Estimating golden-cheeked warbler immigration: implications for the spatial scale of conservation

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Abstract

Understanding the factors that drive population dynamics is fundamental to species conservation and management. Since the golden-cheeked warbler *Setophaga chrysoparia* was first listed as endangered, much effort has taken place to monitor warbler abundance, occupancy, reproduction and survival. Yet, despite being directly related to local population dynamics, movement rates have not been estimated for the species. We used an integrated population model to investigate the relationship between immigration rate, fledging rate, survival probabilities and population growth rate for warblers in central Texas, USA. Furthermore, using a deterministic projection model, we examined the response required by vital rates to maintain a viable population across varying levels of immigration. Warbler abundance fluctuated with an overall positive trend across years. In the absence of immigration, the abundance would have decreased. However, the population could remain viable without immigration if both adult and juvenile survival increased by almost half or if juvenile survival more than doubled. We also investigated the response required by fledging rates across a range of immigration in order to maintain a viable population. Overall, we found that immigration was required to maintain warbler target populations, indicating that warbler conservation and management programs need to be implemented at larger spatial scales than current efforts to be effective. This study also demonstrates that by using limited data within integrated population models, biologists are able to monitor multiple key demographic parameters simultaneously to gauge the efficacy of strategies designed to maximize warbler viability in a changing landscape.

Introduction

Fundamental to species conservation and management is an understanding of the factors driving population dynamics (Williams, Nichols & Conroy, 2002). Temporal population dynamics concern the chronological variation in abundance and can simply be expressed as the inputs and depletions of individuals via recruitment, survival, emigration and immigration over time. Thus, there is a need for a comprehensive understanding of the biotic and abiotic factors that influence these vital rates. Such information helps biologists better understand fluctuations in abundance of a species and the environmental variation individuals are faced with at a variety of spatial and temporal scales.

The golden-cheeked warbler *Setophaga chrysoparia* (hereafter warbler) is a neotropical migrant passerine that breeds exclusively in the mature oak (*Quercus* spp.) – Ashe juniper *Juniperus ashei* woodlands of central Texas, USA, and spends the rest of the year in the pine (*Pinus* spp.) – oak forests ≥ 100 m in elevation in Central America

(Monroe, 1968; Pulich, 1976; Rappole, King & Barrow, 1999). The warbler was listed as endangered in an emergency listing by the US Fish and Wildlife Service (USFWS) in 1990, citing habitat loss and the species' limited breeding range as primary threats to warbler persistence (USFWS, 1990). Since the species was first listed, movement between habitat patches has remained an area of high interest for warbler conservation and management, especially as range-wide breeding habitat loss and fragmentation continue to occur (Duarte *et al*., 2013). Indeed, the need to maintain gene flow across the entire breeding range is directly stated in the warbler recovery criteria (USFWS, 1992) and connectivity between habitat patches is considered essential for warbler persistence (Alldredge *et al*., 2004).

Warbler population models currently assisting in recovery planning use sensitivity analyses or assume a dispersal distance function to assess the influence of dispersal rates on projected population dynamics (Alldredge *et al*., 2004; Vaillant *et al*., 2004; Horne, Strickler & Alldredge, 2011). In

these models, dispersal rate is defined as the proportion of individuals moving from one population to another (Akçakaya, 2004), and as such is a measure of emigration. Notably, emigration can be estimated for avian species through the use of direct or indirect methods (i.e. telemetry, band recoveries, dynamic occupancy models, etc.; reviewed in Kendall & Nichols, 2004). Such techniques, however, require a large amount of data and/or multiple study areas that are spatially structured such that movement between areas can be estimated. Another approach to estimate emigration that might be more pragmatic, in that it overcomes the need to have so much data, is the use of spatial capture-recapture models (Royle *et al.*, 2014; Schaub & Royle, 2014). Nevertheless, carrying out capture-recapture studies is costly. Thus, methods to estimate warbler emigration are impractical to implement across large spatial scales over the long term. Consequently, emigration has remained one of the few population parameters that has yet to be estimated for the species (reviewed in Hatfield, Weckerly & Duarte, 2012).

It seems evident that at the local spatial scale (i.e. the spatial scale of a study area) immigration should be a main focus concerning warbler movements for a few reasons. First, there is the logistical challenge associated with estimating emigration for animals that are capable of traveling large distances, such as the warbler. This challenge is amplified when access to neighboring properties to document movement events is limited, a common scenario across the state of Texas because most properties are privately owned. Second, warbler survival estimates thus far are calculated as apparent or local survival, not true survival (USFWS, 1996*b*; Alldredge *et al.*, 2004; Duarte *et al.*, 2014). Therefore, in this one estimate biologists are already tracking both the mortality and permanent emigration of individuals on a site of interest (Pollock *et al.*, 1990; Lebreton *et al.*, 1992). Lastly, whether or not immigration has a substantial role in local population dynamics has profound consequences for the spatial scale at which warbler conservation and management programs should be implemented. If immigrants from surrounding areas have a substantial role in maintaining a viable local warbler population, management actions applied at a local spatial scale may not be effective.

