THE INFLUENCE OF TREE SPECIES COMPOSITION ON SONGBIRD ABUNDANCE AND PRODUCTIVITY

A Dissertation

by

ASHLEY MARIE LONG

Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Chair of Committee,	Michael L. Morrison
Committee Members,	Heather A. Mathewson
	David M. Cairns
	William E. Rogers
Head of Department,	Michael P. Masser

August 2014

Major Subject: Wildlife and Fisheries Sciences

ABSTRACT

Most avian habitat selection studies are conducted within small spatial and temporal scales and fail to link habitat selection decisions to reproductive success. This limits our understanding of avian demographic patterns across the full continuum of ecological conditions a species inhabits and may result in the application of inappropriate conservation strategies. The golden-cheeked warbler (*Setophaga chrysoparia*; hereafter warbler) is a federally endangered songbird that breeds in oak-juniper woodland of central Texas. Management guidelines indicate that mature, dense Ashe juniper cover is an attribute of high quality warbler breeding habitat, but few studies have examined warbler responses to Ashe juniper across the continuum of vegetation types they inhabit. I used data collected from 899 territories on 90 study sites (2009–2013) located across the warbler's breeding range to investigate the influence of year, geographic location, various Ashe juniper metrics, and dominant oak species on warbler abundance and productivity. My results reiterate that vegetation utilized by warblers is highly variable and that warblers successfully breed in areas with vegetation characteristics outside current descriptions of warbler breeding habitat. Warbler territory density remained constant across the full range of percent Ashe juniper cover in woodland dominated by Lacey (*Quercus laceyi*), live (*Q. fusiformis*), and Texas oak (*Q. buckleyi*). Warbler territory density increased with increasing percent Ashe juniper cover in woodland dominated by post oak (*Q. stellata*) and in mixed oak woodland and warbler territory density decreased with increasing percent Ashe juniper cover in woodland stands dominated by shin oak (*Q. sinuata*). Territories were larger in oak-juniper woodland stands dominated by live oak than oak-juniper woodland stands dominated by all other species but post oak. Results regarding relationships between territory-scale metrics and territory size and pairing and fledging success varied, but indicate that prioritizing sites based on qualitative Ashe juniper metrics or managing sites to promote single-aged stands of mature Ashe juniper cover may not be the most effective strategy for warblers. Management and restoration efforts may be more effective if tailored to local vegetation characteristics associated with tree species composition.

ACKNOWLEDGMENTS

I would like to thank my committee chair, Dr. Michael L. Morrison, and my committee members, Drs. Heather A. Mathewson, William E. Rogers, and David M. Cairns, for their guidance and support throughout the course of my graduate program. I also thank personnel at Texas A&M's Institute of Renewable Natural Resources and Department of Wildlife and Fisheries Sciences for providing time and resources that aided my research efforts, especially T. McFarland and B. Stevener. Thanks also to the many field technicians and landowners who made data collection for my project possible. I am additionally grateful to all of the graduate student members of the Morrison lab for their contributions to my study. I give special thanks to M. Colón, H. Pruett, and L. Stewart, who served not only as colleagues, but also as close friends. In addition, I thank those who served as mentors to me during my undergraduate and graduate school career, particularly W. Jensen and K. Blackmore. Their encouragement was integral to the completion of my degree.

Land access and financial support was provided by the US Army Integrated Training Area Management (ITAM) Program, Office of the Secretary of Defense, Department of Defense, and additionally by Texas Ecolab, Joint Fire Science Program, Texas Parks and Wildlife Department, Texas Department of Transportation, and The Nature Conservancy – Austin.

TABLE OF CONTENTS

LIST OF FIGURES

Page

LIST OF TABLES

CHAPTER I

INTRODUCTION

Studies that explore wildlife-habitat relationships have a rich history and have provided important information regarding species distributions, abundance, and productivity (Hildén 1965, Hutto 1985, Morrison et al. 2006:3-14). Interest in wildlife-habitat relationships remains strong, particularly in light of recent animal population declines, as studies that incorporate both habitat and animal demographic information play a critical role in species conservation (Caughley 1994, Bonebrake et al. 2010). Knowledge gained from such research guides wildlife management, aids species recovery, and advances ecological theory. Unfortunately, our understanding of most wildlife-habitat relationships is limited to information gained from short-term studies conducted at a small number of prioritized study sites. This strategy provides a baseline for natural history and habitat associations at specific locations, but constrains our ability to develop comprehensive range-wide management and restoration plans that are effective across the continuum of ecological conditions a species inhabits. Spatially extensive, replicated studies conducted across the geographic extent of a species' range are necessary if our goals are to fully understand the ecology of a species and ensure the long-term persistence of a population.

The federally endangered golden-cheeked warbler (*Setophaga chrysoparia*; hereafter warbler), is a small, insectivorous songbird that breeds exclusively in central Texas (USFWS 1990). Typical breeding habitat for the warbler is described as oak-juniper woodland with dense canopy cover that is composed of tree species such as Ashe juniper (*Juniperus ashei*), oaks (e.g., live oak, *Quercus fusiformis*; post oak, *Q. stellata*; Texas oak, *Q. buckleyi*), and various other hardwoods (Pulich 1976, Ladd and Gass 1999). Habitat loss and degradation precipitated warbler decline (USFWS 1990). Within oak-juniper woodlands, clearing of Ashe juniper for range management, or urban development, and subsequent lack of oak recruitment were particularly problematic for this species. This is because mature (>20 years) Ashe juniper provides necessary nesting material, nesting sites, and song perches and a combination of oaks and Ashe juniper provide important foraging substrates for warblers (Pulich 1976, Wahl et al. 1990). Oak wilt, an infectious oak-defoliating disease caused by the fungus *Ceratocystis fagacearum*, can alter oak-juniper woodland composition and may negatively impact warblers in the near future (Stewart et al. 2014).

Researchers and land managers obtained most information regarding the distribution of warblers from short-term conducted on prioritized sites. In the eastern portion of the warbler’s breeding range, warbler occurrence (DeBoer and Diamond 2006), density (Peak and Thompson 2013), and nest site selection (Dearborn and Sanchez 2001) were positively related to Ashe juniper cover. Magness (2006) additionally found that warblers were more likely to occur at points with high Ashe juniper cover in the western portion of the warbler’s breeding range. Given the perceived importance of Ashe juniper cover to warbler habitat selection, warbler management guidelines indicate that dense Ashe juniper cover is an attribute of high quality warbler breeding habitat (TPWD 1990, 2012; USFWS 1992). However, few studies have actually examined the influence of Ashe juniper cover on habitat selection across multiple spatial and temporal scales or linked this vegetative characteristic to reproductive success.

Warblers may also exhibit different responses to oak species composition within oak-juniper woodland stands. At the Fort Hood Military Reservation located in the northern portion of the warbler's breeding range, warbler territory density and productivity appeared higher in oak-juniper woodland dominated by Texas oaks than in oak-juniper woodland dominated by post oaks (Marshall et al. 2013, M. L. Morrison *unpublished data*). Similar to studies conducted on other songbird species (e.g., Petit and Petit 1996), variation in food abundance across different tree species may be driving the disparity in warbler habitat selection and productivity (Marshall et al. 2013). The dominant oak species within oak-juniper woodland stands occupied by warblers varies by site and geographic location within the warbler's breeding range (Diamond 1997, Campbell 2003). However, warbler responses to variation in tree species composition outside of the single study conducted at Fort Hood are unknown.

Warbler management guidelines additionally emphasize the importance of Ashe juniper height to warbler habitat selection and quality; thinning guidelines, based on Campbell (2003), approve the removal of Ashe juniper <4.5 m in height from the understory of oak-juniper woodland. The importance of mature Ashe juniper as a nesting and foraging substrate for warblers is well established, but no studies directly link Ashe juniper height or variation in Ashe juniper height to warbler habitat selection or productivity. Again, these particular vegetation metrics vary widely across the warbler's breeding range. Canopy height within warbler habitat typically averages between 4 and

7.5 m, but can be as low as 3 m, particularly in the southwestern portion of the warbler's breeding range (Diamond 1997, Ladd and Gass 1999). Identifying the importance of Ashe juniper height to warbler productivity and quantifying the point (or zone) at which warbler productivity is expected to be high could aid management and restoration efforts for this species.

I used data collected from 899 territories on 90 study sites (2009–2013) located across the warbler's breeding range to investigate the influence of year, geographic location, various Ashe juniper metrics, and dominant oak species on warbler territory density, territory size, pairing success, and fledging success. As described above, researchers and land managers obtained most information regarding the spatial distribution of warblers in relation to vegetation characteristics from short-term studies conducted on prioritized sites. However, many assumptions regarding warbler-habitat relationships remain untested and we have limited information on how these relationships vary across spatial and temporal scales. In addition, we have limited quantitative information regarding the strength or shape of these relationships, which may limit our ability to develop effective management practices and determine appropriate restoration goals. My research could aid our ability to predict warbler responses to habitat alteration, identify warbler habitat where productvity is expected to be high, and help guide future management and restoration practices for this conservation target.

CHAPTER II

TREE SPECIES COMPOSITION INFLUENCES GOLDEN-CHEEKED WARBLER ABUNDANCE AND TERRITORY SIZE

INTRODUCTION

Studies that explore wildlife-habitat relationships have a rich history and have provided important information regarding species distributions, abundance, and productivity (Hildén 1965, Hutto 1985, Morrison et al. 2006:3-14). Interest in wildlife-habitat relationships remains strong, particularly in light of recent animal population declines, as studies that incorporate both habitat and animal demographic information play a critical role in species conservation (Caughley 1994, Bonebrake et al. 2010). Knowledge gained from such research guides wildlife management, aids species recovery, and advances ecological theory. Unfortunately, our understanding of most wildlife-habitat relationships is limited to information gained from short-term studies conducted at a small number of prioritized study sites. This strategy provides a baseline for natural history and habitat associations at specific locations, but constrains our ability to develop comprehensive range-wide management and restoration plans that are effective across the continuum of ecological conditions a species inhabits. Spatially extensive, replicated studies conducted across the geographic extent of a species' range are necessary if our goals are to fully understand the ecology of a species and ensure the long-term persistence of a population.

Identifying the spatial distribution of individuals across habitats is a critical step towards these goals. During the hierarchical process of habitat selection, innate and learned behavioral responses allow animals to distinguish among various components of the environment; general features of the landscape determine whether an organism will explore a given area, while settlement is determined by the subsequent appraisal of fine-scale factors (Svardson 1949, Hildén 1965, Johnson 1980, Cody 1981, Hutto 1985). Across space and time, the process of habitat selection is influenced by natural (e.g., vegetation, weather) or anthropogenic (e.g., urbanization, agricultural development) differences in environmental conditions and resources among locations (Orians and Wittenberger 1991, Block and Brennan 1993). For most species, broad-scale variation in plant physiognomy (i.e., vegetation structure and distribution) (Hildén 1965, James 1971, Dunning et al. 1992) and local variation in plant species composition (Holmes and Robinson 1981, Rotenberry 1985, Bersier and Meyer 1994) drive the process of habitat selection. Additional factors, such as predation (Martin 1993), competition (Svardson 1949, Martin 1993, Petit and Petit 1996), and social information (Danchin et al. 1998, Forsman et al. 1998, Farrell et al. 2012) also influence the process of habitat selection at local scales. However, plants are often the focus of habitat selection studies because vegetation provides wildlife with important resources such as food, protective cover, and nesting, perching, or roosting sites.

The spatial and temporal factors that govern habitat selection decisions additionally contribute to the reproductive success of individuals found therein, which is often described in terms of habitat quality (i.e., a relative measure of the ability of a habitat to contribute to the population) (Block and Brennan 1993, Morrison et al. 2006:56). General models of habitat selection predict that individuals will maximize their reproductive output through spatial distribution, adjusting their spatial location to reflect the distribution of resources necessary for survival and reproductive success (Fretwell and Lucas 1970). Such models are simplistic in that they assume 1) fitness is lower at high densities as a result of some limiting factor, 2) organisms have information about resource availability via direct assessment of resources (Bonnot et al. 2009) or assessment of habitat parameters associated with resource abundance (Smith and Shugart 1987), and 3) personal information does not influence habitat selection decisions (e.g., past reproductive success; Tremblay et al. 2007, Thériault et al. 2012; social information, Danchin et al. 2004). However, they provide a useful theoretical framework from which to explore wildlife-habitat relationships across the unique combination of environmental conditions that occur at any given point in space and time. Empirical evidence supports relationships between the spatial distribution of organisms and habitat quality (Bock and Jones 2004). Many have found positive relationships between density and reproductive success and inverse relationships between reproductive success and the area used by an individual for food acquisition, mating, and rearing young and have linked these responses to variation in resource availability (e.g., Marshall and Cooper 2004, Atuo and Manu 2013, Haché et al. 2013).

From a wildlife management perspective, it is not only important to identify the habitat characteristics that drive the spatial distribution of species across spatial and temporal scales, but also identify the points or zones at which changes in habitat conditions influence the spatial distribution of organisms (i.e., ecological thresholds, Huggett 2005). Many have found nonlinear responses to habitat loss and fragmentation and data indicate that multiple factors often interact to influence threshold shifts across spatial and temporal scales. For example, there may be abrupt changes in the movement patterns of animals at specific proportions of available habitat in the landscape (With and Crist 1995), species richness and the probability of occupancy may decline rapidly after a critical proportion of habitat in the landscape is lost (Radford et al. 2005, Betts et al. 2007), and there may be minimum patch size thresholds for reproductive success of some species (Butcher et al. 2010, Robinson 2013). Quantifying the range of habitat conditions that cause a change in the spatial distribution of a conservation target could aid in the development of more effective land management practices and help land managers set restoration goals (Huggett 2005).

