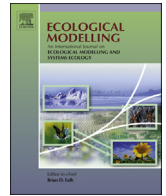Simulating range-wide population and breeding habitat dynamics for an endangered woodland warbler in the face of uncertainty

Simulating range-wide population and breeding habitat dynamics for an endangered woodland warbler in the face of uncertainty

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ABSTRACT

Population viability analyses provide a quantitative approach that seeks to predict the possible future status of a species of interest under different scenarios and, therefore, can be important components of large-scale species' conservation programs. We created a model and simulated range-wide population and breeding habitat dynamics for an endangered woodland warbler, the golden-cheeked warbler (*Setophaga chrysoparia*). Habitat-transition probabilities were estimated across the warbler's breeding range by combining National Land Cover Database imagery with multistate modeling. Using these estimates, along with recently published demographic estimates, we examined if the species can remain viable into the future given the current conditions. Lastly, we evaluated if protecting a greater amount of habitat would increase the number of warblers that can be supported in the future by systematically increasing the amount of protected habitat and comparing the estimated terminal carrying capacity at the end of 50 years of simulated habitat change. The estimated habitat-transition probabilities supported the hypothesis that habitat transitions are unidirectional, whereby habitat is more likely to diminish than regenerate. The model results indicated population viability could be achieved under current conditions, depending on dispersal. However, there is considerable uncertainty associated with the population projections due to parametric uncertainty. Model results suggested that increasing the amount of protected lands would have a substantial impact on terminal carrying capacities at the end of a 50-year simulation. Notably, this study identifies the need for collecting the data required to estimate demographic parameters in relation to changes in habitat metrics and population density in multiple regions, and highlights the importance of establishing a common definition of what constitutes protected habitat, what management goals are suitable within those protected areas, and a standard operating procedure to identify areas of priority for habitat conservation efforts. Therefore, we suggest future efforts focus on these aspects of golden-cheeked warbler conservation and ecology.

1. Introduction

Population viability analyses (PVAs) can be important components of large-scale species' conservation programs (Caswell, 2001; Beissinger and McCullough, 2002; Morris and Doak, 2002; Akçakaya et al., 2004). Such models provide a quantitative approach through computer modeling to predict the possible future status of a species of interest under different environmental and management scenarios. The precision and bias of a PVA are directly related to the precision and bias of demographic parameter estimates (and the parameters of the functional relationships that govern these parameters), our understanding of the population structure of the species of interest, and the available information on the extent, configuration, and temporal dynamics of the species' habitat. Therefore, the structure and parameters of such models must be updated periodically with inferences from recent and on-going research to remain relevant and make meaningful contributions to conservation efforts.

The golden-cheeked warbler (*Setophaga chrysoparia*; hereafter warbler) is a Neotropical migrant passerine that is a habitat specialist, breeding exclusively in the mature mixed woodlands of central Texas, USA that are comprised primarily of oak (*Quercus*
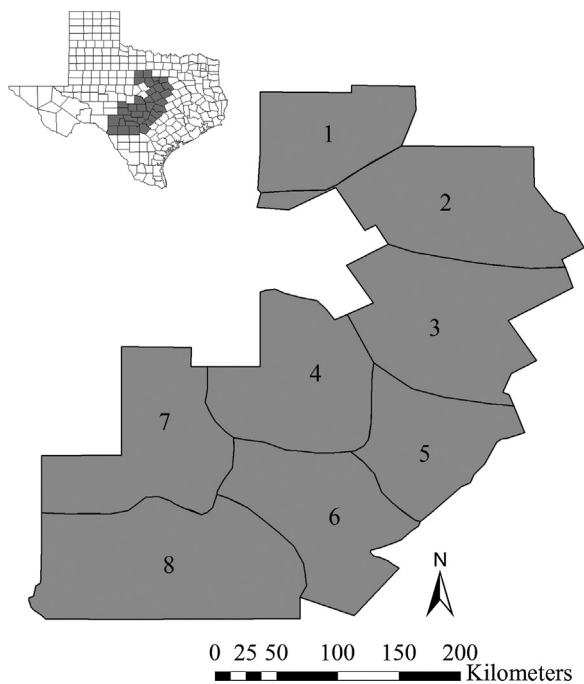
Fig. 1. Golden-cheeked warbler (*Setophaga chrysoparia*) breeding range and federally-designated recovery units in Texas, USA.

spp.) and Ashe juniper (*Juniperus ashei*; Pulich, 1976). Perceived loss of warbler breeding habitat and the species' limited breeding range ultimately led to the warbler being listed as endangered by U.S. Fish and Wildlife Service (USFWS) in 1990 (USFWS, 1990; Wahl et al., 1990). Shortly afterwards, USFWS developed a recovery plan that listed specific goals and objectives needed to achieve the downlisting of the species (USFWS, 1992). In that plan, eight regions were delineated across the species' breeding range to manage the recovery process (Fig. 1), and one of the objectives set by this plan was to protect sufficient breeding habitat "to ensure the continued existence of at least one viable, self-sustaining population in each of eight regions." (USFWS, 1992:iv).

As with many other species of concern, PVAs are currently being used in large-scale warbler conservation programs (reviewed in Hatfield et al., 2012). Previous warbler PVAs estimated the minimum amount of protected habitat required to meet the recovery objectives (USFWS, 1996), assessed the importance of dispersal among habitat patches (Alldredge et al., 2004), and simulated potential land change scenarios to examine their impact on projected population dynamics (Vaillant et al., 2004; Horne et al., 2011). Each of these models provided direction toward fruitful areas of further study, but each was also hampered by the paucity of information then available concerning warbler demography, distribution, abundance, dispersal, and habitat change.

In recent years, much effort has been expended to update our knowledge on these information gaps. Current research suggests the warbler is relatively abundant (Mathewson et al., 2012), widely distributed (Collier et al., 2012), has little genetic differentiation across its breeding range (Lindsay et al., 2008), and has high movement rates among habitat patches (Duarte et al., 2015). Despite the seemingly positive outlook for warbler conservation, large-scale habitat loss and fragmentation have continued to occur across the species' breeding range (Duarte et al., 2013), and survival of adult warblers may actually be 16% lower than what was previously reported (Duarte et al., 2014).