In this paper, we use an integrated population model to estimate warbler immigration. Briefly, integrated population models combine multiple data types (i.e. abundance and demographic data) into a single analysis to assess population dynamics (Besbeas *et al.*, 2002; Brooks, King & Morgan, 2004; Schaub & Abadi, 2011). By combining the likelihoods of multiple datasets, integrated population models allow biologists to estimate population parameters for which little to no explicit data are available (Besbeas *et al.*, 2002; Schaub *et al.*, 2007). Such models have recently been extended to estimate immigration using auxiliary data that are typically already collected by established warbler monitoring programs (Abadi *et al.*, 2010*b*; Schaub, Jakober & Stauber, 2013). This is possible because of the direct relationship between temporal population dynamics and vital rates.

We investigated temporal dynamics of a warbler population in central Texas, USA. The primary aims for this study were to (1) estimate warbler immigration by combining Bayesian integrated population modeling with data regularly collected by established warbler monitoring programs and (2) use the resulting estimates to quantify the demographic conditions required to maintain viable warbler populations for a range of immigration. Given the current warbler demographic estimates (i.e. relatively low survival estimates; Duarte *et al.*, 2014) and the widespread warbler habitat throughout its breeding range, we hypothesize that annual movement is widespread and immigration is needed to maintain stable populations at the local spatial scale. This study is the first to estimate warbler movement rates, which has implications concerning warbler movement ecology, population viability and the spatial scale at which conservation and management programs need to be implemented.

Materials and methods

Study sites

Data and prior information for this study came from the Balcones Canyonlands Preserve (BCP) and the Fort Hood Military Reservation (FHMR; Fig. 1). The BCP is a large (> 12 300 ha), discontinuous collection of properties located in Travis County, Texas, USA (City of Austin, 2012). Several public and private entities manage the collection of properties. The primary goal across the preserve is to protect and enhance habitat for species of concern as part of a habitat mitigation strategy in response to urban sprawl throughout Travis County (USFWS, 1996*a*). The FHMR is an 87 890-ha contiguous property located in Bell and Coryell Counties, Texas, USA. The property is managed by the US Army, with the primary goal to facilitate training of US military personnel (reviewed in Wolfe *et al.*, 2012).