The federally endangered golden-cheeked warbler (*Setophaga chrysoparia*; hereafter warbler), is a small, insectivorous songbird that breeds exclusively in central Texas (Fig. 1; USFWS 1990). Typical breeding habitat for the warbler is described as oak-juniper woodland with dense canopy cover that is composed of tree species such as Ashe juniper (*Juniperus ashei*), oaks (e.g., live oak, *Quercus fusiformis*; post oak, *Q. stellata*; Texas oak, *Q. buckleyi*), and various other hardwoods (Pulich 1976, Ladd and Gass 1999). Habitat loss and degradation precipitated warbler decline (USFWS 1990). Within oak-juniper woodlands, clearing of Ashe juniper for range management, or urban development, and subsequent lack of oak recruitment were particularly problematic for this species. This is because mature (>20 years) Ashe juniper provides necessary nesting material, nesting sites, and song perches and a combination of oaks and Ashe juniper provide important foraging substrates for warblers (Pulich 1976, Wahl et al. 1990). Oak wilt, an infectious oak-defoliating disease caused by the fungus *Ceratocystis fagacearum*, can alter oak-juniper woodland composition and may negatively impact warblers in the near future (Stewart et al. 2014).

Researchers and land managers obtained most information regarding the spatial distribution of warblers in relation to vegetation characteristics from short-term studies conducted on prioritized sites. In the eastern portion of the warbler's breeding range, warbler occurrence was positively related to Ashe juniper cover (DeBoer and Diamond 2006) and warbler density was positively related to woodland cover (Peak and Thompson 2013). Magness (2006) also found that warblers were more likely to occur at points with higher percent woodland cover in the western portion of the warbler's breeding range. Such relationships likely reflect the importance of Ashe juniper as a nesting and foraging substrate for this species. Range-wide predictions also indicate that warbler density may increase with increasing percent woodland cover in at least some portions of the warbler's breeding range (Mathewson et al. 2012). Though Mathewson et al. (2012) did not find a direct relationship between warbler density and increasing percent canopy cover, warbler abundance decreased with increasing latitude. Mathewson et al. (2012) suggested that this south-north abundance gradient results from a higher percentage of available (Groce et al. 2010), more suitable (i.e., large, less fragmented woodland; DeBoer and Diamond 2006, Baccus et al. 2007) warbler habitat in the southern portion of the warbler's breeding range.

Given perceived relationships between Ashe juniper cover and occupancy, warbler management guidelines indicate that dense Ashe juniper cover is an attribute of high quality warbler breeding habitat (TPWD 1990, 2012; USFWS 1992). The positive relationship between canopy cover and warbler productivity is consistent in some (but not all) portions of the warbler's breeding range (Klassen et al. 2012, Campomizzi et al. 2012). Combined with results that directly examined warbler occurance and abundance in relation to canopy cover characteristics, this suggests that warbler territory density may increase and warbler territory size may decrease with increasing Ashe juniper cover. However, warblers will establish territories in oak-juniper woodland with much less canopy cover than currently identified by warbler management guidelines (35-40%; Reemts et al. 2008, Heilbrun et al. 2009), and successfully breed in areas with as low as 20% canopy cover (Klassen et al. 2012). As such, the direction and shape of the relationships between percent Ashe juniper cover and the spatial distribution of warblers may depend on local woodland stand characteristics that vary across spatial and temporal scales.

For example, the relationships between Ashe juniper cover and warbler territory density and territory size may be influenced by dominant oak species within generically classified oak-juniper woodland. In 2009 and 2010, warbler territory density was higher in oak-juniper woodland dominated by Texas oak than oak-juniper woodland dominated by post oak in the eastern portion of the warbler's breeding range (M. L. Morrison *unpublished data*). Data collected at the same location and within the same time period also indicate that oak species within occupied oak-juniper woodland may influence warbler habitat quality, as warbler productivity appeared higher in oak-juniper woodland dominated by Texas oaks than in oak-juniper woodland dominated by post oak

(Marshall et al. 2013). Marshall et al. (2013) linked this difference in habitat quality to disparities in the abundance of certain warbler food resources on Texas oaks when compared to post oaks. The dominant oak species within occupied oak-juniper woodland varies across the warbler's breeding range (Diamond 1997, Campbell 2003). However, the importance of oak species composition (which changes with site characteristics and geographic location) on warbler territory density or territory size has not yet been examined. In addition, Marshall et al. (2013) found that warblers forage more often on oaks at the beginning of the breeding season and switch their foraging efforts to Ashe juniper as the breeding season progresses. Therefore, differences in the proportion of Ashe juniper and oaks across vegetation types could influence warbler territory density and territory size. Spatial and temporal (seasonal or annual) variation in local vegetation characteristics (e.g., differences in the timing of leaf-out) or food abundance (e.g., late frost that kills insects at the beginning of the breeding season), could also influence the distribution of warblers across oak-juniper woodland types.

I used data collected from 2009 to 2013 on 90 study sites located across the warbler's breeding range to examine warbler territory density and territory size in relation to percent Ashe juniper cover and oak species composition. I predicted both linear and nonlinear relationships between percent Ashe juniper and my warbler response variables. For example, given the importance of Ashe juniper as a nesting and foraging substrate for warblers, I predicted that territory density would increase and territory size would decrease with increasing Ashe juniper cover (linearly or until reaching levels where no subsequent increase in Ashe juniper cover changed the spatial distribution of warblers). However, oaks are also an important component of warbler habitat, so I additionally predicted that warbler territory density would be highest and territory size would be smallest in areas with an equal proportion of Ashe juniper and oaks. Because spatial and temporal variation in habitat characteristics can influence habitat selection decisions, I predicted that the strength and shape of these relationships could vary by dominant oak species, geographic location, or year.

As described above, researchers and land managers obtained most information regarding the spatial distribution of warblers in relation to vegetation characteristics from short-term studies conducted on prioritized sites. However, it is unknown if these relationships vary across spatial and temporal scales. In addition, we have limited quantitative information regarding the strength or shape of these relationships, which may limit our ability to develop effective management practices and determine appropriate restoration goals. My research could aid our ability to predict warbler responses to habitat alteration and help guide future management and restoration practices for this species.

METHODS

Study area

I conducted my research from 2009 to 2013 in 11 counties (Kinney, Edwards, Uvalde, Real, Kerr, Bandera, Hays, Travis, Bell, Coryell, and Bosque) across the 3 largest Level-IV Ecoregions located within the warbler's breeding range in central Texas (Fig. 1; Griffith et al. 2004). Ecoregion delineations are based on geography, physiography, vegetation, climate, soils, land use, wildlife, and hydrology and represent areas with generally similar ecosystem responses to disturbance (Omernik 1987). As such, Ecoregions are often used as spatial units for research and natural resource management; I used Ecoregions for my research as the broadest geographic scale within which similar ecological conditions are inhabited by warblers. The Ecoregions included in my research contain 75% percent (1,257,296 ha) of the total predicted warbler habitat in central Texas (1,678,697 ha) and 82% of the total area predicted to have a probability of warbler occurrence >0.50 (Collier et al. 2012).

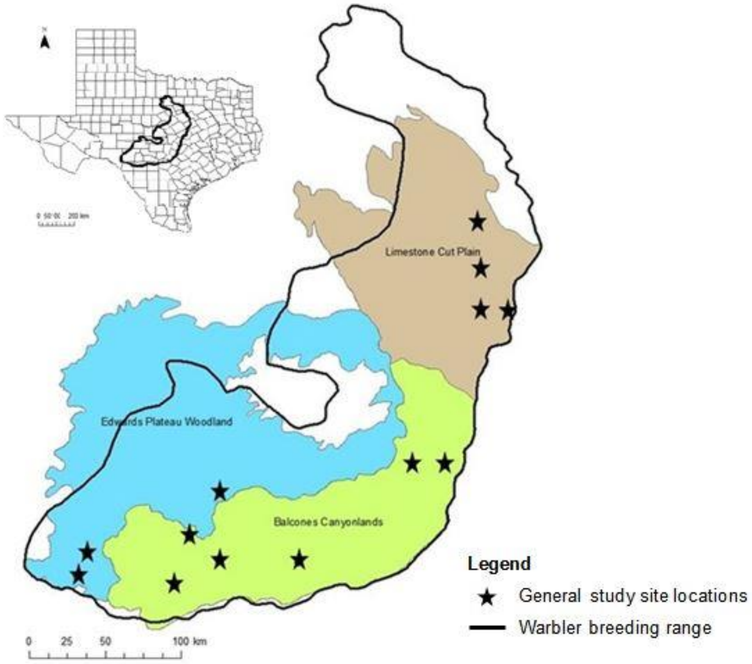

Figure 1. Golden-cheeked warbler study site locations (2009–2013) across the 3 largest Level-4 Ecoregions within the warbler's breeding range in central Texas, USA.

The Edwards Plateau Woodlands Ecoregion (hereafter EPW) is located in the central portion of the Edwards Plateau and is on the southwestern edge of the warbler's breeding range (Fig. 1). The EPW is characterized by rolling hills and intervening broad valleys. It is described as the transition between eastern mesic and western arid climates and is subject to regular drought conditions, dry western winds, and moist, humid updrafts from the Gulf of Mexico (Griffith et al. 2004). Mean minimum and maximum temperatures in January are 1ºC and 15ºC and mean minimum and maximum temperatures in July are 20ºC and 34ºC (NOAA 2014). Mean annual precipitation (56–86 mm) is generally less than found elsewhere in the warbler's breeding range and declines from east to west (NOAA 2014). Vegetation in the EPW is generally dominated by grasslands with scattered oak mottes (Griffith et al. 2004). Warbler habitat in this Ecoregion is composed primarily of Ashe juniper, Lacey oak (*Q. laceyi*), post oak, and live oak (Diamond 1997). The Balcones Canyonlands Ecoregion (hereafter BC) is located on the southern border of the Edwards Plateau (a karst limestone formation with sharp relief and deep soils) and is the central-most Ecoregion represented in my study (Fig. 1; Griffith et al. 2004). Mean minimum and maximum temperatures are similar to that found in the Edwards Plateau Ecoregion (NOAA 2014). However, mean annual precipitation is typically greater in this Ecoregion (66–86 mm) (NOAA 2014). Vegetation in the BC consists of oak-juniper woodland and oak-mesquite savanna, as well as interspersed grasslands (Griffith et al. 2004). Warbler habitat in this Ecoregion is composed primarily of Ashe juniper, Texas oak, live oak, and various other hardwoods (Diamond 1997). The Limestone Cut Plain (hereafter LCP) is the northernmost

Ecoregion included in my study and is located in a transitional area between grassland vegetation to the north and the Edwards Plateau to the south (Fig. 1). This Ecoregion is more geologically varied than either the EPW or BC (Griffith et al. 2004) and generally receives more annual precipitation (76–86 mm) (NOAA 2014). Mean temperatures are similar to those found in the BC and EPW (NOAA 2014). Soils in the LCP are shallow and support oak savannas and juniper-oak woodland (Griffith et al. 2004). Warbler habitat is in this Ecoregion is typically dominated by Texas oak, post oak, live oak, shin oak (*Q. sinuata*), Ashe juniper, and various other hardwoods (Diamond 1997).

Within each Ecoregion, I used data collected on 90 study sites (i.e., sampled area within an oak-juniper woodland stand) selected for the various needs (e.g., impacts of road construction and military training activities, influence of age structure, influence of tree species composition) of warbler research projects conducted by Texas A&M University and the Texas A&M Institute of Renewable Natural Resources (M. L. Morrison *unpublished data*). All study sites were identified as spatially-separated (i.e., >10 m break between oak-juniper woodland stands), potential habitat for warblers (Collier et al. 2012). Oak-juniper woodland stands represented multiple ecological sites (hereafter “Ecosite”) occupied by warblers within each Ecoregion. Ecosite delineations, determined using Ecological Site Description Shapefiles provided by the Texas Natural Resources Department, identify soil types distributed across the state of Texas and have been used to ascertain dominant oak species within areas more generally described as oak-juniper woodlands. For example, in a study conducted at the Fort Hood Military Reservation located in the LCP, Marshall et al. (2013) found that oak-juniper woodland delineated as Ecosite “Redlands” was dominated by post oak, while oak-juniper woodland delineated as Ecosite “Low Stony Hill” was dominated by Texas oak (Marshall et al. 2013). General patterns in oak species composition related to Ecosite delineations are unknown for most areas within the warbler’s breeding range. However, soil type (Catry et al. 2012), soil drainage capabilities (Stuen et al. 1988, Carroll et al. 2011), and soil nutrient availability (Tilgar et al. 1999) can contribute to tree species composition (and the resulting arthropod community). Therefore, I used Ecosite as an initial delineation of oak species composition, but ultimately used vegetation measurements taken across each study site to ensure accurate representation of fine-scale oak species composition (Table 1). Study sites additionally represented a wide range of percent Ashe juniper cover (i.e., percentage of the canopy represented by Ashe juniper) occupied by warblers across their breeding range (Table 1).

