

POPULATION DYNAMICS AND HABITAT CONSERVATION FOR THE
GOLDEN-CHEEKED WARBLER (*SETOPHAGA CHRYSOPARIA*)

by

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DEDICATION

This dissertation is dedicated to my wife, Jennifer JoAnn Duarte, to my daughter, Elizabeth Alli Duarte, and to my son, Lucas Fidel Duarte. Exploring the outdoors with you all is a constant reminder of the true value of our natural resources.



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ABSTRACT

Fundamental to species' conservation and management is an understanding of the factors driving population dynamics. The objective of this dissertation is to update and extend our knowledge on population and habitat dynamics for the federally endangered golden-cheeked warbler (*Setophaga chrysoparia*). In order to achieve this, I carried out 4 interrelated multidisciplinary studies that used modern statistical and geospatial methodologies.

Habitat availability limits the distribution and abundance of wildlife species. Thus, for the first study I quantified the degree of change in range-wide warbler breeding habitat over the past decade using available GIS data and Landsat imagery. Here, I provided quantitative evidence for large-scale reduction in total warbler breeding habitat during the last decade, determining that warbler breeding habitat was removed and became more fragmented at uneven rates across the warbler's breeding range. This information will assist researchers and managers in prioritizing breeding habitat conservation efforts for the species and provides a foundation for more realistic carrying-capacity scenarios when modeling warbler populations over time.

In my second study, I estimated more current, precise adult and juvenile male warbler apparent survival estimates and tested hypotheses about spatial and temporal variation in apparent survival by analyzing long-term warbler capture-resight data. This study did not provide evidence of site-specific variation in warbler apparent survival on

the study area. Nor did it provide strong evidence for temporal association between warbler abundance and apparent survival. Although juvenile apparent survival did not differ greatly from previous estimates, the adult apparent survival estimate suggests previous warbler population models were overly optimistic with respect to adult survival.

After my first two studies, it was apparent that movement among habitat patches was essential for warbler persistence. Unfortunately, movement rates had not been previously estimated for the species. Therefore, for my third study I focused on warbler population dynamics at the local spatial scale using a new extension of integrated population models. This study provided quantitative evidence of the importance of immigration to stabilize local warbler populations, indicating warbler conservation and management programs need to be implemented at larger spatial scales 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.

Finally, for my fourth study I refocused on warbler population and habitat dynamics at the range-wide scale. Specifically, I estimated habitat-transition probabilities across the warbler's breeding range by combining National Land Cover Database classifications with multistate capture-recapture analyses. This enabled a determination of warbler viability into the next 50 years given the current conditions and an evaluation of whether protecting a greater amount of habitat at present day would increase the number

of warblers that can be supported in the future. The estimated habitat-transition probabilities indicated habitat transitions are directional, whereby habitat is more likely to diminish than regenerate. The model results also indicated that population viability could be achieved under current conditions. However, there is considerable uncertainty associated with the population projections due to parametric uncertainty. Further, the 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. This study highlights the importance of prioritizing the conservation of existing, large tracts of warbler breeding habitat due to the directional nature of habitat transitions and the positive outcome of protecting a greater amount of habitat on the future population.

CHAPTER I

GENERAL INTRODUCTION

Central to wildlife conservation and management is the ability to forecast how species will behave and persist under future environmental conditions. To accomplish this, biologists must have a deep understanding in how current environmental conditions impact a species' recruitment, survival, emigration, and immigration at a variety of spatial and temporal scales (Williams et al. 2002). Thus, it is no surprise the use of quantitative and geospatial methods have continued to be an active area of research when studying wildlife population dynamics. By using many of these modern techniques, biologists are able to reliably estimate abundances and vital rates, and by extension, establish effective science-based conservation and management protocols. However, there is often a time lag between the development of such techniques and their application to on-the-ground conservation and management efforts.

The golden-cheeked warbler (*Setophaga chrysoparia*; henceforth, warbler) is a Neotropical migrant passerine that, unlike any other migratory songbird, breeds exclusively in the mature woodlands of the Texas Hill Country and Balcones Escarpment. These woodlands primarily consist of Ashe juniper (*Juniperus ashei*) and various species of oaks (*Quercus* spp.) and are utilized by warblers for foraging habitat, nesting cover, and nesting material (i.e., strips of bark from mature Ashe juniper) during the breeding season (Pulich 1976, Kroll 1980, Ladd and Gass 1999). During wintering months, warblers migrate south and select for mixed pine (*Pinus* spp.) and oak forests that are $\geq 1,100$ m in elevation located within Mexico, Guatemala, Honduras, El Salvador,

and Nicaragua (Monroe 1968, Rappole et al. 1999). The species endemism coupled with perceived high rates of breeding habitat loss across the landscape raised concern for warbler viability (Wahl et al. 1990). In 1990, the warbler was designated as endangered in an emergency federal listing (U.S. Fish and Wildlife Service [USFWS] 1990), despite much controversy (reviewed in Groce et al. 2012). Although habitat loss was cited as the primary threat to warblers, nest predation and nest parasitism were also acknowledged as ongoing threats to warbler viability (USFWS 1990).

Following the species' emergency federal listing, a recovery plan for the warbler was released by the USFWS that described the basic biology of the species, various threats, and recovery criteria that must be met before the species can be downlisted (USFWS 1992). Also, in order to manage the recovery process for the species, the recovery plan delineated 8 recovery units that were based on geology, vegetation, and watershed boundaries (USFWS 1992). Although the recovery plan is currently under revision by the USFWS Golden-cheeked Warbler Recovery Team, the recovery criteria for the current recovery plan are summarized below, copied from the Executive Summary of USFWS (1992:iv):

“The warbler will be considered for delisting when (1) sufficient breeding habitat has been protected to ensure the continued existence of at least one viable, self-sustaining population in each of 8 regions outlined in the plan, (2) the potential for gene flow exists across regions between demographically self-sustaining populations needed for long-term viability, (3) sufficient and sustainable non-breeding habitat exists to support the breeding populations, (4) all existing warbler populations on public lands are protected and

managed to ensure their continued existence, and (5) all of these criteria have been met for 10 consecutive years.”

Since the warbler was first listed as endangered, research has occurred that examined population dynamics (USFWS 1996, Alldredge et al. 2004, Vaillant et al. 2004, Horne et al. 2011), habitat modeling (see Morrison et al. 2010), and survey procedures (Watson et al. 2008, Laake et al. 2011, Peak 2011, Hunt et al. 2012, Warren et al. 2013). Per the recovery plan, population models are currently assisting the USFWS Golden-cheeked Warbler Recovery Team in deciding the amounts of protected breeding habitat necessary to ensure a high probability of warbler persistence into the foreseeable future. However, previous population viability analyses (PVAs) were hampered by the paucity of information concerning warbler demography, distribution, abundance, dispersal, and habitat change (USFWS 1996, Alldredge et al. 2004, Vaillant et al. 2004, Horne et al. 2011). Current research suggests the warbler is abundant (Mathewson et al. 2012) and widely distributed (Collier et al. 2012), with little genetic differentiation across its breeding range (Lindsay et al. 2008). Further, we now have 10 more years of warbler monitoring data that have yet to be analyzed. Estimates from these data could dramatically alter our outlook on warbler demography and viability.

My dissertation is centered on updating and extending our knowledge on warbler population dynamics and habitat conservation at multiple spatial and temporal scales. In order to achieve this, I carried out 4 interrelated multidisciplinary studies that used modern statistical and geospatial methodologies. Understanding how habitat changes over time is crucial for large-scale conservation decision making because habitat availability limits the distribution and abundance of species. Thus, my first objective was

to examine range-wide breeding habitat change. To accomplish this, I conducted a post-classification change-detection analysis using Landsat imagery. The findings of this research project will help prioritize areas for habitat conservation efforts based on rates of habitat loss and fragmentation. Since current survival parameters were calculated using relatively small data sets that are now greater than a decade old, my second objective was to update survival estimates for the species in order to use these estimates in future warbler population models. To meet this goal, I analyzed long-term male warbler capture-resight data that were collected within 7 study plots on the Fort Hood Military Reservation. Here, I also tested hypotheses concerning spatial and temporal variation in warbler survival. Following these research projects two things became apparent. (1) Large-scale habitat loss and fragmentation was occurring across the warbler's breeding range, and (2) local warbler populations might not be self-sustaining given some of the current vital-rate estimates. Therefore, my third objective was to focus on better understanding the various parameters that affect local warbler population dynamics. Specifically, I set out to estimate the first movement parameter for the species and to determine if the spatial scale in which warblers are being monitored is sufficient. To achieve this, I linked survival estimates from the Fort Hood Military Reservation with long-term survey data collected on the Balcones Canyonlands Preserve, and analyzed these data using a new extension of integrated population models. Lastly, I again focused at the range-wide scale and simulated warbler population and habitat dynamics. My goals were to quantify habitat-transition probabilities across the warbler's breeding range, examine if warbler viability is possible given the current conditions, and evaluate if protecting a greater amount of habitat would increase the number of warblers that can be

supported in the future. Here, I used a new approach to estimate habitat transitions across time (e.g., multistate capture-recapture analyses). Further, in order to make the model spatially explicit, I took advantage of the seamless interface between ArcMAP and Python programming. Overall, my dissertation research will enable informed conservation decision making for the golden-cheeked warbler, both at the local and range-wide scale.

Literature Cited

- Allredge, M. W., J. S. Hatfield, D. D. Diamond, and C. D. True. 2004. Golden-cheeked warbler (*Dendroica chrysoparia*) in Texas: importance of dispersal toward persistence in a metapopulation. Pages 372–383 in H. R. Akçakaya, M. A. Burgman, O. Kindvall, C. C. Wood, P. Sjögren-Gulve, J. S. Hatfield, and M. A. McCarthy, editors. Species conservation and management: case studies. Oxford University Press, New York, New York, USA.
- Collier, B. A., J. E. Groce, M. L. Morrison, J. C. Newnam, A. J. Campomizzi, S. L. Farrell, H. A. Mathewson, R. T. Snelgrove, R. J. Carroll, and R. N. Wilkins. 2012. Predicting patch occupancy in fragmented landscapes at the rangewide scale for an endangered species: an example of an American warbler. *Diversity and Distributions* 18:158–167.
- Groce, J. E., K. N. Smith, R. N. Wilkins, and D. Wolfe. 2012. The golden-cheeked warbler: history of a conflict. *Wildlife Society Bulletin* 36:401–407.
- Horne, J. S., K. M. Strickler, and M. Allredge. 2011. Quantifying the importance of patch-specific changes in habitat to metapopulation viability of an endangered songbird. *Ecological Applications* 21:2478–2486.
- Hunt, J. W., F. W. Weckerly, and J. R. Ott. 2012. Reliability of occupancy and binomial mixture models for estimating abundance of Golden-cheeked Warblers (*Setophaga chrysoparia*). *Auk* 129:105–114.
- Kroll, J. C. 1980. Habitat requirements of the golden-cheeked warbler: management implications. *Journal of Range Management* 33:60–65.

- Laake, J. L., B. A. Collier, M. L. Morrison, and R. N. Wilkins. 2011. Point-based mark-recapture distance sampling. *Journal of Agricultural Biological and Environmental Statistics* 16:389–408.
- Ladd, C., and L. Gass. 1999. Golden-cheeked warbler (*Dendroica chrysoparia*). Account 420. in A. Poole, and F. Gill, editors. *The Birds of North America*. The Academy of Natural Sciences, Philadelphia, Pennsylvania, The American Ornithologists' Union, Washington D.C., USA.
- Lindsay, D. L., K. R. Barr, R. F. Lance, S. A. Tweddale, T. J. Hayden, and P. L. Leberg. 2008. Habitat fragmentation and genetic diversity of an endangered, migratory songbird, the golden-cheeked warbler (*Dendroica chrysoparia*). *Molecular Ecology* 17:2122–2133.
- Mathewson, H. A., J. E. Groce, T. M. McFarland, M. L. Morrison, R. T. Newnam, R. T. Snelgrove, B. A. Collier, and R. N. Wilkins. 2012. Estimating breeding season abundance of golden-cheeked warblers in Texas, USA. *Journal of Wildlife Management* 76:1117–1128.
- Morrison, M. L., R. N. Wilkins, B. A. Collier, J. E. Groce, H. A. Mathewson, T. M. McFarland, A. G. Snelgrove, R. T. Snelgrove, and K. L. Skow. 2010. Golden-cheeked warbler population distribution and abundance. Texas A&M Institute of Renewable Natural Resources, College Station, Texas, USA.
- Monroe, B. L. 1968. A distributional survey of the birds of Honduras. *Ornithological Monographs* 7:1–458.

- Peak, R. G. 2011. A field test of the distance sampling method using golden-cheeked warblers. *Journal of Field Ornithology* 82:311–319.
- Pulich, W. M. 1976. *The Golden-Cheeked Warbler: A Bioecological Study*. Texas Parks and Wildlife, Austin, Texas, USA.
- Rappole, J. H., D. I. King, and W. C. Barrow. 1999. Winter ecology of the endangered golden-cheeked warbler. *Condor* 101:762–770.
- U.S. Fish and Wildlife Service. 1990. Endangered and threatened wildlife and plants; final rule to list the golden-cheeked warbler as endangered. *Federal Register* 55:53153–53160.
- U.S. Fish and Wildlife Service. 1992. Golden-cheeked warbler (*Dendroica chrysoparia*) recovery plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.
- U.S. Fish and Wildlife Service. 1996. Golden-cheeked warbler population and habitat viability assessment report. Compiled and edited by C. Beardmore, J. Hatfield, and J. Lewis in conjunction with workshop participants. Report of a August 21–24, 1995 workshop arranged by the U.S. Fish and Wildlife Service in partial fulfillment of U.S. National Biological Service Grant no. 80333–1423, Austin, Texas, USA.
- Vaillant, H., H. R. Akcakaya, D. Diamond, and D. True. 2004. Modeling the effects of habitat loss and fragmentation on the golden-cheeked warbler. Final report, submitted to the Engineering Research and Development Center, Construction Engineering Research Laboratory, Champaign, Illinois, USA.

Wahl, R., D. D. Diamond, and D. Shaw. 1990. The Golden-cheeked Warbler: a status review. U.S. Fish and Wildlife Service Ecological Services. Ft. Worth, Texas, USA.

Warren, C. C., J. A. Veech, F. W. Weckerly, L. O'Donnell, and J. R. Ott. 2013. Detection heterogeneity and abundance estimation in populations of golden-cheeked warblers (*Setophaga chrysoparia*). *Auk* 130:677–688.

Watson, C. A., F. W. Weckerly, J. S. Hatfield, C. C. Farquhar, and P. S. Williamson. 2008. Presence-nonpresence surveys of golden-cheeked warblers: detection, occupancy and survey effort. *Animal Conservation* 11:484–492.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

CHAPTER II

SPATIOTEMPORAL VARIATION IN RANGE-WIDE GOLDEN-CHEEKED WARBLER BREEDING HABITAT¹

ABSTRACT

Habitat availability ultimately limits the distribution and abundance of wildlife species. Consequently, it is paramount to identify where wildlife habitat is and understand how it changes over time in order to implement large-scale wildlife conservation plans. Yet, no work has quantified the degree of change in range-wide breeding habitat for the Golden-cheeked Warbler (*Setophaga chrysoparia*), despite the species being listed as endangered by the U.S. Federal Government. Thus, using available GIS data and Landsat imagery we quantified range-wide warbler breeding habitat change from 1999–2001 to 2010–2011. We detected a 29% reduction in total warbler breeding habitat and found that warbler breeding habitat was removed and became more fragmented at uneven rates across the warbler’s breeding range during this time period. This information will assist researchers and managers in prioritizing breeding habitat conservation efforts for the species and provides a foundation for more realistic carrying capacity scenarios when modeling Golden-cheeked Warbler populations over time. Additionally, this study highlights the need for future work centered on quantifying Golden-cheeked Warbler movement rates and distances in order to assess the degree of connectivity between increasingly fragmented habitat patches.

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INTRODUCTION

It is well accepted that habitat loss and fragmentation caused by anthropogenic modifications to the landscape are primary drivers of wildlife population declines. Although wildlife management actions are usually implemented at the site (or local) level, recovery plans for species of concern are often structured at the range-wide (or regional) level. Thus, monitoring large-scale habitat availability is paramount in wildlife conservation efforts. This information allows researchers and managers to identify factors that may limit the distribution of the species, to create population models based on realistic carrying capacity scenarios, and to prioritize areas for habitat conservation efforts based on habitat availability, habitat patch metrics, as well as previous rates of habitat loss and fragmentation.

The Golden-cheeked Warbler (*Setophaga chrysoparia*; hereafter, warbler) is a migratory songbird that breeds exclusively in the mature (generally ≥ 4.6 m tall and ≥ 12.7 cm in diameter at breast height) juniper-oak/deciduous woodlands of the Texas Hill Country and Balcones Escarpment (Pulich 1976, Kroll 1980, Ladd and Gass 1999). In 1990, the species' endemism coupled with perceived high rates of habitat loss across the landscape resulted in the species' emergency listing as endangered by the U.S. Federal Government (United States Fish and Wildlife Service [USFWS] 1990). Despite the species' federal listing status, most of the warbler's breeding range is comprised of privately owned property. Thus, nearly all breeding habitat can be subject to removal for multiple anthropogenic reasons (i.e., direct human removal due to perceived negative effects of Ashe juniper [*Juniperus ashei*] on livestock herbivory and groundwater availability, urban sprawl, land-use change, and prolonged drought).

In recent years, a suite of warbler habitat suitability models (hereafter referred to as warbler habitat maps) have been developed for the entirety of its breeding range (reviewed in Morrison et al. 2010). Yet, the scope of these warbler habitat maps was to delineate a static description of the locations and metrics of habitat patches in central Texas. Groce et al. (2010) quantified woodland loss/gain across the warbler's breeding range from 1992 to 2001 using the National Land Cover Database (NLCD). However, not all woodland areas in central Texas should be considered warbler breeding habitat. Further, information concerning more recent habitat dynamics across the entire warbler breeding range is lacking. An up-to-date understanding of the dynamics of warbler breeding habitat patch metrics is particularly important since increased forest edge, decreased habitat patch size, and reduced connectivity of habitat patches have been linked to deleterious effects on warbler reproductive success (Peak 2007, Reidy et al. 2009, Butcher et al. 2010), increased genetic differentiation among warbler populations (Lindsay et al. 2008), a decline in genetic diversity over time (Athrey et al. 2011), and reduced warbler occupancy of habitat patches (Collier et al. 2010, Collier et al. 2012, McFarland et al. 2012, Warren et al. 2013). Notably, habitat patches with lower occupancy probabilities have been reported to support lower warbler abundances (Mathewson et al. 2012). Additionally, habitat loss and fragmentation reduce survival in other closely related warbler species (e.g., Black-burnian Warbler [*S. fusca*] and Black-throated Green Warbler [*S. virens*]; Zitske et al. 2011), and therefore, have the potential to negatively affect Golden-cheeked Warbler survival.

The objective of this study was to model range-wide warbler breeding habitat dynamics from 2000 to 2010 using available GIS data and Landsat imagery. In order to

manage the recovery process for warblers, the species' recovery plan delineated eight recovery units that were based on geology, vegetation, and watershed boundaries (USFWS 1992). Therefore, we quantified patch metrics in both time steps for each warbler recovery unit in order to assist researchers and managers in prioritizing breeding habitat conservation efforts for the species, which has recently been highlighted as a research need for warbler conservation (Hatfield et al. 2012).

METHODS

Study area

This study pertains to the entirety of the warbler's breeding range. As stated above, the warbler's breeding range is confined to central Texas, USA and has been divided into eight recovery units to manage the recovery process for the species (Fig. 2.1). Warbler breeding habitat varies in density across the species' breeding range with a sparseness of habitat occurring in the far northern and far western portions of the range. Tree species that are widespread across the Texas Hill Country and Balcones Escarpment include Ashe juniper, live oak (*Quercus fusiformis*), Texas oak (*Q. buckleyi*), post oak (*Q. stellata*), blackjack oak (*Q. marilandica*), Lacey oak (*Q. glaucoides*), shin oak (*Q. sinuata*), sugarberry (*Celtis laevigata*), Texas ash (*Fraxinus texensis*), cedar elm (*Ulmus crassifolia*), black cherry (*Prunus serotina*), pecan (*Carya illinoensis*), and black walnut (*Juglans nigra*).

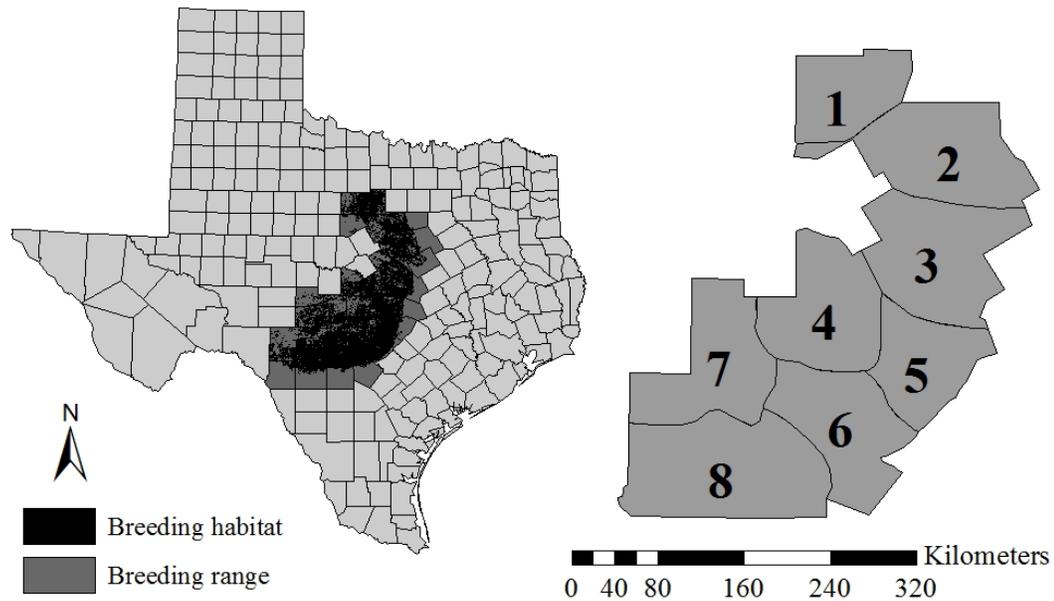


Figure 2.1 Breeding range and habitat (as delineated by Diamond et al. 2010) for the Golden-cheeked Warbler (*Setophaga chrysoparia*) in Texas, USA. On the right, golden-cheeked warbler recovery unit boundaries (USFWS 1992).

Data acquisition

Landsat 5 Thematic Mapper (TM) images at a 30-m spatial resolution were downloaded from the USGS Earth Explorer website (earthexplorer.usgs.gov/). Images were selected if they had <10% cloud cover and were acquired in two seasons, winter (December–January) and summer (late April–July). Using images during both of these periods was desirable because it allowed for identification of areas occupied by evergreen/mixed vegetation vs. deciduous vegetation since both types of vegetation will be green in the summer and deciduous vegetation will be either senesced or defoliated in

winter images. Eighteen images were used per time step (we used two seasons worth of imagery per time step and the total number of images needed to cover the warbler’s breeding range is nine, see Morrison et al. 2010: Fig. 1–5). For the first time step, images used for analysis were obtained from 1999–2001 and for the second time step, images were obtained from 2010–2011. This was necessary since not all Landsat 5 scenes were acquired on days with <10% cloud cover within the restricted seasons in 2000 and 2010. Refer to Table 2.1 for a summary of image acquisition dates for each time step of the analysis.

Table 2.1 Date of acquisitions for Landsat 5 Thematic Mapper images used in a Golden-cheeked Warbler (*Setophaga chrysoparia*) range-wide breeding habitat post-classification change detection analysis.

Image row/path	1999–2001		2010–2011	
	Winter	Summer	Winter	Summer
27_37	31-Dec-99	23-May-00	11-Jan-10	04-Jun-10
27_38	31-Dec-99	23-May-00	13-Dec-10	07-Jun-11
27_39	31-Dec-99	21-Apr-00	13-Dec-10	07-Jun-11
27_40	17-Dec-00	21-Apr-00	13-Dec-10	04-Jun-10
28_37	08-Feb-00	02-Jun-01	05-Jan-11	24-Apr-10
28_38	06-Dec-99	31-Jul-99	04-Dec-10	24-Apr-10
28_39	06-Dec-99	15-Jul-99	04-Dec-10	24-Apr-10
28_40	23-Jan-00	15-Jul-99	04-Dec-10	24-Apr-10
29_39	13-Dec-99	24-May-01	09-Jan-10	05-Jun-11

Note: Images are at a 30-m resolution, selected if they had <10% cloud cover, and were acquired in two seasons, winter (December–January) and summer (April–July).

Spatial analyses

Images were pre-processed in ERDAS Imagine 2011. Image pixel values were converted from brightness values to at-sensor reflectance in the model builder within Imagine using the radiometric coefficients and conversion algorithms presented in

Chander et al. (2009). Multi-date image composites were then created by stacking the reflectance images from different seasons that have the same row/path and were within the same time step.

To mitigate potential classification accuracy issues due to temporal differences attributed to cloud cover (e.g., adjacent scenes acquired during the same season, but different years), we classified the composite path/row images prior to creating a mosaic of the thematic output for each time step. Land cover was classified for each of the 18 multi-date image composites using an unsupervised classification with the ISODATA clustering algorithm into 20 statistically different clusters, with a maximum of 75 iterations and convergence threshold of 0.95 for both time steps. When a cluster was determined to be indistinguishable between two or more classes, cluster busting was used (i.e., clusters that could not be identified were extracted and a separate unsupervised classification was performed). Clusters were then combined into three thematic land cover classes, evergreen/mixed woodlands, deciduous woodlands, or other (comprised of urban, water, barren, etc.). A pixel was considered woodland if at least half of the pixel was covered by woody vegetation, which was assessed by visual observation. Classified images were then mosaicked for each time step.