Abundance and productivity data collection

From 1998 to 2012, warbler surveys have been conducted within five 40.5-ha 'prime' warbler-habitat plots delineated on BCP (City of Austin, 2012). Here, a 'prime' warbler-habitat plot is a plot that contains mature Ashe juniper and oak woodlands with at least 75% of the area containing > 70% canopy cover (Abbruzzese & Koehler, 2002). Spot-mapping survey data were collected to calculate the number of warbler territories (which are comprised of adult male birds) per plot using Verner's counting method (i.e. counting all territories completely within each plot and half of each territory that overlapped the plot boundary; Verner, 1985), following the recommendation of Weckerly & Ott (2008). These surveys were carried out at least twice a week from mid-March until late May. An individual was considered territorial if it was located in the same vicinity during three surveys that were separated by at least 1 week (City of Austin, 2012). For productivity data, biologists actively
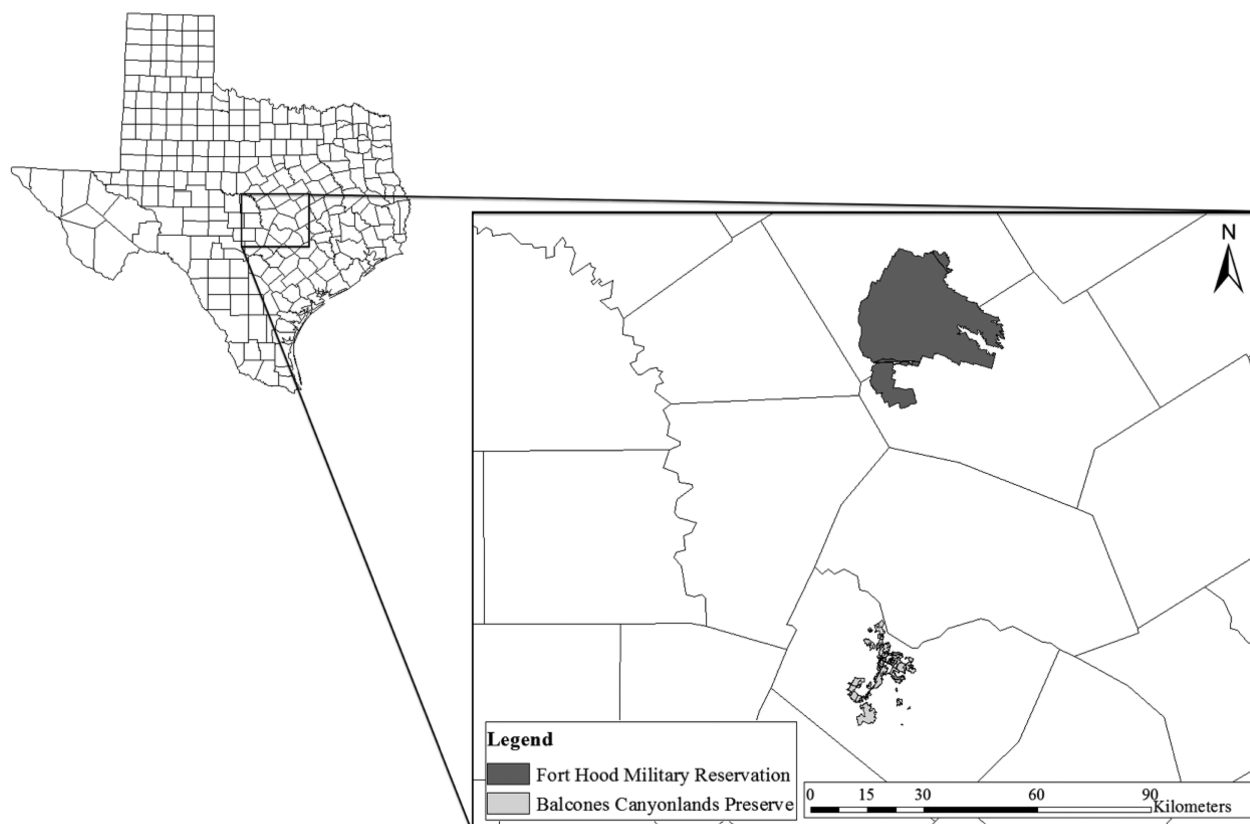
Figure 1 Map of the locations in Texas, USA, where golden-cheeked warbler *Setophaga chrysoparia* data and prior information were collected.

searched for fledglings within the plots. Spot-mapping and productivity surveys were conducted simultaneously, however, productivity surveys extended out until mid-June (City of Austin, 2012). Data were summed across the plots. Because integers are required for this analysis and are more biologically meaningful when referring to the total number of individuals, we rounded the number of territories to integer values by alternating whether we rounded up or down when half territories were present after pooling the data.

Integrated population model

A male-based, pre-breeding projection model was used within the integrated population model because only male demographic data are available for this species due to the cryptic nature of females during the breeding season. The model assumed transient males did not occur in the data, which concurs with long-term capture-resight data for the species (Duarte *et al.*, 2014). The likelihood of the spot-mapping data was constructed using a state-space model (De Valpine & Hastings, 2002). Such a model separates process variation (i.e. true fluctuations in abundance) from observer error when analyzing count data over time (Kéry & Schaub, 2012). The state process portion of the model described the change in the number of adult territorial

males as a function of vital rates, and included three categories of adults: (1) local recruits (N_L) were individuals that were born on the plots the previous year that survived and returned as adults; (2) survivors (N_{Surv}) were adult individuals from the previous year that survived and returned; and (3) immigrants (N_{Im}) were adult individuals that were new to the study area. These numbers change over time in a stochastic manner due to demographic stochasticity:

$$N_{L,t+1} \sim Binomial(N_{F,t}, \phi_{J,t}), \text{ where } N_{F,t} \sim Poisson(0.5N_tF_t),$$

$$N_{Surv,t+1} \sim Binomial(N_t, \phi_{A,t}) \text{ and }$$

$$N_{Im,t+1} \sim Poisson(N_t\omega_t).$$

The total population size in year *t* is then the sum of these three categories:

$$N_t = N_{L,t} + N_{Im,t} + N_{Surv,t}.$$

N_F is the total number of fledglings, *F* is the number of fledglings per territory, ω is immigration rate, ϕ_A is adult apparent survival and ϕ_J is juvenile apparent survival. Immigration rate is defined as the proportion of individuals entering the population in year *t*, relative to the number of

individuals in the population in year $t - 1$. Although a male-based model was used, F corresponds to the total number of juvenile birds that fledge per territory, regardless of sex. We assumed an even sex ratio for fledglings and therefore multiplied F by 0.5. The observer error in the state-space model assumed a Poisson distribution, such that $COUNT_t \sim Poisson(N_t)$, where COUNT represents the calculated abundance from the spot-mapping data using Verner's counting method. Population growth rates ($\lambda_t = N_{t+1}/N_t$) were then calculated as derived parameters within the model to track temporal variation in the number of adult territorial males.

