimated adult survival as 0.57 + 0.06 (posterior mean + SD), with a process variance of 0.019 (Reidy et al. 2018). There were no estimates of juvenile survival for the BCP, so we lacked an empirical estimate for the baseline scenario. Territory monitoring data for the BCP suggested the population was relatively stable during the period of data collection (180–198 territories during 2011–2015, City of Austin and Travis County 2018); therefore, we used an estimate for juvenile survival in our baseline scenario that resulted in a realized λ of approximately 1, which was 0.40. We considered other values in the scenarios described below.

Model Scenarios

We created 14 additional scenarios by varying vital rates and carrying capacities (Table 1). We incorporated normal year-to-year variation or process variation as environmental stochasticity where we selected rates annually based on a mean and SD as described above (Akçakaya 2002, McGowan et al. 2011). We created scenarios in addition to our baseline scenario to span the range of other mean estimates of productivity and survival in the literature and encompass the range of uncertainty reflected in 95% confidence and credible intervals for mean productivity and survival for the BCP (Reidy et al. 2018). This allowed us to address parameter uncertainty or potential changes in rates due to habitat improvements or degradation (McGowan et al. 2011). We created 2 scenarios by varying mean annual productivity from the baseline value of 1.32 to 1.14 and 1.50, which encompassed the 95% CI for mean annual productivity on BCP (Reidy et al. 2018) and included the mean productivity estimates for Fort Hood (1.18 assuming 50:50 sex ratio; Peak and Thompson 2014) and Balcones Canyonlands National Wildlife Refuge (1.16 assuming 50:50 sex ratio; Reidy et al. 2016*b*). We created 2 scenarios by varying mean adult survival from the baseline value of 0.57 to 0.47 and 0.67. This covered the mean survival reported for Fort Hood (0.47; Duarte et al. 2014) and the 95% credible interval for mean annual survival on the BCP (Reidy et al. 2018). We examined 4 additional scenarios with varying rates for juvenile survival. We incrementally increased juvenile survival from 0.28, the most recent estimate from Fort Hood, Texas (Duarte et al. 2014), to 0.44, which was one step above the rate in our baseline scenario and that resulted in a realized λ > 1 (Table 1). Lastly, we created 6 additional scenarios by increasing and decreasing K by 25% from the baseline scenario (K = 2,224) paired with 3 levels of productivity. Increases in carrying capacity could result from improving habitat within the BCP, whereas decreases in carrying capacity could happen as a result of further habitat loss and fragmentation and increases in edge effects or predator abundance within protected woodlands. Changes in productivity could result from management directed at increasing the percent woodland cover or decreasing woodland edge within the landscape (Reidy et al. 2018).

Analysis

We conducted 1,000 simulations for a 50-year period for each scenario. We plotted the median, 2.5 and 97.5 percentiles, and minimum and maximum population size for each year for the baseline scenario. We report median population size at year 50, the asymptotic and realized λ, probability of a 50% population decline, and terminal extinction risk for each scenario. We calculated the asymptotic λ directly from the stage matrix, so it did not include effects of demographic and environmental stochasticity and density dependence. We calculated the realized λ as the median λ from the 1,000 iterations of the 50-year simulation for each scenario. We calculated terminal extinction risk based on an extinction threshold of 100, which represents the probability the population would fall below 100 males by the end of the simulation. We chose 100 because it represents an extremely low density across the BCP. We calculated elasticities as the proportional contribution each element of the stage matrix (S_0m_1, S_0m_2, S_1, S_2) made toward the dominant eigenvalue for the stage matrix under the baseline scenario, however these analytical elasticities do not include the effects of density dependence and stochasticity (Caswell 2001, Akçakaya 2002). To further characterize the importance of m, S_0, and $S_1 + S_2$, we calculated the coefficient of determination for each of these parameters related to λ by treating them as fixed effects in a multiple regression predicting λ based on outputs from all 15 scenarios. Our approach is similar to life-stage simulation analysis in which the coefficient of determination represented the proportion of variation in λ across all scenarios—including stochasticity and density dependence—that was explained by each vital rate (Wisdom et al. 2000, Mills and Lindberg 2002). The elasticities represented the proportional contribution of small changes in each element of the stage matrix to λ, whereas the coefficients of determination represented the percent variance explained across the range of scenarios that encompassed the likely potential range in mean values of each vital rate given parameter uncertainty or directional changes in carrying capacity.

RESULTS

We fit a polynomial regression relating estimated golden-cheeked warbler density from the model by Reidy et al.