We simulated range-wide warbler population and breeding habitat dynamics. There were three primary objectives for this study. First, we estimated habitat-transition probabilities across

the warbler's breeding range. To accomplish this objective, we combined National Land Cover Database (NLCD) imagery with multistate modeling to estimate habitat-transition probabilities. Given current land-cover-change estimates reported by Duarte et al. (2013), we hypothesized that recovery units five, six, and eight would have the highest rates of habitat loss. It likely takes many decades for Ashe juniper to mature sufficiently to become warbler breeding habitat (J. S. Hatfield, *unpublished data*). Thus, we also hypothesized that habitat transitions will be unidirectional, whereby it will be more likely for an area to undergo habitat loss than habitat regeneration. Second, we wanted to simulate warbler population dynamics in response to habitat change and a range in estimates of vital rates to examine if warbler viability is possible given the current knowledge of the species and its breeding habitat. Here, we also assessed various scenarios with differing levels of dispersal since this parameter has yet to be estimated for warblers. Lastly, we evaluated if protecting a greater amount of habitat would increase the number of warblers that can be supported in the future. This last objective seems somewhat intuitive. A greater amount of protected habitat should lead to a higher carrying capacity (K). This might not be the case, however, if the amount of protected habitat is relatively small compared to the total available habitat. To achieve this objective, we systematically increased the amount of protected habitat at the onset of the simulation and compared the estimated terminal K for each recovery unit at the end of 50 years of simulated habitat change.

It is important to point out the distinctions between our modeling approach and the others carried out to simulate warbler population dynamics because our approach is unlike the previous warbler PVAs in several aspects. First, we used a pre-breeding census projection model as opposed to a post-breeding census model, although this should have no effect so long as all models were parameterized correctly. A pre-breeding census model was used because the number of adult territorial males is often the population abundance estimate that is accessible in warbler conservation efforts because of the territorial nature of the species. Second, we integrated a stochastic habitat change component into our model based on real-world data using a novel method to estimate landscape change. Previous warbler population models that incorporated habitat change relied on deterministic changes based on perceived probable scenarios. Third, we simulated warbler population dynamics assuming the entire breeding range consisted of one large population. This population structure was used because current research indicates warblers are a single population distributed patchily across the landscape, rather than a collection of subpopulations with infrequent dispersal events (i.e., a metapopulation; reviewed in Morrison et al., 2012). Many of the previous warbler PVAs (e.g., Alldredge et al., 2004; Vaillant et al., 2004; Horne et al., 2011) presumed a metapopulation structure. However, we note that the difference (i.e., modeling a metapopulation versus a single population) when compared to Alldredge et al. (2004) is primarily based on terminology rather than model structure, given their model did not incorporate a natal-site dispersal-distance limitation and they considered relatively high dispersal probabilities. Fourth, we incorporated dispersers into the model differently. For example, in previous models the dispersers were second-year birds that survived, returned to the habitat patch they hatched in, and then dispersed. In our model, dispersers were sampled from birds that would have been in their second year but did not return to their natal site from the previous year. Dispersers were calculated using these individuals because survival estimates for the species represent apparent, not true, survival. Thus, the survival estimates for the species are the probability an individual survives and returns to the area. By modeling dispersal this way, we were able to directly use the survival estimates for the species within the model, rather than inflating juvenile survival estimates to accommodate

dispersal. Fourth, to create a more realistic model we simulated the entire breeding range simultaneously and always included habitat outside of what we considered protected. Thus, individuals were allowed to disperse among protected and unprotected habitat patches in every scenario. Lastly, we incorporated parametric uncertainty into a subset of scenarios to gauge the uncertainty present in our model results based on the available demographic parameter estimates.

2. Methods

2.1. Habitat transitions

Although change metrics for breeding habitat have recently been estimated for the species using a post-classification change detection approach (e.g., Duarte et al., 2013), using those estimates in population models is problematic because not all changes in habitat will have a substantial impact on warbler population dynamics (i.e., at the spatial scale of a 30 m^2 pixel), and it would be ideal to incorporate stochasticity into the habitat component of the model. Therefore, we estimated habitat change using a different approach for this study. Habitat delineations were based on the 2001 (2011 edition), 2006 (2011 edition), and 2011 NLCD (Homer et al., 2007; Fry et al., 2011; Jin et al., 2013). The NLCD provides categorical land-cover classification derived from Landsat multispectral datasets. Only one NLCD land cover category was of interest: Forest. This category is subdivided into Deciduous Forest, Evergreen Forest, and Mixed Forest. A Forest pixel is any pixel that contains at least 20% total vegetation cover (i.e., canopy cover) that is greater than five meters tall. Notably, this classification system can accurately differentiate Forest from Shrubland (a similar NLCD category that is separated by vegetation height) within the warbler's breeding range (Jensen et al., 2013). Similar to Duarte et al. (2013), habitat was classified as any Evergreen Forest or Mixed Forest pixel as well as any Deciduous Forest pixel that was within 90 m of an Evergreen Forest or Mixed Forest pixel. This habitat classification scheme has been shown to do well when compared to warbler detection/non-detection surveys (N. Heger, *personal communication*).

Habitat-transition probabilities (ψ^{rs}, where r and s denote habitat states) were estimated by fitting multistate models using the habitat data derived from NLCD (Hotaling et al., 2009; Breininger et al., 2010). This innovative approach uses maximum-likelihood methods, which are traditionally coupled with animal capture-recapture/resight encounter data, to estimate habitat-transition probabilities from site-history data. One advantage of using this approach is that the estimates can be used to project habitat dynamics into the future (e.g., Johnson et al., 2011). We wanted our habitat transitions to be meaningful to the species and compatible with current warbler vital-rate estimates. Warbler occupancy of habitat patches is impacted by the amount of habitat up to 200 ha surrounding a point of interest (Magness et al., 2006). Further, current survival parameters are estimated using data collected on plots that are approximately 200 ha in area (Duarte et al., 2014). Therefore, a 200-ha hexagon tessellation that covered the entire warbler breeding range was created, resulting in 34,690 hexagons. The amount of habitat in each hexagon during each time step was calculated, and hexagons were separated into four states based on the proportion of area covered by habitat. A hexagon was classified as high habitat (H) if it was ≥70% habitat, medium habitat (M) if it was ≥40% habitat, low habitat (L) if it was ≥10% habitat, and non-habitat (N) if it was <10% habitat. Hexagons classified as state N were assumed to contain no, or a negligible amount of, habitat because warblers need approximately 15 to 20 ha of habitat to successfully fledge young (Butcher et al., 2010). We considered two models: the first assumed habitat transitions were

similar among recovery units, and the second examined recovery-unit-specific habitat-transition probabilities. Program MARK was used to fit the multistate models (White and Burnham, 1999). Survival and detection probabilities were fixed at 1.0 since all states were observed on each occasion and all hexagons remained in the study. Habitat-transition probabilities were estimated at five-year intervals to match the five year temporal sampling of NLCD images, and for computational efficiency when projecting habitat dynamics within the model. Since we were interested in estimating the average habitat-transition probability over the time series, transition probabilities were modeled as a constant over time. When a transition did not occur in the data, transition parameters were fixed at 0.0 to circumvent numerical estimation problems.