This state-space model contains all the parameters we want to estimate. Yet, most of them are not identifiable (i.e. parameters cannot be estimated separately) based on spot-mapping data alone. More information needs to be included to render all parameters identifiable. Here, we include data that are informative about productivity and informative priors for the survival parameters, which we describe next.

A Poisson regression model was used to analyze the productivity data. The observed number of fledglings (J) assumed a Poisson process with the product of F and the number of territories monitored (T) for fledglings (i.e. the number of full territories within each plot – excluded all territories that extended beyond the boundary of a 40.5-ha plots) in year t, such that $J_t \sim Poisson(T_t F_t)$.

Data are not readily available to estimate time-varying survival probabilities over the time series in which abundance and productivity data were collected on the BCP. Hence, we used age-specific male warbler mean survival probabilities (ϕ) and their associated variances (σ^2_ϕ) that were estimated using long-term capture-resight data from FHMR (adult: $\phi_A = 0.47 \pm 0.02$, $\sigma^2_{\phi-Process,A} = 0.0120$, $\sigma^2_{\phi-Sampling,A} = 0.0113$; juvenile: $\phi_J = 0.28 \pm 0.06$, $\sigma^2_{\phi-Process,J} = 0.0076$, $\sigma^2_{\phi-Sampling,J} = 0.0149$; Duarte *et al.*, 2014) and included this knowledge via informative priors into the integrated population model. Duarte *et al.* (2014) review the protocols used to monitor warblers and provides a detailed description of the data and the methodology used to analyze these capture-resight data.

A random-effects approach was used to model ϕ, F and ω and calculate an overall mean estimate and its associated temporal process variance for each parameter, while accounting for variance associated with the uncertainty in the point estimates due to the sampling process (i.e. sampling variance; Burnham & White, 2002). The model assumed the underlying point estimates are distributed randomly around a central mean over time and these parameters were modeled as follows:

$$logit(\phi_{A,t}) = \beta_0 + \varepsilon_{\phi_{A,t}}, \text{ with } \varepsilon_{\phi_{A,t}} \sim N\left(0, \sigma^2_{\phi-Process,A}\right),$$

$$logit(\phi_{J,t}) = \beta_1 + \varepsilon_{\phi_{J,t}}, \text{ with } \varepsilon_{\phi_{J,t}} \sim N\left(0, \sigma^2_{\phi-Process,J}\right),$$

$$log(F_t) = \beta_2 + \varepsilon_{F_t}, \text{ with } \varepsilon_{F_t} \sim N\left(0, \sigma^2_{F-Process}\right),$$

$$log(\omega_t) = \beta_3 + \varepsilon_{\omega_t}, \text{ with } \varepsilon_{\omega_t} \sim N\left(0, \sigma^2_{\omega-Process}\right),$$

where the intercept coefficients (β_0, β_1, β_2, β_3) are the mean values for each parameter and σ^2 are the process variances. Note that the intercept coefficients and the process variances are on transformed scales.

Because we lacked data to estimate annual survival parameters directly in the model, informative priors were used for mean survival of each age class based on the mean and sampling variance estimates from Duarte *et al.* (2014) as outlined earlier using beta distributions. The sampling variance was used as the variance for the prior on mean survival as this estimate represents the uncertainty in the mean. The process variances were fixed to the estimated process variance from Duarte *et al.* (2014). The implementation of the sampling variance follows the methods used by McGowan, Runge & Larson (2011) when incorporating parametric uncertainty to project piping plover *Charadrius melodus* population dynamics.

The joint likelihood of the integrated population model is composed of the likelihood of the state-space model for the count data and that of the Poisson regression model for the productivity data. The model analysis was implemented using JAGS (Plummer, 2003) called from program R (R Core Team, 2013) with package jagsUI (Kellner, 2014) to estimate the parameters. Non-informative prior distributions were used for all parameters, except survival (see Supporting Information Appendix S1). We ran three independent chains consisting of 1 000 000 iterations, following a burn-in of 500 000 iterations, with a thinning rate of 100. The Brooks and Gelman diagnostic ($\hat{R}$) was used to assess convergence (Brooks & Gelman, 1998), and convergence ($\hat{R} < 1.02$) was obtained for all parameter estimates. Model fit was assessed for the productivity data using a posterior predictive check and calculating a Bayesian *P*-value (Kéry, 2010; Link & Barker, 2010). Specifically, we compared the lack of fit of the model when fitted with the actual and hypothetical replicate (i.e. generated using the parameter estimates from the analysis) data, and calculated the proportion of times the discrepancy measure for the replicate dataset was greater than the discrepancy measure for the actual dataset. Posterior distributions of the estimated parameters were described by their mean (or median) and the 95% credible interval (CI).