Two independent accuracy assessments (hereafter referred to as the accuracy assessment performed by Interpreters (a) and (b)) were conducted for each mosaic by treating NAIP color infrared imagery (1-m resolution; 2004 and 2010) as the reference source. We used 2004 NAIP imagery to assess the accuracy of the 1999–2000 mosaic because 2004 is the closest (in time) available NAIP imagery that covers the entire warbler breeding range. Using the multinomial distribution, we determined that 106 and

102 pixels were needed to assess classification accuracy with an expected accuracy of 90% and precision of 10%, respectively, during both time steps (Tortora 1978, Congalton and Green 1999). Measures of classification accuracy were overall classification accuracy, overall Kappa coefficient of agreement, and user's and producer's accuracy. User's accuracy is the probability that a pixel in the classified image represents the same land cover class on the ground, and is used as a measure of the reliability of the classification. Producer's accuracy indicates the probability that a reference pixel (i.e., the corresponding group of pixels in the NAIP imagery) was correctly classified. Thus, producer's accuracy provides information on how well a certain class/category has been classified.

Thematic land cover classes were then separated into two categories: "habitat" and "other". We classified habitat as any pixel that was originally classified as evergreen/mixed woodland as well as any pixel that was originally classified as deciduous woodland that was within 90 m of an evergreen/mixed woodland pixel. All remaining pixels were considered "other". We chose this warbler breeding habitat classification scheme because it has been shown to do well when compared to warbler detection/non-detection surveys (N. Heger, *personal communication*). Habitat patches were then identified using an eight neighbor rule. All patches <15 ha were not considered breeding habitat because it has been found that warblers need approximately 15–20 ha to successfully fledge young (Butcher et al. 2010).

In post-classification change detection analyses, misclassification of pixels can be misleading if errors in classifications are confused with landscape changes in habitat. This may lead to biased estimates of habitat gains and losses. However, methods to

account for these biases require knowledge of misclassifications of the change (Veran et al. 2012). We cannot determine with certainty that change in warbler habitat at the pixel level is actual change or misclassification since we are using a modeling approach to delineate warbler habitat from classified woodland maps. Therefore, in order to determine if the change we show here is driven by actual change, and not primarily a function of errors in classification, we ran two independent accuracy assessments (hereafter referred to the accuracy assessment performed by Interpreters (a) and (b)) on a change image between the two classified woodland map mosaics. Once again, we used the multinomial distribution with an expected accuracy of 90% (and a precision of 10%) and found it was necessary to check 158 pixels within the woodlands change image. We used the identical measures of classification accuracy as before. If change between evergreen/mixed woodlands, deciduous woodlands, and other between the two time steps has reasonable accuracy then we assumed change in warbler habitat that were based off these woodland maps is actual change in warbler habitat, not compounded classification errors.

A post-classification change detection between the warbler habitat maps for each time step was conducted in Imagine to quantify how habitat changed across the landscape between the two time steps. Areas identified as “converted to habitat” were not considered habitat since these images were roughly 10 years apart and it likely takes several decades for woodlands to mature and be considered viable warbler breeding habitat (Reemts and Hansen 2008). Once these pixels were removed from the second time step’s habitat map, patch sizes were reassessed to be sure all patches were ≥ 15 ha.

Habitat patch metrics were then quantified for each recovery unit in both time steps using FRAGSTATS v4 (McGarigal et al. 2012). Metrics were selected to account for class-specific area, shape characteristics, and aggregation and included mean habitat patch area, total habitat area, number of habitat patches, mean habitat patch shape index, and patch aggregation index. Mean habitat patch size, number of habitat patches, and total habitat area are the base metrics for habitat change that we considered. Mean patch area and total patch area provide information about the composition of the landscape and can be used to assess changes in habitat proportion over time. The number of habitat patches was selected to represent potential subdivision or aggregation of patches over time. An increase in the number of habitat patches combined with a decrease in mean habitat patch size indicates habitat patches are becoming fragmented. Whereas, a decrease in mean habitat patch size with a lack of change in the total number of habitat patches indicates some habitat patches are becoming fragmented, while other habitat patches are being entirely depleted. A decrease in total habitat area indicates habitat loss. Mean shape index is similar to perimeter-area ratio in that it is a measure of patch shape complexity, however, the mean shape index corrects for the size of the patch. The mean shape index is one when all habitat patches are circular and increases as habitat patches become more irregular. Notably, as a habitat patch becomes more irregular the core area of that patch decreases. Aggregation index characterizes the frequency with which like classes are adjacent and provides a spatial component to interpreting landscape fragmentation. Values are low (i.e., 0) when the frequency of like classes is low (indicating habitat fragmentation) and high (i.e., 100) when like classes are maximally aggregated. All habitat patch metrics were quantified using an eight neighbor rule.

RESULTS

Accuracy assessment results for the two land cover classifications are summarized in Table 2.2. The overall classification accuracy for the first time step was 93.4% or 83.2%, depending on the interpreter, (a) or (b). Producer and user accuracies for the evergreen/mixed woodland class for this time step were 90.3% and 93.3% and 70.3% and 86.7% for Interpreters (a) and (b), respectively. Kappa coefficients of agreement were 0.87 and 0.67. Accuracy assessments for the second time step demonstrated similar results, with overall classification accuracies of 93.1% and 86.3%. Producer and user accuracies for the evergreen/mixed woodland class for this time step were 84.6% and 95.7% for Interpreter (a) and 70.0% and 91.3% for Interpreter (b). Kappa coefficients of agreement for the second time step were 0.86 and 0.74.

Accuracy assessment results for the change detection between the two time steps are reported in Table 2.3. Overall classification accuracies were 80.4% and 70.1% for Interpreters (a) and (b) and Kappa coefficients of agreement were lower than for the individually classified maps in each time step (0.68 and 0.58). For Interpreter (a), producer and user accuracies for evergreen/mixed woodland to evergreen/mixed woodland were quite high; 70.0% and 100.0% respectively. However, these same percentages for Interpreter (b) were lower, with only 65.7% for producer accuracy and 82.1% for user accuracy.

As expected, the results indicate warbler habitat has changed (Fig. 2.2). From 1999–2001 to 2010–2011, the total amount of delineated warbler habitat decreased from 2,219,168 ha to 1,578,281 ha (29% loss). As mentioned above, we quantified habitat patch metrics for each warbler recovery unit in each time step (Fig. 2.3). It is worth

noting that changes in habitat patch metrics are not directly comparable between recovery units because the units are different sizes and differ in overall shape. Therefore, one should not expect each unit to have the identical habitat patch metrics. Instead, we should examine how habitat patch metrics changed over time within a recovery unit.

Table 2.2 Error matrices of the two independent accuracy assessments completed for the woodland images in each time step.

Mosaicked image	Producer's accuracy (%)	User's accuracy (%)	Overall accuracy (%)	Kappa coefficient of agreement
1999–2001				
Interpreter (a)				
Evergreen/Mixed Woodlands	90.3	93.3	93.4	0.87
Deciduous Woodlands	80.0	88.9		
Other	96.9	94.0		
Interpreter (b)				
Evergreen/Mixed Woodlands	70.3	86.7	83.2	0.67
Deciduous Woodlands	75.0	33.3		
Other	90.8	88.1		
2010–2011				
Interpreter (a)				
Evergreen/Mixed Woodlands	84.6	95.7	93.1	0.86
Deciduous Woodlands	80.0	72.7		
Other	98.5	95.6		
Interpreter (b)				
Evergreen/Mixed Woodlands	70.0	91.3	86.3	0.74
Deciduous Woodlands	70.0	63.6		
Other	96.8	88.2		

Notes: Interpreter (a) accuracy assessments were performed by A. Duarte. Interpreter (b) accuracy assessments were performed by J. Jensen. Points were generated using random sampling and were assessed using visual interpretation.

Table 2.3 Error matrices of the two independent accuracy assessments completed for the woodland change image.

Mosaicked image	Producer's accuracy (%)	User's accuracy (%)	Overall accuracy (%)	Kappa coefficient of agreement
Interpreter (a)				
Evergreen/Mixed to Evergreen/Mixed	70.0	100.0	80.4	0.68
Evergreen/Mixed to Deciduous	100.0	12.5		
Evergreen/Mixed to Other	85.7	60.0		
Deciduous to Evergreen/Mixed		
Deciduous to Deciduous	18.2	66.7		
Deciduous to Other	100.0	40.0		
Other to Evergreen/Mixed	100.0	33.3		
Other to Deciduous	100.0	33.3		
Other to Other	90.4	94.4		
Interpreter (b)				
Evergreen/Mixed to Evergreen/Mixed	65.7	82.1	70.1	0.58
Evergreen/Mixed to Deciduous		
Evergreen/Mixed to Other	50.0	40.0		
Deciduous to Evergreen/Mixed	0.0	0.0		
Deciduous to Deciduous	16.7	66.7		
Deciduous to Other	33.3	20.0		
Other to Evergreen/Mixed	100.0	66.7		
Other to Deciduous	66.7	33.3		
Other to Other	88.3	92.2		

Notes: Interpreter (a) accuracy assessments were performed by A. Duarte. Interpreter (b) accuracy assessments were performed by J. Jensen. Points were generated using random sampling and were assessed using visual interpretation. Ellipses indicate classes that were not represented in the assessments because of the low number of total pixels in those particular classes.

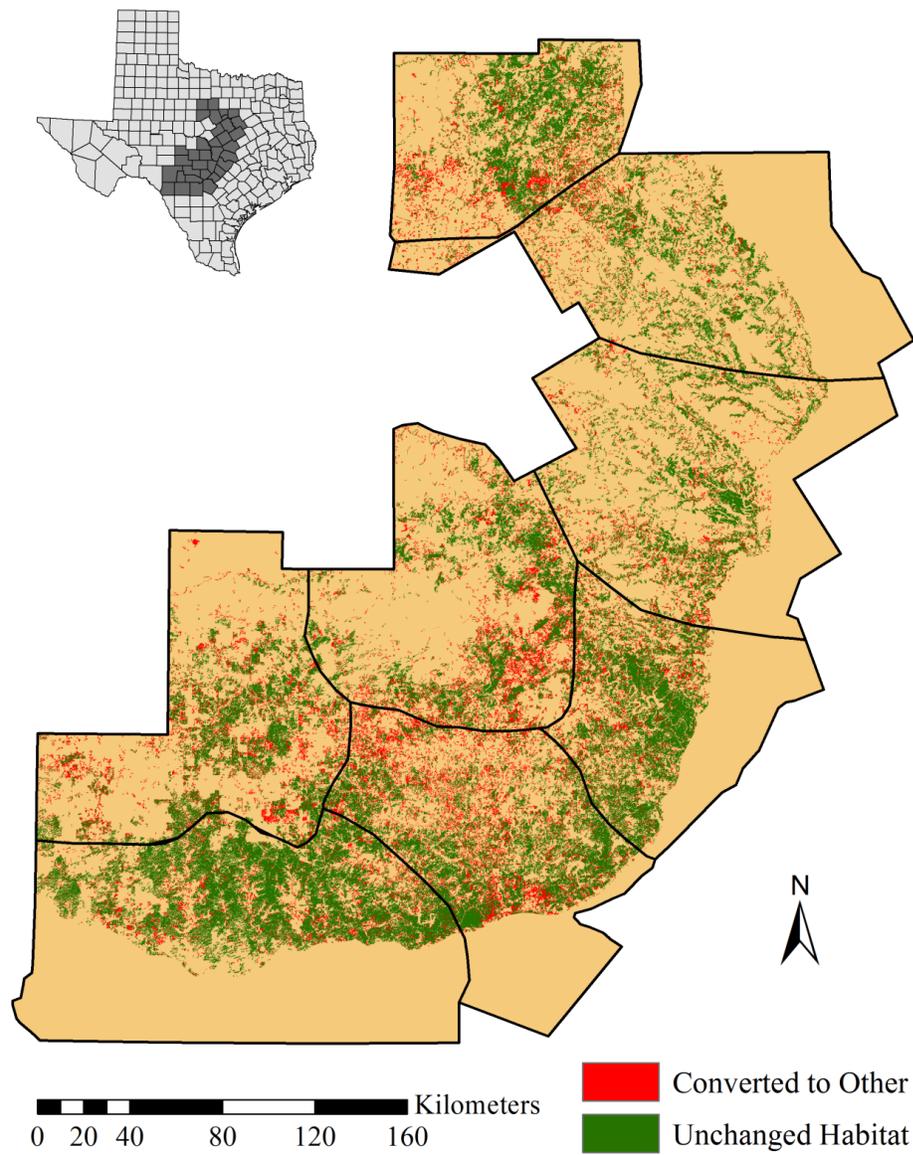


Figure 2.2 Range-wide Golden-cheeked Warbler (*Setophaga chrysoparia*) breeding habitat loss from 1999–2001 to 2010–2011.

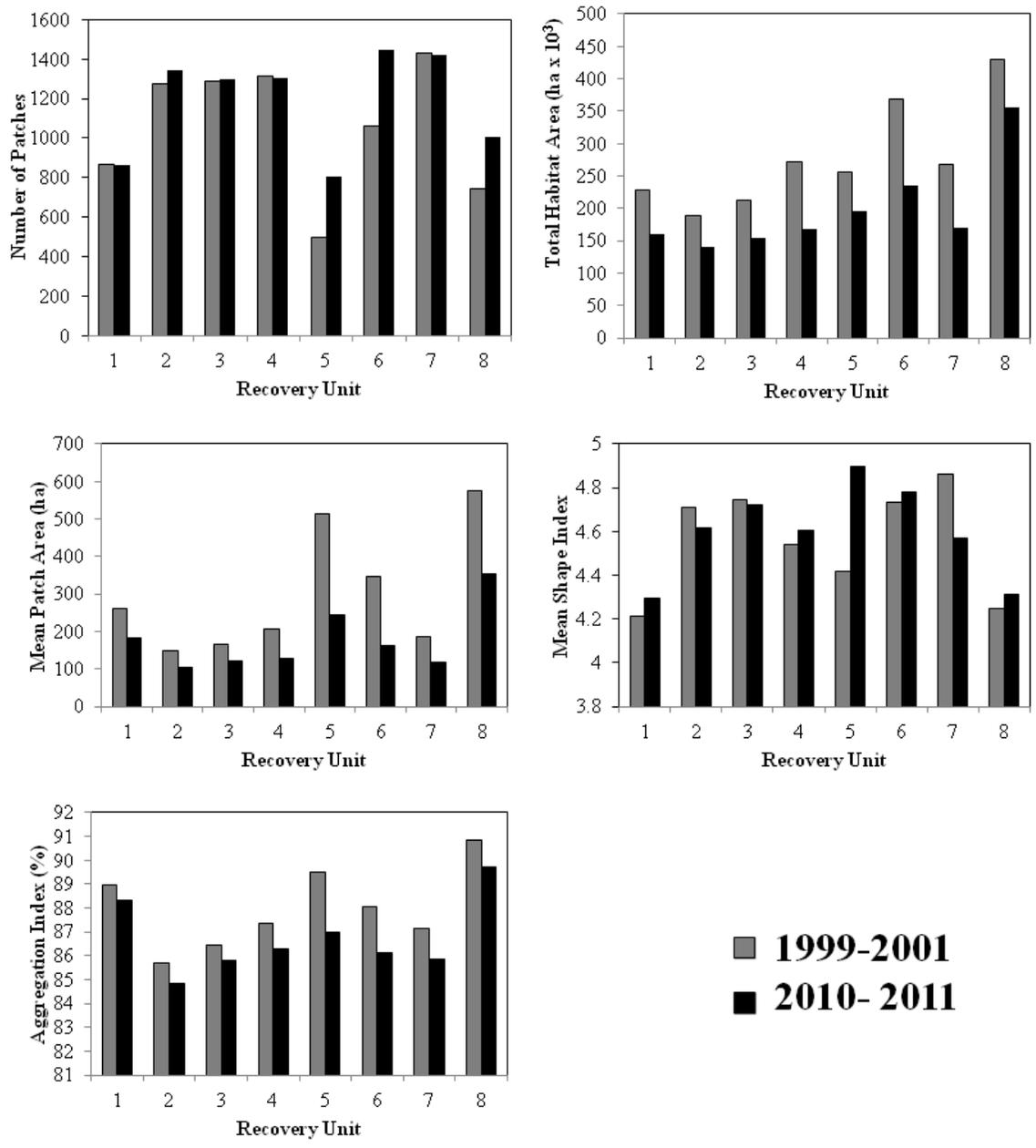


Figure 2.3 Breeding habitat patch metrics per Golden-cheeked Warbler (*Setophaga chrysoparia*) recovery unit at each time step.

DISCUSSION

We were able to quantify the change in range-wide warbler breeding habitat and describe pertinent warbler habitat patch metrics for each of the species' recovery units over a roughly 10 year period. There was an estimated 29% loss in range-wide warbler breeding habitat from 1999–2001 to 2010–2011. Indeed, such a large reduction in breeding habitat is a function of the additive influence of direct warbler breeding habitat loss, our minimum habitat patch size criterion, and that we did not consider gained warbler breeding habitat as habitat. We chose these criteria because we set out to examine the dynamics of habitat patches that were large enough to support warbler reproduction, and it likely takes several decades for woodlands to establish and become viable warbler breeding habitat. In all recovery units, we found the total habitat area, mean habitat patch size, and habitat patch aggregation index decreased from the first time step to the second time step. Percent loss in habitat for recovery units one through eight was 30, 26, 27, 38, 23, 36, 36, and 17, respectively. Reduction in mean habitat patch size was more pronounced in recovery units five, six, and eight. Aggregation index had a greater decrease in recovery units five and six. Mean habitat patch shape index was variable, with the largest change occurring in recovery units five and seven. The total number of habitat patches showed little change in most recovery units (exceptions were units five, six, and eight). Collectively, these patterns suggest that warbler reproductive success and overall carrying capacity has been dramatically reduced during this time period. Moreover, the patterns identified here raise concern regarding habitat connectivity. Alldredge et al. (2004) modeled warbler populations between the Fort Hood Military Reservation and the city of Austin and found movement between habitat patches

was needed in order for populations to persist. Furthermore, reduced connectivity of habitat patches may lead to increased genetic differentiation among warbler populations and a decline in genetic diversity over time (Lindsay et al. 2008, Athrey et al. 2011). Yet, movement rates and distances have not been quantified for this species.

Interestingly, a majority of warbler habitat conservation dollars have been spent conserving warbler breeding habitat on the outskirts of the city of Austin, Travis County (recovery unit five). Yet, our findings suggest warbler habitat is being removed and becoming more fragmented at equal, if not greater, rates (than in recovery unit five) on the outskirts of the city of San Antonio, Bexar County (recovery unit six) and throughout recovery unit eight. Given the scarcity of non-privately owned warbler breeding habitat in recovery unit eight (Hatfield et al. 2012), the greater number of warbler territories that can be supported per hectare in the southern portion of the warbler's breeding range (Mathewson et al. 2012), and the relatively high amount of habitat loss and fragmentation occurring in recovery unit eight, future warbler habitat conservation efforts focused in unit eight might be a more effective range-wide breeding habitat conservation strategy in order to preserve large breeding habitat patches that support a greater number of warblers while they are still available.

Notably, our image for the second time step classifies woodlands in central Texas, and by extension potential warbler breeding habitat, with high accuracy. Thus, it can serve as yet another warbler breeding habitat map to be used in large-scale warbler conservation planning. Each of the more recent warbler breeding habitat maps (i.e., the one produced here, Diamond et al. 2010, and Collier et al. 2012) uses a classification scheme that is considered acceptable to delineate warbler breeding habitat. Yet, each

warbler habitat map has its own advantages, disadvantages, and inherent assumptions. Thus, careful consideration should be conducted to determine which warbler habitat map better meets the requirements of a specific individual conservation objective in order to decide which warbler habitat map to use. Or perhaps all warbler habitat maps could be used in a multi-model inference framework (e.g., ensemble models weighted by differences in imagery age, target metric [occupancy, reproductive success, etc.], and/or other planning value) to identify breeding habitat patches of high conservation value. However, it should be noted that each of these warbler habitat maps (including the one presented here) is based off imagery that can be considered somewhat outdated. The Diamond et al. (2010) warbler habitat map is derived from the vegetation classifications done as part of the Texas Ecological Systems Classification Phase 1. The images used in this classification were acquired from 2005 to 2007. The Collier et al. (2012) warbler habitat map is based off 2007–2008 Landsat TM images. Although we recognize there will always be time lags between satellite image acquisition dates and image classifications, especially at the scale of the warbler’s entire breeding range, all warbler breeding habitat maps are based on imagery taken prior to a significant, landscape altering event. In the summer of 2011, central Texas experienced severe drought conditions that resulted in die offs of many oak and juniper trees (Kukowski et al. 2013). Thus, current warbler habitat maps may have large errors of commission (i.e., false positives), and should be updated, when feasible, for more reliable large-scale warbler conservation planning to take place.

Of particular importance with regard to these results are the differences in classification accuracy and sources of uncertainty that are introduced to the analysis at

different stages. For example, though every effort was made to download temporally consistent satellite image tiles, minor differences in green-up and senescence attributed to temperature or timing of precipitation may have resulted in mislabeled clusters for the individual time steps. Additionally, the use of NAIP imagery as the reference dataset, presents particular challenges with regard to visual interpretation and its use as a reference source. For instance, NAIP imagery for a region is frequently acquired over the course of days to weeks and during inconsistent satellite-sun geometries, whereby shadows and shading can be introduced to the final image product such that overall species composition looks more dense or spectrally similar to different land cover classes (i.e., Ashe juniper and broadleafed evergreen species such as live oak).

Another consideration with regard to land cover classification is the differentiation between forest/woodland and shrubland. Ashe juniper shrublands may appear spectrally similar particularly to the evergreen/mix woodland class, though the difference is based on height, an attribute not available with Landsat imagery. Thus, individual class accuracies may have been influenced by interpreter-specific identification of woodland and shrubland and may have led to artificial gains and losses of warbler habitat. Using LiDAR technology to remotely measure vegetation height could help distinguish woodlands from shrublands and has been shown to do well in predicting warbler occurrence at the site level (Farrell et al. 2013). Still, these types of data are not available for historic imagery spanning the warbler's entire breeding range. Further, optimal LiDAR based vegetation height metrics that accurately represent forest canopy characteristics at a 30 m resolution have not been determined (Jensen et al. 2013).

Therefore, LiDAR based vegetation metrics were not included in this classification scheme.

Regardless, overall classification accuracies of 93.4% (or 83.2%) and 93.1% (or 86.3%) are high, and the overall Kappa coefficient of agreements (0.87 [or 0.67] and 0.86 [or 0.74]) indicated we had moderate-to-strong agreement between our classified maps and the reference dataset. Further, we had decent classification accuracy for the woodland change image, particularly given the geographic extent of the image. Collectively, this indicates we were able to quantify actual change in warbler breeding habitat over time.

It should be noted, however, that in the context of landscape change analyses, land cover classification, habitat identification, and the selection of metrics used to characterize change over time must be considered. Our selection of landscape metrics was guided by the need to quantify changes in warbler breeding habitat area, patch shape, as well as potential fragmentation within each of the species' recovery units. Further, we selected metrics that we considered would be easily interpretable to a wide audience of resource managers and policy makers, regardless of biogeographic, ecological, or geospatial expertise and training. Nonetheless, selection of metrics may in some cases influence how landscape change is quantified and interpreted, particularly when the analysis is focused on characterizing or understanding underlying landscape processes and species modeling.

In summary, we found that there was a large reduction in range-wide warbler breeding habitat and that warbler breeding habitat was removed and became more fragmented at uneven rates across the warbler's breeding range. This information will assist researchers and managers in prioritizing breeding habitat conservation efforts

across recovery units, and highlights the significance in estimating warbler movement rates and distances in order to assess the degree of connectivity between increasingly fragmented habitat patches. Further, it would be useful to incorporate these rates of habitat change into warbler population models in order to extrapolate how long the species can be sustained given current habitat dynamics.

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LITERATURE CITED

- Allredge, M. W., J. S. Hatfield, D. D. Diamond, and C. D. True. 2004. Golden-cheeked warbler (*Dendroica chrysoparia*) in Texas: importance of dispersal toward persistence in a metapopulation. Pages 372–383 in H. R. Akçakaya, M. A. Burgman, O. Kindvall, C. C. Wood, P. Sjögren-Gulve, J. S. Hatfield, and M. A. McCarthy, editors. Species conservation and management: case studies. Oxford University Press, New York, New York, USA.
- Athrey, G., D. L. Lindsay, R. F. Lance, and P. L. Leberg. 2011. Crumbling diversity: comparison of historical archived and contemporary natural populations indicate reduced genetic diversity and increasing genetic differentiation in the golden-cheeked warbler. *Conservation Genetics* 12:1345–1355.
- Butcher, J. A., M. L. Morrison, D. Ransom, R. D. Slack, and R. N. Wilkins. 2010. Evidence of a minimum patch size threshold of reproductive success in an endangered songbird. *Journal of Wildlife Management* 74:133–139.
- Chander, G., B. L. Markham, and D. L. Helder. 2009. Summary of current radiometric calibration coefficients for Landsat MSS, TM, ETM_p, and EO-1 ALI sensors. *Remote Sensing of Environment* 113:893–903.
- Collier, B. A., J. E. Groce, M. L. Morrison, J. C. Newnam, A. J. Campomizzi, S. L. Farrell, H. A. Mathewson, R. T. Snelgrove, R. J. Carroll, and R. N. Wilkins. 2012. Predicting patch occupancy in fragmented landscapes at the rangewide scale for an endangered species: an example of an American warbler. *Diversity and Distributions* 18:158–167.
- Formatted for publication in Ecosphere.

