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Urban land cover and El Niño events negatively impact population viability of an endangered North American songbird

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Abstract

Population dynamics of migratory species are influenced by land use and climate patterns experienced across the full annual cycle. Identifying environmental factors influencing productivity, survival, and their relative contributions to abundance and population growth is critical for the recovery and management of at-risk species in the face of continuing global change. The golden-cheeked warbler (*Setophaga chrysoparia*) is an endangered passerine that breeds exclusively in the mixed Ashe juniper (*Juniperus ashei*)–oak (*Quercus*) woodlands of Central Texas, USA, and winters at high elevations in Central America. We evaluated the effects of precipitation, climate, and land cover on golden-cheeked warbler productivity, adult male survival, and territory abundance using data from a long-term monitoring site, the Balcones Canyonlands Preserve, in Austin, Texas. We jointly analyzed annual productivity, mark–recapture, and territory count data collected on 10 plots from 2011 to 2019 in an integrated population model. The number of young fledged per male territory was negatively related to percent urban land cover within 1 km of monitoring plots, and adult male survival was negatively related to a strong El Niño event. Estimates of population growth and abundance indicated a decline in abundance across our study period. We forecasted population viability 25 years into the future given increases in urban development and frequency of El Niño events. Quasi-extinction probability increased from 0.17 under current urban land cover conditions and El Niño frequency to 0.41 under the scenario of a 10% increase in urban development around all plots and an increase in El Niño frequency. Productivity and adult survival were positively correlated with population growth, highlighting the need for conservation and management actions to maximize these vital rates on the breeding grounds and range-wide.

KEYWORDS
climate change, El Niño, endangered species, golden-cheeked warbler, integrated population model, productivity, *Setophaga chrysoparia*, survival, urban land cover

INTRODUCTION

Land use and climate change are considered primary drivers of biodiversity loss (Fischer & Lindenmayer, 2007; Jetz et al., 2007; Mantyka-Pringle et al., 2012; Newbold, 2018; Oliver & Morecroft, 2014; Thomas et al., 2004), and by extension, primary threats to conservation of endangered species. Demographic rates of populations such as productivity, survival, and population growth are sensitive to characteristics of vegetation and land cover composition and structure such as fragmentation and percent forest cover (Cox et al., 2012; Okada et al., 2017; Robinson et al., 1995). Additionally, demographic rates are affected by local temperature, precipitation, and drought conditions, as well as global climate patterns (Arbeiter et al., 2016; Conrey et al., 2016; Cox et al., 2013; Gyurácz et al., 2016; Sherry et al., 2015; Stokke et al., 2005). Understanding how relationships between environmental conditions and demographic rates influence population growth and viability across the full annual cycle is critical for identifying effective approaches for the conservation of vulnerable species under expectations of future change.

Ongoing anthropogenic land use change is a primary driver of biodiversity loss, both in terms of species richness and abundance, and a main factor cited in decisions regarding species' conservation or protected status (Newbold et al., 2015; Powers & Jetz, 2019; Sala et al., 2000). Historically, most land use change in the United States was conversion of forests and grassland to agriculture. However, much of the current and projected future land use change is attributed to urban expansion (Seto et al., 2011). One common form of urban expansion is low-density residential development in proximity to protected or wilderness areas; such development can increase fragmentation of native vegetation communities, introduce urban-adapted or novel predators, increase the spread of non-native plant and animal species, and increase water pollution, thereby limiting their value to conservation and biodiversity protection (Hansen et al., 2005; Radeloff et al., 2009; Robinson et al., 2005; Wood et al., 2014). Urban expansion is expected to continue around protected areas, and the effects from anthropogenic land use change will likely exacerbate effects associated with climate change (Findell et al., 2017; Hamilton et al., 2013; Lakeman-Fraser & Ewers, 2014; Zhao et al., 2019).

Climate change is expected to have profound effects on local and global weather patterns, with concomitant and far-ranging impacts to abiotic and biotic conditions that can affect species' persistence in a given location (Newbold, 2018; Thomas, 2010). Such long-term changes in weather patterns can lead to drastic changes in the vegetation community (Anderegg et al., 2012; Tietjen et al., 2017), for example, prolonged droughts are associated with higher tree mortality, which could alter forested habitat composition and structure (Allen et al., 2010; Anderegg et al., 2012; Wang et al., 2012). Additionally, cyclical global climate phenomena such as the El Niño-Southern Oscillation (hereafter El Niño) can significantly impact vital rates, and consequently, population growth rates, and may offer additional insight into potential effects on population dynamics from predicted future climate patterns. The effects of El Niño on migratory birds vary by species-specific breeding and wintering ranges, but trends from species breeding in the eastern United States and wintering in areas of Central and South America or the Caribbean suggest populations have lower survival rates (Mazerolle et al., 2005; McKellar et al., 2015; Sillett et al., 2000), reduced body condition prior to migration (Paxton et al., 2014), and lower reproductive success (Mazerolle et al., 2005; Nott et al., 2002) during periods of strong El Niño conditions. The change in frequency and strength of future El Niño phases is disputed under various climate change models, but several climate models have predicted an increase in the frequency of strong El Niño phases (characterized by severe droughts in much of Mexico and Central America during the winter period) as a byproduct of climate change (Cai et al., 2014, 2018; Timmerman et al., 1999; Wang et al., 2017). Knowledge of the impacts of changing land cover and climate variability on population viability is especially critical to management and conservation of species threatened with habitat loss.

The golden-cheeked warbler (*Setophaga chrysoparia*) is an endangered passerine that breeds exclusively within the mature Ashe juniper (*Juniperus ashei*)–oak (*Quercus* spp.) woodlands of Central Texas and winters in the highland oak (*Q.* spp.)–pine (*Pinus* sp.) woodlands of Central America (Ladd & Gass, 2020). Golden-cheeked warblers arrive on the breeding grounds in March and begin migrating to the wintering grounds in mid-June, migrating through a narrow band in central Mexico (Ladd & Gass, 2020). The golden-cheeked warbler was

listed as endangered in the United States in 1990 due to the narrow breeding habitat constraints coupled with increasing habitat loss due to agricultural clearing and urbanization (USFWS, 1990). This species is also considered highly vulnerable to changes in habitat extent and distribution due to land use and climate change (Newbold, 2018; Wilsey et al., 2019).

Precipitation, forest composition and structure, and urban land cover potentially influence golden-cheeked warbler productivity on their breeding grounds. The frequency of drought and extreme precipitation events are expected to increase in Central Texas (Nielson-Gammon et al., 2020). Higher rainfall can alter parental provisioning rates, thereby reducing nestling growth rates or survival (Arlettaz et al., 2010; Öberg et al., 2015). Severe drought on the breeding grounds during 2011 caused crown mortality of ~20% of trees and future droughts in the region could potentially kill 18%–85% of medium to large Ashe junipers in the region (Crouchet et al., 2019; Polley et al., 2018). Golden-cheeked warblers build nests from peeling strips of Ashe juniper bark found on mature trees and forage for insects in mature trees; therefore, large-scale tree mortality not only reduces nesting opportunities but also alters foraging opportunities and insect availability (Carnicer et al., 2011). In addition to these climate-related vegetation changes, Central Texas has experienced high rates of human population growth in the 30 years since the golden-cheeked warbler was listed; for example, Travis County, where our study took place, grew from ~580,000 people in 1990 to over 1.3 million in 2020 (USA Facts, 2023). This growth is predicted to continue, putting extreme pressure from additional human development within the golden-cheeked warbler's breeding range (Dreiss et al., 2022; Duarte et al., 2013).

Global climate patterns potentially influence annual adult survival across their full range. Within the golden-cheeked warbler's wintering range, Central America is expected to experience more frequent drought and severe climatic events (IPCC, 2014). Droughts potentially increase the risk of forest fires and further habitat loss (Briones, 2017; Burton et al., 2020). Droughts or below-average precipitation have also been shown to lower body condition in other migratory songbirds, potentially reducing survival during the wintering period or during migration to and from the breeding grounds (McKinnon et al., 2015; Studds & Marra, 2007).

A comprehensive understanding of how weather, climate, and landscape composition affect full annual cycle population dynamics would aid conservation and management efforts for the golden-cheeked warbler. We estimated productivity, adult male survival, and population growth of the golden-cheeked warbler within an urbanizing preserve within Austin, Texas, from 2011 to 2019 using an integrated population model (IPM). We also compared population viability under alternative scenarios of future climate and land use change. Our objectives were to: (1) evaluate the effects of weather, forest structure, and land cover composition on seasonal productivity; (2) evaluate the effects of global climate patterns on annual adult male survival; (3) estimate population growth and the relative influence of productivity and adult male survival on annual population growth; and (4) forecast future abundance and quasi-extinction probabilities to compare population viability under current conditions to future scenarios of climate and land use change. We predicted productivity was higher in plots with less landscape-level urban land cover, less forest edge within plots, more forest cover within plots, and in years with less precipitation in April and May; and annual adult male survival was lower in years with a strong El Niño effect.

METHODS

Study area

We monitored golden-cheeked warblers on the Balcones Canyonlands Preserve (BCP), in Austin, Texas (30°20′ N, 97°50′ W; Figure 1a). The BCP protects ~14,000 ha of juniper and oak woodland and is the largest protected area in recovery region 5 of the species' USFWS recovery plan (Groce et al., 2010). This region has a humid subtropical climate, with mean monthly temperature of 22.0°C (range of average lows and highs: 17.5 and 27.8°C) and mean monthly precipitation of 92.5 mm during March–June; May is typically the month with the most rainfall during the breeding season. Dominant tree species were Ashe juniper, Texas red oak (*Q. buckleyi*), plateau live oak (*Q. fusiformis*), shin oak (*Q. sinuata* var. *breviloba*), and cedar elm (*Ulmus crassifolia*).