2.2. Projection model

A male-based pre-breeding census projection model was used to simulate range-wide warbler population dynamics. The model is based on the male segment of the species because demographic estimates are available only for males. The model assumes the dynamics of females are similar to those of males, all habitat patches were occupied at the initial starting point of the model, all adult males establish territories, all territories are capable of producing fledglings, and males will only mate with a single female. The latter assumption can be relaxed because productivity data incorporate territories where double brooding may have occurred (see Section 2.3). Lastly, effects of the wintering range on warbler population dynamics were not incorporated within the model with the exception of annual survival. Therefore, the model assumes habitat availability in the warbler's wintering range is not a limiting factor. The model was programed using Python to access preprogramed tools in ArcGIS 10.2 and the scipy and numpy packages (Oliphant, 2007; Environmental Systems Research Institute, 2011). The 200-ha hexagon tessellation created to estimate habitat-transition probabilities was the base structure within the model. Birds within each hexagon were modeled separately, however, individuals were allowed to disperse among hexagons.

The model is initialized using initial abundance and K for each hexagon based on the 2011 habitat classifications described in the previous section, and the region specific mean and upper 95% confidence interval (CI) density estimates reported by Mathewson et al. (2012), respectively. These mean density estimates were used for the initial abundances because these are the most up-to-date density estimates from range-wide surveys for the species. Furthermore, we used the upper 95% CI to represent K because these are some of the highest density estimates reported for the species, and we wanted the K's in the simulations to be biologically realistic. Generalizations were made concerning the amount of habitat within each hexagon in that the midpoint estimate of percent habitat per habitat state was used in the calculations. That is the model assumed a hexagon in state H had 170 ha of habitat (i.e., 85% of 200 ha), a hexagon in state M had 110 ha of habitat (i.e., 55% of 200 ha), a hexagon in state L had 50 ha of habitat (i.e., 25% of 200 ha), and a hexagon in state N had 0 ha of habitat. The number of fledglings in year zero was calculated using the methods described below.

After initialization, the model proceeds by sampling vital rates, simulating population and habitat dynamics, and allowing for dispersal events. For each hexagon, both adult and juvenile survival parameters were sampled from beta distributions and productivity was sampled from a lognormal distribution using the mean and process variance estimates found in the literature (described in the subsequent section). In doing so, vital rates were allowed to vary among hexagons and over time, which captures the spatial and temporal stochasticity observed in a real system. All hexagons shared the same overall mean (and variance) vital rates. Population

dynamics were simulated using binomial and Poisson processes to incorporate demographic stochasticity (Morris and Doak, 2002). The number of adults and fledglings that survived from the previous year was estimated by sampling from binomial distributions with a probability of success equal to the selected survival parameters. Emigrants from each hexagon were estimated using the fledgling birds from the previous year that were "lost" (including both death and emigration) from the hexagon and sampling from a binomial distribution with the probability of success equal to the specified dispersal probability. Therefore, dispersal for this model is defined as the probability a fledgling that did not return from the previous year emigrated to a different hexagon, rather than died. Again, emigrants were estimated using these individuals because survival estimates for the species reflect the probability an individual remains alive and returns to a hexagon from one year to the next, and emigrants are a portion of what did not return. Since emigrants were fledglings the previous year, the dispersal probability represents only natal-site dispersal events. Also, it should be noted that inputting a higher dispersal probability means the underlying survival probabilities of juveniles will have a concomitant increase given the way dispersal was programed. The model incorporated a ceiling type density dependence (Morris and Doak, 2002). Thus, abundances in each hexagon were allowed to fluctuate in the absence of density dependence until the number of adults exceeded K. In the event the number of adults overshoots K within a hexagon, the excess individuals also disperse from the hexagon. These individuals represent possible breeding-site dispersal. The number of emigrants, both natal and breeding-site dispersers, from each hexagon were summed. To simulate dispersal, all hexagons that had available space (i.e., hexagons with fewer adults than K) were identified and the model randomly selected these hexagons (with replacement) to accept an immigrant. The number of selected hexagons was equal to the total number of emigrants. In some cases a hexagon received enough immigrants to overshoot K. When this occurred the excess individuals were allowed to disperse up to two more times. The hexagons that had available space were reevaluated before each dispersal event. If after three dispersal events there were hexagons that had a greater number of adult birds than they could support, the excess individuals died (i.e., the abundances were truncated to K). The number of fledglings in each hexagon was estimated by sampling from a Poisson distribution centered on the product of the number of adults, productivity, and 0.5. Thus, the model assumed an equal sex ratio for fledglings.

Habitat transitions occurred every five years. To simulate habitat change, the model randomly selects a habitat state using the habitat-transition probabilities for the recovery unit in which that hexagon resides. After habitat transitions occurred, the K for each hexagon was recalculated (again, based on the upper 95% CI density estimates reported by Mathewson et al., 2012 and the amount of habitat within each hexagon). Only hexagons on non-protected lands were allowed to transition to an alternate habitat state. The model assumed the amount of habitat on protected lands would not diminish and that natural catastrophes on protected lands did not occur.

2.3. Survival, productivity, and dispersal

To date, most of the warbler survival parameters have been estimated from capture-resight data collected on the Fort Hood Military Reservation (FHMR). U.S. Fish and Wildlife Service (1996) analyzed capture-resight data collected within a single study plot on FHMR from 1991 to 1995, and reported a mean adult survival estimate at 0.57 with a process variance of 0.0119. Alldredge et al. (2004) reported a mean adult survival at 0.56 ($\pm$0.04) with a process variance of 0.007 when analyzing capture-resight data collected from 1997 to 2001 on the identical study plot. More recently,

Duarte et al. (2014) reported a mean adult survival estimate at 0.47 ($\pm$0.02) with a process variance of 0.0120 and sampling variance of 0.0113 when analyzing capture-resight data collected from 1992 to 2011 within seven study plots on FHMR that were monitored for variable numbers of years. In all three of these studies, juvenile survival probabilities were estimated using capture-resight data collected within the identical study plot on FHMR with overlapping time intervals. As expected, the mean juvenile survival did not change substantially. U.S. Fish and Wildlife Service (1996) estimated a mean juvenile survival at 0.30 from 1991 to 1995, Alldredge et al. (2004) estimated a mean juvenile survival at 0.30 ($\pm$0.11) with a process variance of 0.058 from 1997 to 2001, and Duarte et al. (2014) estimated a mean juvenile survival at 0.28 ($\pm$0.06) with a process variance of 0.0076 and a sampling variance of 0.0149 from 1992 to 2000. U.S. Fish and Wildlife Service (1996) also analyzed capture-resight data collected on Balcones Canyonlands National Wildlife Refuge (BCNWR) from 1992 to 1994 and in Kendall County from 1961 to 1964. Adult warbler survival on BCNWR was estimated at 0.61, and adult and juvenile warbler survival from Kendall County was estimated at 0.69 and 0.42, respectively. Unfortunately, process variance could not be estimated using these data, and the quality of the data has been questioned (USFWS, 1996).