Study site occupancy

To establish study site occupancy by warblers, trained observers conducted preliminary surveys across each study site every 7–10 days beginning the second week of March, the approximate time of warbler arrival to their breeding grounds in Texas. During initial surveys, observers walked along parallel transects systematically established 150-200 m apart across each site (ArcGIS 9.3.1) and recorded the GPS coordinates of any warblers seen or heard. I did not use this information for analysis purposes, but observers used these detections to relocate male warblers on subsequent visits to each occupied study site. If observers did not detect warblers on a given study site within the first 4 weeks of the warbler breeding season, observers discontinued transect surveys on the study site and returned only to conduct vegetation surveys prior to the end of the warbler's breeding season.

Territory mapping and monitoring

Observers returned to each occupied study site every 7–10 days for the duration of the warbler breeding season (March to July) to conduct territory mapping, which I used to estimate territory density and approximate the spatial extent of each focal male's territory. Observers relocated male warblers along transects established to determine study site occupancy. Once a warbler was detected, observers recorded the bird's initial location using a GPS unit. The observer then followed the male bird until it was no longer visible or was mapped for no more than 1 hour. After the sampling occasion for the focal male was complete, observers returned to the transect and continued searching for singing males.

In 2009 and 2010, GPS locations of male warblers were recorded if the focal male moved ≥20 m until 3–6 locations were recorded. From 2011–2013, observers recorded GPS locations every 2 minutes until the male was no longer visible or was mapped for no more than 1 hour. The second sampling technique described similarly represents the spatial extent of vegetation used by male warblers and captures movements ≥20 m, but also allowed me to examine the temporal use of vegetation by warblers for a concurrent study on warbler productivity in relation to tree species composition. To address the objectives presented herein, I used data collected using both methods to create minimum convex polygons (MCPs) for each territorial male (i.e., male

Table 1. Distribution of golden-cheeked warbler study sites (2009–2013) across the 3 largest Level-4 Ecoregions (EPW = Edwards Plateau Woodlands, BC = Balcones Canyonlands, and LCP = Limestone Cut Plain) within the warbler's breeding range in central Texas, USA.

Ecoregion	**Study Sites**[a]	**Size (ha)**[b]	**Oak**[c]	**Study Sites**[a]	**Size (ha)**[b]	**AJ (%)**[d]	**Mean AJ % (SD)**[e]	**Terr/ha**[f]	**Territory size (ha)**[g]
EPW	24	5.0–357.0	Lacey	9	5.0–140.0	40–76	57 (14)	0.00–0.33	0.5–4.8
			Live	7	23.0–311.0	64–77	70 (5)	0.01–0.09	1.8–6.1
			Post	3	6.0–10.0	58–75	65 (9)	0.33–0.50	1.1–1.7
			Shin	4	20.0–357.0	34–59	49 (12)	0.03–0.26	1.8–3.1
			Texas	1	12.0	72	N/A	0.25	0.6
BC	15	14.0–928.7	Live	13	15.0–908.0	35–89	62 (15)	0.00–0.14	1.4–5.1
			Texas	2	14.0–23.0	36–69	67 (3)	0.00–0.04	0.8
LCP	51	9.0–595.0	Live	14	46.0–305.0	22–63	41 (11)	0.00–0.19	1.5–4.3
			Mixed	6	22.0–260.0	48–55	52 (3)	0.06–0.13	1.1–3.5
			Post	5	174.0–595.0	20–54	34 (13)	0.03–0.12	1.9–3.0
			Shin	9	14.0–104.0	46–68	58 (7)	0.07–0.24	1.2–2.8
			Texas	17	9.0–104.0	23–69	48 (14)	0.03–0.22	0.9–5.5

[a] Number of study sites

[b] Size range of the area sampled.

[c] Dominate oak species within the sampled area.

[d] Range of the mean percent Ashe juniper cover.

[e] Mean and standard deviation of the mean percent Ashe juniper cover.

[f] Range of territory density (calculated by dividing the number of minimum convex polygons by the sampled area) for each categorization.

[g] Range of mean territory size (calculated using minimum convex polygons) for the area sampled.

relocated for ≥4 weeks) when ≥15 points were recorded over the course of the breeding season. MCPs represent the outermost points in a location dataset, regardless of sampling technique. Using MCPs for the current study allowed me to analyze comparable data across years (2009–2013). I calculated territory density as the number of MCPs per ha of area searched within the oak-juniper woodland stand (Table 1). I calculated the size of each MCP and used the mean MCP size within each oak-juniper woodland stand for calculations of territory size in relation to my explanatory variables (Table 1).

Vegetation measurements

Observers recorded vegetation measurements across each study site at points spaced 100 m apart along grid transects established using ArcGIS 9.3.1. For all vegetation ≥2 m, observers measured percent canopy cover per dominant tree species to the nearest 10% using a tubular densitometer. For each study site, I calculated mean percent Ashe juniper cover (Table 1). Of the remaining hardwoods, I calculated the mean percent cover of each oak species. As such, mean percent Ashe juniper cover and mean percent oak cover were inversely related (Appendix A). Eighty-five percent of study sites were dominated by a single oak species (i.e., >50% cover by a single oak species). When this was the case, I assigned the oak-juniper woodland stand a dominant oak species categorization (e.g., a stand with 80% live oak was categorized as “Live Oak Dominated”) (Table 1). When there was <50% cover of multiple oak species within a single stand of oak-juniper woodland, I categorized the stand as “Mixed” (Table 1).

Data analysis

I developed *a priori* models including variables hypothesized to cause variation in territory density and territory size (i.e., year, Ecoregion as a proxy for geographic location of the study site within the warbler's breeding range, tree species composition metrics, and 2-way interactions between all combinations of variables). *A priori* models included both linear and quadratic trends for hypotheses regarding mean percent Ashe juniper cover. There were statistically significant correlations between Ecoregion and dominant oak species ($\chi_{10}^{2} = 51.97$, $P \leq 0.01$) and Ecoregion and mean percent Ashe juniper cover ($F_{2,87} = 14.27$, $P \leq 0.01$). As such, I did not include these additive interaction models in analyses. The final candidate model set included an intercept-only model, a main effect model for year, and models for Ecoregion, dominant oak species with the oak-juniper woodland stand, and mean percent Ashe juniper cover within the oak-juniper stand (linear and quadratic trends) that included year as a covariate (Table 2). Additionally, I considered a model representing the interaction between dominant oak species and mean percent Ashe juniper cover (again with year as a covariate) (Table 2).

I used a generalized linear model approach to determine which variables best predicted warbler territory density and territory size (Zar 1999:324-376). I used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to rank models (Sugiura 1978, Burnham and Anderson 2002:49-97). I determined the relative support for each model using ΔAIC_c and Akaike Weights (w_i) (Burnham and Anderson 2002:49-97). I considered models with ΔAIC_c <2.0 equally plausible; w_i value used to determine the most plausible model within the top candidate set of models. I used the regression coefficients estimated from the best-fit model to predict territory density and territory size. I then calculated the 95% confidence intervals (hereafter 95% CI) for predicted territory density and territory size to examine the extent of variation around my predicted values (Burnham and Anderson 2002:49-97). I examined the extent of overlap among the 95% CIs to determine the potential statistical or biological significance of each relationship and identified points or zones in habitat conditions that caused a shift in my avian response variables. I performed all analyses using R statistical software (R Development Core Team 2013).

RESULTS

There were 761 territories across the 90 sites included in my study and territory density ranged from 0.00–0.50 territories/ha (Table 1). Mean territory size ranged from 0.5–6.1 ha (Table 1). Mean percent Ashe juniper cover within my study sites ranged from 22–89% (Table 1). The best-fit model for territory density included the interaction between dominant oak species and mean percent Ashe juniper cover (Table 2). Territory density increased with increasing mean percent Ashe juniper in post and mixed oak woodland stands and decreased with increasing percent Ashe juniper in shin oak dominated woodland stands (Fig. 2). Territory density did not vary in relation to percent Ashe juniper in Lacey, live, or Texas oak dominated woodland stands (Fig. 2). Dominant oak species was the only variable included in the best-fit model for mean territory size (Table 2). Territories were larger in oak-juniper woodland stands dominated by live oak than oak-juniper woodland stands dominated by all other species but post oak (Fig. 3).

Table 2. Models of territory density (territories/ha) and territory size (ha) for golden-cheeked warblers monitored on 90 study sites located across the 3 largest Level-4 Ecoregions within the warbler's breeding range in central Texas, USA (2009–2013).

Response	**Model**[a]	***K***[b]	**Log liklihood**	**AIC$_c$**[c]	**ΔAIC$_c$**[d]	***w$_i$***[e]
Density						
	DomOak*PercentAJ +Year	14	114.34	-195.08	0.00	1.0
	DomOak+Year	8	94.72	-171.67	23.41	0.0
	Ecoregion+Year	5	87.54	-164.36	30.72	0.0
	Constant	2	80.95	-157.77	37.31	0.0
	Year	1	81.10	-155.93	39.15	0.0
	PercentAJ+Year	3	82.56	-154.65	40.43	0.0
	PercentAJ^2+Year	6	81.19	-153.66	41.42	0.0
Size						
	DomOak+Year	8	-137.53	292.84	0.00	0.9
	DomOak*PercentAJ+Year	14	-132.43	298.46	5.62	0.1
	Ecoregion+Year	5	-146.03	302.78	9.94	0.0
	Year	3	-149.08	304.44	11.61	0.0
	PercentAJ+Year	4	-148.65	305.77	12.94	0.0
	PercentAJ^2+Year	5	-147.99	306.68	13.85	0.0
	Constant	2	-151.84	307.82	14.98	0.0

[a] Explanatory variable abbreviations are as follows: Constant = null, Year = year, Ecoregion = geographic location, DomOak = dominant oak species within the oak-juniper woodland stand, PercentAJ = percent Ashe cover within the oak-juniper woodland stand. An * indicates when interactions between explanatory variables were considered.

[b] Number of parameters in the model

[c] Akaike's Information Criteria corrected for small sample sizes

[d] AIC$_c$ relative to the best-fit model

[e] Model weight

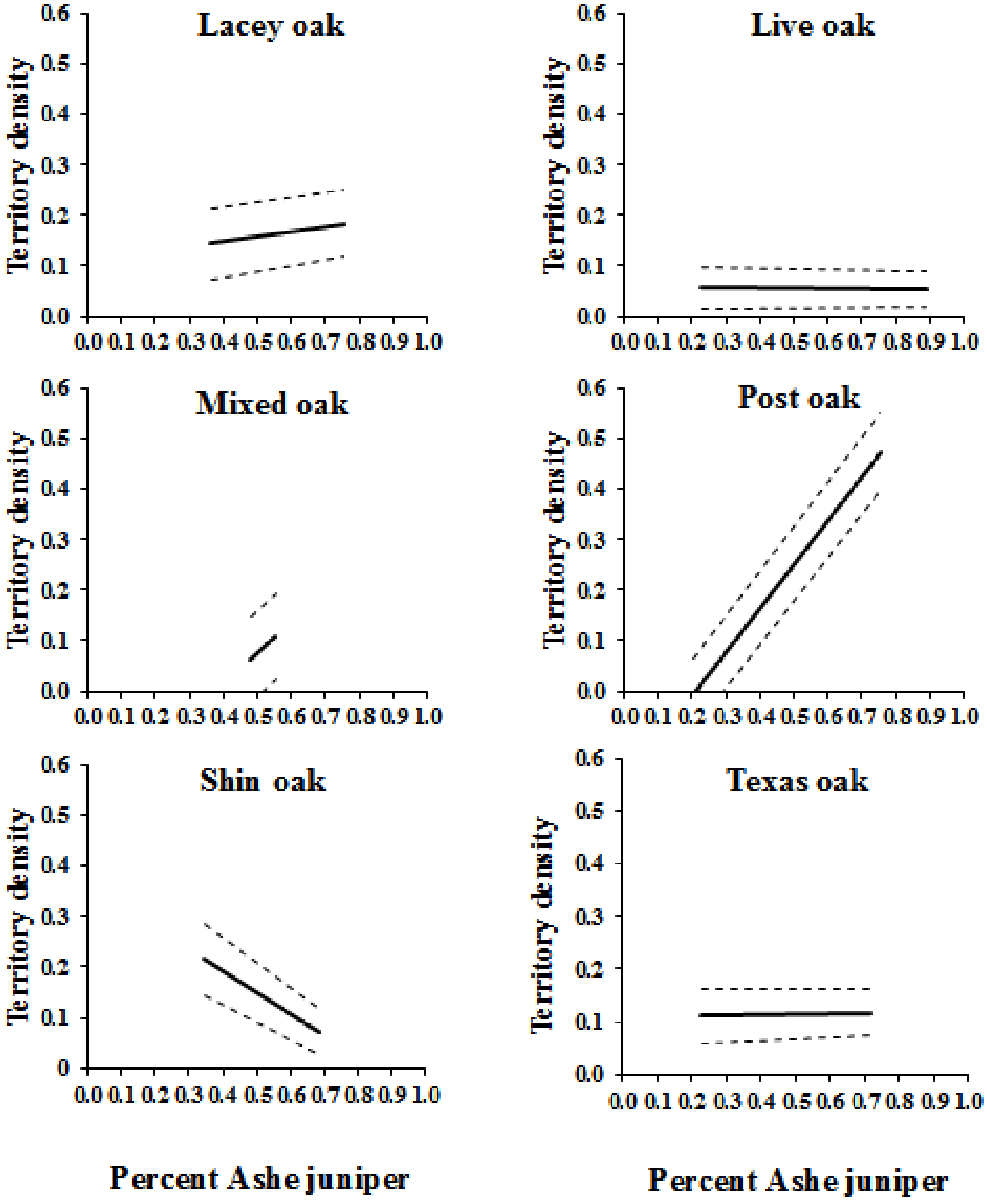

Figure 2**.** Predicted golden-cheeked warbler territory density (territories/ha) and the associated 95% confidence intervals per dominant oak species within oak-juniper woodland stands in relation to mean percent Ashe juniper cover (2009–2013). Study sites (n = 90) were located across the 3 largest Level-4 Ecoregions within the warbler's breeding range in central Texas, USA.