Intensive golden-cheeked warbler monitoring has occurred on a series of plots across the BCP since 2011. We used data collected on 10 plots that were consistently monitored from 2011 to 2019 for the IPM (Figure 1b): eight plots were 40 ha and two additional low-density plots were 96 and 180 ha. Plots were distributed across the BCP and ranged in forest cover (59%–93%) and composition (11%–51% juniper) and in golden-cheeked warbler density (City of Austin, 2019: Exhibit E; Reidy et al., 2020). We also searched additional suitable (wooded habitat) and accessible areas beyond the plot buffers 3–5 times per season for banded golden-cheeked warblers that may have moved off plots to document dispersal and better estimate adult survival; to standardize search effort, the searched area and effort remained consistent

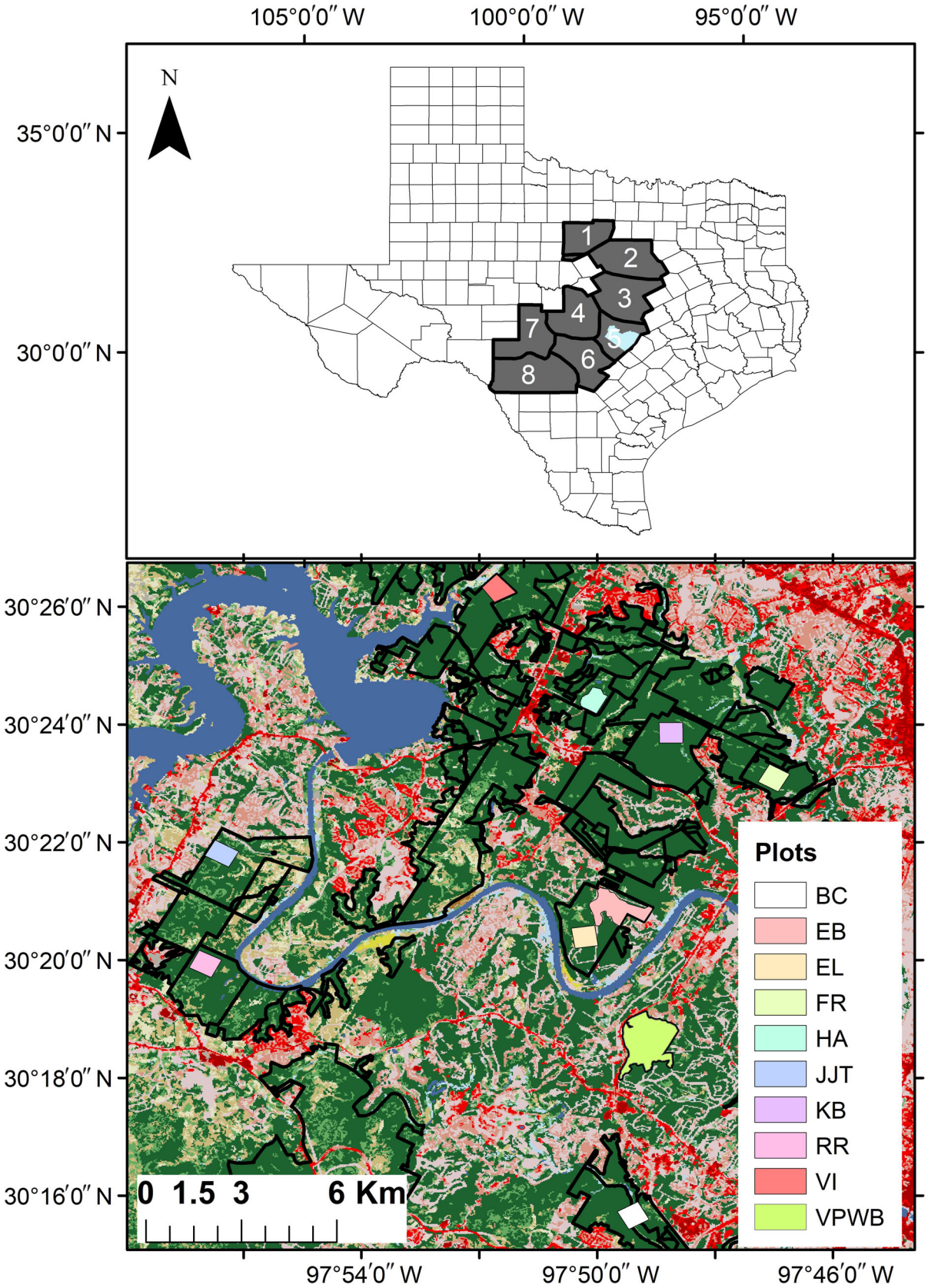

FIGURE 1 Top panel: Our study area was located in Travis County (blue polygon), along the eastern edge of the golden-cheeked warbler's breeding range (gray) in recovery region 5, within Texas, USA. Bottom panel: Locations of intensive monitoring plots (colored polygons, labeled in legend) within Balcones Canyonlands Preserve (black outline) overlaid on National Land Cover data layer; green represents forested land cover and red and pink represent high- and low-density urban land cover, respectively.

and were performed by the same observer(s) within a year.

Data collection

Abundance and productivity data

Observers surveyed each plot 1–3 times per week from early-mid March through mid-June each year to document golden-cheeked warbler locations, breeding activity, and number of fledglings produced. Adults were uniquely color-banded to enable identification of individual territories and accurately assess territory boundaries and breeding success. We determined plot abundance by delineating territories from resighting efforts and considered a male to be territorial if we documented it within the same area over ≥3 weeks; this criterion excluded transitory males. We counted every territorial male wholly or partially within each plot as one and summed these as our measure of abundance for each plot. We monitored every territory for the duration of the breeding season to determine breeding success, and we counted the number of fledglings produced per territory in a breeding season as our measure of productivity. Terrain and behavior (including brood splitting) can make counting golden-cheeked warbler fledglings difficult, and to account for this, we categorized fledgling counts as "complete" or "possibly incomplete" based on the observer's certainty (e.g., number of times observer documented adults with a maximum number of young). We then adjusted the number of total fledglings for "possibly incomplete" counts using plot-level information from "complete" counts (see Reidy et al., 2018 for detailed methods). We did not monitor three plots (EL, RR, and VI) intensively enough in 2016 to estimate abundance and productivity, so these were missing values in our analysis and were treated as latent variables that were estimated within the IPM. Additional details regarding study plots and bird surveys are reported in Reidy et al. (2018, 2020).

Land cover and forest data

We summarized vegetation structure and land cover parameters from publicly available National Land Cover Database (NLCD), National Agricultural Imagery Program (NAIP) imagery, and Lidar data layers. We used multiple data sources in our analysis because we were interested in examining both temporal changes within plots and in the surrounding landscape and in evaluating fine-resolution plot-level differences in habitat composition and structure. We summarized the percent of urban land cover in a 1-km radius around each plot perimeter using NLCD data for each year available during our study period (2011, 2013, 2016, and 2019); this additional area was ~6.4 times larger than the largest plot (1146 ha), ~9.2 times the area of the second largest plot (915 ha), and ~15.3 times the area of the eight 40-ha plots (610 ha). We used leaf-off NAIP imagery from 2014 to 2015 and a leaf-on NAIP imagery from 2016 to distinguish evergreen and deciduous vegetation within the plots. We combined this with Lidar data collected over our study area from 2012 to 2018 to identify vegetation >3 m tall as evergreen or broadleaf forest. We calculated forest edge density as the length of the interface between forest and nonforest. We interpolated the missing annual values for environmental variables using PROC EXPAND in SAS 9.4 to allow analysis of temporal changes in these variables.

Weather and climate data

We obtained precipitation data from the National Centers for Environmental Information (NOAA) Austin Great Hills station (30.4144°, −97.7664°), located within 4–19 km of our plots. We calculated the total monthly precipitation measured in April and May of each year; we chose these months because they are the primary months of incubation and care of dependent young (Reidy et al., 2018).

We calculated an average annual index of the El Niño effect using the Oceanic Niño Index (ONI) from April of one year through March of the next year to coincide with the onset of the breeding season. A strong El Niño, the warming phase of the cycle, often brings below-average temperatures and above-average winter precipitation in the southern portions of North America and drier conditions along the western and central portions of Central America during the rainy season (Giannini et al., 2000; Ropelewski & Halpert, 1986, 1987). The ONI index produces a monthly value based on the three-month mean compared to the 30-year mean; a strong or very strong El Niño year is indicated by values of 1.5–1.9 and ≥2.0, respectively.

Modeling approach

We developed an IPM describing the golden-cheeked warbler's full annual life cycle population dynamics from 2011 to 2019. We jointly analyzed productivity, mark–recapture, and territory count data in a unified framework to simultaneously estimate productivity, survival, and population growth (Schaub & Abadi, 2011). We used a male-based, two age-structured IPM that linked plot-specific sub-models for abundance and productivity with a sub-model estimating annual adult survival probability for the entire preserve (Appendix S1).

Population sub-model

We estimated true abundance $\text{Ntot}_{t,k}$ for each year t at each site k within a state-space model. Annual territory counts were linked to true abundance following a Poisson distribution, $\mathcal{Y}_{t,k} \sim \text{Poisson}(\text{Ntot}_{t,k})$. Abundance was estimated as the sum of the number of new individuals that either hatched in and survived the previous year or immigrated to a site, $\text{N1}_{t,k}$, and the number of adults that survived the same period, $\text{Nad}_{t,k}$ (Equation 1). The number of new individuals added to the population each year was estimated based on population size, $\text{Ntot}_{t-1,k}$, per-capita fecundity, $f_{t-1,k}/2$, and recruitment, $R_{t-1,k}$, from the previous year and modeled with a normal distribution (Equation 2). The number of adults surviving the previous year was modeled with a binomial distribution (Equation 3).

$$\text{Ntot}_{t,k} = \text{N1}_{t,k} + \text{Nad}_{t,k}, \tag{1}$$

$$\text{N1}_{t,k} \sim \text{Normal}\left(\text{Ntot}_{t-1,k}\frac{f_{t-1,k}}{2}R_{t-1,k}, \sigma^2_{\text{N1}}\right), \tag{2}$$

$$\text{Nad}_{t,k} \sim \text{Binomial}(\text{Sad}_{t-1}, \text{Ntot}_{t-1,k}). \tag{3}$$