A number of studies have assessed warbler productivity. Productivity is often reported as the number of fledglings per successful territory (i.e., a territory that had at least one fledgling) or the number of fledglings per territory (i.e., territories that were both successful and unsuccessful). Groce et al. (2010) summarized productivity data from several sites. They reported the number of fledglings per territory ranged 1.13 to 2.06 on FHMR from 1991 to 1999, 0.99 to 1.74 on Travis County properties from 2001 to 2008, and 0.93 to 1.68 on City of Austin properties from 1998 to 2008. They also reported the number of fledglings per successful territory ranged 1.03 to 2.29 on FHMR from 2001 to 2008, 1.86 to 2.87 on BCNWR from 1993 to 1997, and 2.29 to 2.79 on Barton Creek Habitat Preserve from 1996 to 1997. Reidy et al. (2008) studied warbler nesting ecology at FHMR and Balcones Canyonlands Preserve (BCP) in 2005, 2006, and 2008 with the assistance of video surveillance on nests. They reported the number of fledglings per successful territory at 3.6 (95% CI: 3.4–3.8) on FHMR and 3.6 (95% CI: 3.3–3.8) on BCP. Marshall et al. (2013) examined warbler nesting ecology on FHMR from 2009 to 2010 and reported the number of fledglings per successful territory at 1.9 $\pm$ 0.1 and 2.1 $\pm$ 0.1 in Texas oak (*Quercus buckleyi*) habitat and 2.0 $\pm$ 0.2 and 2.1 $\pm$ 0.1 in post oak (*Quercus stellata*) habitat. Duarte et al. (2015) analyzed survey data collected on BCP from 1998 to 2012 and estimated the number of fledglings per territory at 1.42 (95% Credible Interval: 1.18–1.69) with a process variance of 0.2415.

Little is known concerning inter-annual warbler movement events. In the past decade, only two banded adult male warblers were ever documented to disperse outside of a study-plot boundary on FHMR. Still, these individuals were sighted in close proximity to the study plot they were located in the previous year (R. Peak, *personal communication*). Monitoring programs on BCP have documented adult male warblers dispersing 1.2 to 16.0 km (City of Austin, 2012). Nevertheless, 94% of the birds that returned from the previous year displayed high territory site fidelity (City of Austin, 2012). Further, long-term capture-resight data collected on FHMR provided no evidence of transient adult birds (Duarte et al., 2014). Consequently, warbler breeding-site dispersal is assumed to be rare. However, immigration was found to be essential in maintaining the observed warbler population dynamics on BCP (Duarte et al., 2015), breeding habitat is widely distributed across the warbler's breeding range (Diamond et al., 2010; Collier et al., 2012; Duarte et al., 2013), long-distance movements and high dispersal rates are common among migratory birds (reviewed in Haig et al., 2011), and the warbler's breeding range is relatively small (i.e., restricted

Table 1
Productivity (F), juvenile survival (ϕ_J), and adult survival (ϕ_A) estimates and their associated temporal process variances (σ^2) used to simulate golden-cheeked warbler (*Setophaga chrysoparia*) population dynamics under different scenarios.

| | F | | ϕ_J | | ϕ_A | |
Scenario	$\bar{X}$	σ^2	$\bar{X}$	σ^2	$\bar{X}$	σ^2
I	1.42	0.2415	0.28	0.0076	0.47	0.0120
II	2.52	0.2415	0.28	0.0076	0.52	0.0120
III	3.60	0.2415	0.28	0.0076	0.57	0.0120

to central Texas, USA) when compared to the distance traveled during migration. Thus, natal-site dispersal among habitat patches is likely not a limiting factor for the species.

2.4. Model scenarios

We assessed if the range-wide warbler population could achieve a low probability of falling below 5000 individuals (i.e., ≤0.05; hereafter referred to as risk of quasi-extinction) under current conditions of abundance, protected lands, habitat change, and vital-rate estimates. Given the range in vital-rate estimates for the species, there are myriad scenarios we could consider. For simplicity, we restricted the first series of simulations to three scenarios (Table 1). Scenario I represents the lowest estimated mean rates, Scenario III represents the highest estimated mean rates based on quality data, and the rate parameters of Scenario II are intermediate between those of Scenario I and III. We chose to only include the juvenile survival estimates from Duarte et al. (2014) because, as stated earlier, USFWS (1996) and Alldredge et al. (2004) estimated juvenile survival using capture-resight data collected within the identical study plot with overlapping time intervals, the juvenile survival estimates were not statistically different among studies, and Duarte et al. (2014) used the longest time series of data to estimate survival. First, we ran each scenario with a dispersal probability of 0.25. If there was a high risk of quasi-extinction we increased dispersal to 0.55 in increments of 0.10 to assess if a more favorable outcome could be achieved if we assume a greater portion of the fledgling birds that are estimated to have been lost from the site emigrated to sites within the system, rather than died. If there was a low risk of quasi-extinction we decreased dispersal to 0.05 in increments of 0.10 to examine if a low risk of quasi-extinction could be maintained with lower dispersal. In all of these scenarios, habitat within a hexagon was considered protected if greater than 50% of the hexagon intersected 2012 conservation and recreation lands and/or 2010 Department of Defense lands.

We also investigated if increasing the amount of protected habitat at the onset of the simulation would impact the estimated terminal K for each recovery unit after simulating 50 years of habitat change. In particular, we increased the amount of protected habitat in each recovery unit to support approximately 1500, 3000, and 4500 adult male warblers. If protected habitat already exceeded the value within a recovery unit, no change was made. To select hexagons to be converted to protected we began by selecting hexagons in state H and then selected hexagons in state M until the desired K was achieved. See Table 2 for a list of K for protected lands under various scenarios.