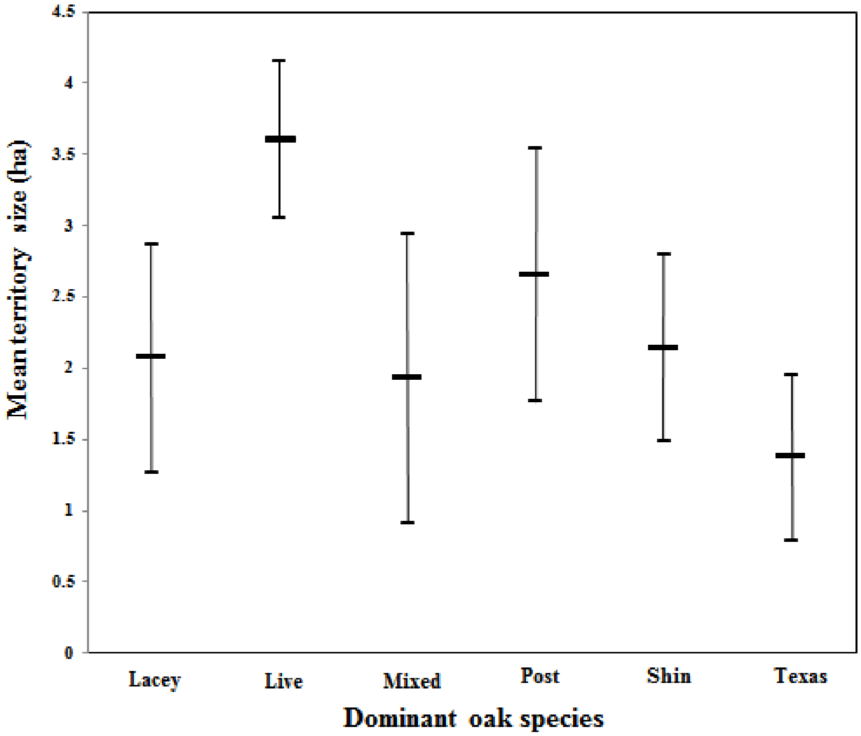

Figure 3. Predicted mean golden-cheeked warbler territory size (ha) and the associated 95% confidence intervals per dominant oak species (2009–2013). Study sites (n = 90) were located across the 3 largest Level-4 Ecoregions within the warbler's breeding range in central Texas, USA.

CONCLUSIONS

My broad-scale study quantitatively demonstrates that local vegetative characteristics of warbler habitat vary widely across the warbler's breeding range and that tree species composition within generically classified oak-juniper woodland stands influence the spatial distribution of warblers across habitats. Warbler territory density was best-predicted by the interaction between percent Ashe juniper cover and dominant oak species within occupied oak-juniper woodland stands. Contrary to current management guidelines, which suggest that high quality habitat has dense canopy cover (Campbell 2003, TPWD 2012) and emphasize the importance of Ashe juniper in the canopy, warbler territory density did not increase with increasing percent Ashe juniper across all oak species categorizations. In Lacey, live, and Texas oak dominated woodland stands, which were the primary oak-juniper woodland stand types represented in my study, predicted warbler territory density remained relatively constant with increasing percent Ashe juniper cover. Previous research on range-wide warbler habitat quality found inconsistent relationships between warbler reproductive success and canopy cover (Campomizzi et al. 2012). If patterns of warbler density track patterns of warbler productivity, my results in live, Texas, and Lacey oak dominated habitat provide an additional reason to question the common assertion that percent Ashe juniper cover is the primary driver of warbler demographics across all occupied habitat.

I did find a positive relationship between territory density and percent Ashe juniper cover in oak-juniper woodland stands dominated by post oak and in mixed oak-juniper woodland stands. In the northern portion of warbler's breeding range, Marshall et al. (2013) found that warblers forage primarily on oaks at the beginning of the breeding season and forage more often on Ashe juniper as the season progresses. The Marshall et al. (2013) study additionally demonstrated that arthropod abundance may be lower on post oak than on Texas oak. It is possible that increased Ashe juniper in post oak dominated warbler habitat provides foraging opportunities that compensate for limited resources on post oaks, thus leading to increased warbler density in post oak dominated woodland when there is a higher percentage of Ashe juniper in the canopy.

Though there was a positive relationship between territory density and percent Ashe juniper cover in mixed oak-juniper woodland stands, my sample size for that particular woodland type was low, it was represented in only one Ecoregion, and the variation in percent Ashe juniper cover across my mixed oak-juniper woodland study sites was small. More information is needed to clarify patterns of warbler territory density in mixed oak juniper woodland stands occupied by warblers.

Conflicting with current assumptions regarding warblers and Ashe juniper cover, I found a negative relationship between territory density and percent Ashe juniper cover in shin oak dominated woodland stands. Pulich (1976) noted the potential importance of shin oak as a foraging substrate for this species and Marshall (2011) found that arthropod density was higher on shin oak than on Ashe juniper when the warbler habitat occurred on the Low Stony Hill Ecosite. Most of my shin oak dominated study sites were located in areas delineated as Low Stony Hill. Birds may initially select habitat via direct assessment of resources (Bonnot et al. 2009) or assessment of habitat parameters associated with resource abundance (Smith and Shugart 1987). In areas where there is variation in percent Ashe juniper cover across woodland stands dominated by shin oak, warbler habitat selection decisions may reflect resource abundance on shin oak rather than Ashe juniper, thus leading to a negative relationship between territory density and Ashe juniper cover in this vegetation type.

With regards to territory size, the spatial extent of vegetation used by an organism for food, mating, and rearing young often reflects the distribution and density of resources found therein; many have found an inverse relationship between territory size and resource abundance (e.g., Village 1982, Marshall and Cooper 2004, Atuo and Manu 2012). Defending a smaller territory may additionally benefit individuals by lowering costs for foraging movement and territory defense (Wolf and Hainsworth 1971, Blake and Hoppes 1986), and reducing exposure to predators (Thompson and Fritzell 1989). As stated throughout much of the literature, Ashe juniper is no doubt a necessary component of warbler breeding habitat, but it was not an important predictor of territory size in my study. Rather, the model including dominant oak species was considered the best-fit model for this warbler response variable; warbler territories were larger in oak-juniper woodland stands dominated by live oak than oak-juniper woodland stands dominated by all other species but post oak. Live- and post oak dominated warbler breeding habitat often occurs on dry, rocky- or clay-based upland soils (Diamond 1997, Campbell), while Texas- and Lacey oak dominated warbler habitat typically occurs on mesic soils associated with slopes, canyons, and creek bottoms (Diamond 1997, Campbell 2003). Soil type (Catry et al. 2012), soil drainage capabilities (Stuen et al. 1988, Carroll et al. 2011), and soil nutrient availability (Tilgar et al. 1999) can contribute to tree species composition and the resulting arthropod community. Therefore, territory size may be larger and more comparable when males selected areas dominated by live- or post oak due to similarities in food resource abundance across these particular vegetation types.

Though I predicted that relationships between warbler territory density and territory size and the vegetation characteristics of occupied oak-juniper woodland stands would vary in relation to year and geographic location, best-fit models for these avian response variables did not include the main effect for year or Ecoregion with year as a covariate. I included a temporal component in my analyses because environmental conditions and resources can vary substantially across warbler breeding seasons. For example, Marshall et al. (2013) reported very different precipitation patterns for 2009 and 2010, which could have contributed to a difference in the abundance of at least some food resources between years. In addition, warbler habitat varies considerably across the warbler's breeding range (Diamond 1997, Ladd and Gass 1999, Groce et al. 2010). Previous studies have found relationships between geographic location and range-wide warbler density (Mathewson et al. 2012) and warbler productivity (Campomizzi et al. 2012). These studies provide support for my hypotheses that warbler territory density and territory size would vary with year and geographic location. However, my study demonstrates that local vegetation characteristics contribute more to warbler territory density and territory size than year alone or geographic location.

My results additionally reiterate that vegetation occupied by warblers is more variable than current definitions of warbler breeding habitat suggest and that Ashe juniper cover does not have a strong effect on the spatial distribution of warblers across all vegetation types occupied by this species. Warbler territory density remained constant across the full range of percent Ashe juniper cover in oak woodland stands dominated by Lacey, live, and Texas oak. Warbler territory density increased with increasing percent Ashe juniper cover in oak woodland stands dominated by post oak and in mixed oak woodland and warbler territory density decreased with increasing percent Ashe juniper cover in oak woodland stands dominated by shin oak. Current management guidelines, based on Campbell (2003), indicate that land managers can remove Ashe juniper <4.5 m in height from warbler breeding habitat. Widespread juniper removal would have obvious consequences for this species. However, my results suggest that thinning in this manner would have less effect on warbler territory density in Lacey, live, or Texas dominated oak juniper woodland when compared to other woodland stand types. For example, Ashe juniper removal in post oak dominated warbler habitat may result in decreased territory density and warblers may need more area to obtain all of their necessary resources if Ashe juniper is thinned from post oak dominated woodland. In addition, lack of oak recruitment, drought, and disease may have a stronger influence on the spatial distribution of warblers in some oak-juniper woodland types.

Understanding the spatial distribution of wildlife across the continuum of ecological conditions they occupy is essential for effective management. Land managers are often limited by time and financial constraints and must find ways to focus their habitat maintenance and restoration efforts. My results suggest that conservation efforts may be more effective if tailored to local vegetation characteristics associated with tree species composition. Future studies should examine how vegetation characteristics contribute to warbler productivity, as density is not always correlated with reproductive success (Van Horne 1983). There is also need for manipulative experiments to directly examine warbler responses to forest management techniques (e.g., prescribed burning, mechanical thinning). Conducting this research across the geographic extent of the warbler’s breeding range is necessary if our goal is to fully understand the ecology of this species and develop more effective site-specific warbler management and restoration strategies.

CHAPTER III

THE INFLUENCE OF LOCAL VEGETATION STRUCTURE AND COMPOSITION ON HABITAT SELECTION AND PRODUCTIVITY OF AN ENDANGERED WARBLER

INTRODUCTION

Identifying the spatial distribution of birds in relation to general features of the landscape is a critical step towards conservation of threatened or endangered species. However, researchers conduct most avian habitat selection studies within small spatial and temporal scales and fail to link habitat selection decisions to reproductive success (Jones 2001, Johnson 2007). This limits our understanding of avian demographic patterns across the full continuum of ecological conditions a species inhabits and may result in the application of inappropriate conservation strategies (Tear et al. 1995, Thompson et al. 1998). Detailed information regarding variation in avian productivity vastly improves our ability to construct effective, comprehensive range-wide management and restoration plans for bird species of conservation concern.

Avian habitat selection is a hierarchical process driven by spatial and temporal variation in environmental conditions and resources (Hildén 1965, Cody 1981, Hutto 1985, Block and Brennan 1993). Innate and learned behavioral responses allow animals to distinguish among various components of the environment; general features of the landscape determine whether an organism will explore a given area, while settlement is determined by the subsequent appraisal of fine-scale factors (Svardson 1949, Hildén 1965, Johnson1980, Cody 1981, Hutto 1985). For Neotropical migrants, this typically includes early arrival of males to the breeding grounds to select and defend territories. Females arrive shortly after, assess potential mates and select territories for their nesting attempt(s). Predation (Martin 1993), competition (Svardson 1949, Martin 1993, Petit and Petit 1996), and social information (Danchin et al. 1998, Forsman et al. 1998, Farrell et al. 2012) can influence the process of male and female habitat selection at local scales. However, plants are often the focus of avian habitat selection studies because vegetation provides birds with important resources such as food, protective cover, and nesting, perching, or roosting sites.

The natural (e.g., vegetation, weather) or anthropogenic (e.g., urbanization, agricultural development) differences in environmental conditions and resources that drive habitat selection among locations additionally contribute to the ability of a pair to fledge young, and thus habitat quality (i.e., a relative measure of the ability of a habitat to contribute to the population) (Block and Brennan 1993, Morrison et al. 2006:56). General models of habitat selection predict that individuals will maximize their reproductive output through spatial distribution, adjusting their spatial location to reflect the distribution of resources necessary for survival and reproductive success (Fretwell and Lucas 1970). These models assume that fitness outcomes depend on some limiting factor, that organisms have information about resource availability via direct (Bonnot et al. 2009) or indirect (Smith and Shugart 1987) assessment of resources, or that personal information influences habitat selection decisions (e.g., social information or past reproductive success; Danchin et al. 2004, Tremblay et al. 2007, Thériault et al. 2012), which may not always be the case. However, empirical evidence supports relationships between the spatial distribution of organisms and habitat quality (Bock and Jones 2004). Many have found positive relationships between density and reproductive success and inverse relationships between reproductive success and the area used by an individual for food acquisition, mating, and rearing young and have linked these responses to spatial and temporal variation in resource availability (e.g., Marshall and Cooper 2004, Atuo and Manu 2013, Haché et al. 2013).