- Collier, B. A., M. L. Morrison, S. L. Farrell, A. J. Campomizzi, J. A. Butcher, K. B. Hays, D. I. Mackenzie, and R. N. Wilkins. 2010. Monitoring golden-cheeked warblers on private lands in Texas. *Journal of Wildlife Management* 74:140–147.
- Congalton, R. G., and K. Green. 1999. Assessing the accuracy of remotely sensed data: principles and practices. Lewis, Boca Raton, Florida, USA.
- Diamond, D. D., L. F. Elliott, C. Blodgett, C. D. True, D. German, and A. Treuer-Kuehn. 2010. Texas Ecological Systems Classification Project. Missouri Resource Assessment Partnership (MoRAP). University of Missouri, Columbia, and the Texas Parks and Wildlife Department, Austin, Texas, USA.
<http://morap.missouri.edu/Projects.aspx?ProjectId/457>
- Farrell, S. L., B. A. Collier, K. L. Skow, A. M. Long, A. J. Campomizzi, M. L. Morrison, K. B. Hays, and R. N. Wilkins. 2013. Using LiDAR-derived vegetation metrics for high-resolution, species distribution models for conservation planning. *Ecosphere* 4:42.
- Groce, J. E., H. A. Mathewson, M. L. Morrison, and N. Wilkins. 2010. Scientific evaluation for the 5-year status review of the golden-cheeked warbler. Texas A&M Institute of Renewable Natural Resources, College Station, Texas, USA.
- Hatfield, J. S., F. W. Weckerly, and A. Duarte. 2012. Shifting foundations and metrics for golden-cheeked warbler recovery. *Wildlife Society Bulletin* 36:415–422.
- Jensen, J. L. R., S. Irvin, and A. Duarte. 2013. Lidar-based detection of shrubland and forest land cover to improve identification of Golden-cheeked Warbler habitat. *Papers in Applied Geography* 36:74–82.

- Kroll, J. C. 1980. Habitat requirements of the golden-cheeked warbler: management implications. *Journal of Range Management* 33:60–65.
- Kukowski, K. R., S. Schwinning, and B. F. Schwartz. 2013. Hydraulic responses to extreme drought conditions in three co-dominant tree species in shallow soil over bedrock. *Oecologia* 171:819–830.
- Ladd, C., and L. Gass. 1999. Golden-cheeked warbler (*Dendroica chrysoparia*). Account 420 in A. Poole and F. Gill, editors. *The birds of North America*. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.
- Lindsay, D. L., K. R. Barr, R. F. Lance, S. A. Tweddale, T. J. Hayden, and P. L. Leberg. 2008. Habitat fragmentation and genetic diversity of an endangered, migratory songbird, the golden-cheeked warbler (*Dendroica chrysoparia*). *Molecular Ecology* 17:2122–2133.
- Mathewson, H. A., J. E. Groce, T. M. McFarland, M. L. Morrison, R. T. Newnam, R. T. Snelgrove, B. A. Collier, and R. N. Wilkins. 2012. Estimating breeding season abundance of golden-cheeked warblers in Texas, USA. *Journal of Wildlife Management* 76:1117–1128.
- McFarland, T. M., H. A. Mathewson, J. E. Groce, M. L. Morrison, J. C. Newnam, R. T. Snelgrove, K. L. Skow, B. A. Collier, and R. N. Wilkins. 2012. Utilization of a species occupancy model for management and conservation. *Wildlife Society Bulletin* 36:432–439.

- McGarigal, K., S. A. Cushman, and E. Ene. 2012. FRAGSTATS v4: Spatial pattern analysis program for categorical and continuous maps. University of Massachusetts, Amherst, Massachusetts, USA.
- Morrison, M. L., R. N. Wilkins, B. A. Collier, J. E. Groce, H. A. Mathewson, T. M. McFarland, A. G. Snelgrove, R. T. Snelgrove, and K. L. Skow. 2010. Golden-cheeked warbler population distribution and abundance. Texas A&M Institute of Renewable Natural Resources, College Station, Texas, USA.
- Peak, R. G. 2007. Forest edges negatively affect golden-cheeked warbler nest survival. *Condor* 109:628–637.
- Pulich, W. M. 1976. *The Golden-cheeked Warbler: A bioecological study*. Texas Parks and Wildlife, Austin, Texas, USA.
- Reemts, C. M., and L. L. Hansen. 2008. Slow recolonization of burned oak-juniper woodlands by Ashe juniper (*Juniperus ashei*): Ten years of succession after crown fire. *Forest Ecology and Management* 255:1057–1066.
- Reidy, J. L., F. R. Thompson, and R. G. Peak. 2009. Factors affecting golden-cheeked warbler nest survival in urban and rural landscapes. *Journal of Wildlife Management* 73:407–413.
- Tortora, R. 1978. A note on sample size estimation for multinomial populations. *American Statistician* 32:100–102.
- U.S. Fish and Wildlife Service. 1990. Endangered and threatened wildlife and plants; final rule to list the golden-cheeked warbler as endangered. *Federal Register* 55:53153–53160.

- U.S. Fish and Wildlife Service. 1992. Golden-cheeked warbler (*Dendroica chrysoparia*) recovery plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.
- Veran, S., K. J. Kleiner, R. Choquet, J. A. Collazo, and J. D. Nichols. 2012. Modeling habitat dynamics accounting for possible misclassification. *Landscape Ecology* 27:943–956.
- Warren, C. C., J. R. Ott, and J. A. Veech. 2013. Comparative occupancy and habitat associations of black-and-white (*Mniotilta varia*) and golden-cheeked warblers (*Setophaga chrysoparia*) in the juniper-oak woodlands of central Texas. *American Midland Naturalist* 169:382–397.
- Zitske, B. P., M. G. Betts, and A. W. Diamond. 2011. Negative effects of habitat loss on survival of migrant warblers in a forest mosaic. *Conservation Biology* 25:993–1001.

CHAPTER III

AGE-SPECIFIC SURVIVAL OF MALE GOLDEN-CHEEKED WARBLERS ON THE FORT HOOD MILITARY RESERVATION, TEXAS¹

ABSTRACT. Population models are essential components of large-scale conservation and management plans for the federally endangered Golden-cheeked Warbler (*Setophaga chrysoparia*; hereafter GCWA). However, existing models are based on vital rate estimates calculated using relatively small data sets that are now more than a decade old. We estimated more current, precise adult and juvenile apparent survival (Φ) probabilities and their associated variances for male GCWAs. In addition to providing estimates for use in population modeling, we tested hypotheses about spatial and temporal variation in Φ . We assessed whether a linear trend in Φ or a change in the overall mean Φ corresponded to an observed increase in GCWA abundance during 1992–2000 and if Φ varied among study plots. To accomplish these objectives, we analyzed long-term GCWA capture-resight data from 1992 through 2011, collected across seven study plots on the Fort Hood Military Reservation using a Cormack-Jolly-Seber model structure within program MARK. We also estimated Φ process and sampling variances using a variance-components approach. Our results did not provide evidence of site-specific variation in adult Φ on the installation. Because of a lack of data, we could not assess whether juvenile Φ varied spatially. We did not detect a strong temporal association between GCWA abundance and Φ . Mean estimates of Φ for adult and juvenile male GCWAs for all years analyzed were 0.47 with a process variance of 0.0120 and a

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sampling variance of 0.0113 and 0.28 with a process variance of 0.0076 and a sampling variance of 0.0149, respectively. Although juvenile Φ did not differ greatly from previous estimates, our adult Φ estimate suggests previous GCWA population models were overly optimistic with respect to adult survival. These updated Φ probabilities and their associated variances will be incorporated into new population models to assist with GCWA conservation decision making.

INTRODUCTION

The Golden-cheeked Warbler (*Setophaga chrysoparia*; hereafter GCWA) is a neotropical migrant passerine that breeds almost exclusively in the mature oak-juniper woodlands of central Texas (Pulich 1976). Motivated by concerns about the GCWA's restricted breeding range and the perceived ongoing loss of breeding habitat, the species was listed as endangered by the U. S. federal government in 1990 (USFWS 1990; R. Wahl, D. D. Diamond, and D. Shaw, *unpublished manuscript*). Following the species' federal listing, a recovery plan was produced that described the species' basic biology and various threats, separated the GCWA's breeding range into eight regions to manage the species' recovery process, and established recovery criteria that must be met before the GCWA can be downlisted (USFWS 1992).

Given that the criteria to downlist the species include "sufficient breeding habitat has been protected to ensure the continued existence of at least one viable, self-sustaining population in each of 8 regions outlined in the plan" (USFWS 1992:iv), it is no surprise that population models are currently being used to assist in GCWA conservation efforts

(USFWS 1996, Alldredge et al. 2004, Vaillant et al. 2004, Horne et al. 2011). Natural resource agencies are currently operating under the population viability analysis (PVA) results of Alldredge et al. (2004). Their model suggests that enough good-quality breeding habitat in each of the eight regions with the potential to support a carrying capacity of 3000 breeding pairs is required to ensure a low probability of extinction for GCWAs over the next 100 years. Fortunately, the amount of breeding habitat currently available is well above this threshold, because it supports an estimated 263,339 (95% confidence interval = 223,927-302,620) male GCWAs across the entire breeding range (Mathewson et al. 2012). However, the current amount of breeding habitat on publicly owned property in each region outlined in the species' recovery plan does not support that many male GCWAs (Hatfield et al. 2012a), and breeding habitat located on privately owned property is not certain to be protected and available in the future (Groce et al. 2010, Duarte et al. 2013).

Fundamental to projecting population dynamics are up-to-date estimates of abundance and vital rates. In the case of territorial songbirds such as the GCWA, females are more difficult to detect than males. Consequently, population parameters are often reported for male birds, and population models focus on the male segment of the species. Previous GCWA PVAs used vital rate estimates that are now more than 10 years old, did not have access to a robust abundance estimate for the initial starting point of abundances at year one of the simulations, did not incorporate geographic variability in reproductive success, and only modeled a portion of the species' breeding range. Thus, a new PVA is warranted and might significantly alter our outlook on GCWA viability. In recent years

much effort has been expended to update our knowledge on GCWA abundance and reproduction both at the local and range-wide scale (e.g., abundance, Hunt et al. 2012, Mathewson et al. 2012, Collier et al. 2013, Peak and Thompson 2013, Warren et al. 2013; reproduction, Campomizzi et al. 2012, Klassen et al. 2012, Marshall et al. 2013). Apparent survival (Φ) has been estimated for juvenile (hatch year, HY) and adult (after hatch year, AHY) male GCWAs while accounting for imperfect detection in the past, where Φ is the probability that an individual remains alive and returns to the study area from one sampling occasion to the next. Still, these estimates were derived from studies consisting of only five years of data collected on a single study plot, with the 2001 field season being the most recent data analyzed (USFWS 1996, Alldredge et al. 2004). In the absence of up-to-date robust Φ estimates, GCWA return rates, i.e., the proportion of marked individuals from one year that are resighted in subsequent years, are often used by resource agencies as an indication of annual survival (Peak and Grigsby 2011, Travis County 2011). However, return rates do not account for imperfect detection and are notorious for being negatively biased (Martin et al. 1995).

Our aim was to update HY and AHY male GCWA annual Φ estimates, and their associated variances, using long-term capture-resight data collected on seven plots within the Fort Hood Military Reservation (hereafter Fort Hood) to use in future population models. Unlike previous studies, we had the opportunity to test for spatial variability in GCWA Φ on the installation. We hypothesized that GCWA Φ would vary among study plots. Our justification for expecting spatial variability in Φ was related to differences in emigration rates because of habitat structure within each plot, rather than carryover

effects of breeding habitat on annual mortality. That is, individuals might choose to breed in alternate locations in subsequent years if the habitat structure within a given plot was not amenable to successful territories, i.e., territories that fledge young, which could result in spatial differences in Φ estimates. Furthermore, long-term point-count data collected on the installation suggest a positive trend in GCWA densities from 1992 to 2001, after which the population began to show evidence of stabilization (Fig 3.2 in Peak 2011a). However, pairing success, territory success, nest survival, and return-rate data do not indicate temporal trends (reviewed in Groce et al. 2010). Golden-cheeked Warbler Φ might be directly related to the observed population dynamics in at least two nonmutually exclusive ways. Apparent survival might be inversely related to abundance because of density dependence. Also, a larger overall mean Φ during the population increase, followed by a lower mean Φ during the population stabilization period, might be driving the observed population dynamics. Thus, we tested two hypotheses concerning temporal variability in GCWA Φ on the installation: (1) a negative linear trend in Φ corresponds to the observed increase in GCWA densities; and (2) the overall mean Φ during intervals between 1992 and 2001 was greater than the overall mean Φ during intervals between 2001 and 2011.

METHODS

Sampling protocol

Field work for this study was conducted on Fort Hood, a 87,890-hectare contiguous parcel of land located in Bell and Coryell counties, central Texas (Fig. 3.1).

Approximately 21,422 hectares of GCWA breeding habitat are within the boundaries of

Fort Hood (Hayden et al. 2001). Baccus et al. (2007) provide a detailed description of the environments on Fort Hood and the protocols used to monitor GCWAs. Briefly, from April to June GCWAs were captured in mist nets using playback recordings of conspecific songs as an attractant. Then age and sex were determined for each bird using methods described by Pyle (1997) and Peak and Lusk (2011). All birds captured were uniquely marked using both U.S. Geological Survey aluminum bands and a distinctive combination of plastic, colored leg bands. Monitoring efforts occurred every five days for at least two hours in an effort to resight birds that were marked in previous years, calculate density estimates via spot mapping, and collect behavioral and reproductive data (Peak 2011*b*).

From 1991 to 2011, 4035 GCWAs, both male and female birds of different age classes, were marked by various entities under different programs to achieve several objectives. However, a minimum of three years of capture-resight data are needed to calculate one estimate of Φ using a fully time-specific model (Pollock et al. 1990), and only the Nature Conservancy, in collaboration with Fort Hood, and the Monitoring Avian Productivity and Survivorship programs surveyed the same plots for at least three years (R. Peak, U.S. Army Garrison-Fort Hood, Directorate of Public Works, *personal communication*). Although the Nature Conservancy program initiated GCWA capture-resight efforts on Fort Hood in 1991, the program did not delineate any study plots until 1992. Since 1992, the Nature Conservancy program has delineated six study plots to monitor GCWA population parameters. However, surveys were not conducted on all plots across the entire time series. The Monitoring Avian Productivity and Survivorship program was

initiated on Fort Hood in 1995 and conducted annual surveys for marked birds in the same plot through the 2008 breeding season. Thus, we used capture-resight data from the seven study plots that were monitored by these two programs for at least three years (Table 3.1). Notably, once a study plot was established it was surveyed annually until monitoring ceased on that particular plot; that is, sampling intervals were all one year.



Figure 3.1 Map of the Fort Hood Military Reservation, Texas, USA, and study plots where Golden-cheeked Warbler (*Setophaga chrysoparia*) capture-resight programs occurred for at least three years. 13 B is Thirteen B, BLORA is Belton Lake Outdoor Recreation Area, SFH is South Fort Hood, M is Manning, NWFH is North West Fort Hood, SWFH is South West Fort Hood, and MAPS is Monitoring Avian Productivity and Survivorship.

Table 3.1 Years and study plots where Golden-cheeked Warbler (*Setophaga chrysoparia*) surveys were conducted by the Nature Conservancy and Monitoring Avian Productivity and Survivorship programs on the Fort Hood Military Reservation, Texas, USA. Banding and monitoring efforts were conducted from April through June. Table excludes 1991 because study plots were not delineated until 1992. 13 B is Thirteen B, BLORA is Belton Lake Outdoor Recreation Area, SFH is South Fort Hood, M is Manning, NWFH is North West Fort Hood, SWFH is South West Fort Hood, and MAPS is Monitoring Avian Productivity and Survivorship.

	Year																			
	92	93	94	95	96	97	98	99	00	01	02	03	04	05	06	07	08	09	10	11
13 B	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
MAPS				X	X	X	X	X	X	X	X	X	X	X	X	X	X			
NWFH						X	X	X	X	X	X	X	X	X						
SWFH						X	X	X	X	X	X									
BLORA							X	X	X	X	X	X								
M									X	X	X	X	X	X	X	X	X	X	X	X
SFH															X	X	X			

Survival analyses

A Cormack-Jolly-Seber model structure was used to estimate Φ (Cormack 1964, Jolly 1965, Seber 1965) with the age-specific extension of Pollock (1981) for HY birds.

During preliminary analyses we determined that six of the seven study plots had an insufficient number of HY captures and subsequent resightings. The exception was study plot Thirteen B. Consequently, two separate analyses were conducted to estimate HY and AHY Φ .

The AHY Φ analysis included capture-resight data from 1434 AHY male GCWAs captured from 1992 to 2011 on seven study plots. These data were insufficient to accommodate interaction terms when modeling sources of variation. Consequently, we began by fitting a model where Φ and resight probability (p) both varied as a function of

the additive effects of study plot and time (model $sp+t$). We then fit a series of models in which Φ and p varied among study plots (model sp), over time (model t), or neither (model $.$). Further, we used the basic structure of the best-supported model and constrained Φ to be constant across years for two sets of years; i.e., we included a separate β parameter to test for differences in Φ during intervals between 1992-2001 and 2001-2011 (model dif). If there was a difference in mean Φ during the two intervals, the separate β parameter would be different than zero. We did not test for linear trends in Φ for this analysis because of the inconsistencies in years in which study plots were monitored. For all AHY models, resight probabilities were constrained to zero for years in which a particular study plot was not monitored because there cannot be a resighting of a marked individual in a plot that was not surveyed in a given year.

Because of a lack of data in subsequent years, the HY Φ analysis only included capture-resight data from 132 HY and 233 AHY male GCWAs captured from 1992 to 2000 on study plot Thirteen B. There were insufficient data to estimate one of the HY Φ parameters when fitting a model with an interaction term between age and time. Thus, we began by fitting a model where Φ varied with age and time additively (model $a+t$) and p varied across time (model t). We then fit models where Φ varied with age (model a), time (model t), or neither (model $.$), and also fit models where p was constant (model $.$). To test for a linear trend in Φ , we used the basic structure of the best-supported model and constrained Φ to be different between age classes, with Φ for each age class having a linear trend across time (model $a+T$).

A variance-components approach was used to decompose the temporal variance of the Φ point estimates into components associated with process variance and sampling variance (Burnham and White 2002). It is suggested that this type of analysis be applied to the global model to estimate variance components for Φ using a model that does not have many constraints. We were interested in estimating a single overall mean Φ with its associated variances to use in GCWA population models. Consequently, we used an intercept variance-components model. Notably, an intercept model assumes that the underlying Φ probabilities are distributed randomly around a central mean over time. As suggested, we applied the variance-components approach to the global models for each age-class analysis, i.e., AHY analysis Φ_{sp^*t}, p_{sp^*t} , and HY analysis Φ_{a^*t}, p_t . All inestimable parameters were excluded. To make direct comparisons concerning the amount of variability in Φ , we used the mean and process variance Φ estimates to calculate the coefficient of variation (CV) of Φ for each age class.

Model selection was based on change in Akaike's Information Criterion corrected for small sample size (ΔAIC_c) and AIC_c weights (w_i), such that the best-supported model had a value of zero for ΔAIC_c and the largest w_i (Burnham and Anderson 2002). Using a parametric-bootstrap approach, the goodness of fit of the most general model, i.e., AHY analysis Φ_{sp+t}, p_{sp+t} , and HY analysis Φ_{a+t}, p_t , was tested by simulating 1000 data sets, computing the deviance for each, and then comparing the observed deviance with the distribution of deviances from the bootstrap to estimate the probability of observing a deviance as extreme as we did. If there was evidence of a lack of fit, a variance-inflation factor (\hat{c}) was estimated by dividing the observed deviance by the average simulated

deviance. All analyses were conducted using program MARK (White and Burnham 1999).

After completing the process of initial model selection, we decided to investigate the potential importance of a phenomenon that was not incorporated into the original model set for AHY birds. One possible cause of spatial variability in Φ , i.e., individuals might choose to breed in alternate locations in subsequent years, implies that transient individuals might be prevalent. However, individuals might be choosing to breed in alternate locations in subsequent years at the same rate across study plots. To test this possibility, we used the basic structure of the model in the original model set that was best supported and set apparent survival in the first interval after initial capture (Φ^1) to differ from apparent survival during subsequent intervals (Φ^2 ; see Pradel et al. 1997), considering three different scenarios: (1) Φ^1 was constant across the time series (model Φ^1, Φ^2_t); (2) Φ^1 varied across time (model Φ^1_{*t}, Φ^2_t); and (3) Φ^1 varied across time, but paralleled Φ^2 (model Φ^1_{+t}, Φ^2_t).

RESULTS

A total of 17 models were included in the original candidate model set for the AHY Φ analysis (Table 3.2). The goodness-of-fit test suggested the most general model did not fit the data well ($P < 0.001$), and \hat{c} was estimated to be 1.25. The best-supported model in the original candidate model set was model Φ_t, p_{sp} . In this model, Φ varied across time, but did not differ among study plots. Resight probabilities varied among study plots but were constant across time. Estimates of Φ ranged from 0.25 to 0.75 (Fig. 3.2), and

estimates of p ranged from 0.32 to 1, depending on the study plot. In the model that tested for temporal differences in the mean Φ , i.e., Φ_{dif}, p_{sp} , the β parameter reflecting the difference between the two periods was estimated at 0.40 (95% confidence interval = 0.19–0.61). Thus, this model suggested the mean Φ during the interval 1992–2001 was 10% higher than mean Φ during the interval 2001–2011. However, this model had little support, ranking tenth overall. Using variance components, we estimated that the overall mean \pm SE AHY Φ was 0.47 ± 0.02 , with process and sampling variances of 0.0120 and 0.0113, respectively. The CV for AHY Φ was 0.23.

As described above, we took the basic structure of the low-AIC model for the AHY analysis and added transient parameters in three different ways. The transient model ($\Phi^1_{+t}, \Phi^2_t, p_{sp}$) actually had a lower AIC_c , by 3.88 AIC_c units, than model Φ_t, p_{sp} . The transient models dealt with the possibility of transient birds by allowing Φ^1 to differ from, i.e., be smaller than, Φ^2 . However, the a posteriori transient models estimated higher, not lower, Φ probabilities for individuals that were newly marked; estimates were 5% to 7% higher. These estimates were not consistent with the existence of transients. We could think of no a posteriori hypothesis for this pattern in Φ that was biologically relevant, so we based our inferences on the original model set shown in Table 3.2.

For the HY Φ analysis, Φ varied additively between age classes and across time, but p was constant across time (Table 3.3). The goodness-of-fit test suggested that the most general model fit the data ($P = 0.11$). Thus, we assumed \hat{c} was equal to one. Estimated HY Φ probabilities ranged from 0.17 to 0.46 (Fig. 3.2). For this analysis, the mean

estimated AHY Φ was 0.54 and estimated p was 0.84. The model that constrained Φ to vary linearly across time, i.e., $\Phi_{a+T}, p.$, suggested there was a negative linear trend in AHY and HY Φ probabilities from 1992 to 2000. This model, however, ranked third overall, with a weight of only 0.06. Using variance components, we estimated that the overall mean \pm SE HY Φ was 0.28 ± 0.06 , with process and sampling variances of 0.0076 and 0.0149, respectively. The CV for HY Φ was 0.31.

Table 3.2 Model selection statistics for after-hatch-year male Golden-cheeked Warbler (*Setophaga chrysoparia*) capture-resight data from seven study plots on the Fort Hood Military Reservation, Texas, USA, 1992–2011. Model selection was corrected for overdispersion and based on change in Akaike’s Information Criterion corrected for small sample size (ΔQAIC_c) and QAIC_c weights (w_i) such that the best-supported model had the smallest ΔQAIC_c and the largest w_i . Φ - apparent survival probability, p - resight probability, $sp+t$ - study plot and time, sp - study plot, t - time, $.$ - constant, dif - separate β parameter for intervals during 1992-2001.

Model	ΔQAIC_c	w_i	K	QDev
$\Phi_b p_{sp}$	0.00	0.87	26	388.70
$\Phi_{sp+b} p_{sp}$	4.01	0.12	32	380.37
$\Phi_b p_{sp+t}$	10.12	0.01	43	363.70
$\Phi_{sp+b} p.$	14.56	0.00	26	403.26
$\Phi_{.} p_{sp+t}$	15.04	0.00	26	403.74
$\Phi_b p.$	15.35	0.00	20	416.31
$\Phi_{sp+b} p_{sp+t}$	17.64	0.00	49	358.69
$\Phi_{sp+b} p_t$	18.01	0.00	43	371.59
$\Phi_b p_t$	18.10	0.00	37	384.14
$\Phi_{dif} p_{sp}$	18.97	0.00	9	442.24
$\Phi_{.} p_t$	19.82	0.00	20	420.78
$\Phi_{sp} p_t$	20.21	0.00	26	408.91
$\Phi_{sp} p_{sp+t}$	23.65	0.00	32	400.02
$\Phi_{.} p_{sp}$	30.75	0.00	8	456.03
$\Phi_{sp} p_{sp}$	40.58	0.00	14	453.73
$\Phi_{.} p.$	47.81	0.00	2	485.15
$\Phi_{sp} p.$	49.57	0.00	8	474.86

Table 3.3 Model selection statistics for capture-resight data for hatch-year and after-hatch-year male Golden-cheeked Warblers (*Setophaga chrysoparia*) from study plot Thirteen B, Fort Hood Military Reservation, Texas, USA, 1992–2000. Model selection was based on change in Akaike’s Information Criterion corrected for small sample size (ΔAIC_c) and AIC_c weights (w_i) such that the best-supported model had the smallest ΔAIC_c and the largest w_i . Φ - apparent survival probability, p - resight probability, $a+t$ - age and time, a - age, t - time, $.$ - constant, T - linear trend.