Lastly, using two scenarios that indicated a low risk of quasi-extinction could be achieved without population size approaching K (see below) we incorporated the additional uncertainty associated with the fact that adult and juvenile survival parameters are estimated and not known (i.e., we used the sampling variance estimated by Duarte et al., 2014). To do this we followed the recommendations of McGowan et al. (2011). Here, mean survival parameters were selected during the initialization of the model by sampling from a beta distribution using the estimated mean

Table 2
Summary of scenarios for carrying capacity (K) on protected lands used to simulate golden-cheeked warbler (*Setophaga chrysoparia*) habitat dynamics. Estimates of K were based on upper 95% CI of density estimates reported by Mathewson et al. (2012) and the amount of habitat within each hexagon.

| | Protected lands scenario | | | |
Recovery unit	K = original	K = 1500	K = 3000	K = 4500
1	37	1516	3024	4500
2	295	1513	3005	4506
3	5669	–	–	–
4	608	1505	3026	4508
5	4327	–	–	4522
6	2877	–	3033	4515
7	433	1504	3016	4528
8	946	1513	3025	4537
All	15,192	20,424	28,125	37,285

Note: "–" indicates a K that was not modified from the original scenario.

and sampling variance. The selected mean survival parameters and their associated process variances were then used to select hexagon-specific survival parameters in each year, again, by sampling from a beta distribution. Therefore, the mean survival was constant within each simulation but variable among iterations.

For each parameterization, 500, 50-year Monte Carlo (replicate stochastic) simulations were run. The number of adults in each year was summarized annually using the mean, 0.025th percentile, and 0.975th percentile across all iterations.

3. Results

Habitat-transition probabilities varied among recovery units based on a likelihood ratio test ($\chi^2_{40} = 493.13$, $P < 0.001$). Notably, observed habitat transitions always resulted in a reduction of habitat and never to a more favorable habitat state (Table 3). Further, habitat transitions rarely skipped states. For example, if a hexagon in state H transitioned to an alternate state it was more likely to transition to state M than state L or N. The estimated five-year habitat-transition probabilities resulted in a 35.5% decrease in terminal K after the simulated 50 years when using the current protected-lands scenario (Table 4). When increasing the amount of protected lands to support a greater number of warblers at the onset of the simulation there was a substantial increase in the terminal K (Table 4). However, the magnitude of increase in terminal K was dependent on the recovery unit (Table 5).

The warbler population can achieve a low risk of quasi-extinction (i.e., ≤0.05 probability of falling below 5000 individuals) given the current knowledge concerning warbler vital rates and habitat dynamics, depending on dispersal (Table 6). Under Scenario III, the simulations indicated K would limit warbler abundance regardless of the dispersal probability. The same was found for Scenario II when the dispersal probability was at least 0.15. When running Scenario II with a dispersal probability of 0.05 there was only a 0.06 probability of quasi-extinction over the next 50 years. Still, the range-wide expected mean adult warbler population size reduced to 5379 (percentiles: 4923–5870; Table 7). Under the conditions of Scenario I, a low risk of quasi-extinction could be achieved with a dispersal probability of 0.55 (Table 6). In this scenario the range-wide expected mean adult warbler population size reduced to 29,406 (percentiles: 27,990–30,990; Table 7).

Scenario I with a dispersal probability of 0.55 and Scenario II with a dispersal probability of 0.05 indicated range-wide warbler viability could be achieved without population size approaching K. Thus, we also ran these scenarios while incorporating parametric uncertainty in the survival parameters. Under these scenarios, Scenario I risk of quasi-extinction increased to 0.39 with a terminal expected population size of 126,382 (percentiles: 0–291,106) and

Table 3

Golden-cheeked warbler (*Setophaga chrysoparia*) habitat-transition probabilities with SE in parentheses. Probabilities were estimated at five-year intervals for each recovery unit. See text for definitions of habitat transitions.

Transition	Recovery unit							
	1	2	3	4	5	6	7	8
ψ^{HH}	0.61 (0.02)	0.59 (0.03)	0.70 (0.02)	0.59 (0.02)	0.63 (0.02)	0.68 (0.01)	0.58 (0.03)	0.80 (0.01)
ψ^{HM}	0.34 (0.02)	0.41 (0.03)	0.30 (0.02)	0.40 (0.02)	0.35 (0.02)	0.30 (0.01)	0.41 (0.03)	0.20 (0.01)
ψ^{HL}	0.05 (0.01)	<0.01 (–)	<0.01 (–)	0.01 (<0.01)	0.02 (<0.01)	0.02 (<0.01)	0.01 (0.01)	<0.01 (<0.01)
ψ^{HN}	<0.01 (–)	0*	0*	0*	0*	0*	0*	0*
ψ^{MH}	0*	0*	0*	0*	0*	0*	0*	<0.01 (–)
ψ^{MM}	0.82 (0.01)	0.88 (0.01)	0.87 (0.01)	0.82 (0.01)	0.87 (0.01)	0.87 (0.01)	0.88 (0.01)	0.92 (0.01)
ψ^{ML}	0.18 (0.01)	0.12 (0.01)	0.13 (0.01)	0.18 (0.01)	0.13 (0.01)	0.13 (0.01)	0.12 (0.01)	0.08 (0.01)
ψ^{MN}	<0.01 (–)	0*	<0.01 (–)	0*	<0.01 (–)	<0.01 (–)	0*	0*
ψ^{LH}	0*	0*	0*	0*	0*	0*	0*	0*
ψ^{LM}	0*	<0.01 (–)	<0.01 (–)	<0.01 (–)	<0.01 (–)	<0.01 (–)	0*	<0.01 (–)
ψ^{LL}	0.97 (<0.01)	0.98 (<0.01)	0.98 (<0.01)	0.98 (<0.01)	0.98 (<0.01)	0.98 (<0.01)	0.98 (<0.01)	0.99 (<0.01)
ψ^{LN}	0.03 (<0.01)	0.02 (<0.01)	0.02 (<0.01)	0.02 (<0.01)	0.02 (<0.01)	0.02 (<0.01)	0.02 (<0.01)	0.01 (<0.01)
ψ^{NH}	0*	0*	0*	0*	0*	0*	0*	0*
ψ^{NM}	0*	0*	0*	0*	0*	0*	0*	0*
ψ^{NL}	<0.01 (–)	<0.01 (–)	<0.01 (–)	<0.01 (–)	0*	0*	0*	<0.01 (–)
ψ^{NN}	1.00 (–)	1.00 (–)	1.00 (–)	1.00 (–)	1.00 (–)	1.00 (–)	1.00 (–)	1.00 (–)

Notes: "–" indicates a SE that could not be estimated because the parameter estimate was on a boundary.

* indicates a transition probability that was fixed to zero because the transition did not occur in the data.