With that said, relationships between density metrics and habitat quality can be decoupled (Van Horne 1983). For birds, such disconnect may occur when: 1) intraspecific competition negates fitness benefits conferred by individuals that occupy habitat with temporarily abundant resources, 2) highly territorial species push subordinates to pack tightly within lower quality habitat, or 3) individuals are unable to identify an area with the potential to be high quality due to sudden changes in habitat conditions (Van Horne 1983). As such, habitat quality should not be inferred from density metrics alone, but rather examined in conjunction with measures of animal performance.

Early research emphasized the broad-scale influence of vegetation structure and distribution on avian demographics (Hildén 1965, Wiens 1969, James 1971); many found that reduced patch size, decreased distance to patch edge, landscape surrounding remnant patches, and isolation of patches can negatively affect bird populations (e.g., Sisk et al. 1997, Moilanen and Nieminen 2002, Fahrig 2003). Relatively few studies have examined avian habitat selection and reproductive success in relation to plant species composition. However, spatial (e.g., Balda 1969, Franzreb 1978, Bohm and

Kalko 2009) and (e.g., Morrison et al. 1985, Lundquist and Manuwal 1990, Strode 2009) temporal variation in food resources among plant species and life forms (i.e., phenological stage, age, or size class) can influence the total area defended by a male, the core area used by a male, and the probability of pairing or fledging success. Information gained from research that links avian habitat selection decisions to productivity metrics in relation to local vegetation characteristics and quantifies the range of habitat conditions that cause a shift in avian-habitat relationships could aid in the development of more effective land management practices and help land managers set restoration goals.

Vegetation structure and composition may influence habitat selection and productivity of the federally endangered golden-cheeked warbler (*S. chrysoparia*; hereafter warbler), a small, insectivorous songbird species that breeds exclusively in central Texas (Fig. 4; USFWS 1990). Breeding habitat for the warbler is described as oak-juniper woodland and is composed of tree species such as Ashe juniper (*Juniperus ashei*), oaks (e.g., live oak, *Quercus fusiformis*; post oak, *Q. stellata*; Texas oak, *Q. buckleyi*), and various other hardwoods (Pulich 1976, Ladd and Gass 1999). Clearing of oak-juniper woodland for range management and urban development contributed to warbler decline (USFWS 1990). This is because warblers use strips of mature (>20 years) Ashe juniper for nesting material and a combination of Ashe juniper and oaks as foraging substrates, nesting sites, and song perches (Pulich 1976, Wahl et al. 1990). Oak wilt, an infectious oak-defoliating disease caused by the fungus *Ceratocystis* *fagacearum*, can alter oak-juniper woodland composition and may negatively impact warblers in the near future (Stewart et al. 2014).

Researchers and land managers have obtained most information regarding the distribution of warblers from short-term conducted on prioritized sites. In the eastern portion of the warbler's breeding range, warbler occurrence (DeBoer and Diamond 2006), density (Peak and Thompson 2013), and nest site selection (Dearborn and Sanchez 2001) were positively related to Ashe juniper cover. Magness (2006) additionally found that warblers were more likely to occur at points with high Ashe juniper cover in the western portion of the warbler's breeding range. Given the perceived importance of Ashe juniper cover to warbler habitat selection, warbler management guidelines indicate that dense Ashe juniper cover is an attribute of high quality warbler breeding habitat (TPWD 1990, 2012; USFWS 1992). However, few studies have actually examined the influence of Ashe juniper cover on habitat selection across multiple spatial scales or linked this vegetative characteristic to reproductive success. Though not typically emphasized, warblers will establish territories in oak-juniper woodland with much less canopy cover than currently identified by warbler management guidelines (35–40%; Reemts et al. 2008, Heilbrun et al. 2009), and successfully breed in areas with as low as 20% canopy cover (Klassen et al. 2012). More recent research indicates that the positive relationships between canopy cover and warbler productivity may not be consistent in all portions of the warbler's breeding range (Campomizzi et al. 2012). This suggests that using Ashe juniper cover as a range-wide indicator of habitat quality may be an overly simplistic approach to warbler management.

For example, there appears to be seasonal variation in warbler foraging behavior among tree species (Wahl et al. 1990, Beardmore 1994, Marshall et al. 2013), similar to patterns in foraging behavior found among tree species for a closely related bird species, the black-throated gray warbler (*S. nigrescens*) (Keane and Morrison 1999). In the case of the golden-cheeked warbler, oaks provide important foraging opportunities during the early part of the breeding season while Ashe juniper provides important foraging opportunities during the middle- and late stages of the breeding season. Therefore, differences in the proportion of Ashe juniper and oaks could influence warbler habitat selection decisions and subsequent productivity. In addition, warblers may exhibit different responses to oak species composition within oak-juniper woodland stands. At the Fort Hood Military Reservation located in the northern portion of the warbler's breeding range, warbler territory density and productivity appeared higher in oak-juniper woodland dominated by Texas oaks than in oak-juniper woodland dominated by post oaks (Marshall et al. 2013, M. L. Morrison *unpublished data*). Similar to studies conducted on other songbird species (e.g., Petit and Petit 1996), variation in food abundance across different tree species may be driving the disparity in warbler productivity. In the case of the warbler, insects in the Order Lepidoptera (a main food source for warblers) were more abundant on Texas than on post oaks (Marshall et al. 2013). The dominant oak species within oak-juniper woodland stands occupied by warblers varies by site and geographic location within the warbler's breeding range (Diamond 1997, Campbell 2003). However, warbler responses to variation in tree species composition outside of the single study conducted at Fort Hood are unknown.

Warbler management guidelines additionally emphasize the importance of Ashe juniper height to warbler habitat quality; thinning guidelines, based on Campbell (2003), approve the removal of Ashe juniper <4.5 m in height from the understory of oak-juniper woodland. The importance of mature Ashe juniper as a nesting and foraging substrate for warblers is well established, but no studies have linked Ashe juniper height to warbler productivity (Staake 2003, Reidy et al. 2009). Again, this particular vegetation metric can vary widely across the warbler's breeding range. Canopy height within warbler habitat typically averages between 4 and 7.5 m, but can be as low as 3 m, particularly in the southwestern portion of the warbler's breeding range (Diamond 1997, Ladd and Gass 1999). Identifying the importance of Ashe juniper height to warbler productivity and quantifying the point (or zone) at which warbler productivity is expected to be high could aid management and restoration efforts for this species.

The degree of variation in vegetation height within oak-juniper woodland stands may also differ with site-specific natural- (e.g., weather, soil type) or anthropogenic (e.g., prescribed burning, thinning) conditions and could be important to warbler habitat selection and productivity. Food availability can influence avian habitat selection decisions and may limit the reproductive success of some songbirds (Rodenhouse and Holmes 1992, Newton 1998, Nagy and Holmes 2004). As found for other species (e.g., Robinson and Holmes 1982, Marshall and Cooper 2004), structural complexity could provide important foraging opportunities for warblers. Nest success (via predation and parasitism) can also be influenced by structural heterogeneity or lack thereof (e.g., Barber et al. 2001, Driscoll et al. 2005), but an understanding of how variation in Ashe juniper height influences warbler productivity is needed.

I used data collected within 899 warbler territories (2009–2013) located across the warbler’s breeding range to investigate the influence of local vegetation characteristics on warbler territory size, pairing success, and fledging success. I additionally used a subset of my data (n = 486 warbler territories) to examine the influence of vegetation structure and composition on the size of the core area used by warblers within their territories and to explore the influence of vegetation structure and composition within the territory cores on warbler pairing and fledging success. Given the perceived importance of Ashe juniper to warblers, I examined my warbler response variables in relation to mean percent Ashe juniper cover, mean Ashe juniper height (m), and variation in Ashe juniper height (m). I also examined my warbler response variables in relation to the dominant oak species within each territory and delineated core area. I additionally included geographic location and year in my analyses because spatial and temporal variation in local vegetation characteristics (e.g., differences in the timing of leaf-out across breeding season) or food abundance (e.g., late frost that kills insects at the beginning of the breeding season) could influence the spatial distribution or productivity of warblers. I predicted both linear and nonlinear relationships between percent Ashe juniper and my warbler response variables. Given the importance of Ashe juniper as a nesting and foraging substrate for warblers, I predicted that territory and core territory size would decrease and pairing and fledging success would increase with increasing Ashe juniper cover within the territory or delineated core area (linearly or until reaching levels where no subsequent increase in Ashe juniper cover changed the spatial distribution or productivity of warblers). However, oaks are also an important component of warbler habitat, so I additionally predicted that warbler territory and core territory size would be smallest and warbler pairing and fledging success would be highest when the territory or delineated core area has an equal proportion of Ashe juniper and oaks. I also predicted that the strength and shape of these relationships could vary by dominant oak species, geographic location, or year.

Since its listing as federally endangered, state and federal agencies have used information obtained from descriptive, short-term studies conducted on prioritized sites to guide warbler management practices. However, many assumptions regarding warbler-habitat relationships remain untested and we have limited information on how these relationships may vary across spatial and temporal scales. In addition, we have limited quantitative information regarding the strength or shape of these relationships, which may limit our ability to develop effective management practices and determine appropriate restoration goals. My research could aid our ability to predict warbler responses to habitat alteration, identify warbler habitat where productvity is expected to be high, and help guide future management and restoration practices for this conservation target.

METHODS

Study area

I conducted my research from 2009–2013 in 11 counties (Kinney, Edwards, Uvalde, Real, Kerr, Bandera, Hays, Travis, Bell, Coryell, and Bosque) across the 3 largest Level-IV Ecoregions located within the warbler's breeding range in central Texas (Fig. 4; Griffith et al. 2004). Ecoregion delineations are based on geography, physiography, vegetation, climate, soils, land use, wildlife, and hydrology and represent areas with generally similar ecosystem responses to disturbance (Omernik 1987). As such, Ecoregions are often used as spatial units for research and natural resource management; I used Ecoregions for my research as the broadest geographic scale within which similar ecological conditions are inhabited by warblers. The Ecoregions included in my research contain 75% percent (1,257,296 ha) of the total predicted warbler habitat in central Texas (1,678,697 ha) and 82% of the total area predicted to have a probability of warbler occurrence $\geq$0.50 (Collier et al. 2012).

The Edwards Plateau Woodlands Ecoregion (hereafter EPW) is located in the central portion of the Edwards Plateau and is on the southwestern edge of the warbler's breeding range (Fig. 1). Mean minimum and maximum temperatures in January are 1°C and 15°C and mean minimum and maximum temperatures in July are 20°C and 34°C (NOAA 2014). Mean annual precipitation (56–86 mm) is generally less than found elsewhere in the warbler's breeding range and declines from east to west (NOAA 2014). Warbler habitat in this Ecoregion is composed primarily of Ashe juniper, Lacey oak (*Q. laceyi*), post oak, and live oak (Diamond 1997). Balcones Canyonlands Ecoregion (hereafter BC) is the central-most Ecoregion represented in my study (Fig. 4; Griffith et al. 2004). Mean minimum and maximum temperatures are similar to that found in the EPW (NOAA 2014). However, mean annual precipitation is typically greater in BC (66–86 mm) (NOAA 2014). Warbler habitat in the BC is typically of Ashe juniper, Texas oak, live oak, and various other hardwoods (Diamond 1997). The Limestone Cut Plain (hereafter LCP) is the northernmost Ecoregion included in my study (Griffith et al. 2004) and generally receives more annual precipitation (76–86 mm) than the other Ecoregions included in my study (Fig. 4; NOAA 2014). Mean temperatures are similar to those found in the BC and EPW (NOAA 2014). Warbler habitat in this Ecoregion is composed primarily of Texas oak, post oak, live oak, shin oak (*Q. sinuata*), Ashe juniper, and various other hardwoods (Diamond 1997).

Across the Ecoregions, I used territory data collected on 90 study sites (i.e., sampled area within an oak-juniper woodland stand) selected for the various needs (e.g., impacts of road construction and military training activities, influence of age structure, influence of tree species composition) of warbler research projects conducted by Texas A&M University and the Texas A&M Institute of Renewable Natural Resources (M. L. Morrison *unpublished data*). Study sites represented a wide-range of vegetation types (i.e., varying percent Ashe juniper cover, Ashe juniper height, and dominant oak species within the stand) occupied by warblers across their breeding range. As such, vegetation characteristics within territories and delineated territory core areas were also variable (Tables 3–4).