(2016*a*) to territory densities on intensively monitored plots. Territory density was related to estimated density by the model:

$$D_t = -0.0440D_m + 3.606D_m^2 - 3.550D_m^3$$

which was significant ($F_{3,15} = 73.8$, $P < 0.0001$) and had an $R^2 = 0.94$. This adjustment minimized bias from the point-count estimates; mean adjusted model-based density was 0.221 males/ha and mean observed territory density was 0.223 males/ha for the intensive monitoring plots (Fig. 2). We estimated territory densities for all 180 × 180-m pixels on the BCP, using pixel-level habitat structure, which resulted in a mean density of 0.141 males/ha, and 1,779 males, which we equated to a starting population of 1,779 males or territories in the baseline scenario (Table 1).

In the baseline scenario (mean productivity of 1.32 male fledglings/territory, adult survival of 0.57, juvenile survival of 0.40), the median population size increased slightly initially and then was relatively stable (Fig. 3, Table 1). The asymptotic and realized λ was 1.098 and 1.003, respectively, and the median population size at year 50 was 2,050 males (Table 1). There was a 0.062 probability of a 50% population decline and a 0.0 probability of extinction when the extinction threshold was 100 males (Table 1).

Population trajectories were sensitive to changes in vital rates. Vital rates at the lower limits resulted in high probability of local extinction at the end of the 50-year simulation, whereas there was virtually no probability of extinction at the upper ranges (Table 1). For example, an increase in m from 1.32 to 1.50 male fledglings/territory resulted in a mean population trajectory that increased above the starting abundance and had no probability of decline or extinction at the end of 50 years, whereas a decrease in m to 1.14 male fledglings/territory resulted in a declining population with a 0.534 probability of a 50% decline and 0.081 probability of local extinction (Fig. 4A, Table 1). Similarly, the population was sensitive to low survival; when S_1/S_2 was 0.47, the probability the population declined 50% was 0.981 and the probability of local extinction was 0.253 (Fig. 4B, Table 1), and when S_0 was 0.28, the probability of a 50% decline was 0.991 and of local extinction was 0.842 (Fig. 4C, Table 1).

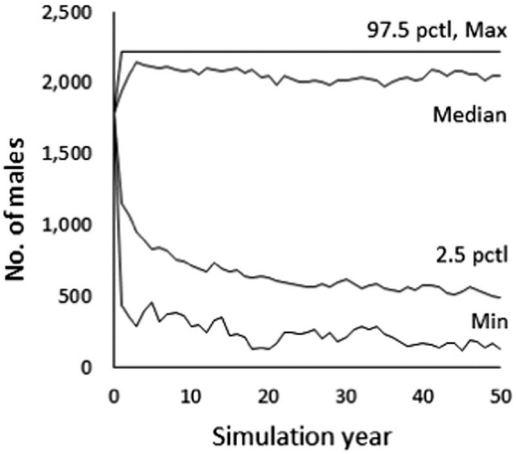

Figure 3. Projected median, minimum (min), maximum (max), and 2.5 and 97.5 percentile abundance of male golden-cheeked warblers on the Balcones Canyonlands Preserve, Austin, Texas, USA, over 50 years based on adult survival (S_1) of 0.57, juvenile survival (S_0) of 0.40, and 1.32 male fledglings/territory (m).

The population was also sensitive to combinations of K and m. By design, abundance can never exceed K so lowering K decreased mean abundance (Table 1). At average and high levels of m, increasing K resulted in greater mean abundance because the population was less constrained by density dependence and grew until it approached K (Fig. 5, Table 1). At low values of m, however, the population was unable to grow and declined to near zero regardless of K (Fig. 5, Table 1).

Elasticities indicated a 1% change in S_0m_1, S_0m_2, S_1, and S_2 would result in a 0.23, 0.25, 0.25, and 0.27% change in λ, respectively. Thus, small changes in each element of the stage matrix contributed almost equally to λ; however, the combined effect of adult survival ($S_1 + S_2$) was 0.52%. By contrast, coefficients of determination for productivity (m_1, m_2), juvenile survival (S_0), adult survival (S_1, S_2), and carrying