Productivity sub-model

We estimated productivity as the mean number of young fledged per male territory and assumed it followed a zero-truncated normal distribution as a Gaussian approximation of a Poisson distribution (Equation 4; Zhao et al., 2019). We first conducted an exploratory analysis to evaluate relationships between the number of young produced, $J_{t,k}$, and weather, forest cover, and landscape composition within an independent model outside of the IPM and determined which effects were most supported (Appendix S2). We considered univariate models composed of the following variables: cumulative spring precipitation, plot-level broadleaf cover, evergreen cover, and forest edge density, as well as percent urban land cover within a 1-km buffer of a plot. All competing candidate models included an intercept α and random effects for year Y_t and plot S_k (Equation 4). We selected the most supported candidate model based on the lowest deviance information criterion (DIC) score. The model that included urban land cover (Urban) had the lowest DIC score and had the greatest posterior support based on the proportion of posteriors that shared the same sign as the mean estimate ($f = 1.00$). All other models had $\Delta\text{DIC} > 4.0$ and CIs overlapping 0 (Appendix S2). Therefore, we opted to include only the urban covariate as a fixed effect within the productivity sub-model of the IPM.

$$J_{t,k} \sim \text{Normal}\left(F_{t,k}, \sigma^2_F\right), \tag{4}$$

$$F_{t,k} = \alpha + \text{Urban} \times x_{t,k} + Y_t + S_k.$$

Adult male survival sub-model

We estimated adult male survival probabilities from encounter histories and location data of banded males within a spatial Cormack–Jolly–Seber model (s-CJS; Reidy et al., 2018). Adult survival probability, Sad_t, for year t was a function of mean survival, μ, the El Niño index ONI, and a random year effect, Y_t (Equation 5). Small sample sizes for some plots precluded the ability to conduct a plot-level survival analysis and a previous study on golden-cheeked warbler survival on Fort Hood did not show survival varied spatially (Duarte et al., 2014), so we assumed annual adult survival did not vary among plots within the study area. We estimated recapture probabilities based on the level of resighting effort, which was classified as high intensity (surveyed 2–3 times week^{-1}), medium intensity (surveyed at least 1 time week^{-1}), and low intensity (areas surrounding high- and medium-intensity areas surveyed 3–5 times season^{-1}).

$$\text{logit}(\text{Sad}_t) = \mu + \text{ONI} \times x_t + Y_t. \tag{5}$$

Model implementation

We fit the IPM in a Bayesian framework using program JAGS and the package jagsUI in R (Kellner, 2019; Plummer, 2003; R Core Team, 2021). We ran models using three chains, each containing 200,000 iterations including a burn-in of 50,000 and a thin rate of 2. We evaluated model convergence by inspecting trace plots and checking for R-hat values of <1.1 for all parameters (Brooks & Gelman, 1998). We present posterior means and 95% credible intervals (CRIs) of estimated parameters. We interpreted support for environmental effects based on the proportion of posteriors that supported a positive or negative effect (f values).

Post-modeling analyses

We conducted a retrospective population analysis to evaluate the relationship of population growth rates to changes in demographic rates given the magnitude of demographic variation observed in the golden-cheeked warbler population (Schaub & Kéry, 2022). We calculated correlation coefficients (r) between adult survival,

productivity, and population growth across their full posterior distributions. We estimated the probability that a demographic rate positively influenced population growth ($p(r > 0)$) to describe mechanisms for population change. We compared estimates of annual adult male survival and productivity to the distribution of posterior samples that resulted in a stable or increasing population size ($\lambda \geq 1.00$) to identify vital rates that may limit population growth.

We used posterior estimates of vital rates and associated environmental covariates from our IPM to conduct a population viability analysis and predict future abundance of golden-cheeked warblers on the BCP through simulations within a population matrix model. We forecasted population size 25 years into the future given current conditions observed from 2011 to 2019 and compared those predictions to three scenarios of land use change (increases in urban land cover by 10% around the three least urbanized plots, the three most urbanized plots, and all plots) and one scenario of change in El Niño patterns (increasing the frequency of strong El Niño events from twice in 25 years to three times). We chose these scenarios because they reflect realistic predicted changes to land use and climate change (Guo & Zhang, 2021; Wang et al., 2017). We used predicted abundance to estimate quasi-extinction probabilities over 25 years for each scenario to evaluate relative conservation risks of land use and climate change to this population. We defined quasi-extinction as fewer than 10 breeding males across all study plots and calculated it as the proportion of posterior estimates of population size that fell below that threshold.

RESULTS

We counted 1056 golden-cheeked warbler territories within the 10 monitoring plots from 2011 to 2019 to predict abundance. We surveyed 951 territories across 10 monitoring plots from 2011 to 2018 to estimate productivity. We used capture histories from 979 males to estimate annual adult survival from 2011 to 2019. Urban land cover varied substantially spatially around plots but changed marginally across the time period of our study (range 7.3%–40.9%; Appendix S3). ONI values varied annually and ranged −0.74 to 1.85 (Appendix S3).

Model estimates of abundance, vital rates, and population growth

We successfully fit our IPM; visual inspection of trace plots and *R*-hat values of <1.1 indicated good mixing among Markov chains and successful model convergence. The IPM estimates of golden-cheeked warbler abundance were consistent with territory counts; observed abundance was within the 95% CRIs for almost every year and plot combination (Figure 2). The IPM also produced estimates of abundance for years in which territory count data were missing based on observed demographic rates. The proportion of new individuals each breeding season that either hatched and survived the previous year or immigrated into the population was approximately 0.44 (95% CRI: 0.34–0.58).

Median productivity across years and plots was 2.25 fledglings/territory (95% CRI: 1.77–2.93). Productivity was greatest in 2012 (median = 2.73, 95% CRI: 2.25–3.19) and lowest in 2015 (median = 2.03, 95% CRI: 1.63–2.39; Figure 3). Productivity was greatest at RR (median = 2.48, 95% CRI: 1.89–3.26) and lowest at VPWB (median = 1.33, 95% CRI: 0.64–2.11; Figure 4). Among years, three plots produced fewer young per territory than estimates that resulted in a stable population (Figure 4). Productivity was negatively related to urban land cover ($\beta_{Urban} = -0.34$, 95% CRI: −0.58 to −0.12; $f = 1.00$) and decreased from 2.59 fledglings/territory (95% CRI: 1.88–3.43) to 1.50 fledglings/territory (95% CRI: 0.68–2.38) as urban land cover increased from 7.3% to 40.9% (Figure 5).

Mean adult survival across years was 0.53 (95% CRI: 0.48–0.59). Recapture probability of marked adults varied with intensity of survey effort ($p_{high} = 0.98$, 95% CRI: 0.94–1.00; $p_{medium} = 0.96$, 95% CRI: 0.87–1.00; $p_{low} = 0.88$, 95% CRI: 0.72–0.99). Adult survival varied annually (Figure 3), but was markedly lower during 2014–2015 and 2015–2016 than estimates that resulted in a stable population (Figure 4). Adult survival was negatively related to the ONI index ($\beta_{ONI} = -0.19$, 95% CRI: −0.44 to 0.05; $f = 0.95$) and decreased from 0.58 (95% CRI: 0.46–0.69) to 0.43 (95% CRI: 0.27–0.60) as the ONI index increased from −0.74 to 1.85 (Figure 5). Variation in productivity of the total population was greater than that of adult survival (coefficient of variation 0.52 and 0.46, respectively).

The geometric mean of population growth, 0.95 (95% CRI: 0.93–0.98), indicated a decline in abundance from 2011 to 2019. Annual population growth was stable in 2012 and 2013; in all other years it was negative, reaching its lowest point in 2015 (Figure 3). Productivity (*r*: 0.18, 95% CRI: −0.02 to 0.41) and adult survival (*r*: 0.77, 95% CRI: 0.12–0.93) were positively correlated with population growth, signifying annual changes in abundance were responsive to both vital rates (Figure 6). Annual adult survival made the greatest relative independent contribution to population growth (61.4%), followed by productivity (38.6%), based on hierarchical partitioning.