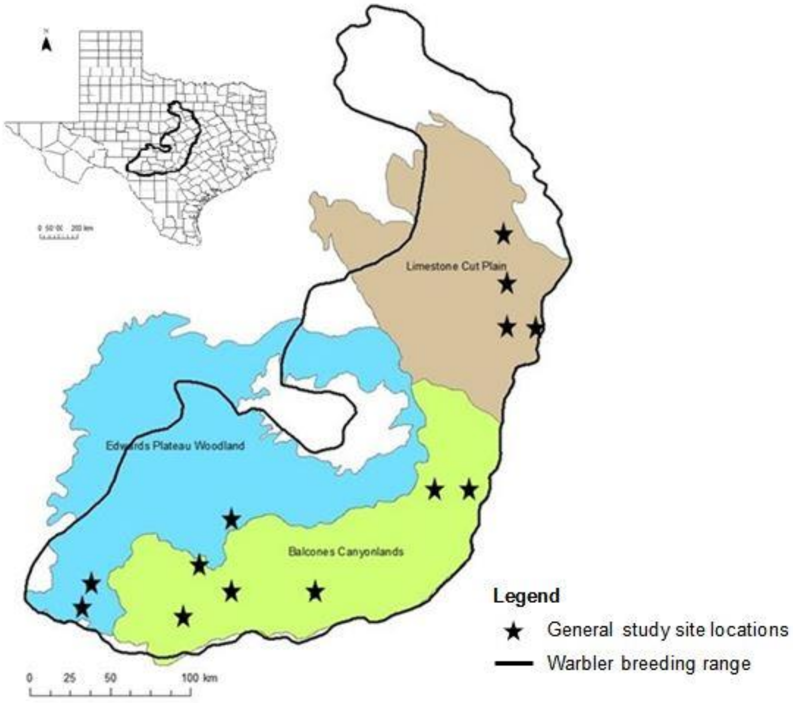

Figure 4. Map of golden-cheeked warbler study sites (2009–2013) located across the 3 largest Level-4 Ecoregions within the warbler's breeding range in central Texas, USA.

Study site occupancy

To establish study site occupancy by warblers, trained observers conducted preliminary surveys across each study site every 7–10 days beginning the second week of March, the approximate time of warbler arrival to their breeding grounds in Texas. During initial surveys, observers walked along parallel transects systematically established 150-200 m apart across each site (ArcGIS 9.3.1) and recorded the GPS coordinates of any warblers seen or heard. I did not use this information for analysis purposes, but rather used these detection points to relocate male warblers on subsequent visits to each occupied study site. If observers did not detect warblers on a given study site within the first 4 weeks of the warbler breeding season, observers discontinued transect surveys on the study site and returned only to conduct vegetation surveys prior to the end of the warbler's breeding season.

Territory mapping

Observers returned to each occupied study site every 7–10 days for the duration of the warbler breeding season (March to July) to conduct territory mapping, which I used to delineate the spatial extent of each focal male's territory and the core area used by each male warbler. Observers relocated male warblers along transects initially established to determine study site occupancy. Once observers detected a warbler, they recorded the bird's initial location using a GPS unit. The observer then followed the male bird until it was no longer visible or was mapped for no more than 1 hour.

In 2009 and 2010, observers recorded GPS locations of male warblers if the focal male moved ≥20 m until 3–6 locations were recorded. From 2011–2013, observers recorded GPS locations every 2 minutes. Both sampling techniques represent the spatial extent of vegetation used by male warblers and capture movements ≥20 m. Therefore, I used data collected using both mapping methods to create minimum convex polygons (MCPs) for each territorial male (i.e., male relocated for ≥4 weeks) monitored between 2009 and 2013 when ≥15 points were recorded over the course of the breeding season. Because MCPs represent the outermost points in a location dataset, I used the total area (ha) within each MCP as an estimate of territory size (Table 3) and examined warbler pairing and fledging success at the territory scale in relation to vegetation data collected across the spatial extent of each MCP.

I additionally used data collected from 2011–2013 to construct individual utilization distributions (UDs) for each territorial male when ≥30 points were recorded over the course of the breeding season. Unlike MCP delineations, which are constructed using only the outermost points in a location data set and can include large areas unused by the target individual (Harris et al. 2009), UD techniques represent the relative frequency distribution of an individual's location for a specified period of time (Fig. 5). There are several classes of UD techniques, but similar to methods used for a closely related species, the cerulean warbler (*S. cerulea*) (Barg et al. 2005), I calculated the UD for each territorial male using fixed kernel density estimation using R package biRdkern (Collier 2012) in R, version 3.0.1 (R Core Team 2013). Kernel estimation allows for the delineation of a territory in terms of a probabilistic model and provides a more accurate and informative calculation of the area used by territorial males (Silverman 1986). I estimated the 50, 75, and 95% kernel isopleths for each territory, but used the 50% kernel to estimate the size of the core area used by each male (Table 4) and examined warbler pairing and fledging success at the core territory scale in relation to vegetation data collected across the spatial extent of each 50% kernel.

Table 3. Distribution of golden-cheeked warbler territories delineated as minimum convex polygons (2009–2013) across the 3 largest Level-4 Ecoregions (EPW = Edwards Plateau Woodland, BC = Balcones Canyonlands, and LCP = Limestone Cut Plain) within the warbler's breeding range in central Texas, USA.

Ecoregion	**Dominant oak spp.**[a]	**No. of Terr**[b]	**Territory size (ha)**[c]	**Mean AJ Cover (%)**[d]	**Mean AJ height (m)**[d]	**SD AJ height (m)**[d]
EPW						
	Lacey	33	0.3–6.2	11–87	0.2–4.2	0.3–2.5
	Live	39	0.6–8.1	0–95	0.5–3.7	0.0–1.6
	Mixed	5	1.6–5.7	48–77	1.4–2.6	0.8–1.4
	Post	1	2.0	80	3.9	2.5
	Shin	24	0.9–5.6	35–86	0.9–3.7	0.4–2.8
	Texas	8	0.5–4.4	10–72	1.7–3.2	0.7–5.2
BC						
	Live	40	0.5–11.0	23–90	0.8–18.3	0.5–7.9
	Mixed	6	0.6–5.7	28–100	2.4–7.9	1.3–3.3
	Shin	3	1.2–2.8	47–100	2.9–8.3	1.6–6.9
	Texas	31	0.7–8.7	14–90	1.0–13.1	1.2–5.1
LCP						
	Live	202	0.1–11.4	23–95	0.6–7.0	0.3–14.8
	Mixed	119	0.5–18.2	21–88	1.0–6.0	0.0–9.9
	Post	53	0.5–8.3	0–82	1.0–4.3	0.0–2.1
	Shin	131	0.3–5.5	18–98	0.4–7.3	0.0–2.9
	Texas	204	0.2–6.7	2–94	0.1–8.5	0.0–14.5

[a] Dominant oak species within the territory.

[b] Number of warbler territories within each Ecoregion and oak species categorization.

[c] Range of territory sizes.

[d] Range of mean percent Ashe juniper cover, mean Ashe juniper height, and standard deviation of Ashe juniper height within warbler territories.

Table 4. Distribution of golden-cheeked warbler core territories delineated as 50% kernel isopleths (2011–2013) across the 3 largest Level-4 Ecoregions (EPW = Edwards Plateau Woodland, BC = Balcones Canyonlands, and LCP = Limestone Cut Plain) within the warbler's breeding range in central Texas, USA.

Ecoregion	**Dominant oak spp.**[a]	**No. of Core Terr**[b]	**Territory size (ha)**[c]	**Mean AJ Cover (%)**[d]	**Mean AJ height (m)**[d]	**SD AJ height (m)**[d]
EPW						
	Lacey	0	N/A	N/A	N/A	N/A
	Live	3	0.8–1.6	15–90	0.4–3.7	1.0– 1.5
	Mixed	0	N/A	N/A	N/A	N/A
	Post	1	0.2	95	6.1	2.9
	Shin	0	N/A	N/A	N/A	N/A
	Texas	4	0.5–1.8	11–51	1.5–3.8	0.7–6.5
BC						
	Live	20	0.4–3.3	11–88	0.5–15.9	1.1–2.2
	Mixed	2	0.9–1.0	32–75	3.5–4.4	2.2–2.5
	Shin	3	0.3–0.9	51–70	5.2–9.9	2.0–7.6
	Texas	20	0.4–2.6	3–92	0.3–3.7	0.9–4.7
LCP						
	Live	183	0.1–10.1	18–92	1.1–9.3	0.0–12.9
	Mixed	49	0.5–5.1	35–85	1.9–5.2	0.3–2.7
	Post	29	0.3–2.7	8–89	0.7–5.4	0.5–2.0
	Shin	83	0.1–3.7	14–93	0.9–6.6	0.0–2.3
	Texas	129	0.1–6.1	12–95	0.8–7.0	0.0–3.6

[a] Dominant oak species within each core territory.

[b] Number of core territories within each Ecoregion and oak species categorization.

[c] Range of core territory sizes.

[d] Range of mean percent Ashe juniper cover, mean Ashe juniper height, and standard deviation of Ashe juniper height within core territories.

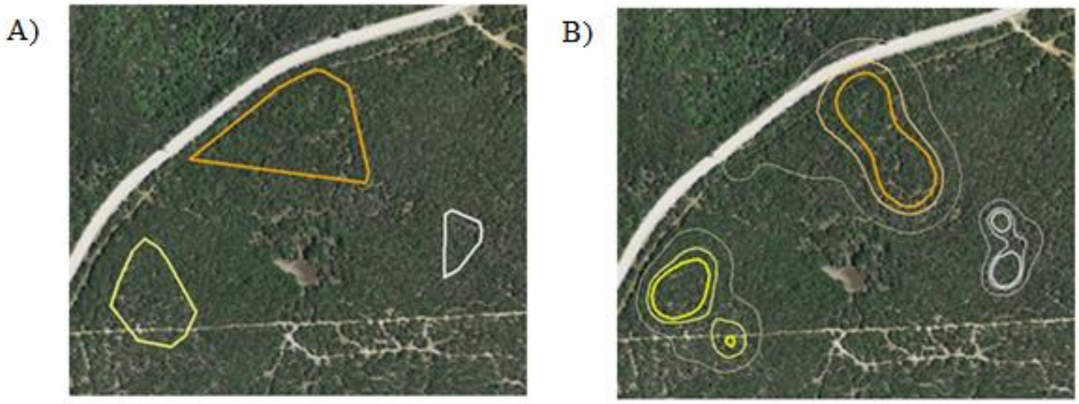

Figure 5. Examples of male warbler territory delineations using minimum convex polygon (A) and fixed kernel density estimation (B) methods. Isopleths in B represent the 50, 75, and 95% kernels.

Productivity estimates

As previously used to assess warbler productivity (e.g., Klassen et al. 2012, Stewart et al. 2014, Marshall et al. 2013), I used a modified version of the Vickery index (Vickery et al. 1992) to examine the reproductive status of each territory (and, thus, each territory core). When time intensive nest searching, nest monitoring, and banding efforts are not possible, this method allows observers to predict the reproductive stage of territorial males or mated pairs and nest outcomes using behavioral observations. The Vickery Index is applicable to short-term studies conducted across broad spatial scales and the methodological effectiveness of the Vickery index has been tested. In a study conducted by Christoferson and Morrison (2001), observers correctly predicted the outcome of 80–92% of painted redstart (*Myioborus pictus*), plumbeous vireo (*Vireo plumbeus*), and western wood-pewee (*Contopus sordidulus*) nests.

During each territory mapping sampling period, observers recorded the behavior of focal birds. We recorded rankings of behavioral observations at each visit to the territory (and, thus, each territory core) as follows: 1) male present >4weeks, 2) pair present, 3) material carried to the presumed nest, 4) food carried to the presumed nestlings, and 5) fledglings sighted by observer. When the behavioral rank recorded by an observer was $\geq$2, I considered the male observed within the territory or core territory successfully paired. When the behavioral rank recorded by the observer was 5, I considered the territory or core area within the territory reproductively successful.

Vegetation measurements

Observers recorded vegetation measurements across each territory, which included the delineated core area(s) within each territory, at points spaced 20 m apart along grid transects established using ArcGIS 9.3.1. For all vegetation $\geq$2 m, observers measured percent canopy cover per dominant tree species to the nearest 10% using a tubular densitometer. Observers also estimated the height of each tree species to the nearest 0.5 m. For each territory and core area within the territory, I calculated mean percent Ashe juniper cover, mean Ashe juniper height (m), and the standard deviation of Ashe juniper height (m) (Tables 3–4). Of the remaining hardwoods, I calculated the mean percent cover of each oak species. Eighty-six percent of territories and 90% of territory cores were dominated by a single oak species (i.e., >50% cover by a single oak species). When this was the case, I assigned the territory or core area within the territory a dominant oak species categorization (e.g., a territory or territory core with 80% live oak was categorized as "Live Oak Dominated") (Table 3). When there was <50% cover of multiple oak species within a single territory or territory core, I categorized the territory or territory core as "Mixed" (Table 4).

Data analysis

I developed *a priori* models including variables hypothesized to cause variation in warbler territory size (i.e., MCP), core territory size (i.e., 50% kernel), and models to address pairing and fledging success at the territory and core territory scales (i.e., year, Ecoregion as a proxy for geographic location of the study site within the warbler's breeding range, tree species composition metrics, and 2-way interactions between all combinations of variables). *A priori* models included both linear and quadratic trends for hypotheses regarding Ashe juniper metrics. There were statistically significant correlations between several variables used to analyze warbler territory size and pairing and fledging success at the territory scale (Appendix B). I did not include these interaction models in my analyses. The final candidate model set for territory size and pairing and fledging success at the territory scale included an intercept-only model, a model representing year as a main effect, and models representing Ecoregion, dominant oak species, mean percent Ashe juniper cover, mean Ashe juniper height, and variation in Ashe juniper height with year as a covariate for each (Table 5). I additionally considered a model representing the interaction between Ecoregion and mean percent Ashe juniper cover with year as a covariate (Table 5).