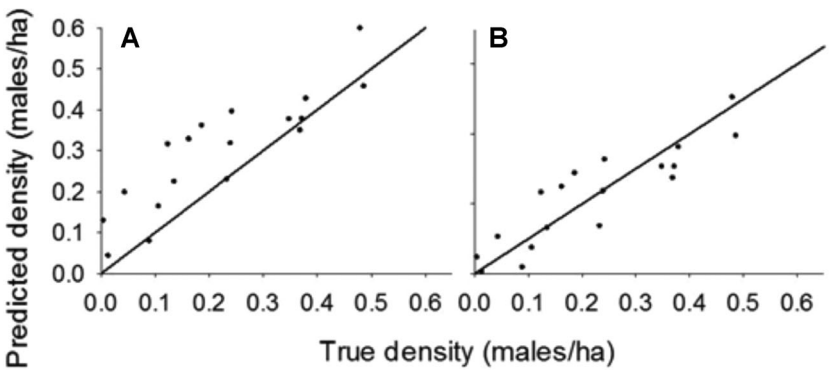

Figure 2. Relationship between estimated densities of golden-cheeked warblers (males/ha) on Balcones Canyonlands Preserve, Texas, USA, 2011–2014, from a model based on point-count surveys (y-axis) and densities from territory mapping of color-marked males on 18 intensive monitoring plots (x-axis) before (A) and after (B) predictions were adjusted with a polynomial regression to match the territory mapping estimates. The line represents a perfect 1:1 correlation between estimated and observed densities.

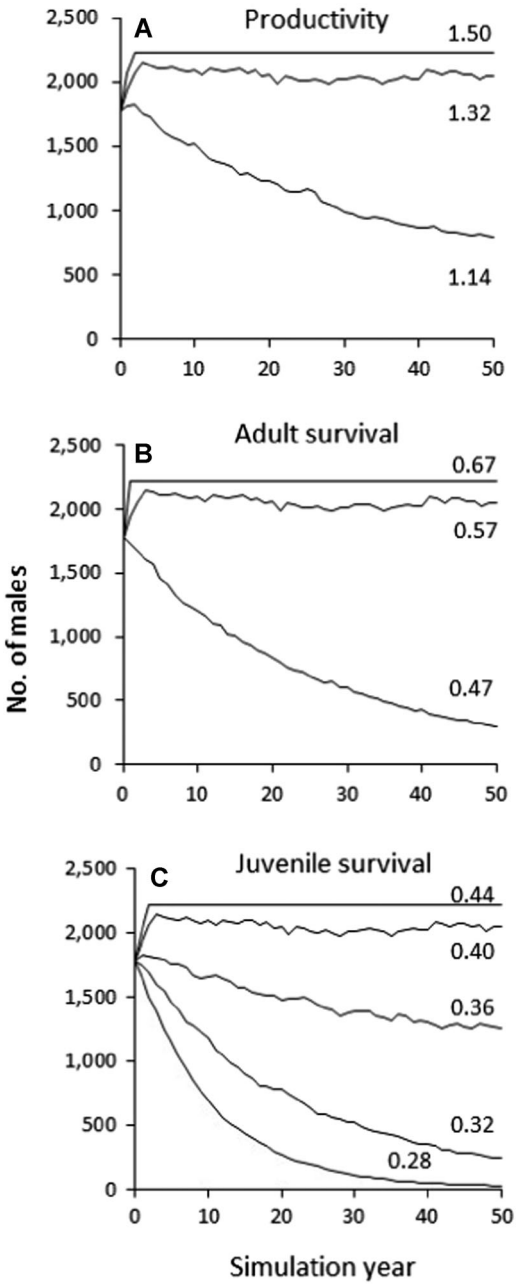

Figure 4. Projected median abundance of male golden-cheeked warblers on the Balcones Canyonlands Preserve, Austin, Texas. USA, over 50 years with (A) varying productivity (*m*) and adult and juvenile survival of 0.57 and 0.40, respectively, (B) varying adult survival (S_1/S_2) and juvenile survival of 0.40 and productivity of 1.32 male fledglings/territory, and (C) varying juvenile survival (S_0) and adult survival of 0.57 and productivity of 1.32 male fledglings/territory.