Model	ΔAIC_c	w_i	K	Dev
$\Phi_{a+t}, p, .$	0.00	0.78	10	117.87
$\Phi_{a}, p, .$	3.36	0.15	3	135.62
$\Phi_{a+T}, p, .$	5.21	0.06	4	135.43
Φ_{a+t}, p, t	8.31	0.01	16	113.52
Φ_{a}, p, t	12.90	0.00	10	130.77
$\Phi_{.}, p, .$	22.19	0.00	2	156.46
Φ_{t}, p, t	30.26	0.00	15	137.60
$\Phi_{.}, p, t$	32.12	0.00	9	152.07

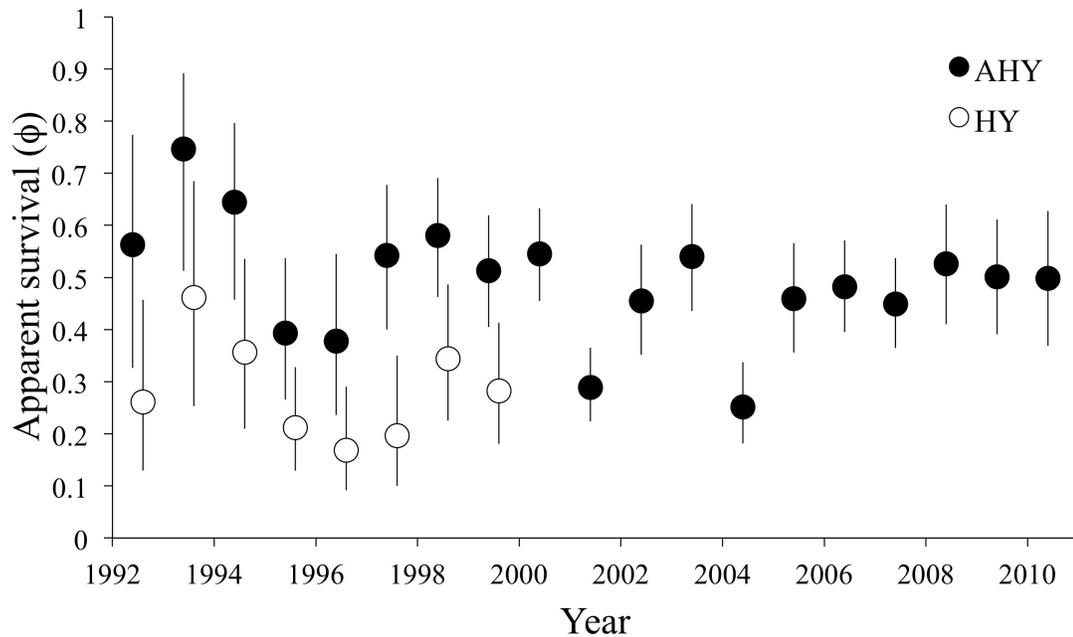


Figure 3.2 Annual probabilities of apparent survival for hatch-year (HY-open circles) and after-hatch-year (AHY-solid circles) male Golden-cheeked Warblers (*Setophaga chrysoparia*) on the Fort Hood Military Reservation, Texas, USA. For AHY birds, apparent survival (Φ) varied across time, and resight probability (p) differed among study plots (Φ_t, p_{sp}). For HY birds, Φ varied additively between age classes and across time, and p was constant ($\Phi_{a+t}, p.$). Error bars are 95% confidence intervals.

DISCUSSION

We present, to our knowledge, the first detailed analysis to estimate Φ for the Golden-cheeked Warbler. Using long-term male GCWA capture-resight data collected within multiple study plots on Fort Hood, we were able to test for spatial and temporal patterns in AHY and HY Φ , and calculate more precise Φ estimates and their process and sampling variances. We found little evidence linking the observed GCWA population dynamics to temporal patterns in Φ . Nor did we detect spatial variation in Φ . The overall mean HY Φ estimate did not differ greatly from previous estimates for the species.

However, the lower overall mean AHY Φ estimate reported herein suggests that previous GCWA PVAs might have been overly optimistic with respect to AHY Φ .

A negative linear trend in Φ from 1992 to 2000 was detected using a model that incorporated a linear trend in the HY analysis, and there was evidence that the mean Φ during intervals between 1992 and 2001 was higher than the mean Φ during intervals between 2001 and 2011 in the AHY analysis. Why these patterns emerged is unclear, because these estimates were the product of both true survival and fidelity, which is the complement of permanent emigration. It is possible that as GCWA densities increased on Fort Hood and approached carrying capacity, GCWA dispersal rates increased as available suitable habitat became more limited; that carryover effects from GCWA densities during the breeding season were impacting true survival; or that a change in overall mean Φ was driving the observed GCWA population dynamics. However, it is also possible that these patterns were a result of a few years with inclement weather conditions during migration that caused Φ to fluctuate in response to increased mortality (Stokke et al. 2005), and/or caused birds to be blown off course and establish territories in alternate locations. Regardless, these models had little support compared with models with time-varying Φ that were not constrained to a trend.

We predicted that GCWA Φ would vary spatially because of potential differences in emigration rates due to habitat structure within each plot. Differences in habitat patch area, landscape composition, i.e., percentage of woodlands within a 400-meter radius, woodland edge, and woodland height have been linked to variation in GCWA occupancy

and abundance across Fort Hood (Collier et al. 2013, Farrell et al. 2013, Peak and Thompson 2013), and therefore support this possibility. However, the results provide no evidence that AHY Φ is site specific. Whether or not HY Φ varies spatially on Fort Hood is yet to be determined because of insufficient data in this study. These study plots are primarily used to monitor GCWA territory size and density, age structure, mated status, the proportion of territories producing at least one fledgling, and nest survival (Peak and Grigsby 2011). Thus, we suspect that the lack of spatial variability in AHY Φ was primarily because study plots were selected based on those areas having high densities of GCWAs outside the live-fire training areas, as opposed to randomly selected sites across the installation; therefore, they were areas with comparable GCWA habitats. Conversely, the apparent lack of spatial differences in Φ might be a result of low discriminatory ability of the model selection procedure (the analog of low statistical power to detect a difference; see Morrison et al. 2004). A retrospective overlay of study-plot boundaries and GCWA habitat (as delineated by Diamond et al. 2010) suggests the first possibility might be true. However, fine-scale vegetation cover and height data are not readily available to test these predictions.

Our three models that tested for transient AHY GCWAs provided no evidence that transients were a part of the banded samples. Current observational reports concerning movement of banded GCWAs on Fort Hood support the possibility that there are no, or negligible numbers of, transient AHY GCWAs in these capture-resight data. In the past decade no movement among study plots has been documented, and only two AHY male birds were ever resighted off a study plot. These birds were found immediately outside

the study-plot boundary where they were banded in the previous year (R. Peak, *personal communication*). However, robust movement data are lacking for the species.

The mean \pm SE annual Φ for male AHY GCWAs was estimated to be 0.47 ± 0.02 , which is within the range of annual male AHY Φ estimates reported for other warbler species such as the Black-throated Blue Warbler (*S. caerulescens*) at 0.51 ± 0.03 and 0.43 ± 0.04 (Sillett and Holmes 2002); the American Yellow Warbler (*S. petechia*) at 0.49 ± 0.03 (Climburg et al. 2002) and a mean of 0.48-0.60 (Mazerolle et al. 2005); Swainson's Warbler (*Limnothlypis swainsonii*) at a mean of ~0.30-0.80 depending on body condition (Bensen and Bednarz 2010); the Prothonotary Warbler (*Protonotaria citrea*) at 0.44 ± 0.07 (Calvert et al. 2010); and the Blackburnian (*S. fusca*) and Black-throated Green Warblers (*S. virens*) at 0.48 ± 0.09 (Zitske et al. 2011). However, our AHY Φ estimate was 16% lower than what was reported for this species in previous Φ analyses. USFWS (1996) analyzed capture-resight data collected by the Nature Conservancy program from 1991 to 1995, and reported a mean AHY Φ estimate of 0.57. We chose to omit data collected in 1991 because study-plot boundaries were not established until 1992. Thus, individuals captured in 1991 had little to no chance of being resighted in subsequent years (R. Peak, *personal communication*). We estimated the mean AHY Φ from 1992 to 1995 as 0.65. Alldredge et al. (2004) reported a mean AHY Φ of 0.56 when analyzing capture-resight data collected on Fort Hood from 1997 to 2001. We estimated a mean AHY Φ of 0.55 for the same interval, i.e., 1997 to 2001. The differences in Φ estimates were likely because we excluded data from 1991 when comparing our estimates with

those of USFWS (1996) and because we included data from different study plots across a greater number of years.

Because of a lack of capture-resight data, HY Φ probabilities for recent years could not be estimated. Both USFWS (1996) and Alldredge et al. (2004) estimated a mean HY Φ of 0.30 when analyzing GCWA capture-resight data from the identical study plot as that for the data used in our analysis, i.e., Thirteen B. The only difference in the time frame in which the data were collected for this analysis is that we chose to omit data from 1991 and 2001 for reasons described earlier and included data from 1996. Thus, it is not surprising that our estimated HY Φ is no different than previous HY Φ estimates when taking into account the approximate 95% confidence interval, i.e., the SE of ± 0.06 . All three of these HY Φ estimates are well above the HY Φ mean \pm SE estimates reported for Prothonotary Warblers, which are 0.06 ± 0.01 and 0.11 ± 0.01 , with and without cowbird nestmates, respectively (McKim-Louder et al. 2013). However, Φ estimates are not directly comparable between studies. McKim-Louder et al. (2013) banded young in nest boxes before fledging occurred and had both males and females in their analysis, and Φ for HY birds can be related to an assortment of factors including differences in dispersal patterns among species and/or subpopulations. We currently do not have the data to assess whether the relatively high HY GCWA Φ estimates are an artifact of the individual study plot, are an outcome of the sampling protocol used to band individuals, or are reasonable for this particular species.

The temporal variance of the Φ point estimates consists of both process and sampling components. Process variance is the true temporal variance in underlying Φ probabilities. On the other hand, sampling variance is a measure of the uncertainty in the estimates of Φ that can be attributed to the sampling process and the inability to capture and detect all animals at all occasions. When the temporal variance of the Φ point estimates is not decomposed into process and sampling variance components, the perceived variability in Φ over time is positively biased as an estimate of process variance, which will artificially increase the risk of extinction for species if incorporated directly into PVAs (Gould and Nichols 1998). Further, incorporating both process and sampling variances into PVAs in an appropriate manner might have a significant impact on projected population dynamics and, by extension, considerably alter conservation decision making (McGowan et al. 2011). Thus, although these Φ variances, i.e., process and sampling variance, are often not reported, these estimates are critical for projecting population dynamics of any species. Herein, sampling variance accounted for 48.5% of the total variance of AHY Φ and 66.2% of the total variance of HY Φ , which illustrates the importance of partitioning the total variance into process and sampling components to gain a better understanding of population dynamics. Our CV estimates indicated that HY Φ had a greater year-to-year variation than AHY Φ . This finding is consistent with the conclusions of Gould and Nichols (1998) when they investigated age-specific differences in temporal variability of Mallard Duck (*Anas platyrhynchos*) Φ . This pattern might be coupled with the experience and/or learned behavior of AHY birds, allowing AHY birds to better compensate during adverse environmental conditions and reduce the year-to-year variation in Φ (Gould and Nichols 1998). We analyzed longer-term capture-resight data than both USFWS (1996)

and Alldredge et al. (2004), which should result in more precise estimates of variance. However, our estimate of process variance for AHY Φ was 0.0120, which is no different than the value of 0.0119 that was calculated by USFWS (1996). Both these estimates are larger than the value of 0.007 that was calculated by Alldredge et al. (2004). Conversely, our estimate of process variance for HY Φ , 0.0076, is substantially smaller than the value of 0.058 that was calculated by Alldredge et al. (2004).

CONSERVATION IMPLICATIONS

The population parameter estimates calculated herein will be used in future Golden-cheeked Warbler population models to aid in large-scale conservation decision making. Given current estimates of vital rates, however, GCWA abundance should be declining dramatically, a scenario that is not supported by the current survey data. This suggests that GCWA movement might be widespread, causing Φ estimates to be biased low because of permanent emigration. Thus, the use of contemporary hierarchical models to estimate GCWA movement parameters is a fruitful area for further study. It can be approached in at least two ways. If the within-season GCWA location data were available, for instance, it would be beneficial to reformat the data analyzed herein to match a robust-design sampling framework and use a spatial Cormack-Jolly-Seber model structure (Royle et al. 2014). Open population spatial capture-recapture models allow for the estimation of Φ during primary sampling periods and density for each trapping session, or in this case each GCWA breeding season, but have the added benefit of being able to explicitly model and estimate dispersal parameters as long as the scale of dispersal is not substantially greater than the scale of the study area. Further, by explicitly

incorporating movement information within the analysis, these models have increased precision and accuracy in the derived Φ estimates (Ergon and Gardner 2013). Another possibility is to combine the capture-resight data analyzed herein with ancillary GCWA population data within an integrated population model (Besbeas et al. 2002, Brooks et al. 2004, Schaub and Abadi 2011). By combining the likelihoods of multiple data sets, integrated population models allow for the estimation of population parameters for which few or no explicit data are available, including immigration rates (Abadi et al. 2010). It is worth noting that these two approaches can be combined within a single analysis using a Bayesian approach. Until movement parameters are better understood for the species, however, the direct estimation of population growth rate (λ) using capture-resight data (see Pradel 1996, Nichols and Hines 2002) or state-space models (see de Valpine and Hastings 2002, Hatfield et al. 2012b) might be a more effective strategy to assess the viability of individual GCWA subpopulations than use of projection matrices with vital rate estimates.

If population models are used to better understand GCWA population dynamics, it should be noted that there is an inherent limitation to using these Φ estimates within models that simulate population dynamics at the range-wide scale. Apparent survival on Fort Hood might not accurately represent Φ across the species' breeding range. The Balcones Canyonlands Preserve, located in Travis County, initiated a GCWA capture-resight program in 2009 (City of Austin 2012). Those data will provide the first estimates of GCWA Φ off Fort Hood. Still, capture-resight data to estimate Φ in the southwest and northern portions of the species' breeding range are lacking and, to our knowledge, no

such study has been initiated. It is essential we understand how population parameters vary across multiple ecoregions and under different management scenarios to model and conserve range-wide populations more effectively. Furthermore, it is vital that such studies are initiated as soon as possible, given it might require 10 Φ estimates, i.e., 11 years of capture-resight data, to provide precise variance estimates using the variance-components approach (Burnham and White 2002).

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LITERATURE CITED

Abadi, F., O. Gimenez, B. Ullrich, R. Arlettaz, and M. Schaub. 2010. Estimation of immigration rate using integrated population models. *Journal of Applied Ecology* 47:393–400. <http://dx.doi.org/10.1111/j.1365-2664.2010.01789.x>

Allredge, M. W., J. S. Hatfield, D. D. Diamond, and C. D. True. 2004. Golden-cheeked Warbler (*Dendroica chrysoparia*) in Texas: importance of dispersal toward persistence in a metapopulation. Pages 372–383 in H. R. Akçakaya, M. A. Burgman, O. Kindvall, C. C. Wood, P. Sjögren-Gulve, J. S. Hatfield, and M. A. McCarthy, editors. *Species conservation and management: case studies*. Oxford University Press, New York, New York, USA.

Baccus, J. T., M. E. Tolle, and J. D. Cornelius. 2007. Response of Golden-cheeked Warblers (*Dendroica chrysoparia*) to wildfires at Fort Hood, Texas. *Texas Ornithological Society, Occasional Publication* 7:1–37.

Benson, T. J., and J. C. Bednarz. 2010. Relationships among survival, body condition, and habitat of breeding Swainson's Warblers. *Condor* 112:138–148. <http://dx.doi.org/10.1525/cond.2010.080089>

Formatted for publication in Avian Conservation and Ecology

Besbeas, P., S. N. Freeman, B. J. T. Morgan, and E. A. Catchpole. 2002. Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics* 58:540–547. <http://dx.doi.org/10.1111/j.0006-341X.2002.00540>.

x

Brooks, S. P., R. King, and B. J. T. Morgan. 2004. A Bayesian approach to combining animal abundance and demographic data. *Animal Biodiversity and Conservation* 27:515–529.

Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. Second edition. Springer, New York, New York, USA.

Burnham, K. P., and G. C. White. 2002. Evaluation of some random effects methodology applicable to bird ringing data. *Journal of Applied Statistics* 29:245–264.
<http://dx.doi.org/10.1080/02664760120108755>

Calvert, A. M., J. Woodcock, and J. D. McCracken. 2010. Contrasting seasonal survivorship of two migratory songbirds wintering in threatened mangrove forests. *Avian Conservation and Ecology* 5:2. [online] URL: <http://www.ace-eco.org/vol5/iss1/art2/>

Campomizzi, A. J., S. L. Farrell, T. M. Mcfarland, H. A. Mathewson, M. L. Morrison, and R. N. Wilkins. 2012. Species conservation at a broad spatial scale: reproductive success of Golden-cheeked Warblers across their breeding range. *Wildlife Society Bulletin* 36:440–449. <http://dx.doi.org/10.1002/wsb.172>

Cilimburg, A. B., M. S. Lindberg, J. J. Tewksbury, and S. J. Hejl. 2002. Effects of dispersal on survival probability of adult Yellow Warblers (*Dendroica petechia*). *Auk* 119:778–789. [http://dx.doi.org/10.1642/0004-8038\(2002\)119\[0778:EODOSP\]2.0.CO;2](http://dx.doi.org/10.1642/0004-8038(2002)119[0778:EODOSP]2.0.CO;2)

City of Austin. 2012. *City of Austin 2012 Golden cheeeked Warbler (Setophaga chrysoparia) monitoring program*. Balcones Canyonlands Preserve annual report FY 2011–12. City of Austin Water Utility Wildland Conservation Division, Austin, Texas, USA.

Collier, B. A., S. L. Farrell, A. M. Long, A. J. Campomizzi, K. B. Hays, J. L. Laake, M. L. Morrison, and R. N. Wilkins. 2013. Modeling spatially explicit densities of endangered avian species in a heterogeneous landscape. *Auk* 130:1–11. <http://dx.doi.org/10.1525/auk.2013.13017>

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51:429–438. <http://dx.doi.org/10.2307/2334149>

de Valpine, P., and A. Hastings. 2002. Fitting population models incorporating process noise and observer error. *Ecological Monographs* 72:57–76.

[http://dx.doi.org/10.1890/0012-9615\(2002\)072\[0057:FPMIPN\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9615(2002)072[0057:FPMIPN]2.0.CO;2)

Diamond, D. D., L. F. Elliott, C. Blodgett, C. D. True, D. German, and A. Treuer-Kuehn. 2010. *Texas ecological systems classification*. Project ID 1/457. Missouri Resource Assessment Partnership. University of Missouri, Columbia, Missouri, and the Texas Parks and Wildlife Department, Austin, Texas, USA. <http://morap.missouri.edu/index.php/texas-ecological-systems-classification/>

Duarte, A., J. L. R. Jensen, J. S. Hatfield, and F. W. Weckerly. 2013. Spatiotemporal variation in range-wide Golden-cheeked Warbler breeding habitat. *Ecosphere* 4:152.

<http://dx.doi.org/10.1890/ES13-00229.1>

Ergon, T., and B. Gardner. 2013. Separating mortality and emigration: modelling space use, dispersal and survival with robust-design spatial capture-recapture data. *Methods in Ecology and Evolution*, early view. <http://dx.doi.org/10.1111/2041-210X.12133>

Farrell, S. L., B. A. Collier, K. L. Skow, A. M. Long, A. J. Campomizzi, M. L. Morrison, K. B. Hays, and R. N. Wilkins. 2013. Using LiDAR-derived vegetation metrics for high-resolution, species distribution models for conservation planning. *Ecosphere* 4:42.

<http://dx.doi.org/10.1890/ES12-000352.1>

Groce, J. E., H. A. Mathewson, M. L. Morrison, and N. Wilkins. 2010. *Scientific evaluation for the 5-year status review of the Golden-cheeked Warbler*. Texas A&M Institute of Renewable Natural Resources, College Station, Texas, USA.

Gould, W. R., and J. D. Nichols. 1998. Estimation of temporal variability of survival in animal populations. *Ecology* 79:2531–2538. [http://dx.doi.org/10.1890/0012-9658\(1998\)079\[2531:EOTVOS\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(1998)079[2531:EOTVOS]2.0.CO;2)

Hatfield, J. S., M. H. Reynolds, N. E. Seavy, and C. M. Krause. 2012b. Population dynamics of Hawaiian seabird colonies vulnerable to sea-level rise. *Conservation Biology* 26:667–678. [http:// dx.doi.org/10.1111/j.1523-1739.2012.01853.x](http://dx.doi.org/10.1111/j.1523-1739.2012.01853.x)

Hatfield, J. S., F. W. Weckerly, and A. Duarte. 2012a. Shifting foundations and metrics for Golden-cheeked Warbler recovery. *Wildlife Society Bulletin* 36:415–422. <http://dx.doi.org/10.1002/wsb.181>

Hayden, T. J., H. J. Cornelius, L. L. Weinburg, L. L. Jette, and R. H. Melton. 2001. *Endangered species management plan for Fort Hood, Texas; FY01–05*. Department of the Army, Engineer Research and Development Center, Construction Engineering Research Laboratory, Champaign, Illinois, USA.

Horne, J. S., K. M. Strickler, and M. Alldredge. 2011. Quantifying the importance of patch specific changes in habitat to metapopulation viability of an endangered songbird.

Ecological Applications 21:2478–2486. <http://dx.doi.org/10.1890/10-2328.1>

Hunt, J. W., F. W. Weckerly, and J. R. Ott. 2012. Reliability of occupancy and binomial mixture models for estimating abundance of Golden-cheeked Warblers (*Setophaga*

chrysoparia). *Auk* 129:105–114. <http://dx.doi.org/10.1525/auk.2012.11093>

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52:225–247.

<http://dx.doi.org/10.1093/biomet/52.1-2.225>

Klassen, J. A., M. L. Morrison, H. A. Mathewson, G. G. Rosenthal, and R. N. Wilkins. 2012. Canopy characteristics affect reproductive success of Golden-cheeked Warblers.

Wildlife Society Bulletin 36:54–60. <http://dx.doi.org/10.1002/wsb.100>

Martin, T. E., J. Clobert, and D. R. Anderson. 1995. Return rates in studies of life history evolution: are biases large? *Journal of Applied Statistics* 22:863–875.

<http://dx.doi.org/10.1080/02664769524676>

Marshall, M. E., M. L. Morrison, and R. N. Wilkins. 2013. Tree composition and food availability affect productivity of an endangered species: the Golden-cheeked Warbler.

Condor 115:882–892. <http://dx.doi.org/10.1525/cond.2013.130013>

Mathewson, H. A., J. E. Groce, T. M. Mcfarland, M. L. Morrison, J. C. Newnam, R. T. Snelgrove, B. A. Collier, and R. N. Wilkins. 2012. Estimating breeding season abundance of Golden-cheeked Warblers in Texas, USA. *Journal of Wildlife Management* 76:1117–1128. <http://dx.doi.org/10.1002/jwmg.352>

Mazerolle, D. F., K. W. Dufour, K. A. Hobson, and H. E. den Haan. 2005. Effects of large-scale climatic fluctuations on survival and production of young in a neotropical migrant songbird, the Yellow Warbler *Dendroica petechia*. *Journal of Avian Biology* 36:155–163. <http://dx.doi.org/10.1111/j.0908-8857.2005.03289.x>

McGowan, C. P., M. C. Runge, and M. A. Larson. 2011. Incorporating parametric uncertainty into population viability analysis models. *Biological Conservation* 144:1400–1408. <http://dx.doi.org/10.1016/j.biocon.2011.01.005>

McKim-Louder, M. I., J. P. Hoover, T. J. Benson, and W. M. Schelsky. 2013. Juvenile survival in a neotropical migratory songbird is lower than expected. *PLoS ONE* 8:e56059. <http://dx.doi.org/10.1371/journal.pone.0056059>

Morrison, S. A., D. T. Bolger, and T. S. Sillett. 2004. Annual survivorship of the sedentary Rufous-crowned Sparrow (*Aimophila ruficeps*): no detectable effects of edge or rainfall in southern California. *Auk* 121:904–916 [http://dx.doi.org/10.1642/0004-8038\(2004\)121\[0904:ASOTSR\]2.0.CO;2](http://dx.doi.org/10.1642/0004-8038(2004)121[0904:ASOTSR]2.0.CO;2)

Nichols, J. D., and J. E. Hines. 2002. Approaches for the direct estimation of λ and demographic contributions to λ , using capture- recapture data. *Journal of Applied Statistics* 29:539–568. [http://dx. doi.org/10.1080/02664760120108809](http://dx.doi.org/10.1080/02664760120108809)

Peak, R. G. 2011a. Population trends of the Golden-cheeked Warbler on Fort Hood, Texas 1992-2011. In *Endangered species monitoring and management at Fort Hood, Texas*. 2011 Annual Report. Fort Hood, Directorate of Public Works, Natural Resources Management Branch, Fort Hood, Texas, USA.

Peak, R. G. 2011b. A field test of the distance sampling method using Golden-cheeked Warblers. *Journal of Field Ornithology* 82:311–319.