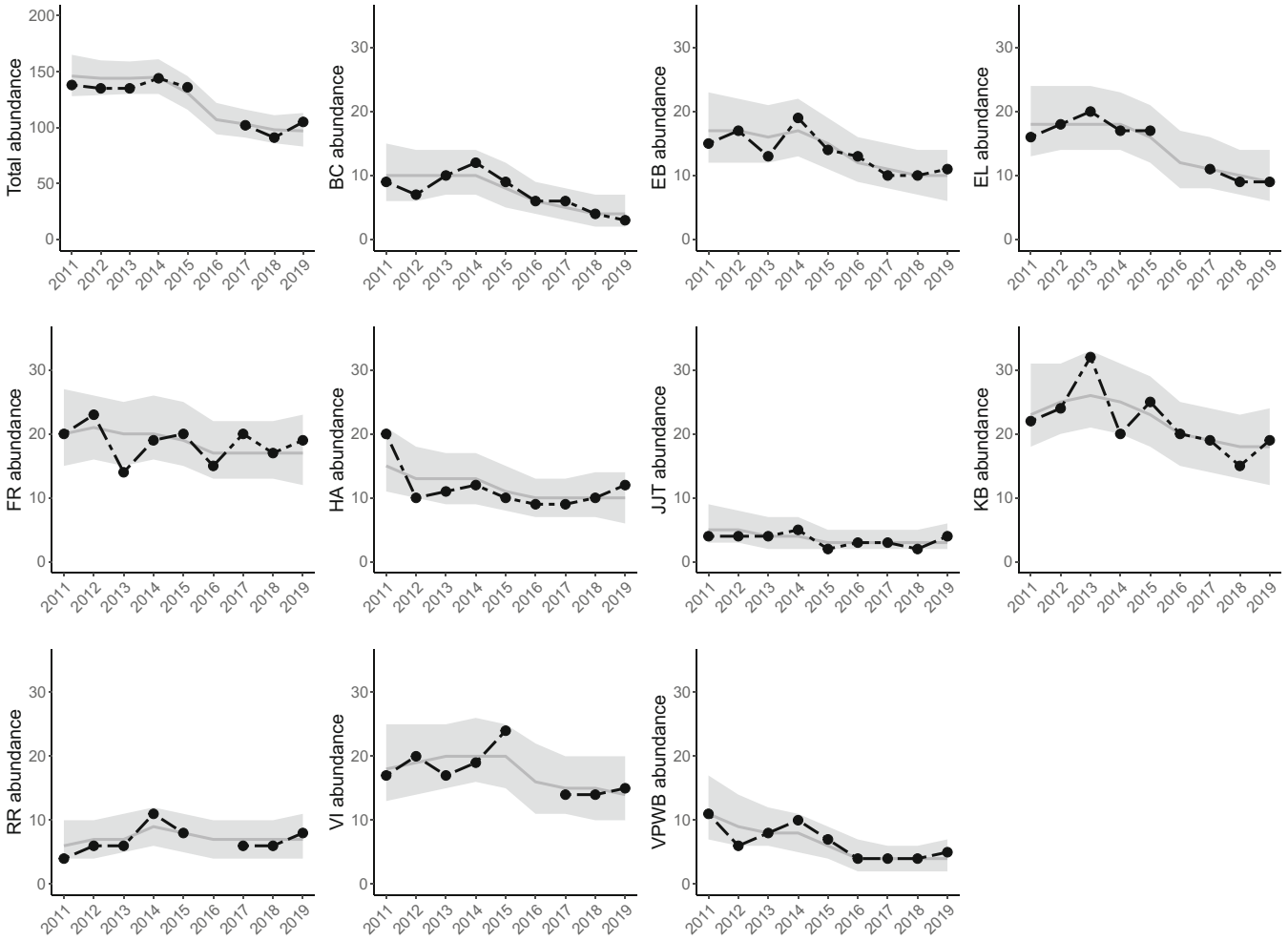

FIGURE 2 Annual total abundance (first panel; note different *y*-axis than plot-level panels) and plot-level observed and model-predicted abundance of golden-cheeked warblers on 10 plots on Balcones Canyonlands Preserve, Austin, Texas, from 2011 to 2019. Black dotted lines represent observed territory counts, gray lines are model-predicted means and gray fill is the 95% credible intervals. Three plots (EL, RR, and VI) were not monitored enough in 2016 to provide territory counts.

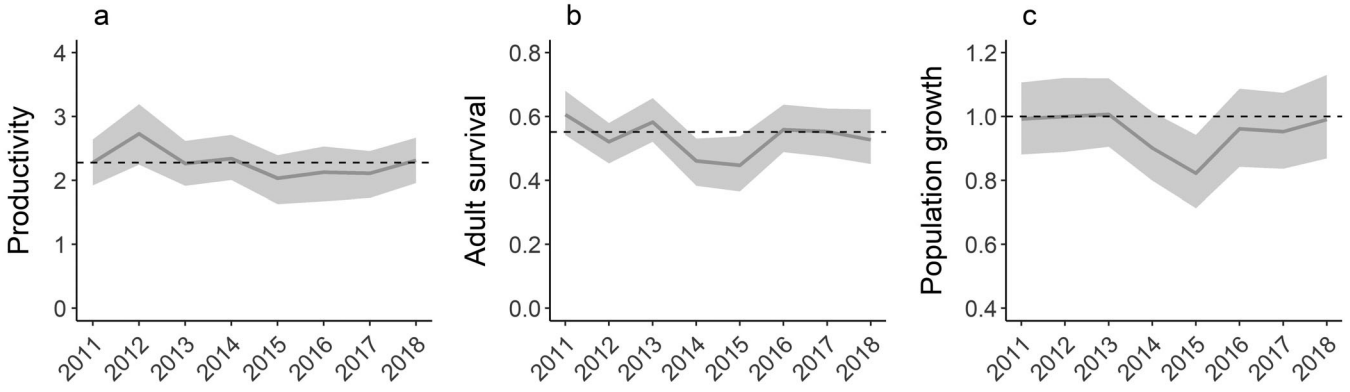

FIGURE 3 Demographic estimates of a golden-cheeked warbler population in Austin, Texas, from 2011 to 2018. Median estimates (gray line) and 95% credible intervals (gray ribbon) are given for (a) productivity, or the number of young produced per territory, (b) adult male survival, and (c) population growth. Population growth rates should be interpreted as 2011–2012 through 2018–2019. Dashed lines represent median values of posterior productivity and adult survival estimates that resulted in a stable population.

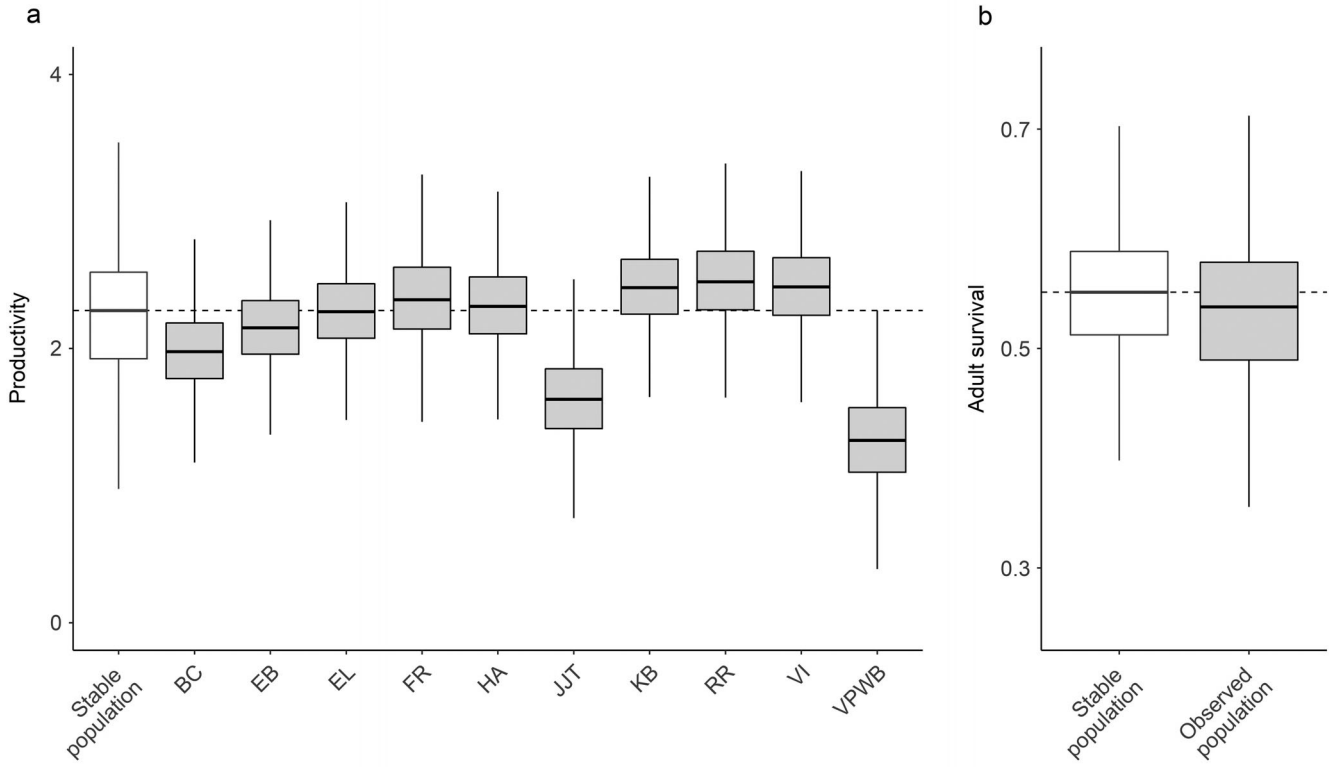

FIGURE 4 Posterior estimates of (a) plot-specific productivity and (b) annual adult male survival of a golden-cheeked warbler population on Balcones Canyonlands Preserve in Austin, Texas, 2011–2018. Productivity is an estimate of the number of young fledged per male territory. Box plots illustrate the variation in rates across all years and allow comparison of observed rates (gray) to distributions of posterior demographic samples that resulted in a stable population (white).

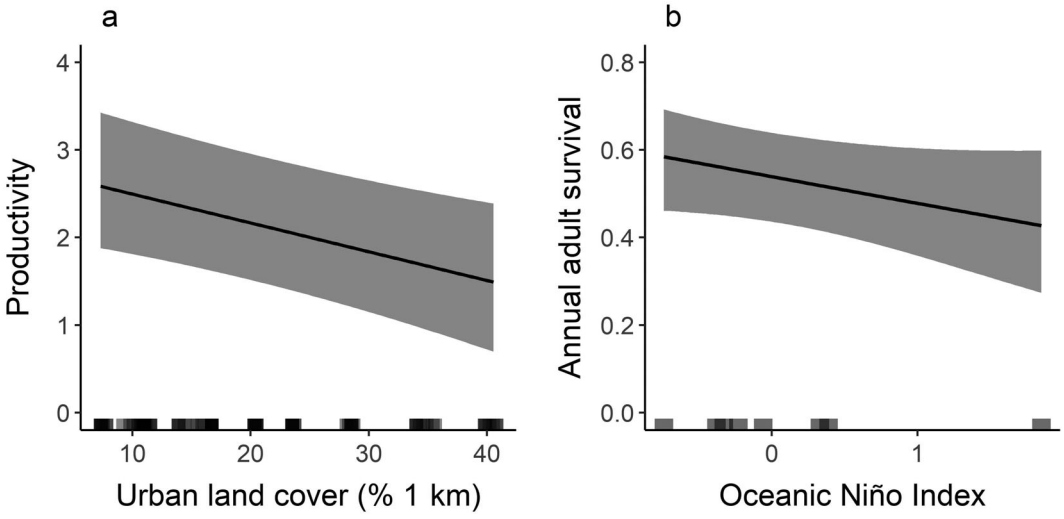

FIGURE 5 Prediction plots showing the relationship between demographic rates and environmental covariates on golden-cheeked warblers breeding on the Balcones Canyonlands Preserve in Austin, Texas, 2011–2018. Posterior predictions reveal the (a) number of young produced per territory was negatively related to percent urban land cover within 1 km of a plot, and (b) annual adult male survival was negatively related to the Oceanic Niño Index (ONI), a measure of El Niño-Southern Oscillation. The rungs along the *x*-axis show the density of values for urban land cover and ONI observed during the study.