Modeling the effect of immigration

To quantify the effect of immigration on λ, we used a deterministic pre-breeding census projection model that was based on the structure of the integrated population model. First, we calculated a hypothetical λ in the absence of immigration. Because every element in the projection model included a survival parameter under this scenario (i.e. when we assume no immigration), we could then calculate the survival multiplier by taking the reciprocal of λ (Whiting *et al.*, 2008). The survival multiplier indicates how much higher average adult and juvenile survival would need to be to maintain a stable population while holding the reproductive parameter constant, and assumes an equal survival multiplier for both juvenile and adult survival. Next, we
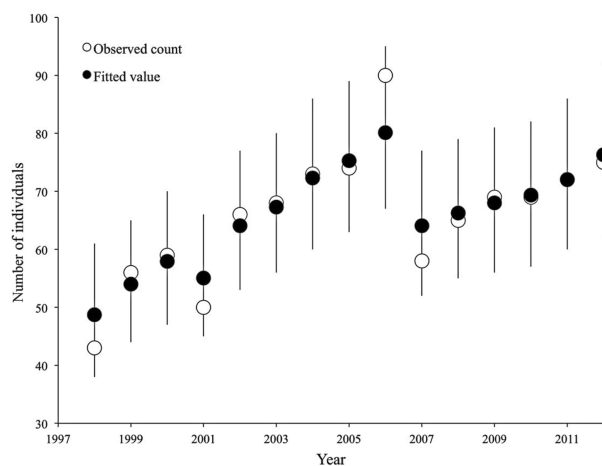
Figure 2 Observed number of territories (open circles) and estimated mean number of territories (solid circles) using a Bayesian state-space model of adult male golden-cheeked warblers *Setophaga chrysoparia* on the Balcones Canyonlands Preserve, Travis County, Texas, USA, 1998–2012. Error bars around fitted values are 95% credible intervals.

assumed adult survival estimates are close to true survival (i.e. adults have high site fidelity) and no immigration occurred and input a range in juvenile survival probabilities (from 0 to 1 in steps of 0.005) to determine which value yielded a stable population (i.e. $\lambda = 1$). Finally, to quantify the response required in fledging rate to maintain a viable population at different levels of immigration, we used a brute-force approach and ran several scenarios with a range in immigration rate (from 0 to 1 in steps of 0.005) and fledging rate (from 0 to 5 in steps of 0.005) to determine which scenarios yielded an approximate stable population (i.e. $\lambda = 0.9, 0.95, 1, 1.05$ or 1.1). This process follows the methods used by Schaub *et al.* (2010) when investigating the relationship between immigration and mortality reduction for an eagle owl *Bubo bubo* population.

Results

Over 15 years, the estimated number of territorial male warblers fluctuated between 48.7 (CI: 38–61, in 1998) and 80.1 (CI: 67–95, in 2006) on a 202.5-ha area (Fig. 2). Although annual estimates of λ were variable, the mean λ was 1.04 (CI: 1.02–1.07), signifying an overall slightly increasing population trend. The mean immigration rate estimate was 0.33 (CI: 0.04–0.62), indicating that about one territorial male will enter the population in year $t + 1$ for every three territorial males present in year t. This implies *c*. 16–27 individuals immigrated into the population each year over the time series. The goodness-of-fit test suggested that the fitted model was adequate for the productivity data (Bayesian *P*-value = 0.55). Estimates of mean/median vital rates and their associated process variances are reported in Table 1. For annual point estimates of demographic parameters see Supporting Information Appendix S2.

Table 1 Estimates of vital rates and their associated process variances for golden-cheeked warblers *Setophaga chrysoparia*. Values in parentheses are the 95% credible intervals

Parameter	Mean/median (β)	Process variance (σ^2)
Immigration rate (ω)	0.33 (0.04, 0.62)	0.0314
Fledging rate (F)	1.42 (1.18, 1.69)	0.2415
Juvenile survival (ϕ_J)	0.26 (0.07, 0.52)	0.0076*
Adult survival (ϕ_A)	0.52 (0.29, 0.73)	0.0120*