Peak, R. G., and N. A. Grigsby. 2011. Golden-cheeked Warbler demography on Fort Hood, Texas, 2011. In *Endangered species monitoring and management at Fort Hood, Texas*. 2011 Annual Report. Fort Hood, Directorate of Public Works, Natural Resources Management Branch, Fort Hood, Texas, USA.

Peak, R. G., and D. J. Lusk. 2011. Test of the plumage characteristics used to sex Golden-cheeked Warblers in the first basic plumage. *North American Bird Bander* 36:110–112.

Peak, R. G., and F. R. Thompson, III. 2013. Amount and type of forest cover and edge are important predictors of Golden-cheeked Warbler density. *Condor* 115:659–668.

<http://dx.doi.org/10.1525/cond.2013.120043>

Pollock, K. H. 1981. Capture-recapture models allowing for age dependent survival and capture rates. *Biometrics* 37:521–529. <http://dx.doi.org/10.2307/2530565>

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107:1–97.

Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52:703–709. <http://dx.doi.org/10.2307/2532908>

Pradel, R., J. E. Hines, J.-D. Lebreton, and J. D. Nichols. 1997. Capture-recapture survival models taking account of transients. *Biometrics* 53:60–72.

<http://dx.doi.org/10.2307/2533097>

Pulich, W. M. 1976. *The Golden-cheeked Warbler: A Bioecological Study*. Texas Parks and Wildlife Department, Austin, Texas, USA.

Pyle, P. 1997. *Identification guide to North American birds, part I*. Slate Creek, Bolinas, California, USA.

Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2014. *Spatial Capture-Recapture*. Academic Press, Waltham, Massachusetts, USA.

Schaub, M., and F. Abadi. 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology* 152:227–237. <http://dx.doi.org/10.1007/s10336-010-0632-7>

Seber, G. A. 1965. A note on the multiple-recapture census. *Biometrika* 52:249–259. <http://dx.doi.org/10.1093/biomet/52.1-2.249>

Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296–308. <http://dx.doi.org/10.1046/j.1365-2656.2002.00599.X>

Stokke, B. G., A. P. Møller, B.-E. Sæther, G. Rheinwald, and H. Gutscher. 2005. Weather in the breeding area and during migration affects the demography of small long-distance passerine migrant. *Auk* 122:637–647. [http://dx.doi.org/10.1642/0004-8038\(2005\)122 \[0637:WITBAA\]2.0.CO;2](http://dx.doi.org/10.1642/0004-8038(2005)122[0637:WITBAA]2.0.CO;2)

Travis County. 2011. *Monitoring of the Golden-cheeked Warbler (Setophaga chrysoparia) on Travis County's Balcones Canyonlands Preserve*. Travis County Parks and Preserves, Austin, Texas, USA.

U.S. Fish and Wildlife Service (USFWS). 1990. Endangered and threatened wildlife and plants; final rule to list the Golden-cheeked Warbler as endangered. *Federal Register* 55(87):53153–53160.

U.S. Fish and Wildlife Service (USFWS). 1992. *Golden-cheeked warbler (Dendroica chrysoparia) recovery plan*. U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.

U.S. Fish and Wildlife Service (USFWS). 1996. *Golden-cheeked warbler population and habitat viability assessment report*. Compiled and edited by C. Beardmore, J. Hatfield, and J. Lewis in conjunction with workshop participants. Report of a August 21-24, 1995 workshop arranged by the U.S. Fish and Wildlife Service in partial fulfillment of U.S. National Biological Service grant no. 80333–1423. U.S. Fish and Wildlife Service, Austin, Texas, USA.

Vaillant, H., H. R. Akcakaya, D. Diamond, and D. True. 2004. *Modeling the effects of habitat loss and fragmentation on the Golden-cheeked Warbler*. Final report, submitted to the Engineering Research and Development Center, Construction Engineering Research Laboratory. Engineering Research and Development Center, Construction Engineering Research Laboratory, Champaign, Illinois, USA.

Warren, C. C., J. A. Veech, F. W. Weckerly, L. O'Donnell, and J. R. Ott. 2013. Detection heterogeneity and abundance estimation in populations of Golden-cheeked Warblers (*Setophaga chrysoparia*). *Auk* 130:677–688. <http://dx.doi.org/10.1525/auk.2013.13022>

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (suppl 1):S120–S139.
<http://dx.doi.org/10.1080/00063659909477239>

Zitske, B. P., M. G. Betts, and A. W. Diamond. 2011. Negative effects of habitat loss on survival of migrant warblers in a forest mosaic. *Conservation Biology* 25:993–1001.
<http://dx.doi.org/10.1111/j.1523-1739.2011.01709.x>

CHAPTER IV

ESTIMATING GOLDEN-CHEEKED WARBLER IMMIGRATION: IMPLICATIONS FOR THE SPATIAL SCALE OF CONSERVATION¹

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. Further, 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

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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 and spends the rest of the year in the pine (*Pinus* spp.) - oak forests ≥ 1100 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 U.S. 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 and 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, 2012b).

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 data sets, 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 by 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. The primary aims for this study were to (i) estimate warbler immigration by combining Bayesian integrated population modeling with data regularly collected by established warbler monitoring programs, and (ii) 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.

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. 4.1). The BCP is a large (>12,300 ha), discontinuous collection of properties located in Travis County, Texas (City of Austin [COA], 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, 1996a). The FHMR is an 87,890-ha contiguous property located in Bell and Coryell Counties, Texas. The property is managed by the U.S. Army, with the primary goal to facilitate training of U.S. military personnel (reviewed in Wolfe et al., 2012).

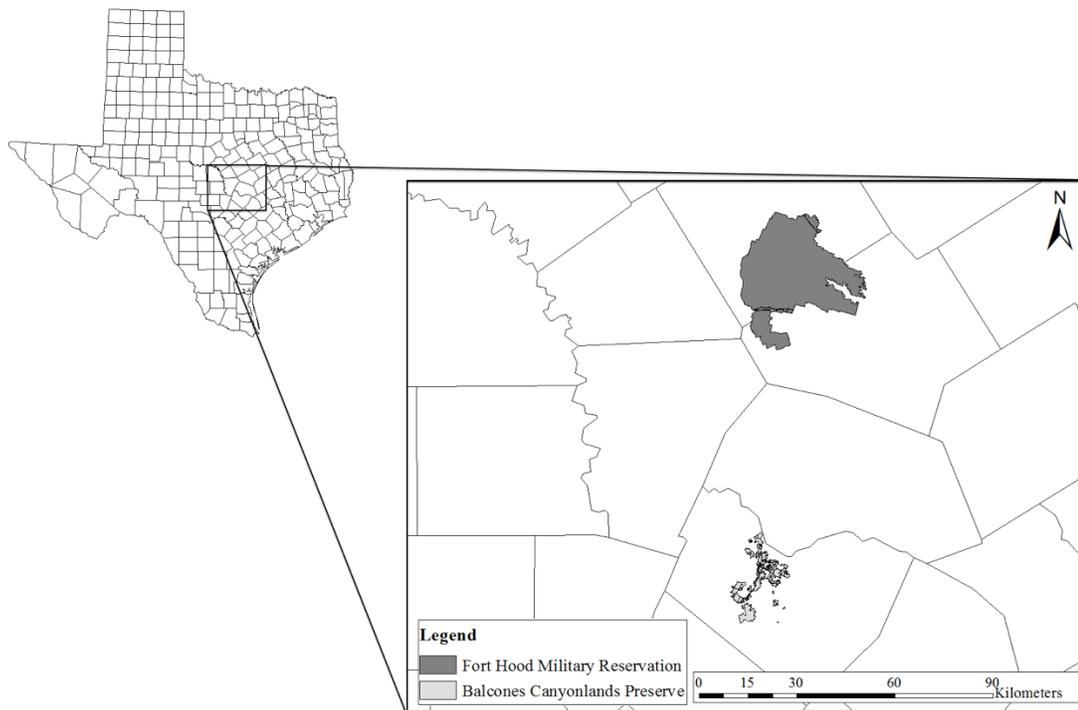


Figure 4.1 Map of the locations in Texas where golden-cheeked warbler (*Setophaga chrysoparia*) data and prior information were collected.

Abundance and productivity data collection

From 1998–2012, warbler surveys have been conducted within five 40.5-ha “prime” warbler-habitat plots delineated on BCP (COA, 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 till late May. An individual was considered territorial if it was located in the same vicinity during three surveys that were separated by at least one week (COA, 2012). For productivity data, biologists actively searched for fledglings within the plots. Spot-mapping and productivity surveys were conducted simultaneously, however, productivity surveys extended out until mid-June (COA, 2012). Data were summed across the plots. Since 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:

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

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

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

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 $COUNT_t \sim \text{Poisson}(N_t)$, 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 $J_t \sim \text{Poisson}(T_t F_t)$.

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_ϕ^2) that were estimated using long-term capture-resight data from FHMR (adult: $\phi_A = 0.47 \pm 0.02$, $\sigma_{\phi\text{-Process}, A}^2 = 0.0120$, $\sigma_{\phi\text{-Sampling}, A}^2 = 0.0113$; juvenile: $\phi_J = 0.28 \pm 0.06$, $\sigma_{\phi\text{-Process}, J}^2 = 0.0076$, $\sigma_{\phi\text{-Sampling}, J}^2 = 0.0149$; Duarte et al., 2014) and included this knowledge via informative priors into the integrated population model. Duarte et al. (2014) reviews 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 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:

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

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

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

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

where the intercept coefficients ($\beta_0, \beta_1, \beta_2, \beta_3$) 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 above using beta distributions. The sampling variance was used as the variance for the prior on mean survival since 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 likelihoods 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 Supplementary Material). 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. 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. Since 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 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., $\lambda = 0.9, 0.95, 1, 1.05, \text{ or } 1.1$). 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. 4.2).

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 approximately 16 to 27 individuals immigrating into the population each year over the time series. Estimates of mean/median vital rates and their associated process variances are reported in Table 4.1. For annual point estimates of demographic parameters see Supplemental Fig. 4.1.

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. 4.3). Notably, a stable population can be achieved with a mean immigration rate of approximately 0.30 or a mean fledging rate of approximately 1.21, while holding all other parameters constant.

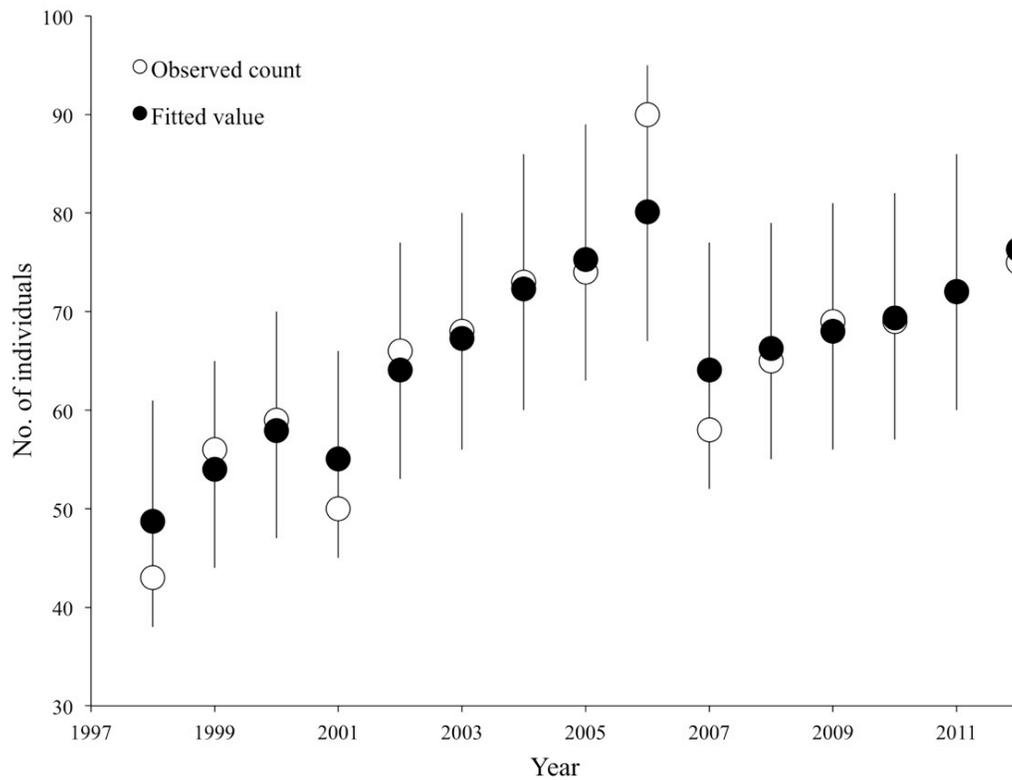


Figure 4.2 Observed number of territories (open circles) and estimated mean number of territories (solid circles) using a Bayesian state-space model of adult male golden-cheeked warblers (*Setophaga chrysoparia*) on the Balcones Canyonlands Preserve, Travis County, Texas, USA, 1998–2012.

Table 4.1 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*

Note: “*” signifies process variance estimates that were calculated using capture-resight data in a different study.

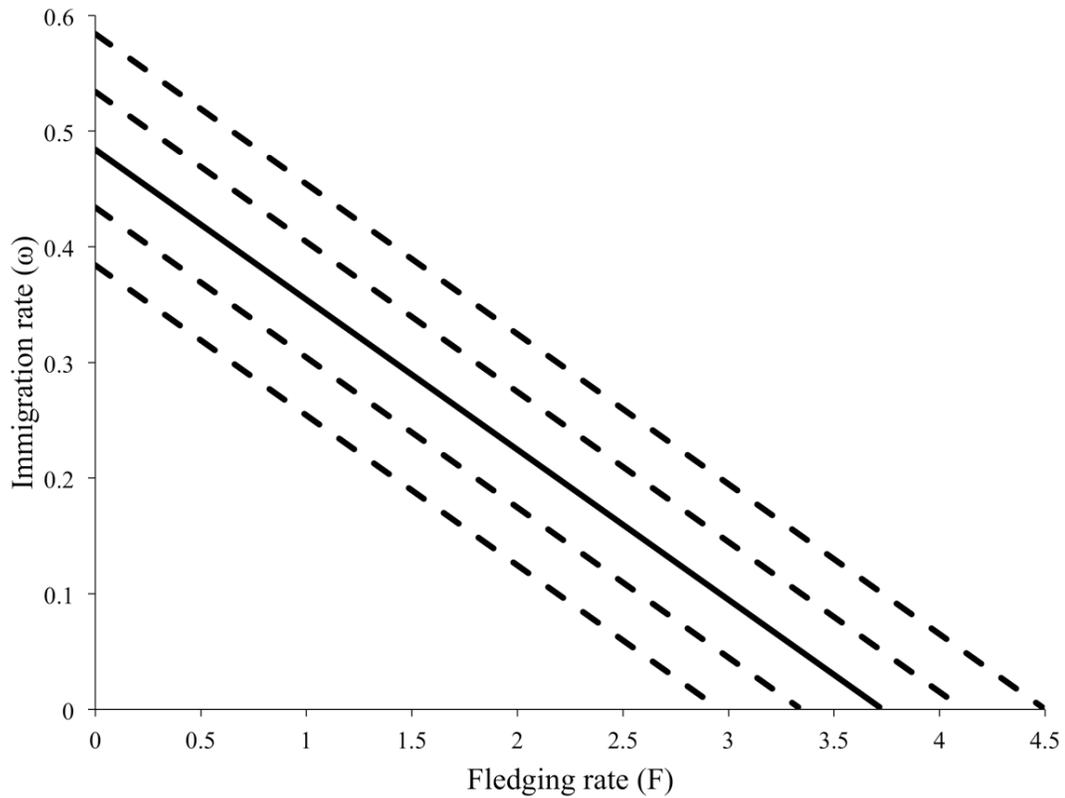


Figure 4.3 Relationship between fledging rate, immigration rate, and population growth rate for golden-cheeked warblers (*Setophaga chrysoparia*). The solid line represents a stable subpopulation ($\lambda = 1$) and the broken lines from top to bottom represent $\lambda = 1.10, 1.05, 0.95,$ and 0.90 . Estimates were derived using a deterministic projection model.

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, since 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 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 Supplemental Fig. 4.1). There was a sudden decline in territory density in 2007 (Fig. 4.2). 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 analyses 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 done 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, successful warbler conservation and management programs need to focus at larger spatial scales (i.e., the site, regional, or perhaps even the range-wide scale) to be effective in maximizing the viability of populations.

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, *personal communication*). 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 COA and U.S. Forest Service, is the documentation of movement distances ranging 1.2–16.0 km by male individuals banded as second-year birds (COA, 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 (COA, 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.

The estimated survival multiplier, which indicates how much higher average adult and juvenile survival would need to be to maintain a stable warbler population while holding the reproductive parameter constant, suggested that juvenile and adult survival probabilities must increase by 43% in order to maintain a stable warbler population in the absence of immigration. This implies 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 approximately 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 stability 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. 4.3) 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 approximately 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 data sets used in the model (i.e., abundance, survival, and productivity data) are assumed to be independent from each other. The two data sets used here did violate this assumption because the surveys for territorial males and fledglings were conducted within the same

plots. However, Abadi et al. (2010a) 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 assumptions. 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 is likely to be fulfilled as well, given that both study sites are close in proximity and the data for each study cover similar time spans. Further, 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. 4.2).

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). Further, 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 1991–1999 and 0.99–1.74 on Travis County properties from 2001–2008. Thus, our fledging-rate estimate is comparable to 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 in order to be effective. Further, 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.

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References

- Abadi, F., Gimenez, O., Arlettaz, R. & Schaub, M. (2010a). An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. *Ecology* **91**, 7–14.
- Abadi, F., Gimenez, O., Ullrich, B., Arlettaz, R. & Schaub, M. (2010b). Estimation of immigration rate using integrated population models. *J Appl Ecol* **47**, 393–400.
- Abadi, F., Gimenez, O., Jakober, H., Stauber, W., Arlettaz, R. & Schaub, M. (2012). Estimating the strength of density dependence in the presence of observation errors using integrated population models. *Ecol Modell* **242**, 1–9.
- Abbruzzese, C. M. & Koehler, D. L. (2002). 2002 Golden-cheeked Warbler and Black-capped Vireo monitoring program: Annual report FY 2001–02. Austin: City of Austin Water Utility Wildland Conservation Division, Balcones Canyonlands Preserve.
- Akçakaya, H. R. (2004). Using models for species conservation and management: an introduction. Species conservation and management: case studies (eds Akçakaya, H. R., Burgman, M. A., Kindvall, O., Wood, C. C., Sjögren-Gulve, P., Hatfield, J. S. & McCarthy, M. A.), pp. 3–14. New York: Oxford University Press.
- Altwegg, R., Jenkins, A. & Abadi, F. (2014). Nestboxes and immigration drive the growth of an urban peregrine falcon *Falco peregrinus* population. *Ibis* **156**, 107–115.

- Allredge, M. W., Hatfield, J. S., Diamond, D. D. & True, C. D. (2004). Golden-cheeked warbler (*Dendroica chrysoparia*) in Texas: importance of dispersal toward persistence in a metapopulation. *Species conservation and management: case studies* (eds Akçakaya, H. R., Burgman, M. A., Kindvall, O., Wood, C. C., Sjögren-Gulve, P., Hatfield, J. S. & McCarthy, M. A.), pp. 372–383. New York: Oxford University Press.
- Besbeas, P., Freeman, S. N., Morgan, B. J. T. & Catchpole, E. A. (2002). Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics* **58**, 540–547.
- Brooks, S. P. & Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *J Comp Graph Stat* **9**, 266–285.
- Brooks, S. P., King, R. & Morgan, B. J. T. (2004). A Bayesian approach to combining animal abundance and demographic data. *Anim Biodivers Conserv* **27.1**, 515–529.
- Brown, J. L. & Collopy, M. W. (2013). Immigration stabilizes a population of threatened cavity-nesting raptors despite possibility of nest box imprinting. *J Avian Biol* **44**, 141–148.
- Burnham, K. P. & White, G. C. (2002). Evaluation of some random effects methodology applicable to bird ringing data. *J Appl Stat* **29**, 245–264.
- City of Austin (2007). City of Austin 2007 Golden-cheeked Warbler (*Dendroica chrysoparia*) and Black-capped Vireo (*Vireo atricapilla*) Monitoring Program Balcones Canyonlands Preserve Annual Report Fiscal Year 2016–07. Austin: City of Austin Water Utility Wildland Conservation Division, Balcones Canyonlands Preserve.

- City of Austin (2012). 2012 Annual Report: Golden-cheeked Warbler (*Setophaga chrysoparia*) Monitoring Program Balcones Canyonlands Preserve annual report FY 2011–12. Austin: City of Austin Water Utility Wildland Conservation Division, Balcones Canyonlands Preserve.
- Collier, B. A., Groce, J. E., Morrison, M. L., Newnam, J. C., Campomizzi, A. J., Farrell, S. L., Mathewson, H. A., Snelgrove, R. T., Carroll, R. J. & Wilkins, R. N. (2012). Predicting patch occupancy in fragmented landscapes at the rangewide scale for an endangered species: an example of an American warbler. *Divers Distrib* **18**, 158–167.
- Cooch, E., Rockwell, R. F. & Brault, S. (2001) Retrospective analysis of demographic responses to environmental change: a lesser snow goose example. *Ecol Monogr* **71**, 377–400.
- De Valpine, P. & Hastings, A. (2002). Fitting population models incorporating process noise and observer error. *Ecol Monogr* **72**, 57–76.
- Duarte, A., Jensen, J. L. R., Hatfield, J. S. & Weckerly, F. W. (2013). Spatiotemporal variation in range-wide golden-cheeked warbler breeding habitat. *Ecosphere* **5**, 152.
- Duarte, A., Hines, J. E., Nichols, J. D., Hatfield, J. S. & Weckerly, F. W. (2014). Age-specific survival of male golden-cheeked warblers on the Fort Hood Military Reservation, Texas. *Avian Conserv Ecology* **9**, 4.
- Groce, J. E., Mathewson, H. A., Morrison, M. L., & Wilkins, N. (2010). Scientific evaluation for the 5-year status review of the golden-cheeked warbler. College Station: Texas A&M Institute of Renewable Natural Resources.

- Hatfield, J. S., Weckerly, F. W. & Duarte, A. (2012b). Shifting foundations and metrics for golden-cheeked warbler recovery. *Wildl Soc Bull* **36**, 415–422.
- Horne, J. S., Strickler, K. M. & Alldredge, M. W. (2011). Quantifying the importance of patch-specific changes in habitat to metapopulation viability of an endangered songbird. *Ecol Appl* **21**, 2478–2486.
- Kellner, K. (2014). jagsUI: Run JAGS from R (an alternative user interface for rjags). R package version 1.0.
- Kendall, W. L. & Nichols, J. D. (2004). On the estimation of dispersal and movement of birds. *Condor* **106**, 720–731.
- Kéry, M. & Schaub, M. (2012). Bayesian population analysis using WinBUGS. A hierarchical perspective. Waltham: Academic Press.
- Knape, J., Jonzén, N. & Sköld, M. (2011). On observation distributions for state space models of population survey data. *J Anim Ecol* **80**, 1269–1277.
- Lebreton, J. -D., Burnham, K. P., Clobert, J. & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* **62**, 67–118.
- Lindsay, D. L., Barr, K. R., Lance, R. F., Tweddale, S. A., Hayden, T. J. & Leberg, P. L. (2008). Habitat fragmentation and genetic diversity of an endangered, migratory songbird, the golden-cheeked warbler (*Dendroica chrysoparia*). *Mol Ecol* **17**, 2122–2133.

- Mathewson, H. A., Groce, J. E., McFarland, T. M., Morrison, M. L., Newnam, J. C., Snelgrove, R. T., Collier, B. A. & Wilkins, R. N. (2012). Estimating breeding season abundance of golden-cheeked warblers in Texas, USA. *J Wildl Manage* **76**, 1117–1128.
- McGowan, C. P., Runge, M. C. & Larson, M. A. (2011). Incorporating parametric uncertainty into population viability analysis models. *Biol Conserv* **144**, 1400–1408.
- Monroe, B. L. (1968). A distributional survey of the birds of Honduras. *Ornithol Monogr* **7**, 1–458.
- Morrison, M. L. (2012). The habitat sampling and analysis paradigm has limited value in animal conservation: a prequel. *J Wildl Manage* **76**, 438–450.
- Peak, R. G. (2011). Population trends of the Golden-cheeked Warbler on Fort Hood, Texas 1992–2011. In *Endangered species monitoring and management at Fort Hood, Texas. 2011 Annual Report*. Fort Hood: Fort Hood, Directorate of Public Works, Natural Resources Management Branch.
- Plummer, M. (2003). JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003) (eds Hornik, K., Leisch, F., Zeileis A.), pp. 1–10. Vienna.
- Pollock, K. H., Nichols, J. D., Brownie, C. & Hines, J. E. (1990). Statistical inference for capture-recapture experiments. *Wildl Monogr* **107**, 1–97.
- Pulich, W. M. (1976). *The Golden-Cheeked Warbler: A Bioecological Study*. Texas Parks and Wildlife, Austin.