There were also statistically significant correlations between several variables used to analyze core territory size and pairing and fledging success at the core territory scale (Appendix B). Again, I did not include these interaction models in my analyses. The final candidate model set for core territory size and pairing and fledging success within the territory cores included an intercept-only model, a model representing year as a main effect, and models representing Ecoregion, dominant oak species, mean percent Ashe juniper cover, mean Ashe juniper height, and variation in Ashe juniper height with year as a covariate for each (Table 6). I additionally considered models representing the interactions between dominant oak species and mean Ashe juniper heights within the territory cores and dominant oak species and variation in Ashe juniper height within the territory cores; year was added as a covariate for both interaction models (Table 6).

I used a generalized linear model approach to determine which variables best predicted warbler territory size, core territory size, and pairing and fledging success at the territory and core territory scales (Zar 1999:324-376). I used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to rank models (Burnham and Anderson 2002:49-97). I determined the relative support of each model using ΔAIC_c and Akaike Weights (w_i) (Sugiura 1978, Burnham and Anderson 2002:49-97). I considered models with $\Delta AIC_c < 2.0$ equally plausible models and used w_i values to determine the most plausible model within the top candidate set of models. I used the regression coefficients estimated from the best-fit model to predict territory size, core territory size, and warbler pairing and fledging success at the territory and core territory scales. I then calculated the 95% confidence intervals (hereafter 95% CI) for each predicted warbler response variable to examine the extent of variation around my predicted values (Burnham and Anderson 2002:49-97). I examined the extent of overlap among the 95% CIs to determine the potential statistical or biological significance of each relationship and identified points or zones in habitat conditions that caused a shift in my avian response variables. I performed all analyses using R statistical software (R Development Core Team 2013).

RESULTS

From 2009–2013, observers monitored 899 warbler territories on 90 study sites across the 3 Ecoregions included in my study (Table 3). Territory size ranged from 0.2–18.2 ha (Table 3). Percent Ashe juniper cover within territories ranged from 0–100%, mean Ashe juniper height ranged from 0.1–18.3 m, and the standard deviation in Ashe juniper height ranged from 0.0–14.8 m (Table 3). Overall pairing success (n = 899 territories) was 81% (EPW pairing success = 81% [n = 110 territories], BC pairing success = 75% [n = 80 territories], and LCP pairing success = 82% [n = 709 territories]). Of the 728 successfully paired territories, 93% successfully fledged $\geq$1 young fledging success (EPW fledging success = 81% [n = 89 paired territories], BC fledging success = 89% [n = 60 paired territories], and LCP fledging success = 96% [n = 579 paired territories]).

Using data collected from 2011–2013, I constructed 50% kernel isopleths, which represented the core area used by warblers, for 486 territories (Table 4). Core territory size ranged from 0.1–10.1 ha (Table 4). Percent Ashe juniper cover within core territories ranged from 3–100%, mean Ashe juniper height ranged from 0.3–15.9 m, and the standard deviation in Ashe juniper height ranged from 0.0–12.9 m (Table 4). Overall pairing success within my 486 core territories was 86% (EPW pairing success = 100% [n = 8 core territories], BC pairing success = 69% [n = 45 core territories], and LCP pairing success = 88% [n = 433 core territories]). Of the 419 successfully paired core territories, 81% successfully fledged $\geq$1 young fledging success (EPW fledging success = 63% [n = 8 paired core territories], BC fledging success = 71% [n = 31 paired core territories], and LCP fledging success = 82% [n = 380 paired core territories]).

The best-fit model for territory size included the main effect for dominant oak species within the territory (Table 5). Territories were larger when dominated by live, mixed, and post oak than territories dominated by Lacey, shin, and Texas oak (Fig. 6). Based on ΔAIC_c values, there were three plausible models in the candidate set for pairing success within territories. Given redundancy in the explanatory variables included in the three top models, I did not use a model averaging approach to make inferences regarding pairing success (Table 5; Burnham and Anderson 2002:149-205, Mazerolle 2013). I instead considered the most parsimonious model (i.e., the model predicting pairing success as a function of percent Ashe juniper cover) the best-fit model for this warbler response (Table 5). The predicted probability of warbler pairing success increased with increasing percent Ashe juniper cover (Fig. 7). The best-fit model for fledging success within territories included the interaction between Ecoregion and percent Ashe juniper cover (Table 5). The predicted probability of warbler fledging success increased with increasing percent Ashe juniper cover in each Ecoregion.

However, overlapping confidence intervals indicated no substantial difference between fledging success and percent Ashe juniper cover across the 3 Ecoregions (Fig. 8).

Table 5. Models of territory size, pairing success, and fledging success for 899 golden-cheeked warbler territories monitored on 90 study sites located across the 3 largest Level-4 Ecoregions within the warbler's breeding range in central Texas, USA (2009–2013).

Response[a]	**Model**[b]	***K***[c]	**Log liklihood**	**AIC$_c$**[d]	**ΔAIC$_c$**[e]	***w$_i$***[f]
Size						
	DomOak+Year	8	-1759.12	3534.39	0.00	1.0
	PercentAJ^2+Year	5	-1779.02	3568.10	33.71	0.0
	Ecoregion*PercentAJ+Year	8	-1778.81	3573.78	39.39	0.0
	Ecoregion+Year	5	-1783.52	3577.11	42.72	0.0
	SDAJHt^2+Year	5	-1783.61	3577.28	42.89	0.0
	SDAJHt+Year	4	-1784.88	3577.80	43.41	0.0
	AvgAJHt^2+Year	5	-1784.69	3579.45	45.06	0.0
	AvgAJHt+Year	4	-1786.00	3580.05	45.66	0.0
	Year	3	-1788.54	3583.10	48.71	0.0
	PercentAJ+Year	4	-1788.47	3584.98	50.58	0.0
	Constant	2	-1798.55	3601.12	66.73	0.0
Pairing						
	PercentAJ+Year	3	-433.71	873.45	0.00	0.3
	Ecoregion*PercentAJ+Year	7	-430.03	874.19	0.75	0.2
	PercentAJ^2+Year	4	-433.36	874.77	1.32	0.2
	AvgAJHt+Year	3	-435.29	876.60	3.15	0.1
	Constant	1	-437.39	876.78	3.34	0.1
	AvgAJHt^2+Year	4	-434.76	877.56	4.11	<0.1
	Year	2	-437.07	878.16	4.71	<0.1
	DomOak+Year	7	-432.81	879.75	6.30	<0.1
	SDAJHt+Year	3	-436.89	879.80	6.35	<0.1
	Ecoregion+Year	4	-435.98	880.00	6.55	<0.1
	SDAJHt^2+Year	4	-435.99	880.03	6.58	<0.1
Fledging						
	Ecoregion*PercentAJ+Year	7	-468.90	951.92	0.00	0.8

Table 5 Continued

Response[a]	**Model**[b]	***K***[c]	**Log liklihood**	**AIC$_c$**[d]	**ΔAIC$_c$**[e]	***w$_i$***[f]
Fledging						
	PercentAJ^2+Year	4	-474.09	956.23	4.31	0.1
	PercentAJ+Year	3	-475.31	956.64	4.72	0.1
	DomOak+Year	7	-472.89	959.90	7.97	0.0
	Ecoregion+Year	4	-477.03	962.11	10.18	0.0
	AvgAJHt+Year	3	-478.59	963.21	11.29	0.0
	AvgAJHt^2+Year	4	-477.62	963.29	11.37	0.0
	Year	2	-480.80	965.61	13.69	0.0
	SDAJHt+Year	3	-480.74	967.51	15.59	0.0
	SDAJHt^2+Year	4	-480.31	968.66	16.74	0.0
	Constant	1	-499.12	1000.25	48.33	0.0

[a] Territory size measured as the area within each delineated minimum convex polygon.

[b] Explanatory variable abbreviations are as follows: Constant = null model, Ecoregion = geographic location of the territory, DomOak = dominant oak species within the territory, PercentAJ = percent Ashe juniper cover within the territory, AvgAJHt = mean AJ height within the territory, SDAJHt = standard deviation of Ashe juniper height within the territory. An * indicates when interactions between explanatory variables were considered.

[c] Number of parameters in the model

[d] Akaike's Information Criteria corrected for small sample sizes

[e] AIC$_c$ relative to the best-fit model

[f] Model weight

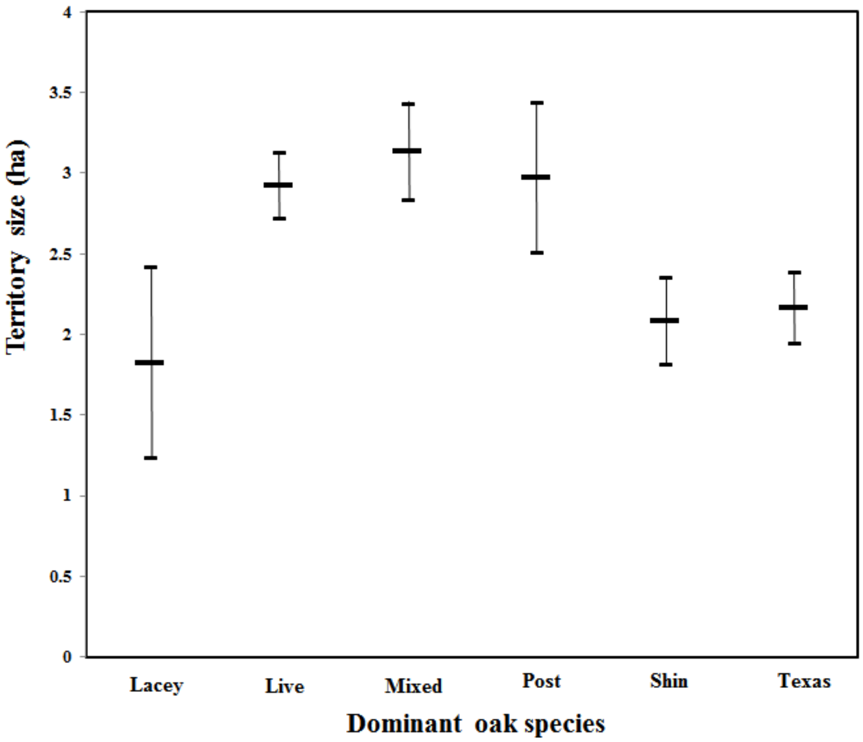

Figure 6. Predicted golden-cheeked warbler territory size (ha) and their associated 95% confidence intervals per dominant oak species (2009–2013). Territories delineated as minimum convex polygons (n = 899) were located across the 3 largest Level-4 Ecoregions within the warbler's breeding range in central Texas, USA.

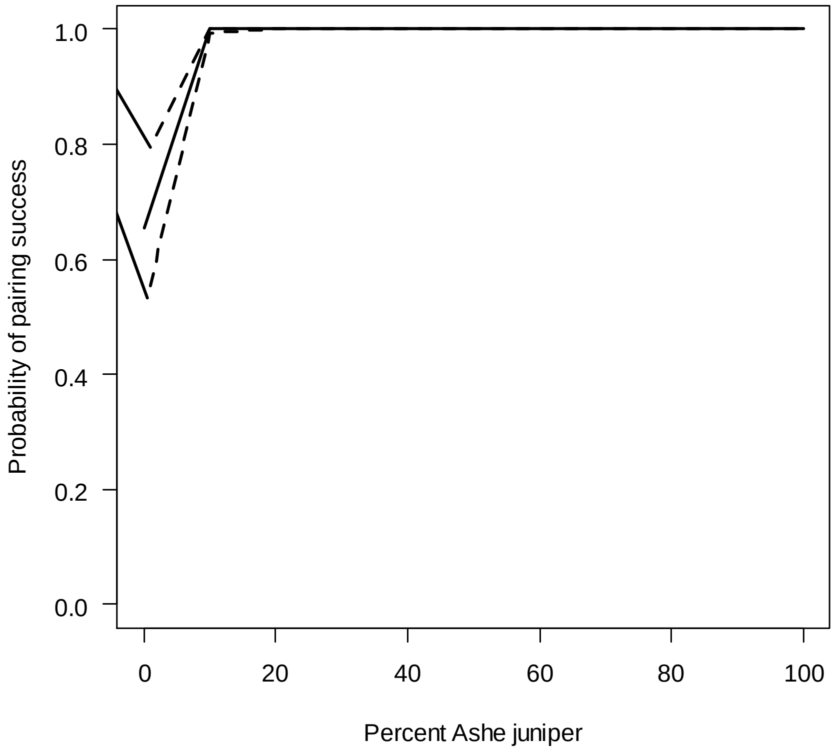

Figure 7. Predicted probability of golden-cheeked pairing success and the associated 95% confidence interval (2009–2013). Territories delineated as minimum convex poloygons (n = 899) were located across the 3 largest Level-4 Ecoregions within the warbler's breeding range in central Texas, USA.