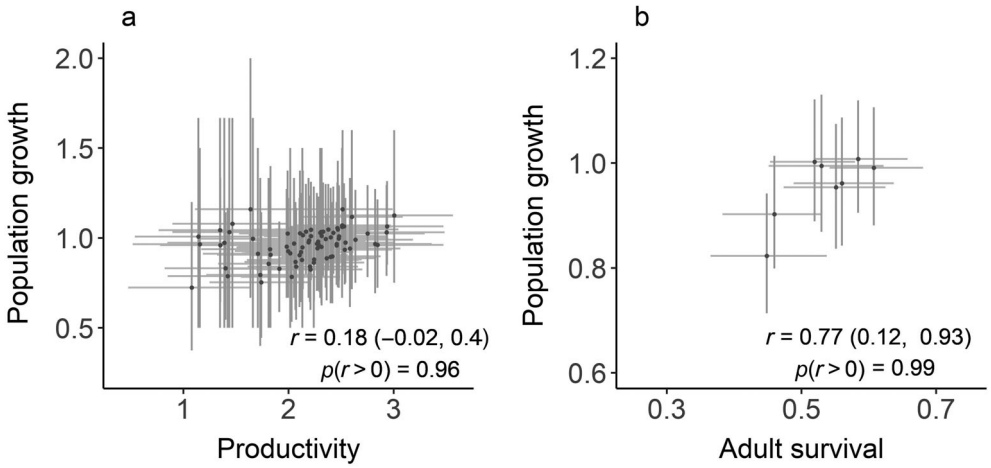

FIGURE 6 Correlations between golden-cheeked warbler population growth and (a) plot-specific productivity and (b) annual adult male survival in Balcones Canyonlands Preserve in Austin, Texas, 2011–2018. Correlation coefficients (r), 95% credible intervals, and the estimated probability of a positive relationship $p(r > 0)$ suggest a positive relationship between population growth and both productivity and adult survival.

Forecasts of abundance and quasi-extinction probability

Uncertainty in golden-cheeked warbler abundance estimates was high among scenarios of forecasted environmental change, but median estimates indicated declining populations (Figure 7). Under conditions observed during 2011–2019, median population growth over 25 years was 0.99 (95% CRI: 0.77–1.24) and quasi-extinction probability after 25 years was 0.17 (Table 1). Increasing urban development by 10% of land cover in less urbanized landscapes and surrounding all plots resulted in the greatest reduction in population growth and the greatest increases in quasi-extinction probability (Table 1). Population growth declined to 0.91 (95% CRI: 0.68–1.15) and the quasi-extinction probability after 25 years was 0.41 under the worst-case scenario in which an additional 10% of land cover surrounding all plots was developed and the frequency of strong El Niño years increased from two to three every 25 years (Table 1). Forecasted quasi-extinction probability was greatest under all scenarios with increased urban development around all plots (Figure 8).

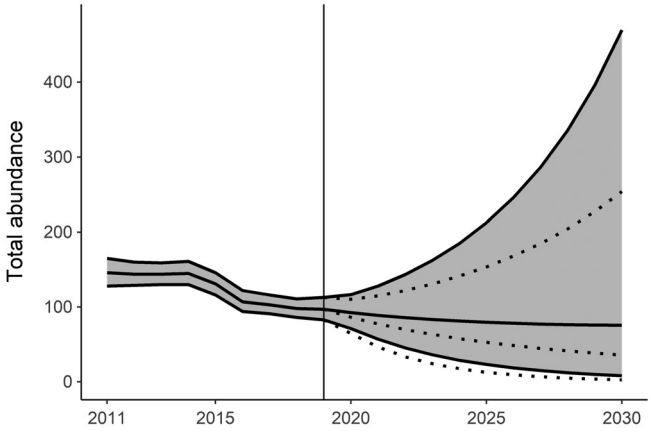

FIGURE 7 Population viability analysis of golden-cheeked warblers in Balcones Canyonlands Preserve, Austin, Texas. Total abundance across 10 plots was estimated from 2011 to 2019 and predictions of future population size were forecasted under observed conditions (thick solid line, gray fill represents 95% credible intervals) and with both an additional year characterized by a high Oceanic Niño Index and 10% development of land surrounding all plots (thick dotted line, smaller dotted lines represent 95% credible intervals) from 2019 to 2044.

DISCUSSION

We developed an IPM for an endangered songbird investigating factors associated with human-caused habitat change and large-scale climate patterns. Urban land cover and a strong El Niño event had significant negative impacts on golden-cheeked warbler population viability, and these factors are projected to increase during this century. Golden-cheeked warbler breeding habitat is threatened by increasing demand for more urban development. Furthermore, it is improbable that woodlands will easily or quickly propagate elsewhere, either due to climatic shifts or due to the need to host suitable habitat away from rapidly urbanizing areas, because of geologic and topographic constraints that create suitable conditions for Ashe juniper woodlands and ideal breeding habitat (US EPA, 2009).

TABLE 1 Predictions of golden-cheeked warbler population growth and persistence within the Balcones Canyonlands Preserve, Austin, TX, 25 years into the future (2019–2044) given current conditions, three scenarios of urban development, and one scenario of change in El Niño-Southern Oscillation (ENSO) patterns.

	Current ENSO patterns		Additional strong ONI year	
Scenario	**Q-extinction**	**λ**	**Q-extinction**	**λ**
Current development	0.17	0.99 (0.77, 1.24)	0.19	0.99 (0.76, 1.24)
Development surrounding high-urban plots ↑ 10%	0.17	0.99 (0.77, 1.24)	0.19	0.99 (0.76, 1.24)
Development surrounding low-urban plots ↑ 10%	0.25	0.96 (0.74, 1.20)	0.27	0.96 (0.72, 1.20)
Development surrounding all plots ↑ 10%	0.40	0.91 (0.70, 1.15)	0.41	0.91 (0.68, 1.15)

Note: The probability of quasi-extinction (Q-extinction), or reaching a total abundance of fewer than 10 breeding territories, and population growth (λ) were estimated for each combination of current conditions and scenarios of land use or climate change. The ↑ under the scenarios indicates an increase of 10% in the 1-km landscape surrounding the plots.
Abbreviation: ONI, Oceanic Niño Index.

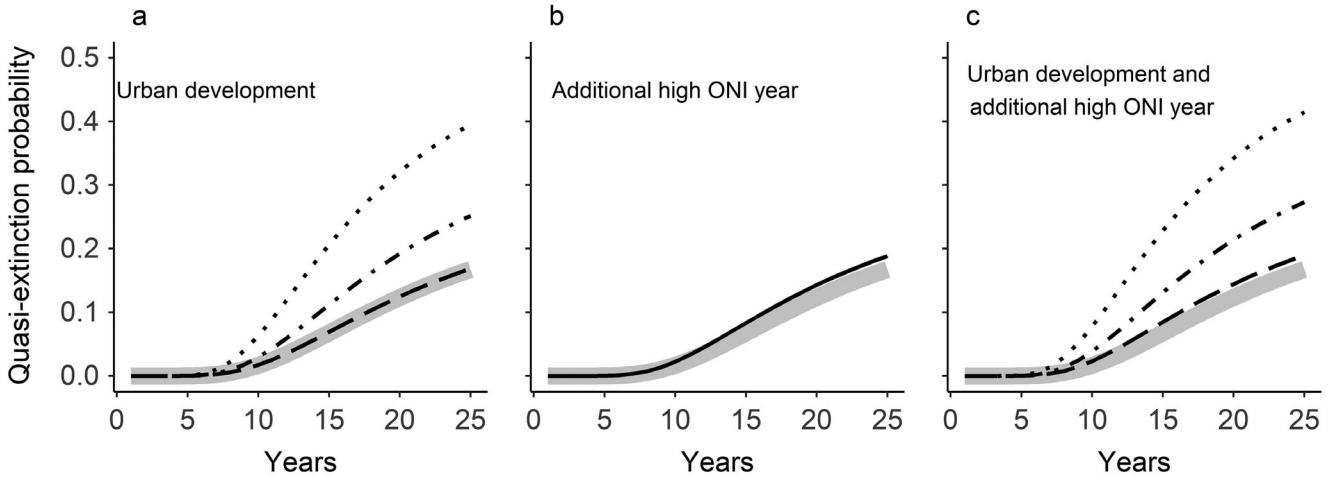

FIGURE 8 Quasi-extinction probabilities over time for a simulated golden-cheeked warbler population in Balcones Canyonlands Preserve, Austin, Texas. The quasi-extinction threshold was defined as the point at which total abundance across 10 plots dropped to fewer than 10 breeding territories. Future scenarios of changes in land cover and climate were compared with a "no change" scenario (gray line). (a) Quasi-extinction probability predicted 25 years into the future from 2019 under three scenarios of land use change: (1) An additional 10% of land cover within 1 km of study plots was converted to development surrounding the three most urbanized plots (dashed line); (2) an additional 10% of land cover within 1 km of study plots was converted to development surrounding the three least urbanized plots (dot-dashed line); (3) an additional 10% of land cover within 1 km of all study plots was converted to development (dotted line). (b) Quasi-extinction probability predicted under a climate scenario in which an additional strong El Niño occurred every 25 years (solid black line). (c) Quasi-extinction probability predicted 25 years into the future under the conditions of both urban development and an additional year with a strong El Niño. ONI, Oceanic Niño Index.

Increasing urban land cover is expected to be a major driver of biodiversity loss globally (Li et al., 2022; Simkin et al., 2022). Central Texas is considered a high-priority area for habitat protection due to its high level of biodiversity and endemism and low amounts of protected areas (Hamilton et al., 2022; Jenkins et al., 2015). Much of the golden-cheeked warbler's breeding range remains unprotected and threatened with increasing urban development. Human infrastructure and population centers are expanding along the eastern edge of the golden-cheeked warbler's range, especially between the Austin and San Antonio metropolitan areas. Counties along this corridor support some of the highest predicted occupancy of woodland patches, but have also experienced high levels of forest disturbance and fragmentation (Collier et al., 2012; Dreiss et al., 2022; Duarte et al., 2013). The BCP is an urbanizing preserve with increasing fragmentation by high-density and low-density roads and varying types of development, mostly residential, at the boundaries. These conditions likely reduce the conservation value of some portions of the BCP to golden-cheeked warbler viability (Wood et al., 2014) and provide a warning to similar protected areas adjacent to increasing exurban and residential development such as the nearby Balcones

Canyonlands National Wildlife Refuge that simply protecting an area may not be sufficient. In addition, our results highlight the need to protect additional breeding habitat away from urbanizing areas.