*Signifies process variance estimates that were calculated using capture-resight data in a different study.
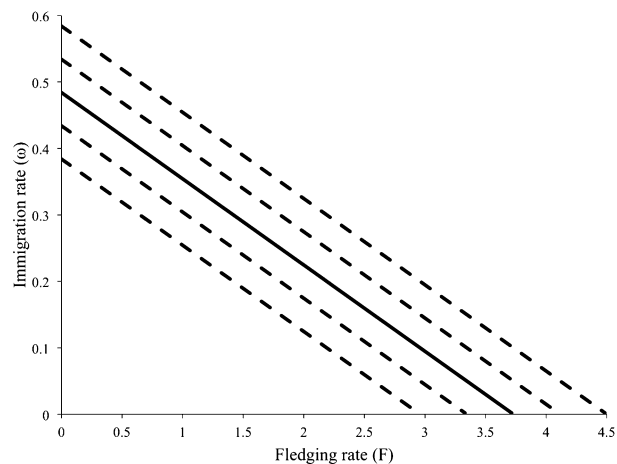
Figure 3 Relationship between fledging rate, immigration rate and population growth rate for golden-cheeked warblers *Setophaga chrysoparia*. The solid line represents a stable population ($\lambda = 1$) and the broken lines from top to bottom represent $\lambda = 1.10, 1.05, 0.95$ and 0.90. Estimates were derived using a deterministic projection model.

In the absence of immigration and with all other vital rates remaining constant, λ would have decreased to 0.70 (CI: 0.42–0.98). Thus, we examined the response required by vital rates to maintain a stable population across varying levels of immigration. The survival multiplier was 1.43, indicating that in the absence of immigration the population could remain stable if both juvenile and adult survival increased by 43%. However, if we assume the adult survival estimate is (or is close to) true survival and only allow juvenile survival to fluctuate, juvenile survival must increase to 0.685 to maintain a stable population. We also examined the relationship between immigration and fledging rates, while holding survival parameters constant (Fig. 3). Notably, a stable population can be achieved with a mean immigration rate of *c*. 0.30 or a mean fledging rate of *c*. 1.21, while holding all other parameters constant.

Discussion

Using a Bayesian integrated population model, we combined limited, but long-term, data and prior information to gain a better understanding of golden-cheeked warbler

population dynamics. The warblers on the 'prime' habitat plots within the BCP varied in overall abundance with a positive trend across the time series. We estimated the first movement parameter for the species in the form of immigration. Notably, because we modeled total immigration, the estimated immigration parameter in our study is comprised of both natal and breeding dispersers returning from wintering grounds to establish breeding territories. Our results indicate that movement rates were high and that immigration was indeed driving local warbler population dynamics.

The overall increasing population trend across the time series is in concert with long-term point count data collected on FHMR (Peak, 2011). Why such patterns in territory densities have occurred on these two properties is unclear. City of Austin (2007) postulated the overall increasing territory density on the BCP might be directly related to the loss of warbler breeding habitat in the surrounding area, causing the ingress of individuals to exceed the number of individuals egressing from the population as available habitat becomes limited. This certainly is a plausible explanation for the increase in territory densities on both BCP and FHMR. Warbler habitat within these regions has undergone dramatic loss and fragmentation in the last decade (Duarte *et al.*, 2013). However, such an increase on BCP might also be linked to the apparent increase in annual warbler productivity (see Supporting Information Appendix S2). There was a sudden decline in territory density in 2007 (Fig. 2). Again, such a pattern could be related to an assortment of reasons. It is worth noting that it is not likely due to observer bias or a reduction in the quality of the survey procedures. When analyzing a subset of the data from BCP (that included 2007), Weckerly & Ott (2008) did not detect an influence of observer bias on annual territory counts and determined that the number of surveys conducted was adequate to detect all territorial males each year. Therefore, the sudden decline in territory density is likely related to natural or anthropogenic induced year-to-year variability in vital rates and/or negative density-dependent feedbacks. Unfortunately, robust data to test these predictions are lacking.

In the absence of immigration, warbler abundance would have declined. Although this suggests immigration is required for local persistence of warbler populations, this does not necessarily indicate the population is a sink. The apparent survival parameters are low, suggesting that a large number of individuals from this area emigrate and serve as immigrants in other areas. Although the study population depends on immigrants, it also exports individuals, and thus has characteristics of a source population. The significant permanent emigration out of a roughly 200-ha area should not be too surprising given the large number of occupied habitat patches with a high density of warblers across the breeding range (Collier *et al.*, 2012; Mathewson *et al.*, 2012) and the inherent long-distance dispersal capabilities of migratory songbirds. Moreover, the data and prior information used in our analysis were collected on properties that actively manage

for the species through habitat-enhancement and nest predator-removal programs. Finally, central to defining source and sink populations is the ability to accurately distinguish a biological population or subpopulation, something that has yet to be performed for the species because there is little genetic differentiation across its breeding range (Lindsay *et al.*, 2008). Collectively, this indicates that the importance of immigration to this population is related to the spatial scale at which warblers are currently being monitored. In other words, the spatial scale of the target population (i.e. the population within the study plots) is not biologically relevant for the species (see Morrison, 2012). Therefore, spatially structured monitoring data are needed to identify if warbler conservation and management programs should occur at the site, regional, or perhaps even the range-wide scale to be effective.