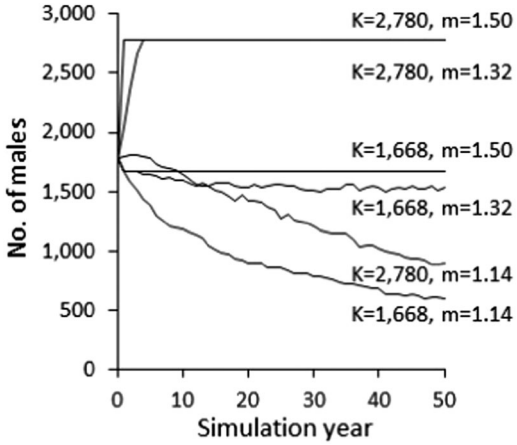

Figure 5. Projected median abundance of male golden-cheeked warblers on the Balcones Canyonlands Preserve, Austin, Texas, USA, over 50 years under different carrying capacities (K) and varying productivities (*m*). Adult and juvenile survival was modeled at 0.57 and 0.40, respectively.

capacity indicated they explained 5.4, 45.2, 5.3, and 1.2% of the variation in λ, respectively. The large contribution of S_0 is a result of the wide range of values considered because of uncertainty in this parameter, and at its lowest value S_0 resulted in the lowest λ among all 15 scenarios.

DISCUSSION

We determined the BCP could support a viable, stand-alone population of golden-cheeked warblers under certain conditions, assuming the extent and quality of habitat within the BCP remains the same. However, the population response was sensitive to changes in vital rates and, at baseline levels, elasticities indicated both productivity and survival were equally important to population growth. The BCP population was fairly stable when adult survival, juvenile survival, and productivity were high, but declined toward local extinction at low values. The ranges we used spanned the range of vital rates we estimated for the population from 2009 to 2015, as well as those estimated for other populations (Duarte et al. 2014, Peak and Thompson 2014, Reidy et al. 2016*b*). Importantly, the BCP population was predicted to decline using similar vital rates as those estimated for Fort Hood and elsewhere (Marshall et al. 2013; Peak and Thompson 2014; Duarte et al. 2016*a*, *b*). We modeled the population trend for each vital rate independent of other vital rates, however, it is possible that processes operating on one vital rate may affect or interact with others, and if positively correlated, would exacerbate population increases or decreases. For example, factors that cause low productivity may also influence juvenile survival. Plausible explanations for this include increased predator abundance, lower food abundance, or poor health of adults. Similarly, favorable conditions during the breeding season may result in greater seasonal productivity and juvenile survival.

We found that a higher carrying capacity resulted in virtually no probability of local extinction over our time period under average or high productivity, but the BCP population declined toward local extinction when productivity was low. The response was similar under lower carrying capacity, except that there was an initial decline in the population size rather than initial increase under average and above average productivities. A benefit of greater carrying capacity was that in years when productivity or survival were high, the population could increase to greater levels, potentially buffering the extent of declines in years when productivity or survival were low. Our findings support the need for

management practices that promote or sustain breeding habitat that has high seasonal productivity, which can be accomplished by maintaining large, contiguous patches of tall, closed-canopy, mixed Ashe juniper–oak forests with a well-developed understory and minimal edge (Peak and Thompson 2014; Reidy et al. 2017, 2018). Site-specific threats to breeding habitat—such as habitat loss and fragmentation, tree mortality from drought or disease, and changes in the predator community—may also need to be considered, especially because these may be exacerbated by climate change (Cox et al. 2013, Moore et al. 2016, Polley et al. 2018).

Our population model differs from previous population models for the golden-cheeked warbler because we used empirically derived and validated data collected on our study area to predict the population trajectory for the BCP population. We used the most informative and intensively gathered data available for this population, but we caution there are still limitations to our model. Because the original density model from Reidy et al. (2016*a*) tended to overpredict density, we relied on a double-sampling approach to adjust density to more closely match density observed on monitoring plots with uniquely marked birds. We suggest additional refinement of design or analysis to more accurately predict density of golden-cheeked warblers across the entire density spectrum (O'Donnell et al. 2019). Additionally, our starting abundance was estimated using habitat conditions occurring within and around the BCP during our study. Most habitat changes since then have been external to the BCP, however, changes within the BCP such as expanding tree mortality following the extreme 2011 drought could affect the number of golden-cheeked warblers that the BCP can support (Schwantes et al. 2017, Crouchet et al. 2019). Future models should use updated land-cover maps that reflect current live canopy cover to predict abundance. We also recommend using updated population trend data because continued monitoring following our study indicates a slightly declining population on the BCP (City of Austin and Travis County 2018, exhibit F).