Table 4

Estimated mean carrying capacity (K) with 2.5th and 97.5th percentiles in parentheses for each golden-cheeked warbler (*Setophaga chrysoparia*) recovery unit after simulating 50 years of habitat change. Estimates of K were based on the upper 95% confidence interval of density estimates reported by Mathewson et al. (2012) and the habitat state of each hexagon.

Unit	Initial K	Protected lands scenario			
		K = original	K = 1500	K = 3000	K = 4500
1	27,600	15,623 (15,233–16,025)	16,584 (16,213–16,957)	17,569 (17,201–17,966)	18,485 (18,096–18,876)
2	31,700	22,328 (21,922–22,731)	23,037 (22,611–23,435)	23,815 (23,403–24,188)	24,459 (24,047–24,823)
3	35,900	26,422 (25,993–26,851)	–	–	–
4	63,200	42,507 (41,964–43,066)	43,099 (42,513–43,639)	44,046 (43,464–44,606)	44,962 (44,347–45,579)
5	47,100	30,101 (29,527–30,655)	–	–	30,214 (29,700–30,786)
6	76,500	49,353 (48,612–50,063)	–	49,449 (48,702–50,184)	50,294 (49,501–51,055)
7	48,900	33,925 (33,151–34,680)	34,530 (33,759–35,297)	35,419 (34,763–36,147)	36,345 (35,677–37,060)
8	118,000	69,487 (68,353, 70,554)	69,914 (68,908–70,973)	70,845 (69,894–72,095)	71,918 (70,948–72,968)
All	449,000	289,741 (287,739–291,550)	293,023 (291,222–294,980)	297,676 (295,893–299,504)	303,093 (301,343–304,960)

Note: "–" indicates a K that was not modified from the original scenario. Initial K is the estimated K prior to simulating habitat change.

Table 5

Percent increase in the terminal mean carrying capacity (K) from the original protected lands scenario for each golden-cheeked warbler (*Setophaga chrysoparia*) recovery unit after simulating 50 years of habitat change. Estimates of K were based on the upper 95% confidence interval of density estimates reported by Mathewson et al. (2012) and the habitat state of each hexagon.

Unit	Protected lands scenario		
	K = 1500	K = 3000	K = 4500
1	6.2	12.5	18.3
2	3.2	6.7	9.5
3	–	–	–
4	1.4	3.6	5.8
5	–	–	0.4
6	–	0.2	1.9
7	1.8	4.4	7.1
8	0.6	2.0	3.5
All	1.1	2.7	4.6

Note: "–" indicates a K that was not modified from the original scenario, implying a 0% increase in terminal mean K.

Table 6

Range-wide risk of quasi-extinction (i.e., probability of falling below 5000 individuals) for golden-cheeked warblers (*Setophaga chrysoparia*) after simulating 50 years of population dynamics for various scenarios.

Dispersal	Scenario		
	I	II	III
0.05	NA	0.06	0.00
0.15	NA	0.00	0.00
0.25	1.00	0.00	0.00
0.35	1.00	NA	NA
0.45	1.00	NA	NA
0.55	0.00	NA	NA

Note: "NA" indicates a scenario that was not simulated.

the Scenario II risk of quasi-extinction increased to 0.51 with a terminal expected population size of 101,922 (percentiles: 0–291,004; Fig. 2).

4. Discussion

We simulated range-wide golden-cheeked warbler population and breeding habitat dynamics. Habitat-transition probabilities supported the predictions that there has been a substantial decrease in warbler habitat over the past decade, habitat transitions were unidirectional, and that the magnitude of change varied among recovery units. The model results suggested warbler population viability could be achieved with the current vital-rate estimates and recent habitat conditions, depending on dispersal. However, there is considerable uncertainty associated with these population projections. Further, the simulations indicated that increasing the amount of protected lands would have a substantial positive impact on terminal carrying capacities at the end of a 50-year simulation.

Table 7
Range-wide expected mean adult male golden-cheeked warbler (*Setophaga chrysoparia*) population size with 2.5th and 97.5th percentiles in parentheses after simulating 50 years of population dynamics for various scenarios. Under this protected lands scenario, terminal carrying capacity (*K*) was approximately 289,741 (percentiles: 287,739–291,550).

Dispersal	Scenario		
	I	II	III
0.05	NA	5379 (4923–5870)	289,712[*] (287,935–291,624)
0.15	NA	288,515[*] (286,487–290,380)	289,708[*] (287,761–291,510)
0.25	4 (0–14)	289,719[*] (287,901–291,588)	289,669[*] (287,780–291,625)
0.35	100 (58–152)	NA	NA
0.45	1847 (1619–2096)	NA	NA
0.55	29,406 (27,990–30,990)	NA	NA

Note: "NA" indicates a scenario that was not simulated.

[*] Indicates a scenario in which the terminal population size approached *K*.