- Rappole, J. H., King, D. I. & Barrow Jr, W. C. (1999). Winter ecology of the endangered golden-cheeked warbler. *Condor* **101**, 1–9.
- Reidy, J. L., Stake, M. M. & Thompson III, F. R. (2008). Golden-cheeked warbler nest mortality and predators in urban and rural landscapes. *Condor* **110**, 458–466.
- R Core Team (2013). R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.
- Royle, J. A., Chandler, R. B., Sollmann, R. & Gardner, B. (2014). Spatial Capture-Recapture. Waltham: Academic Press.
- Schaub, M., Aebischer, A., Gimenez, O., Berger, S. & Arlettaz, R. (2010). Massive immigration balances high anthropogenic mortality in a stable eagle owl population: lessons for conservation. *Biol Conserv* **143**, 1911–1918.
- Schaub, M., Gimenez, O., Sierro, A. & Arlettaz, R. (2007). Use of integrated population modeling to enhance estimates of population dynamics obtained from limited data. *Conserv Biol* **21**, 945–955.
- Schaub, M. & Abadi, F. (2011). Integrated population models: a novel analysis framework for deeper insights into population dynamics. *J Ornithol* **152**, 227–237.
- Schaub, M., Jakober, H. & Stauber, W. (2013). Strong contribution of immigration to local population regulation: evidence from a migratory passerine. *Ecology* **94**, 1828–1838.
- Schaub, M. & Royle, J. A. (2014). Estimating true instead of apparent survival using spatial Cormack-Jolly-Seber models. *Methods Ecol. Evol.* **5**, 1316–1326.

- Schaub, M. & Fletcher, D. (2015). Estimating immigration using a Bayesian integrated population model: choice of parametrisation and priors. *Ecol Environ Stat*. DOI 10.1007/s10651-015-0309-8.
- Szostek, K.L., Schaub, M. & Becker, P.H. (2014). Immigrants are attracted by local pre-breeders and recruits in a seabird colony. *J Anim Ecol* **83**, 1015–1024.
- Tittler, R., Villard, M. -A. & Fahrig, L. (2009). How far do songbirds disperse? *Ecography* **32**, 1051–1061.
- U.S. Fish and Wildlife Service (1990). Endangered and threatened wildlife and plants; final rule to list the golden-cheeked warbler as endangered. Federal Register 55, 53153–53160.
- U.S. Fish and Wildlife Service (1992). Golden-cheeked warbler (*Dendroica chrysoparia*) recovery plan. Albuquerque: U.S. Fish and Wildlife Service.
- U.S. Fish and Wildlife Service (1996a). Final environmental impact statement/habitat conservation plan for proposed issuance of a permit to allow incidental take of golden-cheeked warbler, black-capped vireo, and six karst invertebrates in Travis County, Texas. Albuquerque: Regional Environmental Consultants (RECON) and U.S. Fish and Wildlife Service.
- U.S. Fish and Wildlife Service (1996b). Golden-cheeked warbler population and habitat viability assessment report. (eds Beardmore, C., Hatfield, J. & Lewis J.). Austin: U.S. Fish and Wildlife Service.

- Vaillant, H., Akçakaya, H. R., Diamond & D., True, D. (2004). Modeling the effects of habitat loss and fragmentation on the golden-cheeked warbler. Champaign: Engineering Research and Development Center, Construction Engineering Research Laboratory.
- Verner, J. (1985). Assessment of counting techniques. *Current ornithology*, Vol. 2 (ed Johnston, R. F.), pp. 247–302, New York: Plenum Press.
- Weckerly, F. W. & Ott, J. R. (2008). Statistical trends of golden-cheeked warblers on Balcones Canyonlands Preserve, City of Austin, Texas. San Marcos: Texas State University.
- Whiting, M. J., Dixon, J. R., Greene, B. D., Mueller, J. M., Thonton Jr., O. W., Hatfield, J. S., Nichols, J. D. & Hines, J. E. (2008). Population dynamics of the Concho water snake in rivers and reservoirs. *Copeia* **2**, 438–445.
- Williams, B. K., Nichols, J. D. & Conroy, M. J. (2002). Analysis and management of animal populations. San Diego: Academic Press.
- Wolfe, D. W., Hays, K. B., Farrell, S. L. & Baggett, S. (2012). Regional credit market for species conservation: developing the Fort Hood Recovery Credit System. *Wildl Soc Bull* **36**, 423–431.

Supplementary Material

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

Adam Duarte, Floyd W. Weckerly, Michael Schaub, and Jeff S. Hatfield

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, and abundance.

```
model {
  *****
  # Define the regression equations & priors
  *****
  for (i in 1:(ti-1)){
    *****
    # Juvenile survival
    *****
    logit(phij[i]) <- beta.phij + eps.phij[i]
    eps.phij[i] ~ dnorm(0, tau.phij)

    *****
    # Adult survival
    *****
    logit(phia[i]) <- beta.phia + eps.phia[i]
    eps.phia[i] ~ dnorm(0, tau.phia)

    *****
    # Immigration
    *****
    log(im[i]) <- beta.im + eps.im[i]
    eps.im[i] ~ dnorm(0, tau.im)
  }

  for (i in 1:ti){
    *****
    # Fledgling rate
    *****
    log(F[i])<-log.F[i]
    log.F[i] ~ dnorm(beta.F,tau.F)
  }

  *****
  # Priors for regression parameters
  *****
  a.juv <- 0.28*(((0.28*(1-0.28))/0.0149)-1)
  b.juv <- (1-0.28)*(((0.28*(1-0.28))/0.0149)-1)
  mean.phij ~ dbeta(a.juv, b.juv) # mean juvenile survival with sampling variance
  beta.phij <- log(mean.phij / (1-mean.phij))
}
```

```

logit.temp.phij <- 0.0076/((0.28^2)*((1-0.28)^2)) # logit trans. of juvenile survival process variance
tau.phij <- pow(logit.temp.phij,-1)
sig2.phij <- 1 / tau.phij

a.ad <- 0.47*(((0.47*(1-0.47))/0.0113)-1)
b.ad <- (1-0.47)*(((0.47*(1-0.47))/0.0113)-1)
mean.phia ~ dbeta(a.ad, b.ad) # mean adult survival with sampling variance
beta.phia <- log(mean.phia / (1-mean.phia))
logit.temp.phia <- 0.0120/((0.47^2)*((1-0.47)^2)) # logit trans. of adult survival process variance
tau.phia <- pow(logit.temp.phia,-1)
sig2.phia <- 1 / tau.phia

mean.im ~ dunif(0, 3)
beta.im <- log(mean.im)
sigma.im ~ dunif(0, 10)
tau.im <- pow(sigma.im, -2)
sig2.im <- 1 / tau.im

beta.F ~ dnorm(0,1.0E-6) # mean of the log fecundity

#####
# Priors for the precision of error terms
#####
sig.F ~ dunif(0,2)
tau.F <- pow(sig.F,-2)

#####
# Derived parameters
#####
for(tt in 1:(ti-1)){
lambda[tt]<-AHY[tt+1]/AHY[tt]
logla[tt] <- log(lambda[tt])
}

PGR<-mean(lambda[])
r<-(1/(ti-1))*sum(logla[])
sig2.F <- sig.F*sig.F
mf<-exp(beta.F)

#####
# Likelihoods
#####
#####
# Reproductive data
#####
for (tt in 1:ti){
fledglings[tt] ~ dpois(rho[tt])
rho[tt] <- f_terr[tt]*F[tt]
}

#####
# Priors for inital population sizes
#####
mu.fledge[1] <- AHY[1]*F[1]*0.5
HY[1] ~ dpois(mu.fledge[1]) # hatch-year birds
N1[1] ~ dcat(pop1[])

```

```

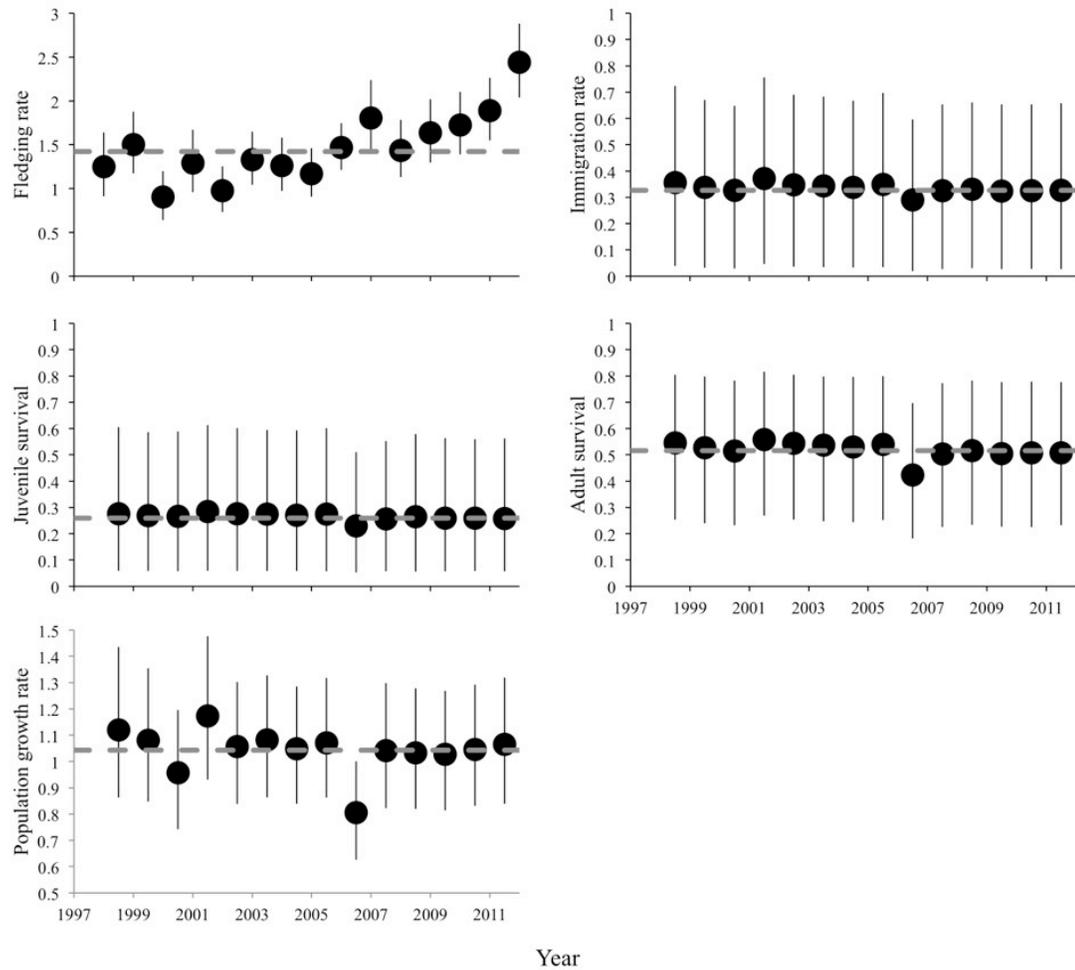
Na[1] ~ dcat(pop1[])
Naim[1] ~ dcat(pop1[])

#####
# System process
#####
for (tt in 2:ti){
mu.fledge[tt] <- AHY[tt]*F[tt]*0.5
HY[tt] ~ dpois(mu.fledge[tt])
N1[tt] ~ dbin(phiij[tt-1],HY[tt-1])
Na[tt] ~ dbin(phia[tt-1],AHY[tt-1])
mu.imm[tt] <- AHY[tt-1]*im[tt-1]
Naim[tt] ~ dpois(mu.imm[tt])
}

for (tt in 1:ti){
AHY[tt] <- Na[tt] + Naim[tt]+ N1[tt]
Ntot[tt] <- HY[tt] + AHY[tt]
}

#####
# Observation process
#####
for(tt in 1:ti){
popcount[tt] ~ dpois(AHY[tt])
}
}

```



Supplemental Figure 4.1 Annual point estimates of fledging rate, immigration rate, survival, 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.

CHAPTER V

POPULATION DYNAMICS OF GOLDEN-CHEEKED WARBLERS IN A STOCHASTIC LANDSCAPE¹

Abstract

Population viability analyses provide a quantitative approach that seek to predict the possible future status of a species of interest under different scenarios and therefore, are essential components of large-scale species' conservation programs. We investigated range-wide population and habitat dynamics for the golden-cheeked warbler (*Setophaga chrysoparia*). Habitat-transition probabilities were estimated across the warbler's breeding range by combining National Land Cover Database images with multistate capture-recapture analyses. 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 directional, whereby habitat is more likely to diminish than regenerate. The model results indicated population viability could be achieved under current conditions. However, there is considerable uncertainty associated with the population projections due to parametric uncertainty. Further, the model results suggested that increasing the amount

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of protected lands would have a substantial impact on terminal carrying capacities at the end of a 50-year simulation. Notably, this study identifies conservation needs for the species. In particular, there is currently no definition on what constitutes protected habitat, demographic data are lacking from a majority of the species' breeding range, and the magnitude of emigration from a target population has yet to be estimated with field data. Further, this study highlights the importance of prioritizing the conservation of large tracts of currently available warbler breeding habitat because habitat transitions are shown to be directional and there is a positive outcome of protecting a greater amount of habitat on the future carrying capacity for the species.

1. Introduction

Population viability analyses (PVAs) are essential 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 scenarios. The precision and bias of a PVA are directly related to the precision and bias of demographic estimates, our understanding of the population structure of the species of interest, and the habitat parameters that are input within the model. Therefore, these models must be updated periodically with inferences from recent and on-going research in order 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 that are comprised primarily of oak (*Quercus* 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 the 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 in an effort to eventually 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. 5.1), 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 assisting with 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 modeled 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 towards fruitful areas of further studies, 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 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., *in review*). 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 investigated 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. 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 m² pixel), and it would be ideal to incorporate stochasticity into the habitat component of the model. To accomplish this objective, we combined National Land Cover Database (NLCD) images with multistate capture-recapture analyses to estimate habitat-transition probabilities. Given current land-cover-change estimates reported by Duarte et al. (2013), we hypothesize recovery units five, six, and eight have the highest rates of habitat loss. It likely takes several decades for Ashe juniper to mature sufficiently to become warbler breeding habitat (J. S. Hatfield, *unpublished data*). Thus, we also hypothesize that habitat transitions will be directional, 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 to examine if warbler viability is possible given the current habitat dynamics and vital rate estimates for the species. Here, we assessed

various scenarios with differing levels of dispersal, survival, and productivity. 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). However, this might not be the case 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 and compared the estimated terminal K for each recovery unit at the end of 50 years of simulated habitat change.

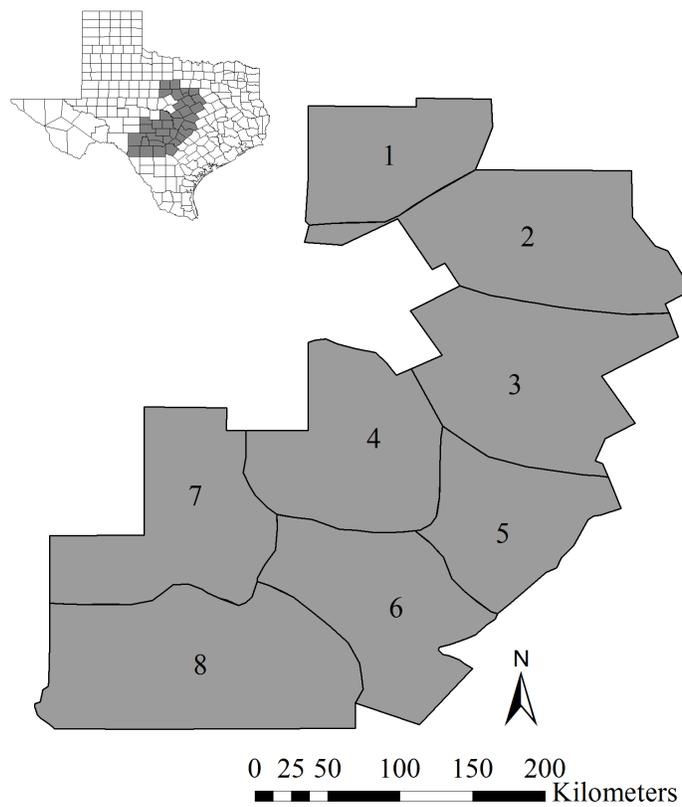


Figure 5.1 Golden-cheeked warbler (*Setophaga chrysoparia*) breeding range and federally-designated recovery units in Texas, USA.

2. Methods

2.1. Habitat transitions

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 percent 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 pixel that was classified as Evergreen Forest or Mixed Forest 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 capture-recapture models using the habitat data derived from NLCD (Hotelling et al., 2009; Breininger et al., 2010). We considered two models. The first model assumed habitat transitions were similar among recovery units. The second model examined recovery-unit-specific, habitat-transition probabilities. 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 34690 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 $\geq 70\%$ habitat, medium habitat (M) if it was $\geq 40\%$ habitat, low habitat (L) if it was $\geq 10\%$ 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 15–20 ha of habitat to successfully fledge young (Butcher et al., 2010). Program MARK was used to fit the multistate models (White and Burnham, 1999). Here, survival and detection probabilities were fixed to 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 because NLCD images were separated by five years and for computational efficiency when projecting habitat dynamics within the population 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 to 0.0 in order to circumvent numerical estimation problems.

2.2. Projection model

A male-based pre-breeding census projection model was used to simulate breeding range-wide warbler population dynamics. The model is based on the male segment of the species because demographic estimates are available only for males due to the cryptic nature of females. The model assumes the dynamics of females are similar to those of males, that all habitat patches were occupied at the initial starting point of the model, and that all adult males establish territories that produce fledglings. 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 programmed using Python in order to access preprogrammed tools in ArcMAP 10.2 and the scipy and numpy packages. The 200-ha hexagon tessellation was the base unit within the model. Each hexagon was modeled individually, however, birds were allowed to disperse among hexagons.

Two main loops were used in the model. The first loop was the iteration, or replication, loop. At this stage the model determines 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. 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. The model assumed an H hexagon had 170 ha of habitat (i.e., 85 percent of 200 ha), an M hexagon had 110 ha of habitat (i.e., 55 percent of 200 ha), L hexagon had 50 ha of habitat (i.e., 25 percent of 200

ha), and an N hexagon had 0 ha of habitat. The number of fledglings for year zero was calculated using the methods described below.

The second loop was the annual loop. At this stage the model samples vital rates, simulates population dynamics, and allows for dispersal and habitat-change 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 (i.e., environmental stochasticity), but 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 were 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 that “died” from the previous year and sampling from a binomial distribution with the probability of success equal to the specified dispersal parameter. 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. Notably, emigrants were estimated using these individuals because survival estimates for the species are apparent survival, not true survival. Thus, the survival estimates for the species represent 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 parameter represents only natal-site dispersal events. Density

dependence was incorporated within the model using a ceiling model (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.

The model also assumed the amount of habitat on protected lands would not diminish and that natural catastrophes on protected lands did not occur. Only hexagons on non-protected lands were allowed to transition to an alternate habitat state. 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.

All simulations were run for 500 iterations. Each iteration was comprised of 50 years. The number of adults in each year was summarized using the mean, 0.025th percentile, and 0.975th percentile across all iterations.

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 1991–1995, 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 (± 0.04) with a process variance of 0.007 when analyzing capture-resight data collected from 1997–2001 on the identical study plot. More recently, Duarte et al. (2014) reported a mean adult survival estimate at 0.47 (± 0.02) with a process variance of 0.0120 and sampling variance of 0.0113 when analyzing capture-resight data collected from 1992–2011 within seven study plots on FHMR that were monitored for variable numbers of years. In all three of these studies, the capture-resight data used to estimate juvenile survival were 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 1991–1995, Alldredge et al. (2004) estimated a mean juvenile survival at 0.30 (± 0.11) with a process

variance of 0.058 from 1997–2001, 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 1992–2000. U.S. Fish and Wildlife Service (1996) also analyzed capture-resight data collected on Balcones Canyonlands National Wildlife Refuge (BCNWR) from 1992–1994 and in Kendall County from 1961–1964. 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).

There are a number of studies that have assessed warbler productivity. Warbler 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 1.13–2.06 on FHMR from 1991–1999, 0.99–1.74 on Travis County properties from 2001–2008, and 0.93–1.68 on City of Austin properties from 1998–2008. They also reported the number of fledglings per successful territory ranged 1.03–2.29 on FHMR from 2001–2008, 1.86–2.87 on BCNWR from 1993–1997, and 2.29–2.79 on Barton Creek Habitat Preserve from 1996–1997. 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–

2010 and reported a number fledglings per successful territory at 1.9 ± 0.1 and 2.1 ± 0.1 in Texas oak (*Q. buckleyi*) habitat and 2.0 ± 0.2 and 2.1 ± 0.1 in post oak (*Q. stellata*) habitat. Duarte et al. (in review) analyzed survey data collected on BCP from 1998–2012 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 1.2–16.0 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., in review), breeding habitat is widely distributed across the warbler's breeding range (Diamond et al., 2010; Collier et al., 2012; Duarte et al., 2013), and long-distance movements and high dispersal rates are common among migratory birds (reviewed in Haig et al., 2011). 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 abundance could achieve a low probability of falling below 5000 individuals (hereafter referred to as the terminal extinction risk to fall below 5000 individuals) 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 a myriad of scenarios we could consider. For simplicity, we restricted the first series of analyses to three models (Table 5.1). Model I represents the lowest estimated mean rates, Model III represents the highest estimated mean rates based on quality data, and the rate parameters of Model II are intermediate between those of Model I and III. First, we ran each model with a dispersal parameter of 0.25. If there was a high terminal extinction risk 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 never resighted emigrated to sites within the system, rather than died. If there was a low terminal extinction risk we decreased dispersal to 0.05 in increments of 0.10 to examine if a low terminal extinction risk could be maintained with lower dispersal. In all of these scenarios, 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 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 5.2 for a list of K for protected lands under various scenarios.

Lastly, using two models that indicated a low terminal extinction risk could be achieved without approaching K (see below) we incorporated the additional uncertainty associated with the adult and juvenile survival parameters (i.e., 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 in the iteration loop of the model by sampling from a beta distribution using the estimated mean 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 an iteration but variable among iterations. Due to the increased variability in projected abundance among iterations, the number of iterations that were run was increased to 1000 for these scenarios.

Table 5.1 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.

Model	F		ϕ_J		ϕ_A	
	\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

Table 5.2 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.

Recovery Unit	Protected Lands Scenario			
	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	15192	20424	28125	37285

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

3. Results

Habitat-transition probabilities varied among recovery units ($\chi^2_{40} = 493.13$, $P < 0.001$).

Notably, habitat transitions always resulted in a reduction of habitat and never to a more favorable habitat state (Table 5.3). Further, habitat transitions rarely skipped states. For example, if an H hexagon transitioned to an alternate state it was more likely to transition to an M hexagon than an L or N hexagon. The estimated 5-year habitat-transition probabilities resulted in a 35.5 percent decrease in terminal K after the simulated 50 years when using the current protected-lands scenario (Table 5.4). 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 5.4). However, the magnitude of increase in terminal K was dependent on the recovery unit (Table 5.5).

The warbler population can remain viable (i.e., not fall below 5000 individuals) given the current information available for warbler vital rates and habitat dynamics (Table 5.6). Under Model III, the simulations indicated K would limit warbler abundance regardless of the dispersal parameter. The same was found for Model II when dispersal was at least 0.15. When running Model II with a dispersal of 0.05 there was only 0.06 terminal extinction risk of falling below to 5000 adult male warblers in the next 50 years. Still, the range-wide expected mean adult warbler population size reduced to 5379 (percentiles: 4923–5870; Table 5.7). Under the conditions of Model I, a low terminal extinction risk could be achieved with a dispersal parameter of 0.55 (Table 6). In this scenario the range-wide expected mean adult warbler population size reduced to 29406 (percentiles: 27990–30990; Table 5.7).

Model I with a dispersal parameter of 0.55 and Model II with a dispersal parameter of 0.5 indicated range-wide warbler viability could be achieved without approaching K. Thus, we also ran these scenarios while incorporating parametric uncertainty in the survival parameters. Under these scenarios, Model I terminal extinction risk increased to 0.39 with a terminal expected population size of 121278 (percentiles: 0–291022) and the Model II terminal extinction risk increased to 0.50 with a terminal expected population size of 107289 (percentiles: 0–291075; Fig. 5.2).

Table 5.3 Golden-cheeked warbler (*Setophaga chrysoparia*) habitat-transition probabilities with SE in parentheses. Probabilities were estimated at five-year intervals for each recovery unit.

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* (-)						
ψ^{MH}	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* (-)							
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* (-)							
ψ^{NM}	0* (-)							
ψ^{NL}	<0.01 (-)	<0.01 (-)	<0.01 (-)	<0.01 (-)	0* (-)	0* (-)	0* (-)	<0.01 (-)
ψ^{NN}	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 5.4 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	27600	15623 (15233–16025)	16584 (16213–16957)	17569 (17201–17966)	18485 (18096–18876)
2	31700	22328 (21922–22731)	23037 (22611–23435)	23815 (23403–24188)	24459 (24047–24823)
3	35900	26422 (25993–26851)	–	–	–
4	63200	42507 (41964–43066)	43099 (42513–43639)	44046 (43464–44606)	44962 (44347–45579)
5	47100	30101 (29527–30655)	–	–	30214 (29700–30786)
6	76500	49353 (48612–50063)	–	49449 (48702–50184)	50294 (49501–51055)
7	48900	33925 (33151–34680)	34530 (33759–35297)	35419 (34763–36147)	36345 (35677–37060)
8	118000	69487 (68353,70554)	69914 (68908–70973)	70845 (69894–72095)	71918 (70948–72968)
All	449000	289741 (287739–291550)	293023 (291222–294980)	297676 (295893–299504)	303093 (301343–304960)

Note: “–” indicates a K that was not modified from the original scenario. Initial K is the estimated warbler carrying capacity prior to simulating habitat change.

Table 5.5 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.

Table 5.6 Range-wide terminal extinction risk of falling below 5000 adult male golden-cheeked warblers (*Setophaga chrysoparia*) in 50 years for various scenarios.

Dispersal	Model		
	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.