Herein we did not evaluate mechanisms underlying the negative relationship between productivity and urban land cover, but other studies have found lower occupancy and reproductive success of golden-cheeked warblers in small patches within urbanized landscapes or proximate to housing development (Robinson et al., 2018; Sperry, 2007). Woodland patch sizes on the BCP varied from 180 to >2100 ha and productivity was lowest on plots with the smallest woodland patch size, and concomitantly the largest proportion of urban land cover (BC, JJT, and VPWB). Predation is the largest source of nest mortality for this species (Reidy et al., 2008); therefore, we speculate that golden-cheeked warblers in areas with more urban cover around the plot are experiencing higher nest predation rates. One possible explanation for higher predation pressure in urbanized woodland fragments is the introduction of a novel predator, the blue jay (*Cyanocitta cristata*); this species was historically absent from juniper–oak woodlands but has been moving westward for >30 years and now occupies fragmented woodland areas on the fringes of the BCP (J. Reidy, unpublished data; Hutchinson & Scalise, 2019; Sexton, 1987). Another possible source is increased abundance of fox squirrels (*Sciurus niger*), a known nest predator, in urban fragments associated with higher densities of oak species such as live oaks in residential neighborhoods (McCleery et al., 2007). Lastly, it is also possible that predation on adult females attending the nest is higher in areas with increased urban–forest edge. Texas rat snakes (*Elaphe obsoleta*) are known to prey on adult females attending the nest and are associated with habitat edges (Reidy et al., 2009; Sperry et al., 2009). Other possible effects of a more urban landscape include increased noise and disturbance that could alter parental behavior at the nest or reduce body condition of the adults or nestlings (Francis & Barber, 2013; Frid & Dill, 2002; Sperry, 2007).

We did not find strong support for our effects of weather or other habitat variables on productivity. Relationships of spring precipitation, evergreen cover, broadleaf cover, and forest edge density were in the direction hypothesized but not strong enough to include in our IPM. Previous studies showed golden-cheeked warbler productivity increased with the proportion of woodland within a landscape and decreased with increasing forest edge density (Peak & Thompson, 2014; Reidy et al., 2018); however, these studies were conducted at the territory level, whereas our current study was plot level. Likewise, spring precipitation was weakly related to lower seasonal productivity, but effects of precipitation may be better linked to individual nest outcomes than to season-long productivity or to some other measure of precipitation such as winter precipitation.

We found the global climate pattern El Niño reduced annual adult survival and threatened population viability. The 2015–2016 El Niño event was among the strongest on record (Huang et al., 2016). Strong El Niño cycles cause major disruptions in local weather patterns within the golden-cheeked warbler's breeding and wintering ranges, especially during winter months. The wintering range experienced much drier than normal conditions from July to October 2015 (the rainy season), which coupled with a previous El Niño-type year in 2014 caused a severe drought (FIU, 2016). Contrary to expectation, Central Texas experienced a warmer and drier winter (after an unusually rainy fall) over 2015–2016 (Chiodi & Harrison, 2016; Reimer, 2016). These combined effects may have disrupted or altered arthropod communities available to golden-cheeked warblers both on the wintering grounds and migratory path, but also what was available on the breeding grounds upon their return in spring. Prolonged drought on the wintering grounds can have profound impacts on the arthropod community, and therefore subsequent body condition prior to spring migration (Akresh et al., 2019; McKinnon et al., 2015); this lowered condition could lead to lower survival. Future research investigating the role of precipitation patterns on arthropod abundance and availability and body condition of migrant birds in Mexico and Central America would provide a better understanding of the mechanisms driving the negative relationship between El Niño and survival. While we did not look directly at climate change projections on golden-cheeked warbler viability, we found a link between climate patterns and adult survival that can be used for future modeling scenarios to better understand the golden-cheeked warbler's vulnerability to climate change patterns on the breeding and wintering grounds.

Our population viability analysis predicted a weak declining trend across the next 25 years under current conditions, resulting in an approximately 17% probability of this population declining to our quasi-extinction threshold. Additionally, the probability of quasi-extinction varied depending on the pattern of urban development, that is, the probability of quasi-extinction was higher when development increased around areas of low-urban land cover and across the study region, but not when development increased around more urbanized areas. This is likely because the more urbanized plots already supported fewer breeding pairs and fewer young were produced in each territory. Increasing the frequency of strong El Niño events likewise increased the probability of quasi-extinction in 25 years, although to a lesser degree compared with

increasing urban land cover. Most importantly, the probability of quasi-extinction was >40% when we simulated both an increase in urban land cover around the study area and an increase in frequency of strong El Niño events. These results have important implications for the viability of golden-cheeked warbler populations, given that urban land cover is expected to continue to increase across the Central Texas landscape and conditions similar to those caused by El Niño are expected to become more common as a result of future climate change. Cumulative results highlight the need to protect large patches of breeding habitat both within and beyond urbanizing areas, and for management strategies to minimize urban effects and increase conservation value. Maximizing productivity and population growth in urban settings may require more intensive management, including reforestation to reduce fragmentation and edge, providing buffers along the periphery of habitat patches, removing non-native species, and public outreach and education. Additional research on weather patterns and factors occurring on the wintering grounds is needed to better elucidate effects on productivity and survival.

CONCLUSIONS

Increasing urban land cover and increased frequency of El Niño events were associated with reduced productivity and annual survival, respectively, and threatened population viability of the golden-cheeked warbler. This has important conservation implications because urbanization and altered climate regimes characterize projected patterns of global change. Protecting, maintaining, and creating additional high-quality juniper–oak woodland, both within and beyond urban areas, and conserving large remnant patches will benefit viability of golden-cheeked warbler populations. The decline in abundance over this 10-year study appeared to be in part the result of a single, strong El Niño event that occurred from 2015 to 2016. Population growth has been positive and approaching 1 since the 2015–2016 El Niño, but it will take several more years of data to confirm if the population has rebounded. Besides general efforts to mitigate land use and climate change, additional research is needed to determine specific mechanisms driving these effects on survival of migratory songbirds to develop more specific conservation actions addressing these changes. We found important relationships between the demography of golden-cheeked warblers and landscape and climate factors. However, our study was limited to 10 sites in Austin, and a better understanding of the species' demography is needed from across its range for more effective conservation planning. Longer term demographic monitoring would also provide more power to detect weather effects and more certainty in projected trends.

AUTHOR CONTRIBUTIONS

Jennifer L. Reidy, Frank R. Thompson III, and Lisa O'Donnell conceived the study design. Jennifer L. Reidy and Lisa O'Donnell led data collection efforts. Emily A. Sinnott conducted the IPM analysis with assistance from Jennifer L. Reidy and Frank R. Thompson III. Jennifer L. Reidy and Emily A. Sinnott led manuscript writing, and Frank R. Thompson III and Lisa O'Donnell provided editing and comments.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Reidy et al., 2023) are available from Dryad: https://doi.org/10.5061/dryad.p2ngf1vvc.

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. Jennifer L. Reidy and Lisa O'Donnell held appropriate state, federal, and banding permits to conduct field activities.

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REFERENCES

Akresh, M. E., D. I. King, and P. P. Marra. 2019. "Rainfall and Habitat Interact to Affect the Condition of the Wintering Migratory Songbird in The Bahamas." *Ecology and Evolution* 9: 8042–61.

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, et al. 2010. "A

Global Review of Drought and Heat-Induced Tree Mortality Reveals Emerging Climate Change Risks for Forests." *Forest Ecology and Management* 259: 660–84.

Anderegg, W. R. L., J. M. Kane, and L. D. L. Anderegg. 2012. "Consequences of Widespread Tree Mortality Triggered by Drought and Temperature Stress." *Nature Climate Change* 3: 30–6.

Arbeiter, S., M. Schulze, P. Tamm, and S. Hahn. 2016. "Strong Cascading Effect of Weather Conditions on Prey Availability and Annual Breeding Performance in European Bee-Eaters *Merops apiaster*." *Journal of Ornithology* 157: 155–63.

Arlettaz, R., M. Schaad, T. S. Reichlin, and M. Schaub. 2010. "Impact of Weather and Climate Variation on Hoopoe Reproduction Ecology and Population Growth." *Journal of Ornithology* 151: 889–99.

Briones, F. 2017. "How Did Central America Cope with El Niño 2015-2016?: Lessons and Challenges." Report for El Niño-Ready Nations. https://www.researchgate.net/publication/321038131_How_did_Central_America_cope_with_El_Nino_2015-2016_Lessons_and_challenges.html.

Brooks, S. P., and A. Gelman. 1998. "General Methods for Monitoring Convergence of Iterative Simulations." *Journal of Computational and Graphical Statistics* 7: 434–55.

Burton, C., R. A. Betts, C. D. Jones, T. E. Feldpausch, M. Cardoso, and L. O. Anderson. 2020. "El Niño Driven Changes in Global Fire 2015/2016." *Frontiers in Earth Science* 8: 199.

Cai, W., S. Borlace, M. Lengaigne, P. van Rensch, M. Collins, G. Vecchi, A. Timmerman, et al. 2014. "Increasing Frequency of Extreme El Niño Events due to Greenhouse Warming." *Nature* 4: 111–6.

Cai, W., G. Wang, B. Dewitte, L. Wu, A. Santoso, K. Takahashi, Y. Yang, A. Carréric, and M. J. McPhaden. 2018. "Increased Variability of Eastern Pacific El Niño under Greenhouse Warming." *Nature* 564: 201–6.

Carnicer, J., M. Coll, M. Ninyerola, G. Sánchez, and J. Peñuelas. 2011. "Widespread Crown Condition Decline, Food Web Disruption, and Amplified Tree Mortality with Increased Climate Change-Type Drought." *Proceedings of the National Academy of Sciences* 108: 1474–8.