4.1. Habitat dynamics

As expected, we found habitat transitions were unidirectional in that habitat states transitioned to less favorable conditions. There was no evidence that the amount of habitat within a hexagon would increase across time in our study. This finding is consistent with the current knowledge on Ashe juniper growth rates in central Texas, USA. Reemts and Hansen (2008) monitored succession of woodlands on FHMR following a high-intensity fire from 1996 to 2005. Approximately 10 years after the fire, they found only six individual Ashe juniper trees exceeded 1.8 m in height. Rasmussen and Wright (1989) had similar results when examining vegetation regeneration in the Edwards Plateau. In their study, Ashe juniper dramatically increased in canopy cover 14 years following prescribed fire, however, less than 25% of the trees were greater than 1 m tall. Moreover, Fuhlendorf et al. (1996) modeled Ashe juniper in the Edwards Plateau. Their model results suggested that in the absence of fire, dense-canopy Ashe juniper woodlands would not form for 75 years. We estimated state *N* to be an absorbing habitat state (i.e., $\psi^{NN} = 1$), indicating that eventually all habitat subject to our habitat-transition matrices (i.e., all unprotected habitat) will be in state *N* with probability = 1. Collectively, this underscores the
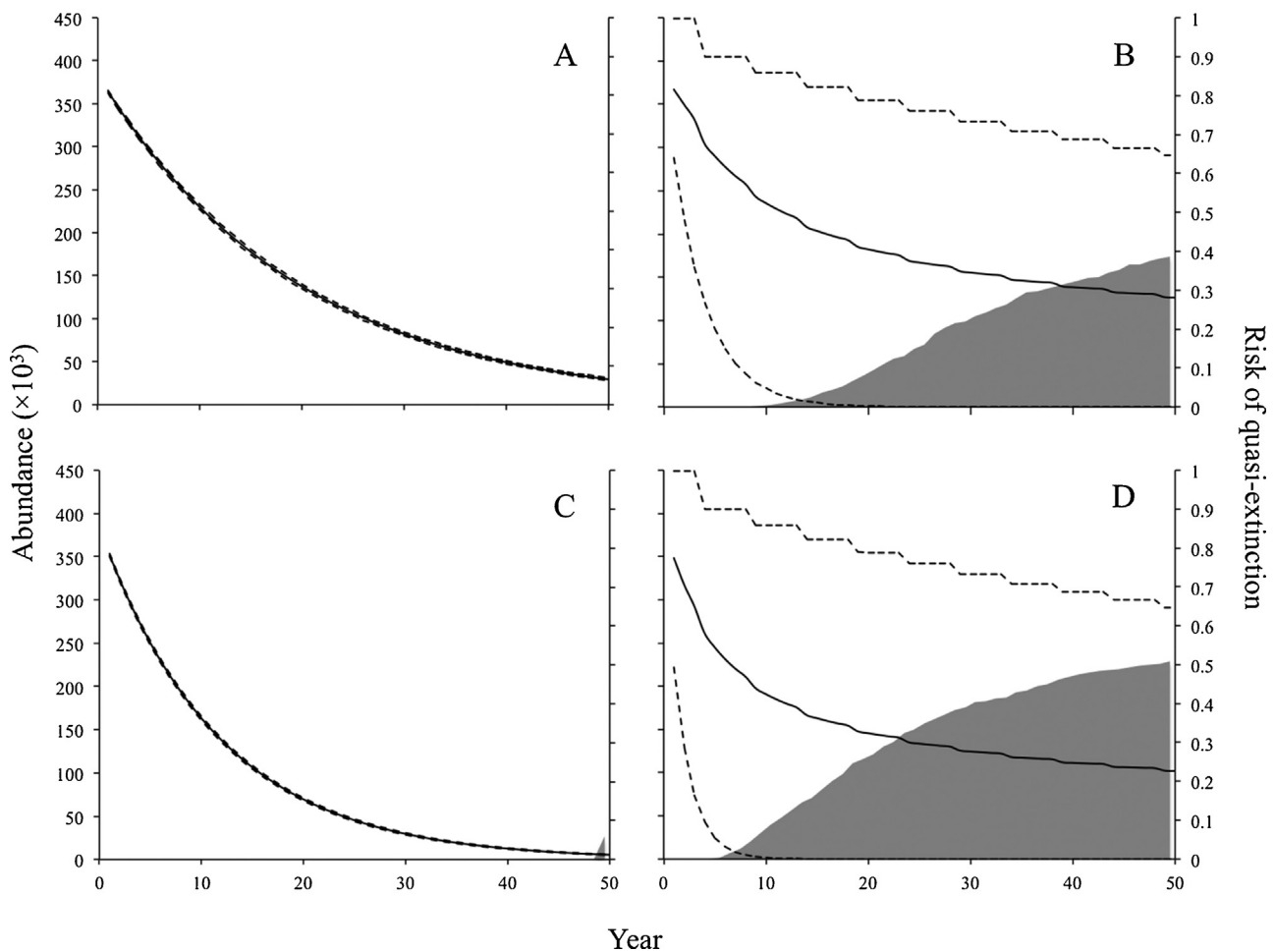

Fig. 2. Range-wide mean golden-cheeked warbler (*Setophaga chrysoparia*) abundance (solid line) with 2.5th and 97.5th percentiles (dashed lines; primary *y*-axis) and risk of quasi-extinction (i.e., probability of falling below 5000 individuals; shaded area; secondary *y*-axis) from Scenario I without parametric uncertainty (A), Scenario I with parametric uncertainty (B), Scenario II without parametric uncertainty (C), and Scenario II with parametric uncertainty (D). Scenario I simulations were run with a dispersal probability of 0.55, and Scenario II simulations were run with a dispersal probability of 0.05.

importance of protecting current warbler breeding habitat, rather than waiting for habitat to regenerate on currently protected lands.

Contrary to our predictions, recovery units five, six, and eight did not have the highest rates of habitat loss. No difference was found for habitat-transition probabilities among recovery units when a hexagon was in state *L* or *N* (based on the point estimates and standard errors). A hexagon in state *M* was more likely to transition to a less favorable state in recovery units one and four, and most likely to remain stable in recovery unit eight. Hexagons in state *H* were also more stable in recovery unit eight, followed by recovery unit three. We based our predictions on the findings of Duarte et al. (2013). However, differences in the methods used to quantify habitat change make comparisons between the two studies problematic. Duarte et al. (2013) quantified habitat change using unsupervised classifications on Landsat imagery followed by a post-classification change detection analysis, where change was quantified for each recovery unit based on 30 m^2 pixels. Here we quantified habitat change for each recovery unit at the spatial scale of a 200-ha hexagon via multistate modeling. Although both methods are suitable approaches to quantify habitat change, we used the multistate modeling approach to incorporate stochastic habitat change within the PVA, and comparisons of habitat change among recovery units are more directly comparable via the methods used herein. Regardless of the method used, both studies found a significant reduction in warbler breeding habitat.

The magnitude of habitat change we present here is dependent on the size of the hexagons and the number of habitat states that were considered. Intuitively, smaller hexagons and an increase in the number of habitat states might lead to greater habitat change. As stated earlier, we chose 200 ha because this spatial scale is directly related to the presence/absence of the species and is compatible with current warbler vital-rate estimates. We restricted the analysis to four habitat states because we felt this was sufficient to model habitat dynamics relevant to birds at the range-wide scale. It is worth noting that the number of transition probabilities to be estimated is the number of states squared. Thus, even slight increases in the number of habitat states considered will lead to dramatic increases in the number of estimated transition probabilities.

Current estimates of habitat transitions indicate there will be a large reduction in warbler *K* in the future. We simulated 50 years, which resulted in 10 opportunities for a hexagon to transition to an alternate habitat state. Under current conditions the range-wide warbler *K* will reduce by approximately 35.5%. Increasing the amount of protected lands substantially increased terminal *K*. However, even when increasing the amount of protected lands to support 4500 adult male warblers per recovery unit there was still an approximately 32.5% reduction in range-wide *K* over the simulated 50 years. Although this might not seem like an overly positive outcome, it is still a 4.6% increase in terminal range-wide *K* from the potential outcome at current conditions. The magnitude of increase in terminal *K* was dependent on the recovery unit. The simulations suggest that the greatest positive impact on terminal *K* can be achieved by creating more habitat-conservation areas in recovery units one, two, and seven.