Table 5.7 Range-wide expected mean adult male golden-cheeked warbler (*Setophaga chrysoparia*) population size with 2.5th and 97.5th percentiles in parentheses after 50 years for various scenarios. Under this protected lands scenario, terminal carrying capacity (K) was approximately 289741 (percentiles: 287739–291550).

Dispersal	Model		
	I	II	III
0.05	NA	5379 (4923–5870)	289712* (287935–291624)
0.15	NA	288515* (286487–290380)	289708* (287761–291510)
0.25	4 (0–14)	289719* (287901–291588)	289669* (287780–291625)
0.35	100 (58–152)	NA	NA
0.45	1847 (1619–2096)	NA	NA
0.55	29406 (27990–30990)	NA	NA

Note: “NA” indicates a scenario that was not simulated. “*” indicates a scenario in which the terminal population size approached K.

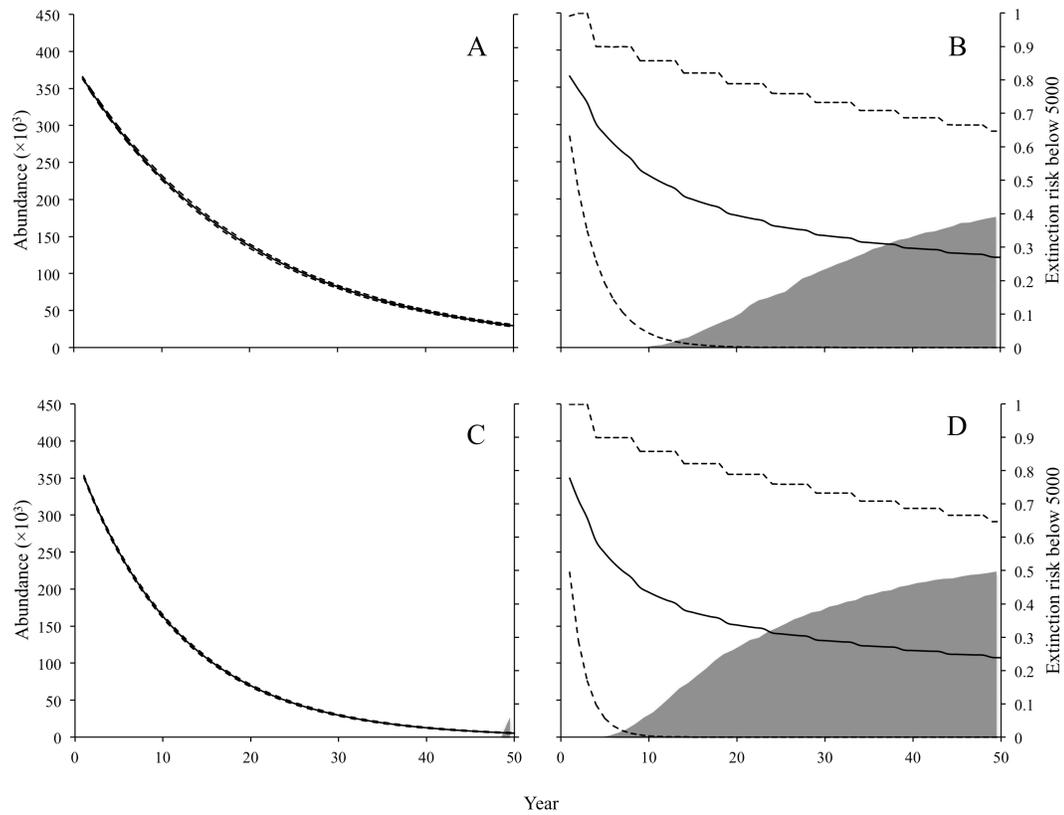


Figure 5.2 Range-wide mean golden-cheeked warbler (*Setophaga chrysoparia*) abundance (solid line) with 2.5th and 97.5th percentiles (dashed lines; primary y-axis) and the extinction risk to fall below 5000 individuals (shaded area; secondary y-axis) from Model I without parametric uncertainty (A), Model I with parametric uncertainty (B), Model II without parametric uncertainty (C), and Model II with parametric uncertainty (D). Model I scenarios were run with a dispersal parameter of 0.55, and Model II scenarios were run with a dispersal parameter of 0.05.

4. Discussion

We projected range-wide golden-cheeked warbler population and habitat dynamics. Habitat-transition probabilities supported the prediction that there has been a substantial decrease in warbler habitat over the past decade and that habitat transitions were directional. The population model suggested warbler population viability could be achieved with the current vital-rate estimates and recent habitat conditions. 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.

4.1. Habitat dynamics

As expected, we found habitat transitions were directional 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. Reemts and Hansen (2008) monitored succession of woodlands on FHMR following a high-intensity fire from 1996–2005. 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, Texas. 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. Fuhlendorf et al. (1996) modeled Ashe juniper in the Edwards Plateau, Texas. Their model results suggested that in the absence of fire, dense-canopy Ashe juniper woodlands would not form for 75 years. Moreover, one of the authors of this manuscript (J. S. Hatfield) is currently conducting a long-term longitudinal study on Ashe juniper growth in Travis County, Texas and is documenting growth rates that indicate Ashe juniper might take as long as a century to mature and contribute to warbler habitat. Collectively, these studies underscore the importance of protecting current warbler breeding habitat, rather than waiting for habitat to regenerate on currently protected lands.

Recovery units five, six, and eight did not have the highest rates of habitat loss as we predicted. No difference was found for habitat-transition probabilities among recovery units when a hexagon was in state L or N. An M hexagon 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. H hexagons 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 at the recovery-unit scale. Here we quantified habitat change at a 200-ha hexagon scale via multistate capture-recapture analyses. Although both methods are suitable approaches to quantify habitat change, we used the multistate approach here in order to incorporate stochastic habitat change within the PVA.

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 and 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. This is directly related to the size of each recovery unit, the current amount of protected habitat within each recovery unit, and the habitat-transition probabilities for each recovery unit.

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 H hexagons first and then selected M hexagons 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 modeling approach for warbler population dynamics is unlike the previous warbler PVAs in several aspects. We used a pre-breeding census projection model as opposed to a post-breeding census model. Thus, our terminal extinction risk estimates only consider adult male birds. 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. 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 when compared to Alldredge et al. (2014) is primarily based on terminology rather than model structure given their model also did not incorporate a natal-site dispersal-distance limitation and they considered relatively high dispersal parameters. How we incorporated dispersers into the model was also different than previous warbler PVAs. For example, in previous models the dispersers were second-year birds that survived, returned to the habitat patch they were born in, and then dispersed. In our model, dispersers were sampled from birds that would have been in their second year but did not return from the previous year. Again, dispersers were calculated using these individuals because survival estimates for the species represent 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 the dispersal parameter. 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 models to gauge the uncertainty present in our model results based on the available demographic estimates.

The PVA results suggest warbler viability can be achieved given the current information available for warbler vital rates and habitat dynamics. Under Model I, warbler terminal extinction risk to fall below 5000 individuals reduced to 0 only when the dispersal parameter was set at 0.55. This input parameter assumes that 55 percent of the fledglings that are estimated to never return to the area they were born 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 Model 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 Model II, warbler abundance was constrained by K when dispersal was at least 0.15. When dispersal reduced to 0.05 under this model the range-wide expected mean adult warbler population size declined by approximately 98.5%. Although alarming, a natal-site dispersal parameter of 0.05 is low and is not likely to occur for a migratory songbird in a natural setting. Under Model III, warbler abundance was constrained by K regardless of the dispersal parameter. The vital rates in Model III are a best-case scenario. In this model mean productivity and adult survival were 3.6 and 0.57, respectively. Although a mean survival of 0.57 has been reported, a mean productivity of 3.6 is not likely to occur across all territories because not all territories are successful. This model is intentionally overly optimistic, and inferences using this model should not be given a large amount weight.

Although Model I with a dispersal parameter of 0.55 and Model II with a dispersal parameter of 0.05 indicated a low terminal extinction risk to fall below 5000 individuals could be achieved, there was a considerable amount of uncertainty associated with these projections (Fig. 5.2). When incorporating parametric uncertainty, some of the replicates fell below 5000 individuals within the first 10 years of the simulation due to the low survival parameters. On the other hand, some of the replicates approached K and remained there throughout the 50-year simulation because of high survival parameters. 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).

Our projections were based on limited vital-rate estimates. These estimates were calculated using data that were collected on properties that actively manage for the species through habitat management and nest-parasite and predator-removal programs. Moreover, these properties only represent 3 of the 35 counties that comprise the warbler's breeding range. Population parameters estimated in different regions of the breeding range and under different management scenarios are essential to model warblers more realistically. This, along with projections that incorporated parametric uncertainty, emphasizes the need for greater field efforts to quantify warbler vital rates across its breeding range.

5. Conservation Implications

We projected range-wide golden-cheeked warbler population and habitat dynamics. The model results indicate warbler viability can be achieved under current conditions.

Although promising, as with any model, there is considerable uncertainty associated with our population projections. The estimated habitat-transition probabilities supported the hypothesis that habitat transitions are directional, whereby habitat is more likely to diminish than regenerate. Further, the model results suggested 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. Thus, conserving large tracts of warbler habitat to ensure their availability in the future is warranted. Nevertheless, there is currently no definition on what constitutes protected habitat, demographic data are lacking from a majority of the species' breeding range, and the magnitude of emigration from a target population has yet to be estimated with field data. Therefore, we recommend future efforts focus on these aspects of warbler conservation and ecology.

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shapefiles were provided by Texas Parks & Wildlife Department Land and Water Resources Conservation and Recreation Plan Statewide Inventory—2012 and military-land shapefiles were downloaded from the Defense Installation Spatial Data Infrastructure website ([http:// www.acq.osd.mil/ie/](http://www.acq.osd.mil/ie/)).

References

- Akçakaya, H. R., Burgman, M. A., Kindvall, O., Wood, C. C., Sjögren-Gulve, P., Hatfield, J. S., McCarthy, M. A. (Eds.), 2004. Species Conservation and Management: Case Studies. Oxford University Press, New York.
- Allredge, M. W., Hatfield, J. S., Diamond, D. D., True, C. D., 2004. Golden-cheeked warbler (*Dendroica chrysoparia*) in Texas: importance of dispersal toward persistence in a metapopulation. Species Conservation and Management: Case Studies (Eds. Akçakaya, H. R., Burgman, M. A., Kindvall, O., Wood, C. C., Sjögren-Gulve, P., Hatfield, J. S., McCarthy, M. A.), pp. 372–383. Oxford University Press, New York.
- Beissinger, S. R., McCullough, D. R. (Eds.), 2002. Population Viability Analysis. The University of Chicago Press, Chicago.
- Breiner, D. R., Nichols, J. D., Duncan, B. W., Stolen, E. D., Carter, G. M., Hunt, D. K., Dreese, J. H., 2010. Multistate modeling of habitat dynamics: factors affecting Florida scrub transition probabilities. *Ecology* 91, 3354–3364.
- Butcher, J. A., Morrisson, M. L., Random JR., D., Slack, R. D., Wilkins, R. N., 2010. Evidence of a minimum patch size threshold of reproductive success in an endangered songbird. *Journal of Wildlife Management* 74, 133–139.
- Caswell, H., 2001. Matrix population models, second edition. Sinauer Associates, Sunderland.

Formatted for publication in Biological Conservation

- City of Austin, 2012. 2012 Annual Report: Golden-cheeked Warbler (*Setophaga chrysoparia*) Monitoring Program Balcones Canyonlands Preserve annual report FY 2011–12. City of Austin Water Utility Wildland Conservation Division, Balcones Canyonlands Preserve, Austin.
- Collier, B. A., Groce, J. E., Morrison, M. L., Newnam, J. C., Campomizzi, A. J., Farrell, S. L., Mathewson, H. A., Snelgrove, R. T., Carroll, R. J., Wilkins, R. N., 2012. Predicting patch occupancy in fragmented landscapes at the rangewide scale for an endangered species: an example of an American warbler. *Diversity and Distributions* 18, 158–167.
- Diamond, D. D., Elliott, L. F., Blodgett, C., True, C. D., German, D., Treuer-Kuehn, A., 2010. Texas ecological systems classification. Project ID 1/457. Missouri Resource Assessment Partnership. University of Missouri, Columbia and the Texas Parks and Wildlife Department, Austin.
- Duarte, A., Jensen, J. L. R., Hatfield, J. S., Weckerly, F. W., 2013. Spatiotemporal variation in range-wide golden-cheeked warbler breeding habitat. *Ecosphere* 5, 152.
- Duarte, A., Hines, J. E., Nichols, J. D., Hatfield, J. S., Weckerly, F. W., 2014. Age-specific survival of male golden-cheeked warblers on the Fort Hood Military Reservation, Texas. *Avian Conservation and Ecology* 9, 4.
- Duarte, A., Weckerly, F. W., Schaub, M., Hatfield, J. S., *in review*. Estimating golden-cheeked warbler immigration: implications for the spatial scale of conservation. *Animal Conservation*.

- Fuhlendorf, S. D., Smeins, F. E., Grant, W. E., 1996. Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. *Ecological Modelling* 90, 245–255.
- Fry, J., Xian, G., Jin, S., Dewitz, J., Homer, C., Yang, L., Barnes, C., Herold, N., Wickham, J., 2011. Completion of the 2006 National Land Cover Database for the Conterminous United States. *Photogrammetric Engineering and Remote Sensing* 77, 858–864.
- Groce, J. E., Mathewson, H. A., Morrison, M. L., Wilkins, N., 2010. Scientific evaluation for the 5-year status review of the golden-cheeked warbler. Texas A&M Institute of Renewable Natural Resources, College Station.
- Haig, S. M., Bronaugh, W. M., Crowhurst, R. S., D’Elia, J., Eagles-Smith, C. A., Epps, C. W., Knaus, B., Miller, M. P., Moses, M. L., Oyler-McCance, S., Robinson, W. D., Sidlauskas, B., 2011. Genetic applications in avian conservation. *Auk* 128, 205–229.
- Hatfield, J. S., Weckerly, F. W., Duarte, A., 2012. Shifting foundations and metrics for golden-cheeked warbler recovery. *Wildlife Society Bulletin* 36, 415–422.
- Homer, C., Dewitz, J., Fry, J., Coan, M., Hossain, N., Larson, C., Herold, N., McKerrow, A., VanDriel, J. N., Wickham, J., 2007. Completion of the 2001 National Land Cover Database for the Conterminous United States. *Photogrammetric Engineering and Remote Sensing* 73, 337–341.

- Horne, J. S., Strickler, K. M., Alldredge, M. W., 2011. Quantifying the importance of patch-specific changes in habitat to metapopulation viability of an endangered songbird. *Ecological Applications* 21, 2478–2486.
- Hotaling, A. S., Martin, J., Kitchens, W. M., 2009. Estimating transition probabilities among everglades wetland communities using multistate models. *Wetlands* 29, 1224–1233.
- Jensen, J. L. R., Irvin, S., Duarte, A., 2013. Lidar-based detection of shrubland and forest land cover to improve identification of golden-cheeked warbler habitat. *Papers in Applied Geography*. 36, 74–82.
- Jin, S., Yang, L., Danielson, P., Homer, C., Fry, J., Xian, G., 2013. A comprehensive change detection method for updating the National Land Cover Database to circa 2011. *Remote Sensing of Environment* 132, 159–175.
- Johnson, F. A., Breininger, D. R., Duncan, B. W., Nichols, J. D., Runge, M. C., Williams, B. K., 2011. A Markov decision process for managing habitat for Florida scrub jays. *Journal of Fish and Wildlife Management*. 2, 234–246.
- Lindsay, D. L., Barr, K. R., Lance, R. F., Tweddale, S. A., Hayden, T. J., Leberg, P. L., 2008. Habitat fragmentation and genetic diversity of an endangered, migratory songbird, the golden-cheeked warbler (*Dendroica chrysoparia*). *Molecular Ecology* 17, 2122–2133.
- Magness, D. R., Wilkins, R. N., Hejl, S. J., 2006. Quantitative relationships among golden-cheeked warbler occurrence and landscape size, composition, and structure. *Wildlife Society Bulletin*. 34, 473–479.

- Marshall, M. E., Morrison, M. L., Wilkins, R. N., 2013. Tree species composition and food availability affect productivity of an endangered species: the golden-cheeked warbler. *Condor* 115, 882–892.
- Mathewson, H. A., Groce, J. E., McFarland, T. M., Morrison, M. L., Newnam, J. C., Snelgrove, R. T., Collier, B. A., Wilkins, R. N., 2012. Estimating breeding season abundance of golden-cheeked warblers in Texas, USA. *Journal of Wildlife Management* 76, 1117–1128.
- McGowan, C. P., Runge, M. C., Larson, M. A., 2011. Incorporating parametric uncertainty into population viability analysis models. *Biological Conservation* 144, 1400–1408.
- Morris, W. F., Doak, D. F., 2002. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sinauer Associates, Sunderland.
- Morrison, M. L., Collier, B. A., Mathewson, H. A., Groce, J. E., Wilkins, R. N., 2012. The prevailing paradigm as a hindrance to conservation. *Wildlife Society Bulletin* 36, 408–414
- Pulich, W. M., 1976. *The Golden-Cheeked Warbler: A Bioecological Study*. Texas Parks and Wildlife, Austin.
- Rasmussen, G. A., Wright, H. A., 1989. Succession of secondary shrubs on Ashe juniper communities after dozing and prescribed fire. *Journal of Range Management* 42, 295–298.
- Reemts, C. M., Hansen, L. L., 2008. Slow recolonization of burned oak-juniper woodlands by Ashe juniper (*Juniperus ashei*): Ten years of succession after crown fire. *Forest Ecology and Management* 255:1057–1066.

- Reidy, J. L., Stake, M. M., Thompson III, F. R., 2008. Golden-cheeked warbler nest mortality and predators in urban and rural landscapes. *Condor* 110, 458–466.
- U.S. Fish and Wildlife Service, 1990. Endangered and threatened wildlife and plants; final rule to list the golden-cheeked warbler as endangered. *Federal Register* 55, 53153–53160.
- U.S. Fish and Wildlife Service, 1992. Golden-cheeked warbler (*Dendroica chrysoparia*) recovery plan. U.S. Fish and Wildlife Service, Albuquerque.
- U.S. Fish and Wildlife Service, 1996. Golden-cheeked warbler population and habitat viability assessment report. (eds Beardmore, C., Hatfield, J., Lewis, J.). U.S. Fish and Wildlife Service, Austin.
- Vaillant, H., Akçakaya, H. R., Diamond, D., True, D., 2004. Modeling the effects of habitat loss and fragmentation on the golden-cheeked warbler. Engineering Research and Development Center, Construction Engineering Research Laboratory, Champaign.
- Wahl, R., D. D. Diamond, and D. Shaw. 1990. The golden-cheeked warbler: a status review. Unpublished report submitted to Ecological Services. U.S. Fish and Wildlife Service, Ft. Worth.
- White, G. C., Burnham, K. P., 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46, S120–S139.
- Wolfe, D. W., Hays, K. B., Farrell, S. L., Baggett, S., 2012. Regional credit market for species conservation: developing the Fort Hood Recovery Credit System. *Wildlife Society Bulletin* 36, 423–431.

Supplementary Material

Population dynamics of golden-cheeked warblers in a stochastic landscape

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Appendix S1

This Python script was used to simulate range-wide golden-cheeked warbler (*Setophaga chrysoparia*) population and breeding habitat dynamics.

```
import arcpy
from arcpy.sa import*
import numpy as np

arcpy.env.workspace=r"C:\Users\..." #set working directory
arcpy.env.overwriteOutput=True
arcpy.CheckOutExtension("Spatial")

Hexagons = "GCWAHabHex.shp"

print "PVA Started ..."

DispRate=0.15 #define dispersal rate

#Model I
##phia=0.47
##fec=0.2940962 #Mean on the transformed scale
##fec_tvar=0.3363353 #sd on the transformed scale

#Model II
phia=0.52
fec=0.905597 #Mean on the transformed scale
fec_tvar=0.1931937 #sd on the transformed scale

#Model III
##phia=0.57
##fec=1.271702 #Mean on the transformed scale
##fec_tvar=0.1358778 #sd on the transformed scale

#No. of iterations in simulation
it=500
R=0 #track iterations

#No. of years in simulation
yrs=50

#Create empty matrices to track abundances
RangeWide=np.zeros((it,yrs))
ProtectedRangeWide=np.zeros((it,yrs))
RU1=np.zeros((it,yrs))
RU2=np.zeros((it,yrs))
RU3=np.zeros((it,yrs))
```

```

RU4=np.zeros((it,yrs))
RU5=np.zeros((it,yrs))
RU6=np.zeros((it,yrs))
RU7=np.zeros((it,yrs))
RU8=np.zeros((it,yrs))
PRU1=np.zeros((it,yrs))
PRU2=np.zeros((it,yrs))
PRU3=np.zeros((it,yrs))
PRU4=np.zeros((it,yrs))
PRU5=np.zeros((it,yrs))
PRU6=np.zeros((it,yrs))
PRU7=np.zeros((it,yrs))
PRU8=np.zeros((it,yrs))
K_tot=np.zeros((it,yrs))
KRU1=np.zeros((it,yrs))
KRU2=np.zeros((it,yrs))
KRU3=np.zeros((it,yrs))
KRU4=np.zeros((it,yrs))
KRU5=np.zeros((it,yrs))
KRU6=np.zeros((it,yrs))
KRU7=np.zeros((it,yrs))
KRU8=np.zeros((it,yrs))

#set vital rates and variances
phij=0.28
phij_tvar=0.0076
phij_svar=0.0149
phia_tvar=0.0120
phia_svar=0.0113

#Alpha and beta shape parameters to derive mean survival at iteration level
Aphia=phia*(((phia*(1-phia))/phia_svar)-1)
Bphia=(1-phia)*(((phia*(1-phia))/phia_svar)-1)
Aphij=phij*(((phij*(1-phij))/phij_svar)-1)
Bphij=(1-phij)*(((phij*(1-phij))/phij_svar)-1)

arcpy.AddField_management(Hexagons, "K", "SHORT")
arcpy.AddField_management(Hexagons, "SaH", "FLOAT", "5", "3")
arcpy.AddField_management(Hexagons, "SjH", "FLOAT", "5", "3")
arcpy.AddField_management(Hexagons, "F", "FLOAT", "10", "8")
arcpy.AddField_management(Hexagons, "Adults", "LONG")
arcpy.AddField_management(Hexagons, "Juveniles", "SHORT")
arcpy.AddField_management(Hexagons, "mu_fledge", "FLOAT", "6", "2")
arcpy.AddField_management(Hexagons, "Emigrants", "SHORT")
arcpy.AddField_management(Hexagons, "Immigrants", "LONG")
arcpy.AddField_management(Hexagons, "S_juv", "SHORT")
arcpy.AddField_management(Hexagons, "S_ad", "SHORT")
arcpy.AddField_management(Hexagons, "Disdead", "SHORT")
arcpy.AddField_management(Hexagons, "NClass", "SHORT")
arcpy.CalculateField_management(Hexagons, "K", 0, "PYTHON_9.3")
arcpy.CalculateField_management(Hexagons, "SaH", 0.01, "PYTHON_9.3")
arcpy.CalculateField_management(Hexagons, "SjH", 0.01, "PYTHON_9.3")
arcpy.CalculateField_management(Hexagons, "F", 0.01, "PYTHON_9.3")
arcpy.CalculateField_management(Hexagons, "Adults", 0, "PYTHON_9.3")
arcpy.CalculateField_management(Hexagons, "NClass", 0, "PYTHON_9.3")
arcpy.CalculateField_management(Hexagons, "Emigrants", 0, "PYTHON_9.3")

```

```

arcpy.CalculateField_management(Hexagons, "Immigrants", 0, "PYTHON_9.3")
arcpy.CalculateField_management(Hexagons, "Juveniles", 0, "PYTHON_9.3")
arcpy.CalculateField_management(Hexagons, "mu_fledge", 0.01, "PYTHON_9.3")
arcpy.CalculateField_management(Hexagons, "S_juv", 0, "PYTHON_9.3")
arcpy.CalculateField_management(Hexagons, "S_ad", 0, "PYTHON_9.3")
arcpy.CalculateField_management(Hexagons, "Disdead", 0, "PYTHON_9.3")

#Mean Survival Parameters for each iteration
Sai=np.zeros(it)
Sji=np.zeros(it)

#initiates iteration loop
for i in range(0,it): # it because it doesnt use last value
    R=R+1
    print 'iteraton ' + repr(R)
    C=1
    print 'year ' + repr(C-1)

#####
## Set initial K and Set initial Adults
#####
cursor =
arcpy.da.UpdateCursor(Hexagons,["Region", "NClass", "K", "Adults", "F", "Class", "mu_fledge", "Juveniles"])
for row in cursor:
    # Reset Habitat Classes
    row[1]=row[5]

#Fledging rate
row[4]=float(np.random.lognormal(fec, fec_tvar, 1))

#Set up initial K and adult Abundance
if(row[0]==1):
    if (row[1]==1):
        row[2]= round(0.17 * 170) #upperbound from Mathewson et al. times 85% of total hexagon
        row[3]= round(0.15 * 170)
    elif (row[1]==2):
        row[2]= round(0.17 * 110) #upperbound from Mathewson et al. times 55% of total hexagon
        row[3]= round(0.15 * 110)
    elif (row[1]==3):
        row[2]= round(0.17 * 50) #upperbound from Mathewson et al. times 25% of total hexagon
        row[3]= round(0.15 * 50)
    else:
        row[2]= 0      #no habitat
        row[3]= 0
elif(row[0]==2):
    if (row[1]==1):
        row[2]= round(0.23 * 170) #upperbound from Mathewson et al. times 85% of total hexagon
        row[3]= round(0.19 * 170)
    elif (row[1]==2):
        row[2]= round(0.23 * 110) #upperbound from Mathewson et al. times 55% of total hexagon
        row[3]= round(0.19 * 110)
    elif (row[1]==3):
        row[2]= round(0.23 * 50) #upperbound from Mathewson et al. times 25% of total hexagon
        row[3]= round(0.19 * 50)
    else:
        row[2]= 0      #no habitat