Chiodi, A. M., and D. E. Harrison. 2016. "2015–16 El Niño Seasonal Weather Impacts from the OLR Event Perspective." Science and Technology Infusion Climate Bulletin. NOAA's National Weather Service. 41st NOAA Annual Climate Diagnostics and Prediction Workshop. Orono, Maine. October 3–6, 2016.

City of Austin. 2019. "Golden-Cheeked Warbler (*Setophaga chrysoparia*) Monitoring Program. Balcones Canyonlands Preserve Annual Report 2019." https://www.traviscountytx.gov/images/tnr/Docs/bccp/2016/appendix-f-cityofaustingcwamonitoring.pdf.

Collier, B. A., J. E. Groce, M. L. Morrison, J. C. Newman, A. J. Campomizzi, S. L. Farrell, H. A. Mathewson, R. T. Snelgrove, R. J. Carroll, and R. N. Wilkins. 2012. "Predicting Patch Occupancy in Fragmented Landscapes at the Rangewide Scale for an Endangered Species: An Example of an American Warbler." *Diversity and Distributions* 18: 158–67.

Conrey, R. Y., S. K. Skagen, A. A. Yackel Adams, and A. O. Panjabi. 2016. "Extremes of Heat, Drought and Precipitation Depress Reproductive Performance in Shortgrass Prairie Passerines." *Ibis* 158: 614–29.

Cox, W. A., F. R. Thompson, III, and J. Faaborg. 2012. "Landscape Forest Cover and Edge Effects on Songbird Nest Predation Vary by Nest Predator." *Landscape Ecology* 27: 659–69.

Cox, W. A., F. R. Thompson, III, and J. L. Reidy. 2013. "The Effects of Temperature on Nest Predation by Mammals, Birds, and Snakes." *Auk* 130: 784–90.

Crouchet, S. E., J. Jensen, B. F. Schwartz, and S. Schwinning. 2019. "Tree Mortality after a Hot Drought: Distinguishing Density-Dependent and -Independent Drivers and Why It Matters." *Frontiers in Forests and Global Change* 2: 21.

Dreiss, L. M., P. Sanchez-Navarro, and B. Bird. 2022. "Spatiotemporal Patterns in Golden-Cheeked Warbler Breeding Habitat Quality and Quantity." *Avian Conservation and Ecology* 17: 14.

Duarte, A., J. E. Hines, J. D. Nichols, J. S. Hatfield, and F. W. Weckerly. 2014. "Age-Specific Survival of Male Golden-Cheeked Warblers on the Fort Hood Military Reservation, Texas." *Avian Conservation and Ecology* 9: 4.

Duarte, A., J. L. R. Jensen, J. S. Hatfield, and F. W. Weckerly. 2013. "Spatiotemporal Variation in Range-Wide Golden-Cheeked Warbler Breeding Habitat." *Ecosphere* 4: 1–12.

Findell, K. L., A. Berg, P. Gentine, J. P. Krasting, B. R. Lintner, S. Malyshev, J. A. Santanello, Jr., and E. Shevliakova. 2017. "The Impact of Anthropogenic Land Use and Land Cover Change on Regional Climate Extremes." *Nature Communications* 8: 989.

Fischer, J., and D. B. Lindenmayer. 2007. "Landscape Modification and Habitat Fragmentation: A Synthesis." *Global Ecology and Biogeography* 16: 265–80.

Florida State University (FIU). 2016. "El Niño Southern Oscillation (ENSO) 2015-2016: Latin American and Caribbean Region." FIU-DRR Report No. 3. https://drr.fiu.edu/enso-201516/report-no3_jan2016_english.pdf.

Francis, C. D., and J. R. Barber. 2013. "A Framework for Understanding Noise Impacts on Wildlife: An Urgent Conservation Priority." *Frontiers in Ecology and the Environment* 11: 305–13.

Frid, A., and L. Dill. 2002. "Human-Caused Disturbance Stimuli as a Form of Predation Risk." *Conservation Ecology* 6: 11.

Giannini, A., Y. Kushner, and M. A. Cane. 2000. "Interannual Variability of Caribbean Rainfall, ENSO, and the Atlantic Ocean." *Journal of Climate* 13: 297–311.

Groce, J. E., H. A. Mathewson, M. L. Morrison, and R. N. Wilkins. 2010. "Scientific Evaluation for the 5-Year Status Review of the Golden-Cheeked Warbler." Final Report Submitted to the Texas Parks and Wildlife Department, Austin, TX, and to the U.S. Fish and Wildlife Service, Region 2, Albuquerque, NM, USA.

Guo, J., and M. Zhang. 2021. "Exploring the Patterns and Drivers of Urban Expansion in the Texas Triangle Megaregion." *Land* 10: 1244.

Gyurácz, J., P. Bánhidi, J. Góczán, P. Illés, S. Kalmár, Z. Lukács, C. Németh, and L. Varga. 2016. "Temperature and Precipitation Effects on Breeding Productivity of Some Passerines – A Multivariate Analysis of Constant Effort Mist-Netting Data." *Biologia* 71: 1298–303.

Hamilton, C. M., S. Martinuzzi, A. J. Plantinga, V. C. Radeloff, D. J. Lewis, W. E. Thogmartin, P. J. Heglund, and A. M. Pidgeon. 2013. "Current and Future Land Use around a Nationwide Protected Area Network." *PLoS One* 8: e55737.

Hamilton, H., R. L. Smyth, B. E. Young, T. G. Howard, C. Tracey, S. Breyer, D. R. Cameron, et al. 2022. "Increasing Taxonomic Diversity and Spatial Resolution Clarifies Opportunities for Protecting U.S. Imperiled Species." *Ecological Applications* 32: e2534.

Hansen, A. J., R. L. Knight, J. M. Marzluff, S. Powell, K. Brown, P. H. Gude, and K. Jones. 2005. "Effects of Exurban Development on Biodiversity: Patterns, Mechanisms, and Research Needs." *Ecological Applications* 15: 1893–905.

Huang, B., M. L'Heureux, Z.-Z. Hu, and H.-M. Zhang. 2016. "Ranking the Strongest ENSO Events while Incorporating SST Uncertainty." *Geophysical Research Letters* 43: 9165–72.

Hutchinson, D. M., and J. L. Scalise. 2019. "First Observation of Blue Jay (*Cyanocitta cristata*) Depredating a Golden-Cheeked Warbler (*Setophaga chrysoparia*) Nest." *Southwestern Naturalist* 64: 53–5.

IPCC. 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by Core Writing Team, R. K. Pachauri, and L. A. Meyer. Geneva: IPCC, 151 pp.

Jenkins, C. N., K. S. Van Houtan, S. L. Pimm, and J. O. Sexton. 2015. "US Protected Lands Mismatch Biodiversity Priorities." *Ecology* 112: 5081–6.

Jetz, W., D. S. Wilcove, and A. P. Dobson. 2007. "Projected Impacts of Climate and Land-Use Change on the Global Diversity of Birds." *PLoS Biology* 5: 1211–9.

Kellner, K. 2019. "jagsUI: A Wrapper around 'rjags' to Streamline 'JAGS' Analyses." R Package Version 1.4.2. https://github.com/kenkellner/jagsUI.

Ladd, C., and L. Gass. 2020. "Golden-Cheeked Warbler (*Setophaga chrysoparia*), Version 1.0." In *Birds of the World*, edited by P. G. Rodewald. Ithaca, NY: Cornell Lab of Ornithology.

Lakeman-Fraser, P., and R. M. Ewers. 2014. "Untangling Interactions: Do Temperature and Habitat Fragmentation Gradients Simultaneously Impact Biotic Relationships?" *Proceedings of the Royal Society B: Biological Sciences* 281: 20140687.

Li, G., C. Fang, Y. Li, Z. Wang, S. Sun, S. He, W. Qi, et al. 2022. "Global Impacts of Future Urban Expansion on Terrestrial Vertebrate Diversity." *Nature Communications* 13: 1628.

Mantyka-Pringle, C. S., T. G. Martin, and J. R. Rhodes. 2012. "Interactions between Climate and Habitat Loss Effects on Biodiversity: A Systematic Review and Meta-Analysis." *Global Change Biology* 18: 1239–52.

Mazerolle, D. F., K. W. Dufour, K. A. Hobson, and H. E. den Haan. 2005. "Effects of Large-Scale Climatic Fluctuations on Survival and Production of Young in a Neotropical Migrant Songbird, the Yellow Warbler *Dendroica petechia*." *Journal of Avian Biology* 36: 155–63.

McCleery, R. A., R. R. Lopez, N. J. Silvy, and S. N. Kahlick. 2007. "Habitat Use of Fox Squirrels in an Urban Environment." *Journal of Wildlife Management* 71: 1149–57.

McKellar, A. E., M. W. Reudink, P. P. Marra, L. M. Ratcliffe, and S. Wilson. 2015. "Climate and Density Influence Annual Survival and Movement in a Migratory Songbird." *Ecology and Evolution* 5: 5892–904.

McKinnon, E. A., J. A. Rotenberg, and B. J. M. Stutchbury. 2015. "Seasonal Change in Tropical Habitat Quality and Body Condition for a Declining Migratory Songbird." *Behavioral Ecology* 179: 363–75.

Newbold, T. 2018. "Future Effects of Climate and Land-Use Change on Terrestrial Vertebrate Community Diversity under Different Scenarios." *Proceedings of the Royal Society* 285: 20180792.

Newbold, T., L. N. Hudson, S. L. L. Hill, S. Contu, I. Lysenko, R. A. Senior, L. Börger, et al. 2015. "Global Effects of Land Use on Local Terrestrial Biodiversity." *Nature* 520: 45–50.

Nielson-Gammon, J., J. Escobedo, C. Ott, J. Dedrick, and A. Van Fleet. 2020. "Assessment of Historic and Future Trends of Extreme Weather in Texas, 1900–2036." Texas A&M University, Document OSC-202001. https://climatexas.tamu.edu/files/ClimateReport-1900to2036-2021Update.

Nott, M. P., D. F. DeSante, R. B. Siegel, and P. Pyle. 2002. "Influences of the El Niño/Southern Oscillation and the North Atlantic Oscillation on Avian Productivity in Forests of the Pacific Northwest of North America." *Global Ecology and Biogeography* 11: 333–42.