It is important to note that the simulated habitat-change results we present here are contingent upon what we defined as protected habitat and how we selected additional hexagons to be considered protected. In our study, a hexagon was originally considered protected if greater than 50% of the hexagon intersected 2012 conservation and recreation lands and/or 2010 Department of Defense lands. This is not entirely accurate because programs are currently in place that allow for the mitigation of habitat take on military lands (Wolfe et al., 2012). Further, many of the conservation and recreation lands might not actively manage for warblers and therefore might inadvertently remove warbler habitat to achieve alternate objectives. We used conservation, recreation, and military lands to indicate protected lands because there currently are no criteria set to define what is protected habitat for the species and many of these lands are parks, greenbelts, and state operated natural areas and wildlife management areas that appear likely to have minimal destruction of wildlife habitat. When running scenarios with increased protected habitat we did not select hexagons at random. Instead, hexagons were selected according to their current habitat state. We selected hexagons in state *H* first and then selected hexagons in state *M* until the desired *K* on protected lands was achieved. Thus, we assumed that warbler habitat conservation efforts would target areas with greater coverage of habitat. In many cases, however, areas are incorporated into warbler habitat-mitigation banks based upon their availability as opposed to resource agencies selecting areas based on habitat metrics (Charlotte Kucera, *personal communication*). Thus, alternate protected land scenarios should be considered in the future.

4.2. Population dynamics

Our PVA results suggest warbler viability can be achieved given the current information available for warbler vital rates and habitat dynamics, depending on dispersal. Under Scenario I, the risk of quasi-extinction approached 0 only when the dispersal probability was set at 0.55. This input parameter assumes that 55% of the fledglings that are estimated to never return to the area they were hatched emigrated. Although 0.55 is a relatively high value, this should not be of extraordinary concern given high dispersal rates are common among migratory birds and this value was paired with the lowest vital-rate estimates for the species. Since the mean adult survival parameter used in Scenario I is the lowest reported for the species and productivity estimates are likely biased low due to the difficulty associated with surveying for fledglings, we also considered scenarios with increased vital rates. Under Scenario II, warbler abundance was constrained by *K* when dispersal was at least 0.15. When dispersal reduced to 0.05 under this scenario the range-wide expected mean adult warbler population size declined by approximately 98.5%. Although alarming, a natal-site dispersal probability of 0.05 is low and is not likely to occur for a migratory songbird in a natural setting. Under Scenario III, warbler abundance was constrained by *K* regardless of the dispersal probability. The vital rates in Scenario III are a best-case scenario. In this scenario mean productivity and adult survival were 3.6 and 0.57, respectively. Although a mean survival of 0.57 has been estimated from field data, a mean productivity of 3.6 is not likely to occur across all territories because not all territories are successful. This scenario is intentionally overly optimistic, and inferences using this scenario should not be given a large amount weight.

Although Scenario I with a dispersal probability of 0.55 and Scenario II with a dispersal probability of 0.05 indicated a low risk of quasi-extinction could be achieved, there was a considerable amount of uncertainty associated with these projections (Fig. 2). When incorporating parametric uncertainty, some of the replicates fell below 5000 individuals within the first 10 years of the simulation due to the low realized survival. On the other hand, some of the replicates approached *K* and remained there throughout the 50-year simulation because of high realized survival. Parametric uncertainty can be attributed to an assortment of factors; however, the magnitude of the uncertainty can be reduced with greater precision in the parameter estimates, which can be obtained via increased field work and larger sample sizes (reviewed in McGowan et al., 2011).

As with any model, the model presented here represents a simplification of reality, and the simulation results are conditional on the model assumptions. The model simulated population dynamics at multiple sites (i.e., hexagons) using vital-rate estimates

from a handful of localized sites. This is a common scenario for many species, particularly those that are endangered. Due to a lack of region-specific vital-rate estimates, the model assumed the means and variances for these parameters were identical across all hexagons. Also, data and estimates are unavailable to model density-dependent vital rates. Therefore, we were forced to model K in such a way that it was dependent solely on the amount of habitat within a hexagon. Furthermore, data are lacking to examine potential correlations in vital rates among sites so the model omitted this process. It should be noted that a negative correlation in vital rates among sites would increase the chances for rescue effects and concomitantly decrease the range-wide risk of quasi-extinction (reviewed in Morris and Doak, 2002). On the other hand, a positive correlation among sites would have the opposite effect on the range-wide risk of quasi-extinction. Having vital-rate estimates from multiple regions and under different environmental and management scenarios would allow us to simulate variation in warbler vital rates (and by extension, population dynamics) more realistically. Our model did not incorporate a dispersal-distance limitation because (as reviewed earlier) there currently is no evidence to support this limitation for the species. This does not necessarily mean that distance between habitat patches does not play a role in warbler population dynamics. It should be stated that if the ability to traverse distances among habitat patches between breeding seasons is a limitation for the species, then our results are overly optimistic. Indeed, limited dispersal among hexagons would alter any source-sink dynamics among hexagons and lead to habitat changes playing a stronger role in the projected population dynamics.

5. Conclusions

We simulated range-wide golden-cheeked warbler population and breeding habitat dynamics. Depending on dispersal, the model results indicate warbler viability can be achieved under current conditions. Although promising, there is considerable uncertainty associated with our population projections that may result in drastically different outcomes at the end of a 50-year simulation (see Fig. 2). Therefore, any change in the listing status of the species based on these projections is *not* warranted. Specifically, demographic data are lacking from a majority of the species' breeding range, and the magnitude and distance of emigration from a target population, particularly for second-year birds returning from the wintering ground, has yet to be estimated with field data. Further, our treatment of carrying capacity as dependent solely on the amount of habitat and the absence of a direct relationship between warbler density and demographic parameters such as survival or productivity was dissatisfying. Estimates of the relationship between vital rates and some metric reflecting warbler density (with respect to habitat) could be used to draw inferences about carrying capacity directly. Notably, the functional relationships among vital rates and habitat metrics at varying densities can be estimated within a unified framework using integrated population models if the appropriate data (i.e., data to estimate productivity, abundance, and survival) are available (reviewed in Duarte et al., 2015). This emphasizes the need for a considerable amount of effort focused on modifying existing annual survey work toward collecting the data required to estimate these relationships. The habitat-dynamics portion of this study suggests that conserving large tracts of warbler habitat to ensure their availability in the future is necessary. Future warbler habitat conservation efforts could beneficially focus on a common definition of what constitutes protected habitat, identify what management goals are suitable within those protected areas, and develop a standard operating procedure to identify areas of priority for habitat conservation efforts.

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