Another important uncertainty in our model is juvenile survival. Previous population models have used juvenile survival estimates ranging from 0.28 to 0.50 (USFWS 1996, Alldredge et al. 2004, Horne et al. 2011, Duarte et al. 2016*a*). When we used a value of 0.28 for juvenile survival, which represented approximately one-half of our adult survival, and was the recent mean juvenile survival estimate for Fort Hood (Duarte et al. 2014), the golden-cheeked warbler population declined precipitously toward local extinction. We determined that a juvenile survival rate of approximately 0.40 was required to achieve a realized λ of 1 when adult survival and productivity were at baseline levels. Apparent juvenile survival (which is confounded with potentially high natal dispersal) ranged from 0.17 to 0.46 annually, and confidence intervals included 0.40 for several years, on Fort Hood (Duarte et al. 2014). Therefore, we believe a juvenile survival rate of 0.40 is biologically reasonable and feasible, at least in some years. If juvenile survival is lower than in our baseline scenario (0.40), the observed stability in abundance on the BCP intensive monitoring plots during our study could be due in part to immigration by birds displaced from the surrounding rapidly urbanizing landscape. Obtaining accurate estimates of juvenile survival and dispersal remains unlikely, but integrating vital rates and abundance data over many years in a single framework may provide more insight into juvenile survival and dispersal (Duarte et al. 2016*b*, Zipkin and Saunders 2018).

Lastly, we did not include spatial variation across the BCP for vital rates in our population model, but we consider it worth exploring in future population models. We suspect spatial variation in adult survival is less important than productivity at the local scale because adults spend most of their year elsewhere and Duarte et al. (2014) did not find support for it using a much larger data set for Fort Hood. However, future viability analyses could incorporate spatial variation in productivity, such as reported by Peak and Thompson (2014) and Reidy et al. (2018), dispersal (Reidy et al. 2018), and habitat selection based on abundance relationships (Peak and Thompson 2013; Reidy et al. 2016*a*, 2017; Sesnie et al. 2016). Spatial variation in productivity resulting from variation in habitat patches could potentially result in source–sink dynamics that exacerbate population declines (Donovan and Thompson 2001). Additionally, we chose to simulate simple scenarios, using constant habitat conditions and without risk of catastrophic events such as wildfire; whereas, in reality, habitat is dynamic and resulting dynamic demographic rates can be simulated in more complicated models with additional data and effort (Bonnot et al. 2017). Future models should also consider the effects of climate change, which is expected to bring warmer temperatures, more frequent droughts and wildfire, and more extreme precipitation events to this region (Hayhoe 2014). Climate change can affect the golden-cheeked warbler directly by changing weather patterns that affect nest survival, productivity, juvenile survival, or habitat selection, or indirectly through changes in habitat quality and quantity (Mueller et al. 2005, Auer and Martin 2012, Bonnot et al. 2018). The golden-cheeked warbler is expected to be exceedingly vulnerable to effects associated with climate change (Galbraith and Price 2009).

MANAGEMENT IMPLICATIONS

We found the BCP could sustain a golden-cheeked warbler population of approximately 1,800 males (assuming the extent and quality of the habitat remain unchanged), adult survival of 0.57, productivity of 1.32 male fledglings/territory, and an assumed juvenile survival of 0.40. However, the population declined toward local extinction when vital rates were at the low end of rates considered, which were similar to those reported in earlier studies (0.47 adult survival, 1.14 male fledglings/territory, 0.28 juvenile survival). Both productivity and survival were important to population growth; however, management actions on the BCP are more likely to affect productivity (and possibly postfledging survival) than adult survival, and as such we recommend actions that favor habitat with high productivity, such as

large, unfragmented patches of tall, closed-canopy, mixed juniper–oak woodland with a well-developed understory (Reidy et al. 2017, 2018), and areas of high juniper cover that may favor greater survival of newly fledged young (Trumbo 2019). Increasing carrying capacity would permit greater average population size and help buffer declines in years when productivity or survival were low. In addition, if juvenile survival is actually closer to that estimated for Fort Hood (0.28; Duarte et al. 2014) and the observed stability of the population is dependent on immigration, maintaining connectivity with other large patches such as the nearby Balcones Canyonlands National Wildlife Refuge may be important for the long-term viability of the BCP population. These examples illustrate the importance of continuing to refine population models with updated habitat and vital rate data and test the accuracy of the model's predictions. Many monitoring programs rely on trends in abundance which could mask threats to a population because of potential immigration from outside the population due to habitat loss in the surrounding landscape, source–sink dynamics, or ecological traps; therefore, we suggest some level of demographic monitoring is justified for high-concern species to provide a better assessment of a population's status, especially if additional information on the factors limiting a population are needed for conservation and management planning. Data from demographic monitoring can also be used in future efforts based on integrated population modeling to overcome some of the uncertainties highlighted here and produce better estimates of net population growth and population viability (Schaub and Abadi 2011).

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