```

```

        row[3]= 0
    else:
        if (row[1]==1):
            row[2]= round(0.37 * 170) #upperbound from Mathewson et al. times 85% of total hexagon
            row[3]= round(0.32 * 170)
        elif (row[1]==2):
            row[2]= round(0.37 * 110) #upperbound from Mathewson et al. times 55% of total hexagon
            row[3]= round(0.32 * 110)
        elif (row[1]==3):
            row[2]= round(0.37 * 50) #upperbound from Mathewson et al. times 25% of total hexagon
            row[3]= round(0.32 * 50)
        else:
            row[2]= 0    #no habitat
            row[3]= 0

    row[6]=row[3]*row[4]*0.5
    if(row[3]>0):
        row[7]=np.random.poisson(row[6],1)
    else:
        row[7]=0
    cursor.updateRow(row)

#Select mean survival for each itteration from a beta distribution
## Sai[i]=np.random.beta(Aphia,Bphia,1) #For parametric uncertainty
## Sji[i]=np.random.beta(Aphij,Bphij,1)
Sai[i]=phia
Sji[i]=phij

#Alpha and beta shape parameters to derive survival at annual level
aphia=Sai[i]*(((Sai[i]*(1-Sai[i]))/phia_tvar)-1)
bphia=(1-Sai[i]*(((Sai[i]*(1-Sai[i]))/phia_tvar)-1)
aphij=Sji[i]*(((Sji[i]*(1-Sji[i]))/phij_tvar)-1)
bphij=(1-Sji[i]*(((Sji[i]*(1-Sji[i]))/phij_tvar)-1)

#Initiate annual loop
for j in range(0,ysrs): #used yrs-1 because year one is set before this loop starts
    C=C+1
    print 'year ' + repr(C-1)
    emigrants=0
    HC=C%5.0
    if (HC==0):
        ###Change that habitat state based on NLCD probabilities every 5 years
        cursor = arcpy.da.UpdateCursor(Hexagons,["NClass","RU","Protected","Region","K"])
        for row in cursor:
            if(row[2]==0):
                if(row[0]==1):
                    if(row[1]==1):

whichClass=np.random.multinomial(1,pvals=[0.6086956,0.3444818,0.0468226,0],size=1)
            elif(row[1]==2):
                whichClass=np.random.multinomial(1,pvals=[0.5884341,0.4115659,0,0],size=1)
            elif(row[1]==3):
                whichClass=np.random.multinomial(1,pvals=[0.6970586,0.3029414,0,0],size=1)
            elif(row[1]==4):

whichClass=np.random.multinomial(1,pvals=[0.5866831,0.4020103,0.0113066,0],size=1)

```

```

elif(row[1]==5):
    whichClass=np.random.multinomial(1,pvals=[0.631016,0.3529412,0.0160428,0],size=1)
elif(row[1]==6):
    whichClass=np.random.multinomial(1,pvals=[0.68197,0.3030049,0.0150251,0],size=1)
elif(row[1]==7):

whichClass=np.random.multinomial(1,pvals=[0.5838923,0.4060406,0.0100671,0],size=1)
else:
    whichClass==np.random.multinomial(1,pvals=[0.796931,0.203069,0,0],size=1)
elif(row[0]==2):
    if(row[1]==1):
        whichClass=np.random.multinomial(1,pvals=[0,0.8184844,0.1815156,0],size=1)
    elif(row[1]==2):
        whichClass=np.random.multinomial(1,pvals=[0,0.8766588,0.1233412,0],size=1)
    elif(row[1]==3):
        whichClass=np.random.multinomial(1,pvals=[0,0.8660391,0.1339609,0],size=1)
    elif(row[1]==4):
        whichClass=np.random.multinomial(1,pvals=[0,0.8167895,0.1832105,0],size=1)
    elif(row[1]==5):
        whichClass=np.random.multinomial(1,pvals=[0,0.8652247,0.1347753,0],size=1)
    elif(row[1]==6):
        whichClass=np.random.multinomial(1,pvals=[0,0.8655391,0.1344609,0],size=1)
    elif(row[1]==7):
        whichClass=np.random.multinomial(1,pvals=[0,0.8829902,0.1170098,0],size=1)
    else:
        whichClass=np.random.multinomial(1,pvals=[0,0.9151854,0.0848146,0],size=1)
elif(row[0]==3):
    if(row[1]==1):
        whichClass=np.random.multinomial(1,pvals=[0,0,0.9666161,0.0333839],size=1)
    elif(row[1]==2):
        whichClass=np.random.multinomial(1,pvals=[0,0,0.9805263,0.0194737],size=1)
    elif(row[1]==3):
        whichClass=np.random.multinomial(1,pvals=[0,0,0.9753598,0.0246402],size=1)
    elif(row[1]==4):
        whichClass=np.random.multinomial(1,pvals=[0,0,0.9832613,0.0167387],size=1)
    elif(row[1]==5):
        whichClass=np.random.multinomial(1,pvals=[0,0,0.9767321,0.0232679],size=1)
    elif(row[1]==6):
        whichClass=np.random.multinomial(1,pvals=[0,0,0.9819594,0.0180406],size=1)
    elif(row[1]==7):
        whichClass=np.random.multinomial(1,pvals=[0,0,0.9804448,0.019552],size=1)
    else:
        whichClass=np.random.multinomial(1,pvals=[0,0,0.9862042,0.0137958],size=1)
else:
    whichClass=np.random.multinomial(1,pvals=[0,0,0,1],size=1)

whichClass2=-1
for l in range(0,4):
    whichClass2=whichClass2+1
    if(whichClass[0][whichClass2]==1):
        row[0]=l+1
else:
    row[0]=row[0]
##Update K
if(row[3]==1):
    if(row[0]==1):

```

```

        row[4]= round(0.17 * 170) #upperbound from Mathewson et al. times 85% of total hexagon
    elif(row[0]==2):
        row[4]= round(0.17 * 110) #upperbound from Mathewson et al. times 55% of total hexagon
    elif(row[0]==3):
        row[4]= round(0.17 * 50) #upperbound from Mathewson et al. times 25% of total hexagon
    else:
        row[4]= 0      #no habitat
elif(row[3]==2):
    if(row[0]==1):
        row[4]= round(0.23 * 170) #upperbound from Mathewson et al. times 85% of total hexagon
    elif(row[0]==2):
        row[4]= round(0.23 * 110) #upperbound from Mathewson et al. times 55% of total hexagon
    elif(row[0]==3):
        row[4]= round(0.23 * 50) #upperbound from Mathewson et al. times 25% of total hexagon
    else:
        row[4]= 0      #no habitat
else:
    if(row[0]==1):
        row[4]= round(0.37 * 170) #upperbound from Mathewson et al. times 85% of total hexagon
    elif(row[0]==2):
        row[4]= round(0.37 * 110) #upperbound from Mathewson et al. times 55% of total hexagon
    elif(row[0]==3):
        row[4]= round(0.37 * 50) #upperbound from Mathewson et al. times 25% of total hexagon
    else:
        row[4]= 0      #no habitat
    cursor.updateRow(row)
#print "Habitat Changed"

cursor =
arcpy.da.UpdateCursor(Hexagons,["SaH","SjH","F","Adults","Juveniles","S_juv","S_ad","Disdead","Emig
rants","K","mu_fledge"])
for row in cursor:

    ###Select survival and fledging rate parameters for each hexagon
    row[0]=float(np.random.beta(aphia,bphia,1))
    row[1]=float(np.random.beta(aphij,bphij,1))
    row[2]=float(np.random.lognormal(fec, fec_tvar, 1))

    ###Calculate number of "survivors"
    if (row[4] > 0):
        row[5]=np.sum(np.random.binomial(row[4],row[1],1))
    else:
        row[5]=0

    if (row[3] > 0):
        row[6]=np.sum(np.random.binomial(row[3],row[0],1))
    else:
        row[6]=0

    row[3]=row[5]+row[6]

    ###How many emigrants?
    row[7]=row[4]-row[5]
    if (row[7] > 0):
        row[8]=np.sum(np.random.binomial(row[7],DispRate,1))
    else:

```

```

    row[8]=0

    ###Zero out the number of juveniles
    row[4] = 0

    ###Deal with hexagons that have greater than K individuals
    if (row[3] > row[9]):
        extra = row[3]-row[9]
        row[8] = row[8]+extra
        row[3] = row[3]-extra

    ###Sum emigrants
    emigrants=emigrants+row[8]

    ###Zero out emigrants
    row[8]=0
    cursor.updateRow(row)

    ###Simulate dispersal
    if (emigrants > 0):
        arcpy.MakeFeatureLayer_management(Hexagons, "AllHex")
        arcpy.SelectLayerByAttribute_management("AllHex", 'NEW_SELECTION',"Adults"<"K")
        n_selected=arcpy.GetCount_management("AllHex") #count how many hexagons are selected
        count = int(n_selected.getOutput(0))
        if (count > 0):
            who=np.random.randint(1,high=count+1,size=emigrants)
            m=max(who)
            ex=count-m
            count2=np.bincount(who)
            if (ex > 0):
                zeros=np.zeros(ex)
                zeros2=zeros.astype(int)
                count2=np.append(count2,zeros2)
            em_it=0 #track who gets what
            cursor = arcpy.da.UpdateCursor("AllHex",["Immigrants", "Adults"])
            for row in cursor:
                em_it=em_it+1
                row[0]=row[0]+count2[em_it]
                row[1]=row[1]+count2[em_it]
                cursor.updateRow(row)
            arcpy.SelectLayerByAttribute_management("AllHex", 'CLEAR_SELECTION') #clear selection
            arcpy.Delete_management("AllHex")

    emigrants2=0
    cursor = arcpy.da.UpdateCursor(Hexagons,["Adults", "K"])
    for row in cursor:
        if (row[0] > row[1]):
            extra2=row[0]-row[1]
            emigrants2=emigrants2+extra2
            row[0]=row[0]-extra2
        else:
            row[0]=row[0]
        cursor.updateRow(row)

    if (emigrants2 > 0):
        arcpy.MakeFeatureLayer_management(Hexagons, "AllHex")

```

```

arcpy.SelectLayerByAttribute_management("AllHex", 'NEW_SELECTION',"Adults"<"K")
n_selected=arcpy.GetCount_management("AllHex") #count how many hexagons are selected
count = int(n_selected.getOutput(0))
if (count > 0):
    who=np.random.randint(1,high=count+1,size=emigrants2)
    m=max(who)
    ex=count-m
    count2=np.bincount(who)
    if (ex > 0):
        zeros=np.zeros(ex)
        zeros2=zeros.astype(int)
        count2=np.append(count2,zeros2)
    em_it=0 #track who gets what
    cursor = arcpy.da.UpdateCursor("AllHex",["Immigrants","Adults"])
    for row in cursor:
        em_it=em_it+1
        row[0]=row[0]+count2[em_it]
        row[1]=row[1]+count2[em_it]
        cursor.updateRow(row)
    arcpy.SelectLayerByAttribute_management("AllHex", 'CLEAR_SELECTION') #clear selection
    arcpy.Delete_management("AllHex")

emigrants3=0
cursor = arcpy.da.UpdateCursor(Hexagons,["Adults","K"])
for row in cursor:
    if (row[0] > row[1]):
        extra3=row[0]-row[1]
        emigrants3=emigrants3+extra3
        row[0]=row[0]-extra3
    else:
        row[0]=row[0]
    cursor.updateRow(row)

if (emigrants3 > 0):
    arcpy.MakeFeatureLayer_management(Hexagons, "AllHex")
    arcpy.SelectLayerByAttribute_management("AllHex", 'NEW_SELECTION',"Adults"<"K")
    n_selected=arcpy.GetCount_management("AllHex")
    count = int(n_selected.getOutput(0))
    if (count > 0):
        who=np.random.randint(1,high=count+1,size=emigrants3)
        m=max(who)
        ex=count-m
        count2=np.bincount(who)
        if (ex > 0):
            zeros=np.zeros(ex)
            zeros2=zeros.astype(int)
            count2=np.append(count2,zeros2)
        em_it=0 #track who gets what
        cursor = arcpy.da.UpdateCursor("AllHex",["Immigrants","Adults"])
        for row in cursor:
            em_it=em_it+1
            row[0]=row[0]+count2[em_it]
            row[1]=row[1]+count2[em_it]
            cursor.updateRow(row)
        arcpy.SelectLayerByAttribute_management("AllHex", 'CLEAR_SELECTION') #clear selection
        arcpy.Delete_management("AllHex")

```

```

cursor = arcpy.da.UpdateCursor(Hexagons,["Adults","K"])
for row in cursor:
    if (row[0] > row[1]):
        extra4=row[0]-row[1]
        row[0]=row[0]-extra4
    else:
        row[0]=row[0]
    cursor.updateRow(row)

cursor = arcpy.da.UpdateCursor(Hexagons,["F","Adults","Juveniles","mu_fledge"])
for row in cursor:
    ###Calculate number of juveniles per hexagon
    row[3]=row[1]*row[0]*0.5
    if(row[1]>0):
        row[2]=np.random.poisson(row[3],1)
    else:
        row[2]=0
    cursor.updateRow(row)

RW_total = 0
PRW_total = 0
RU1_total = 0
RU2_total = 0
RU3_total = 0
RU4_total = 0
RU5_total = 0
RU6_total = 0
RU7_total = 0
RU8_total = 0
PRU1_total = 0
PRU2_total = 0
PRU3_total = 0
PRU4_total = 0
PRU5_total = 0
PRU6_total = 0
PRU7_total = 0
PRU8_total = 0
K_total = 0
KRU1_total = 0
KRU2_total = 0
KRU3_total = 0
KRU4_total = 0
KRU5_total = 0
KRU6_total = 0
KRU7_total = 0
KRU8_total = 0
cursor = arcpy.da.SearchCursor(Hexagons,["Adults","RU","Protected","K"])
for row in cursor:
    RW_total = RW_total + row[0]
    K_total = K_total + row[3]
    if(row[2]==1):
        PRW_total = PRW_total + row[0]

    if(row[1]==1):
        RU1_total = RU1_total + row[0]

```

```

    KRU1_total = KRU1_total + row[3]
    if (row[2]==1):
        PRU1_total = PRU1_total + row[0]
elif(row[1]==2):
    RU2_total = RU2_total + row[0]
    KRU2_total = KRU2_total + row[3]
    if (row[2]==1):
        PRU2_total = PRU2_total + row[0]
elif(row[1]==3):
    RU3_total = RU3_total + row[0]
    KRU3_total = KRU3_total + row[3]
    if (row[2]==1):
        PRU3_total = PRU3_total + row[0]
elif(row[1]==4):
    RU4_total = RU4_total + row[0]
    KRU4_total = KRU4_total + row[3]
    if (row[2]==1):
        PRU4_total = PRU4_total + row[0]
elif(row[1]==5):
    RU5_total = RU5_total + row[0]
    KRU5_total = KRU5_total + row[3]
    if (row[2]==1):
        PRU5_total = PRU5_total + row[0]
elif(row[1]==6):
    RU6_total = RU6_total + row[0]
    KRU6_total = KRU6_total + row[3]
    if (row[2]==1):
        PRU6_total = PRU6_total + row[0]
elif(row[1]==7):
    RU7_total = RU7_total + row[0]
    KRU7_total = KRU7_total + row[3]
    if (row[2]==1):
        PRU7_total = PRU7_total + row[0]
else:
    RU8_total = RU8_total + row[0]
    KRU8_total = KRU8_total + row[3]
    if (row[2]==1):
        PRU8_total = PRU8_total + row[0]

#fill matrices
RangeWide[i,j] = RW_total
ProtectedRangeWide[i,j] = PRW_total
RU1[i,j] = RU1_total
RU2[i,j] = RU2_total
RU3[i,j] = RU3_total
RU4[i,j] = RU4_total
RU5[i,j] = RU5_total
RU6[i,j] = RU6_total
RU7[i,j] = RU7_total
RU8[i,j] = RU8_total
PRU1[i,j] = PRU1_total
PRU2[i,j] = PRU2_total
PRU3[i,j] = PRU3_total
PRU4[i,j] = PRU4_total
PRU5[i,j] = PRU5_total
PRU6[i,j] = PRU6_total

```

```
PRU7[i,j] = PRU7_total
PRU8[i,j] = PRU8_total
K_tot[i,j] = K_total
KRU1[i,j] = KRU1_total
KRU2[i,j] = KRU2_total
KRU3[i,j] = KRU3_total
KRU4[i,j] = KRU4_total
KRU5[i,j] = KRU5_total
KRU6[i,j] = KRU6_total
KRU7[i,j] = KRU7_total
KRU8[i,j] = KRU8_total
```

```
np.savetxt('RangeWideOutput.txt', RangeWide, delimiter=',')
np.savetxt('ProtectedRangeWide.txt', ProtectedRangeWide, delimiter=',')
np.savetxt('RU1.txt', RU1, delimiter=',')
np.savetxt('RU2.txt', RU2, delimiter=',')
np.savetxt('RU3.txt', RU3, delimiter=',')
np.savetxt('RU4.txt', RU4, delimiter=',')
np.savetxt('RU5.txt', RU5, delimiter=',')
np.savetxt('RU6.txt', RU6, delimiter=',')
np.savetxt('RU7.txt', RU7, delimiter=',')
np.savetxt('RU8.txt', RU8, delimiter=',')
np.savetxt('PRU1.txt', PRU1, delimiter=',')
np.savetxt('PRU2.txt', PRU2, delimiter=',')
np.savetxt('PRU3.txt', PRU3, delimiter=',')
np.savetxt('PRU4.txt', PRU4, delimiter=',')
np.savetxt('PRU5.txt', PRU5, delimiter=',')
np.savetxt('PRU6.txt', PRU6, delimiter=',')
np.savetxt('PRU7.txt', PRU7, delimiter=',')
np.savetxt('PRU8.txt', PRU8, delimiter=',')
np.savetxt('K_tot.txt', K_tot, delimiter=',')
np.savetxt('KRU1.txt', KRU1, delimiter=',')
np.savetxt('KRU2.txt', KRU2, delimiter=',')
np.savetxt('KRU3.txt', KRU3, delimiter=',')
np.savetxt('KRU4.txt', KRU4, delimiter=',')
np.savetxt('KRU5.txt', KRU5, delimiter=',')
np.savetxt('KRU6.txt', KRU6, delimiter=',')
np.savetxt('KRU7.txt', KRU7, delimiter=',')
np.savetxt('KRU8.txt', KRU8, delimiter=',')
```

```
print "done"
```

CHAPTER VI

CONCLUSIONS

This dissertation centered on updating and extending our knowledge on golden-cheeked warbler (*Setophaga chrysoparia*, hereafter warbler) population dynamics and habitat conservation. To accomplish this, I carried out four interrelated multidisciplinary studies that used modern statistical and geospatial methodologies to examine factors that influence warbler population and habitat dynamics at multiple spatial and temporal scales. Such information is invaluable in order to establish effective science-based conservation and management programs. In the subsequent paragraphs I outline the major findings of this dissertation research and how those findings relate to on-the-ground management. I also provide recommendations concerning future research and monitoring efforts for the species in order to overcome some of the shared data limitations and knowledge gaps that became evident through the completion of these studies.

Chapters II and V used different techniques to quantify range-wide warbler breeding habitat change over the last decade. In Chapter II, I took advantage of freely available Landsat imagery to quantify habitat change from 1999–2001 to 2010–2011 using a post-classification change detection analysis. I found that there was a large reduction in range-wide warbler breeding habitat and that warbler breeding habitat was removed and became more fragmented at uneven rates across the warbler's breeding range. Specifically, the imagery suggested warbler habitat was being removed and becoming more fragmented at faster rates around the city of Austin (recovery unit five), on the outskirts of the city of San Antonio (recovery unit six), and throughout recovery unit eight. A couple limitations to this approach were that vegetation height data cannot

be derived from Landsat scenes, which is needed in order to reliably distinguish shrublands from woodlands, and the results cannot subsequently be used to project habitat dynamics while incorporating stochasticity. Thus, in Chapter V I used the National Land Cover Database to examine range-wide habitat change from 2001–2011. Here, I partitioned the warbler’s breeding range into equal size hexagons and fitted a multistate capture-recapture models to estimate recovery-unit-specific, habitat-transition probabilities. Using this approach led to slightly different conclusions when comparing habitat change among recovery units. In particular, I found areas with a moderate amount of habitat in recovery units one and four were more likely to diminish and that habitat in recovery unit eight was more stable. Differences in the findings should not be too surprising given the different approaches used (as discussed in Chapter V). It should be acknowledged that habitat change in Chapter II was quantified at the recovery unit scale (i.e., total change), whereas Chapter V quantified habitat change at the 200-ha hexagon scale. Thus, comparisons in habitat change among recovery units are more directly comparable via the methods used in Chapter V. Regardless of the method used, both studies found a significant reduction in warbler breeding habitat and present estimates of habitat destruction that can assist researchers and managers in prioritizing breeding habitat conservation efforts across recovery units. However, neither of these studies found an increase in habitat to occur over the time series. This is related to the time span over which each of these studies quantified habitat change (i.e., roughly 10 years). Although this is probably is not an issue when projecting habitat dynamics over 50 years (as I did in Chapter V), it does limit how far warbler habitat can realistically be projected into the future because at some point habitat can regenerate.

In Chapter III I set out to estimate more current, precise adult and juvenile apparent survival probabilities and their associated variances for male warblers, and test hypotheses concerning possible spatial and temporal variation in apparent survival. To accomplish these objectives, I analyzed long-term warbler capture-resight data collected across seven study plots on the Fort Hood Military Reservation. The results did not provide evidence of site-specific variation in adult apparent survival on the installation, which is probably due to study plots containing similar habitat metrics. However, I could not assess whether juvenile apparent survival varied spatially because of a lack of data. Further, the data did not provide strong support for a temporal association between warbler abundance and apparent survival. The overall mean juvenile apparent survival estimate did not differ greatly from previous estimates for the species. However, the overall mean adult apparent survival estimate suggested that previous warbler population models might have been overly optimistic with respect to adult survival. Further, given the estimated vital rates (i.e., survival), warbler abundance should have significantly declined, a scenario that is not supported by the current survey data. Thus, this study suggested warbler movement might be widespread causing apparent survival estimates to be substantially lower than true survival. Moreover, this study highlighted the need to have capture-resight collected on plots with different habitat metrics.

Although Chapter III suggested movement among habitat patches was essential for warbler persistence, movement rates had not been estimated for the species. Therefore, in Chapter IV I focused on warbler population dynamics at the local spatial scale using a new extension of integrated population models. Specifically, I investigated the relationships among warbler immigration rate, fledging rate, survival probabilities,

and population growth rate. Further, using a deterministic projection model, I examined the response required by vital rates to maintain a stable population across varying levels of immigration. This study provided quantitative evidence of the importance of immigration to stabilize local warbler populations, indicating warbler conservation and management programs need to be implemented at larger spatial scales than current efforts to be effective. This study also demonstrated that biologists are able to monitor warbler movement (i.e., immigration) in the field using practical, reliable methods. Such information is imperative to gauge the efficacy of conservation and management strategies designed to maximize warbler viability in a changing landscape.

Finally, for Chapter V I refocused on warbler population and habitat dynamics at the range-wide scale. Specifically, I examined if warbler viability is possible given the current conditions and evaluated if protecting a greater amount of habitat would increase the number of warblers that can be supported in the future. The model results indicated population viability could be achieved under current conditions for the next 50 years. However, there was considerable uncertainty associated with the population projections due to parametric uncertainty. Further, the model results suggested that increasing the amount of protected lands at the onset of the simulation would have a substantial impact on terminal carrying capacities at the end of the 50-year simulation. This study highlights the importance of conserving large tracts of warbler breeding habitat that is currently available due to the directional nature of habitat transitions and the positive outcome of protecting a greater amount of habitat.

Collectively, these studies help us understand the current and potential future status of the golden-cheeked warbler. Current estimates of warbler vital and movement

rates, distribution, and abundance, along with my population model, suggest there is much hope for warbler persistence into the foreseeable future. It is important to note, however, that there is still much work to be done. Although the long-term capture-resight data collected on the Fort Hood Military Reservation allowed for the estimation of precise survival probabilities, the study design (i.e., only monitoring plots with similar habitat structure), inconsistencies with surveys (i.e., not monitoring every plot every year), and lack of hatch-year bird capture-resight data limited what could be tested using these data. I estimated warbler movement rates (i.e., immigration) by combining long-term spot-mapping and productivity survey data collected on the Balcones Canyonlands Preserve. However, because capture-resight data were lacking I had to rely on the use of informative priors based on the survival estimates from Fort Hood Military Reservation, and again, was limited on what could be tested using the data. Further, warbler survival and productivity estimates used within the range-wide population model were limited. Warbler survival probabilities have yet to be estimated in different regions and under different management programs as they relate to habitat metrics. Moreover, warbler reproductive ecology research typically focuses on the number of territories that produce at least one fledgling, not the number of fledglings per territory. Thus, generalizations had to be made within the population model. Specifically, the model assumed the available survival and productivity estimates were representative of these demographic parameters across the warbler's breeding range. Further, the model assumed the habitat structure within a given hexagon did not impact vital rates. This emphasizes the need for resource agencies to focus a considerable amount of effort on modifying existing annual survey work toward collecting the data needed to estimate these demographic parameters

under different environmental settings. Lastly, the studies related to habitat dynamics within this dissertation emphasize the need for 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.