Öberg, M., D. Arlt, T. Pärt, A. T. Laugen, S. Eggers, and M. Low. 2015. "Rainfall during Parental Care Reduces Reproductive and Survival Components of Fitness in a Passerine Bird." *Ecology and Evolution* 5: 345–56.

Okada, S., D. B. Lindenmayer, J. T. Wood, M. J. Crane, and J. C. Pierson. 2017. "How Does a Transforming Landscape Influence Bird Breeding Success?" *Landscape Ecology* 32: 1039–48.

Oliver, T. H., and M. D. Morecroft. 2014. "Interactions between Climate Change and Land Use Change on Biodiversity: Attribution Problems, Risks, and Opportunities." *Climate Change* 5: 317–35.

Paxton, K. L., E. B. Cohen, E. H. Paxton, Z. Németh, and F. R. Moore. 2014. "El Niño-Southern Oscillation Is Linked to Decreased Energetic Condition in Long-Distance Migrants." *PLoS One* 9: e95383.

Peak, R. G., and F. R. Thompson, III. 2014. "Seasonal Productivity and Nest Survival of Golden-Cheeked Warblers Vary with Forest Type and Edge Density." *Condor* 116: 546–59.

Plummer, M. 2003. "JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling." In *Proceedings of the 3rd International Workshop on Distributed Statistical Computing* (DSC 2003), Volume 124, Vienna, Austria.

Polley, H. W., D. M. Johnson, and R. B. Jackson. 2018. "Projected Drought Effects on the Demography of Ashe Juniper Populations Inferred from Remote Measurements of Tree Canopies." *Plant Ecology* 219: 1259–67.

Powers, R. P., and W. Jetz. 2019. "Global Habitat Loss and Extinction Risk of Terrestrial Vertebrates under Future Land-Use-Change Scenarios." *Nature Climate Change* 9: 323–9.

R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Radeloff, V. C., S. I. Stewart, T. J. Hawbaker, and D. P. Helmers. 2009. "Housing Growth in and Near United States Protected Areas Limits Their Conservation Value." *Proceedings of the National Academy of Sciences* 107: 940–5.

Reidy, J., E. Sinnott, F. Thompson, and L. O'Donnell. 2023. "Golden-Cheeked Warbler Integrated Population Model (IPM)

Data in Austin, TX (2011–2019).” Dryad. Dataset. https://doi.org/10.5061/dryad.p2ngf1vvc.

Reidy, J. L., M. M. Stake, and F. R. Thompson, III. 2008. “Golden-Cheeked Warbler Nest Mortality and Predators in Urban and Rural Landscapes.” *Condor* 110: 458–66.

Reidy, J. L., M. M. Stake, and F. R. Thompson, III. 2009. “Nocturnal Predation of Females on Nests: An Important Source of Mortality for Golden-Cheeked Warblers?” *Wilson Journal of Ornithology* 121: 416–21.

Reidy, J. L., F. R. Thompson, III, G. M. Connette, and L. O’Donnell. 2018. “Demographic Rates of Golden-Cheeked Warblers in an Urbanizing Woodland Preserve.” *Condor* 120: 249–64.

Reidy, J. L., F. R. Thompson, III, and L. O’Donnell. 2020. “Population Viability of Golden-Cheeked Warblers in an Urbanizing Landscape.” *Wildlife Society Bulletin* 44: 502–11.

Reimer, D. 2016. “Looking Back at the Lackluster Winter; What Might Spring Bring?” https://texasstormchasers.com/weather/43318/.

Robinson, D. H., H. A. Mathewson, M. L. Morrison, and R. N. Wilkins. 2018. “Habitat Effects on Golden-Cheeked Warbler Productivity in an Urban Landscape.” *Wildlife Society Bulletin* 42: 48–56.

Robinson, L., J. P. Newell, and J. M. Marzluff. 2005. “Twenty-Five Years of Sprawl in the Seattle Region: Growth Management Responses and Implications for Conservation.” *Landscape and Urban Planning* 71: 51–72.

Robinson, S. K., F. R. Thompson, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. “Regional Forest Fragmentation and the Nesting Success of Migratory Birds.” *Science* 267: 1987–90.

Ropelewski, C. F., and M. S. Halpert. 1986. “North American Precipitation and Temperature Patterns Associated with the El Niño/Southern Oscillation.” *Monthly Weather Review* 114: 2352–62.

Ropelewski, C. F., and M. S. Halpert. 1987. “Global and Regional Scale Precipitation Patterns Associated with the El Niño/Southern Oscillation.” *Monthly Weather Review* 115: 1606–26.

Sala, O. E., F. S. Chapin, III, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, et al. 2000. “Global Biodiversity Scenarios for the Year 2100.” *Science* 287: 1770–4.

Schaub, M., and F. Abadi. 2011. “Integrated Population Models: A Novel Analysis Framework for Deeper Insights into Population Dynamics.” *Journal of Ornithology* 152: 227–37.

Schaub, M., and M. Kéry. 2022. *Integrated Population Models: Theory and Ecological Applications with R and JAGS*. London: Academic Press.

Seto, K. C., M. Fragkias, B. Güneralp, and M. K. Reilly. 2011. “A Meta-Analysis of Global Urban Land Expansion.” *PLoS One* 6: e23777.

Sexton, C. W. 1987. “A Comparative Analysis of Urban and Native Bird Populations in Central Texas.” PhD diss., University of Texas.

Sherry, T. W., S. Wilson, S. Hunter, and R. T. Holmes. 2015. “Impacts of Nest Predators and Weather on Reproductive Success and Population Limitation in a Long-Distance Migratory Songbird.” *Journal of Avian Biology* 46: 559–69.

Sillett, T. S., R. T. Holmes, and T. W. Sherry. 2000. “Impacts of a Global Climate Cycle on Population Dynamics of a Migratory Songbird.” *Science* 288: 2040–2.

Simkin, R. D., K. C. Seto, R. I. McDonald, and W. Jetz. 2022. “Biodiversity Impacts and Conservation Implications of Urban Land Expansion Projected to 2050.” *Proceedings of the National Academy of Sciences* 119: 12.

Sperry, C. S. 2007. “Influences of Borders on Golden-Cheeked Warbler Habitat in the Balcones Canyonlands Preserve, Travis County, Texas.” Thesis, Texas State University.

Sperry, J. H., D. A. Cimprich, R. G. Peak, and P. J. Weatherhead. 2009. “Is Nest Predation on Two Endangered Bird Species Higher in Habitats Preferred by Snakes?” *Ecoscience* 16: 111–8.

Stokke, B. G., A. P. Møller, B.-E. Sœther, G. Rheinwald, and H. Gutscher. 2005. “Weather in the Breeding Area and during Migration Affects the Demography of a Small Long-Distance Passerine Migrant.” *Auk* 122: 637–47.

Studds, C. E., and P. P. Marra. 2007. “Linking Fluctuations in Rainfall to Nonbreeding Season Performance in a Long-Distance Migratory Bird, *Setophaga ruticilla*.” *Climate Research* 35: 115–22.

Thomas, C. D. 2010. “Climate, Climate Change and Range Boundaries.” *Biodiversity Review* 16: 488–95.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Eramus, et al. 2004. “Extinction Risk from Climate Change.” *Nature* 427: 145–8.

Tietjen, B., D. R. Schlaepfer, J. B. Bradford, W. K. Lauenroth, S. A. Hall, M. C. Duniway, T. Hochstrasser, et al. 2017. “Climate Change-Induced Vegetation Shifts Lead to More Ecological Droughts Despite Projected Rainfall Increases in Many Global Temperate Drylands.” *Global Change Biology* 23: 2743–27541.

Timmerman, A., J. Oberhuber, A. Bacher, M. Esch, M. Latif, and E. Roeckner. 1999. “Increased El Niño Frequency in a Climate Model Forced by Future Greenhouse Warming.” *Nature* 398: 694–7.

U.S. Environmental Protection Agency (US EPA). 2009. *A Framework for Categorizing the Relative Vulnerability of Threatened and Endangered Species to Climate Change*. Washington, DC: National Center for Environmental Assessment. https://nepis.epa.gov/Exe/ZyPDF.cgi/P100QR9T.PDF?Dockey=P100QR9T.PDF.

U.S. Fish and Wildlife Service (USFWS). 1990. “Final Rule to List the Golden-Cheeked Warbler as Endangered.” *Federal Register* 55(249): 53153–60.

U.S.A. Facts (USAFacts). 2023. “Our Changing Population: Travis County, Texas.” https://usafacts.org/data/topics/people-society/population-and-demographics/our-changing-population/state/texas/county/travis-county?endDate=2020-01-01&startDate=1990-01-01.

Wang, G., W. Cai, B. Gan, A. Santoso, X. Lin, Z. Chen, and M. J. McPhaden. 2017. “Continued Increase of Extreme El Niño Frequency Long after 1.5°C Warming Stabilization.” *Nature Climate Change* 7: 567–72.

Wang, W., C. Peng, D. D. Kneeshaw, G. R. Larocque, and Z. Luo. 2012. “Drought-Induced Tree Mortality: Ecological Consequences, Causes, and Modeling.” *Environmental Reviews* 20: 109–21.

Wilsey, C., B. Bateman, L. Taylor, J. X. Wu, G. LeBaron, R. Shephard, C. Koseff, S. Friedman, and R. Stone. 2019. *Survival by Degrees: 389 Bird Species on the Brink*. New York: National Audubon Society. https://nas-national-prod.s3.amazonaws.com/climatereport-2019-english-lowres.pdf.

Wood, E. M., A. M. Pidgeon, V. C. Radeloff, D. Helmers, P. D. Dulbert, N. S. Keuler, and C. H. Flather. 2014. “Housing Development Erodes Avian Community Structure in U.S. Protected Areas.” *Ecological Applications* 24: 1445–62.

Zhao, Q., T. W. Arnold, J. H. Devries, D. W. Howerter, R. G. Clark, and M. D. Weegman. 2019. "Land-Use Change Increases Climatic Vulnerability of Migratory Birds: Insights from Integrated Population Modelling." *Journal of Animal Ecology* 88: 1625–37.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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