It is difficult to say the distance over which inter-annual warbler movement occurs. In the past decade, no movement between plots has been documented and only two adult male birds were ever resighted off a plot on FHMR (R. Peak, pers. comm.). These birds were found immediately outside the plot where they were banded in the previous year. An outcome of a recent increase in warbler monitoring efforts on the BCP, a collaborative effort between the City of Austin and US Forest Service, is the documentation of movement distances ranging 1.2–16.0 km by male individuals banded as second-year birds (City of Austin, 2012). Still, of the birds that were documented to return to the area, 94% established territories in close proximity to where the individuals established a territory in the previous year (City of Austin, 2012). Consequently, the current paradigm is that adult male warblers return to the same territory, or at least within close proximity, year after year. Given the current reports of adult warbler movement distances and that warbler habitat is available surrounding the boundaries of the plots monitored for this study, it is probable that some of the immigrants were short-distance breeding dispersers. However, long-distance, inter-annual movement has been reported in a number of songbird species (Tittler, Villard & Fahrig, 2009). Therefore, it is also possible that our results are further indicating that distance between habitat patches is not a limiting factor for the species given the current spatial pattern of its breeding habitat and the dispersal capabilities of the species.

Immigration was modeled as a rate parameter within the integrated population model and therefore was a function of the number of adult territorial males the previous year. This is simply a statistical parameterization to derive an estimate of immigration and we are not suggesting that these two parameters (i.e. immigration and population size the previous year) are necessarily biologically linked to each other. Notably, we could have also directly estimated the number of immigrants each year (Szostek, Schaub & Becker, 2014). We preferred to model immigration as a rate, rather than the total number of immigrants, because it can be directly incorporated within projection models in a straightforward way (e.g. Cooch, Rockwell & Brault, 2001). Schaub & Fletcher (2015) ran simulations with similar sample sizes

and data structures as we had for this study and found that immigration as a rate parameter was reliably estimated when immigration was high (such is the case for the data analyzed herein). Moreover, they showed that immigration estimates are nearly identical regardless of whether they are specified as a number or as a rate.

There was a lack of data to estimate warbler survival parameters directly in the integrated population model. Hence, we took advantage of the ability to use informative priors in Bayesian analyses to estimate an overall mean survival for each age class, while incorporating the uncertainty associated with the estimates and allowing for temporal variation. However, the need for informative priors limited what we could examine using the data. For example, when having the data to estimate survival parameters directly in the model, one could examine factors that influence survival or immigration (Abadi *et al.*, 2010*b*; Brown & Collopy, 2013; Altwegg, Jenkins & Abadi, 2014) and test for density-dependent feedbacks on vital rates (Abadi *et al.*, 2012). Thus, the use of data to directly estimate warbler survival parameters in the model should not be discounted in future analyses, if possible.

We estimated the survival probabilities required to maintain a viable warbler population in the absence of immigration. The estimated survival multiplier (1.43), which indicates how much higher average adult and juvenile survival would need to be to maintain a stable warbler population, suggested juvenile and adult survival would need to increase to 0.37 and 0.73, respectively. Again, this technique assumes the magnitude of change in survival probabilities is the same for both age classes. If we assume the current estimate for adult survival is close to true survival (i.e. adults have high site fidelity – a current hypothesis for the species) and only allow juvenile survival to vary, juvenile survival must be *c.* 0.685 in the absence of immigration to maintain a stable population. Current juvenile warbler apparent survival estimates range 0.28–0.30 (USFWS, 1996*b*; Alldredge *et al.*, 2004; Duarte *et al.*, 2014). This needed level of juvenile survival for population viability in the absence of immigration is unrealistically high and further implies adult male birds may also participate in inter-annual movement causing adult apparent-survival estimates to be lower than true survival. Both of these approaches assume fledging rates remain unchanged and immigration into the population does not occur. Other scenarios are certainly plausible, and therefore, the survival estimates derived under these scenarios (i.e. survival estimates when modeling the effect of immigration) should be used with caution.

We focused on the relationship between fledging and immigration rates using a deterministic projection model (Fig. 3) because effects of breeding habitat on annual mortality (and by extension, population dynamics) are not especially likely given the relatively small proportion of time warblers spend in the breeding range (i.e. warblers migrate to their breeding range in March and migrate back down to their wintering range in July). Therefore, managing for specific annual survival probabilities in the breeding range

alone might not be effective. Conversely, fledging rates can be managed on the breeding grounds through nest-parasite and predator-removal programs and habitat management, and immigration might be directly related to the proximity of the surrounding habitat patches. Our results indicate that if immigration does not occur, fledging rate must be *c.* 3.715 to maintain a stable population. The mean number of fledglings per successful territory is 3.6 (95% confidence interval: 3.3–3.8; Reidy, Stake & Thompson, 2008). Thus, an average fledging rate of 3.715 across all territories (i.e. both successful and unsuccessful territories) is not likely to be biologically possible. Our results also indicated a stable population could be achieved with an immigration rate of 0.485 and fledging rate of zero. Although neither scenario is likely to occur in a natural system, looking at these extremes gives a better understanding of the dynamics of this warbler population.

Of particular importance with regard to the reliability of these estimates is whether assumptions of the analysis are met. For integrated population models, the datasets used in the model (i.e. abundance, survival and productivity data) are assumed to be independent from each other. The two datasets used here did violate this assumption because the surveys for territorial males and fledglings were conducted within the same plots. However, Abadi *et al.* (2010*a*) and Schaub & Fletcher (2015) showed through simulations that this violation has minimal effects on parameter estimates and their precision. The information about survival stems from another study clearly fulfilling the independence assumption. Yet, the satisfaction of the independence assumption comes at the price of another assumption, namely that survival from FHMR is representative of survival from BCP. The latter assumption is likely to be fulfilled as well, given that both study sites are close in proximity, the adult bird data for each study cover similar time spans, and each property manages for the species using similar protocols. Furthermore, the choice of the observation model distribution used in state-space models can substantially affect parameter estimates (Knape, Jonzén & Sköld, 2011). In preliminary analyses, however, we found no evidence of a strong effect on parameter estimates when using these data with various distributions (i.e. Poisson, normal and lognormal distributions), a finding similar to what was discussed by Kéry & Schaub (2012). We chose a Poisson distribution to model our count data because this distribution implies that the observer error in the count data increases as abundance increases. We felt this relationship was a reasonable assumption for the potential survey error when using spot-mapping data, which is further supported by the agreement in the observed counts and the fitted values (Fig. 2).

The deterministic projection model we used to examine the effect of varying levels of immigration assumed every territory successfully fledged young. This assumption can be relaxed because the fledging-rate estimate was calculated as the number of fledglings per territory, regardless of whether the territory successfully fledged young (i.e. the estimate was calculated using data from both successful and unsuccessful

territories). Furthermore, the difficulty associated with searching for fledglings means the estimate is probably biased low. The degree to which the fledging-rate estimate is biased low is difficult to quantify. We estimated a mean fledging rate of 1.42 (95% CI: 1.18–1.69) fledglings per territory. Groce *et al.* (2010) summarized productivity data from FHMR and Travis County. They reported the number of fledglings per territory ranged 1.13–2.06 on FHMR from 1991 to 1999 and 0.99–1.74 on Travis County properties from 2001 to 2008. Thus, our fledging-rate estimate is comparable with that of other studies for the species. However, these properties monitor for fledglings in the same manner and therefore suffer from the same potential bias. It is worth noting that if the probability of detecting a fledgling is substantially low then the fledging-rate estimate will also be biased low. By extension, this will lead to the immigration estimate being biased high and the results when modeling the effect of varying levels of immigration on population dynamics will be altered. Thus, studies that account for imperfect detection when surveying for fledglings are a fruitful area of further warbler research.

Conservation implications

We demonstrate that biologists can monitor abundance, productivity, survival and immigration simultaneously for golden-cheeked warbler populations via integrated population models. Our results indicate immigration was indeed required to maintain viable warbler populations at the local spatial scale, suggesting that conservation and management programs need to be implemented at a larger spatial scale than current efforts to be effective. Furthermore, we explored the response required by vital rates that can be used as a rule of thumb to maintain a stable local warbler population at various levels of immigration. Such information is imperative to gauge the efficacy of conservation and management strategies designed to maximize warbler viability in a changing landscape.

Acknowledgments

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1 This JAGS code is the Bayesian integrated population model that was used to estimate annual golden-cheeked warbler *Setophaga chrysoparia* fledgling rate, immigration rate, survival probability and abundance.

Appendix S2 Annual point estimates of fledging rate, immigration rate, survival probability and population growth rate for golden-cheeked warblers *Setophaga chrysoparia* on the Balcones Canyonlands Preserve, Travis County, Texas, USA, 1998–2012. Estimates were calculated using a Bayesian integrated population model. Error bars are the 95% credible intervals and the gray dotted lines are the mean/median estimate across all years.