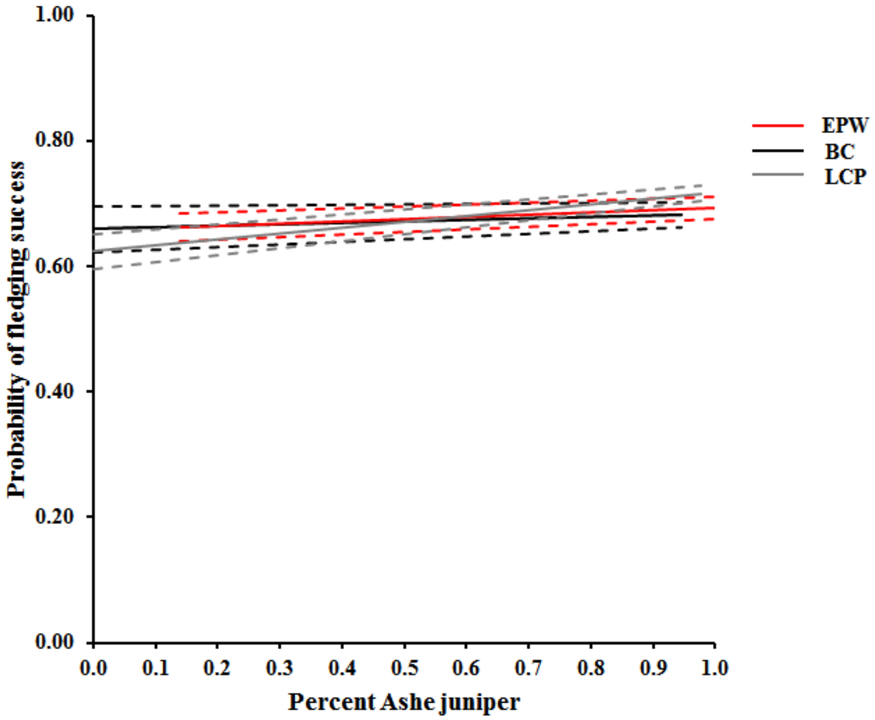

Figure 8. Predicted probability of golden-cheeked fledging success and the associated 95% confidence interval (2009–2013). Territories delineated as minimum convex polygons (n = 899) were located across the 3 largest Level-4 Ecoregions (EPW = Edwards Plateau Wooldand, BC = Balcones Canyonland, and LCP = Limestone Cut Plain) within the warbler's breeding range in central Texas, USA.

The best-fit model for the delineated core area within each territory included the interaction between dominant oak species and standard deviation of Ashe juniper height within the territory (Table 6). Core areas of territories increased with increasing variation in Ashe juniper height across the dominant oak species categorizations (Fig. 10). However, overlapping confidence intervals indicate no substantial relationship between core territory size and variation in Ashe juniper height across the dominant oak species categories (Fig. 10). The best-fit model for pairing success within territory cores included Ecoregion (Table 6). Overlapping confidence intervals indicate that the predicted probability of warbler pairing success was similar across the 3 Ecoregions (Fig. 11). The two plausible models for fledging success within territory cores included Ecoregion and the quadratic trend for mean Ashe juniper height within the territory core (Table 6). The predicted probability of warbler fledging success was slightly higher in the LCP than in the BC. The predicted probability of warbler fledging success generally decreased with increasing mean Ashe juniper height within the core territories (Fig. 12).

Table 6. Models of territory size, pairing success, and fledging success for 486 golden-cheeked warbler territory cores monitored on 90 study sites located across the 3 largest Level-4 Ecoregions within the warbler's breeding range in central Texas, USA (2009–2013).

Response[a]	**Model**[b]	***K***[c]	**Log liklihood**	**AIC$_c$**[d]	**ΔAIC$_c$**[e]	***w$_i$***[f]
Size						
	DomOak*SDAJHt+Year	11	-641.19	1304.93	0.00	0.9
	SDAJHt+Year	3	-652.33	1310.71	5.78	0.1
	SDAJHt^2+Year	4	-652.25	1312.57	7.64	0.0
	DomOak*AvgAJHt+Year	12	-643.97	1312.61	7.67	0.0
	DomOak+Year	7	-649.74	1313.72	8.79	0.0
	PercentAJ^2 +Year	5	-653.84	1317.80	12.86	0.0
	AvgAJHt+Year	4	-658.52	1325.12	20.19	0.0
	AvgAJHt^2+Year	5	-657.56	1325.24	20.31	0.0
	Constant	2	-661.23	1326.49	21.55	0.0
	Year	3	-660.60	1327.25	22.32	0.0
	PercentAJ+Year	4	-659.85	1327.79	22.85	0.0
	Ecoregion	4	-660.66	1329.40	24.47	0.0
Pairing						
	Ecoregion+Year	4	-188.79	385.66	0.00	0.7
	PercentAJ+Year	3	-191.62	389.30	3.64	0.1
	PercentAJ^2+Year	4	-191.21	390.50	4.84	0.1
	SDAJHt+Year	3	-192.29	390.63	4.98	0.1

Table 6. Continued

Response[a]	**Model[b]**	***K*[c]**	**Log liklihood**	**AIC$_c$[d]**	**ΔAIC$_c$[e]**	***w$_i$*[f]**
Pairing						
	Constant	1	-194.92	391.84	6.18	0.0
	Year	2	-193.97	391.97	6.31	0.0
	SDAJHt^2+Year	4	-192.29	392.67	7.01	0.0
	AvgAJHt+Year	3	-193.97	393.99	8.33	0.0
	DomOak*SDAJHt+Year	11	-185.80	394.16	8.50	0.0
	DomOak+Year	6	-191.41	395.00	9.34	0.0
	AvgAJHt^2+Year	4	-193.91	395.90	10.25	0.0
	DomOak*AvgAJHt+Year	11	-190.88	404.32	18.66	0.0
Fledging						
	Ecoregion+Year	4	-289.54	587.16	0.00	0.6
	AvgAJHt^2+Year	4	-289.92	587.92	0.76	0.4
	PercentAJ+Year	3	-295.58	597.22	10.05	0.0
	Constant	1	-297.89	597.79	10.62	0.0
	PercentAJ^2+Year	4	-295.31	598.71	11.54	0.0
	SDAJHt+Year	3	-296.69	599.43	12.27	0.0
	Year	2	-297.85	599.73	12.57	0.0
	AvgAJHt+Year	3	-296.94	599.94	12.77	0.0
	SDAJHt^2+Year	4	-296.69	601.46	14.30	0.0
	DomOak*AvgAJHt+Year	11	-290.51	603.58	16.42	0.0
	DomOak+Year	6	-296.85	605.88	18.71	0.0
	DomOak*SDAJHt+Year	11	-291.92	606.39	19.23	0.0

[a] Core territory size measured as the area within each delineated 50% kernel isopleth.

[b] Explanatory variable abbreviations are as follows: Constant = null model, Ecoregion = geographic location of the territory, DomOak = dominant oak species within the 50% kernel, PercentAJ = percent Ashe juniper cover within the 50% kernel, AvgAJHt = mean AJ height within the 50% kernel, SDAJHt = standard deviation of Ashe juniper height within the 50% kernel. An * indicates when interactions between explanatory variables were considered.

[c] Number of parameters in the model

[d] Akaike's Information Criteria corrected for small sample sizes

[e] AIC$_c$ relative to the best-fit model

[f] Model weight

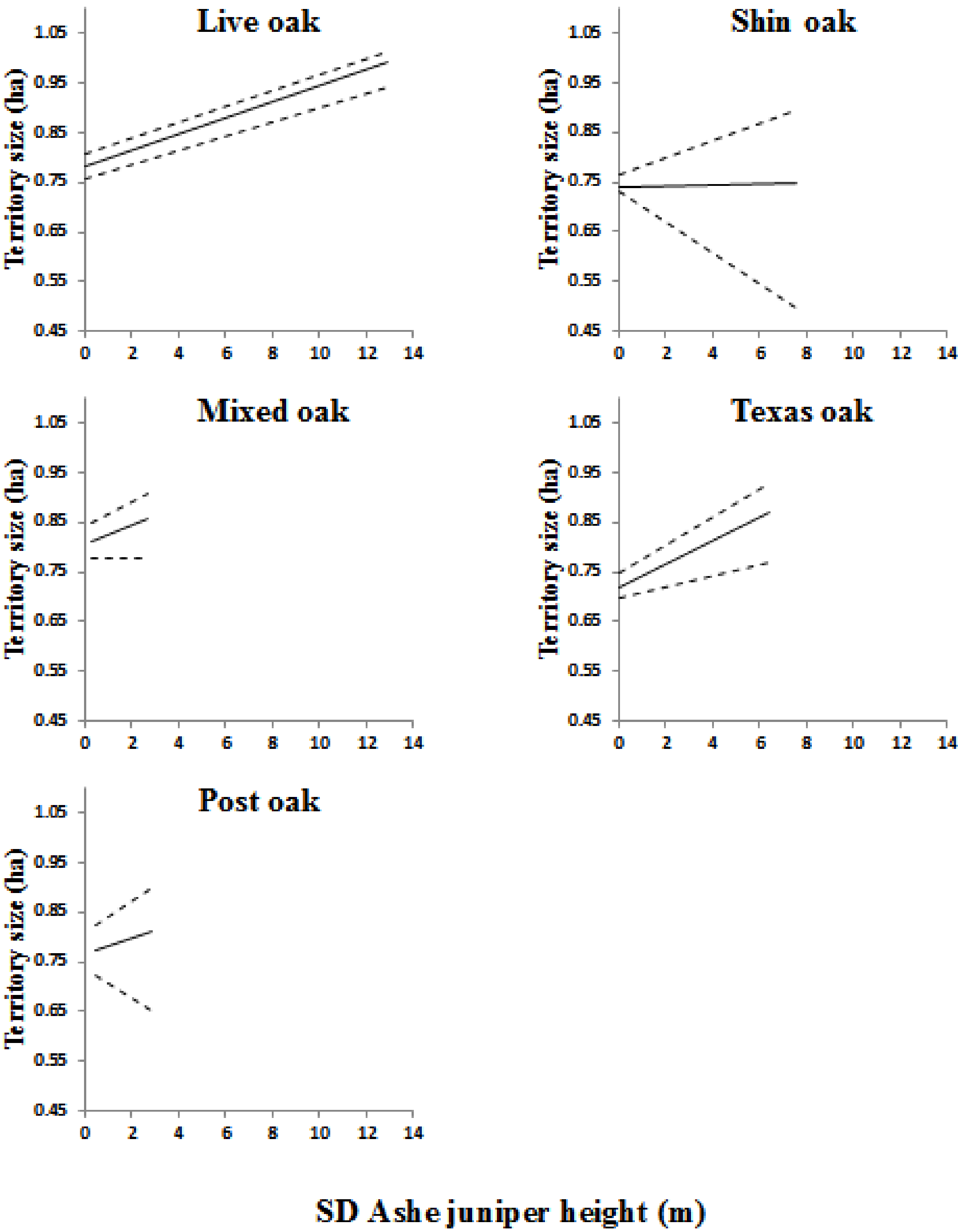

Figure 9. Predicted golden-cheeked warbler core territory size (ha) and the associated 95% confidence intervals per dominant oak species (2011–2013) in relation to the standard deviation of Ashe juniper height within each kernel. Territory cores delineated as 50% kernel isopleths (n = 486) were located across the 3 largest Level-4 Ecoregions within the warbler's breeding range in central Texas, USA.

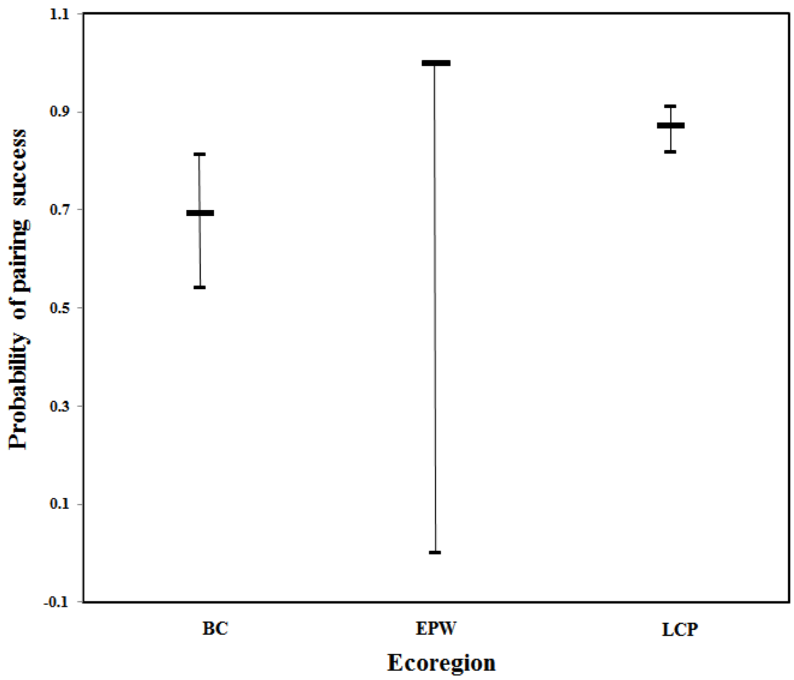

Figure 10. Predicted probability of golden-cheeked pairing success and the associated 95% confidence intervals (2011–2013). Territory cores delineated as 50% kernel isopleths (n = 486) were located across the 3 largest Level-4 Ecoregions within the warbler's breeding range in central Texas, USA (BC = Balcones Canyonlands, EPW = Edwards Plateau Woodland, and LCP = Limestone Cut Plain).

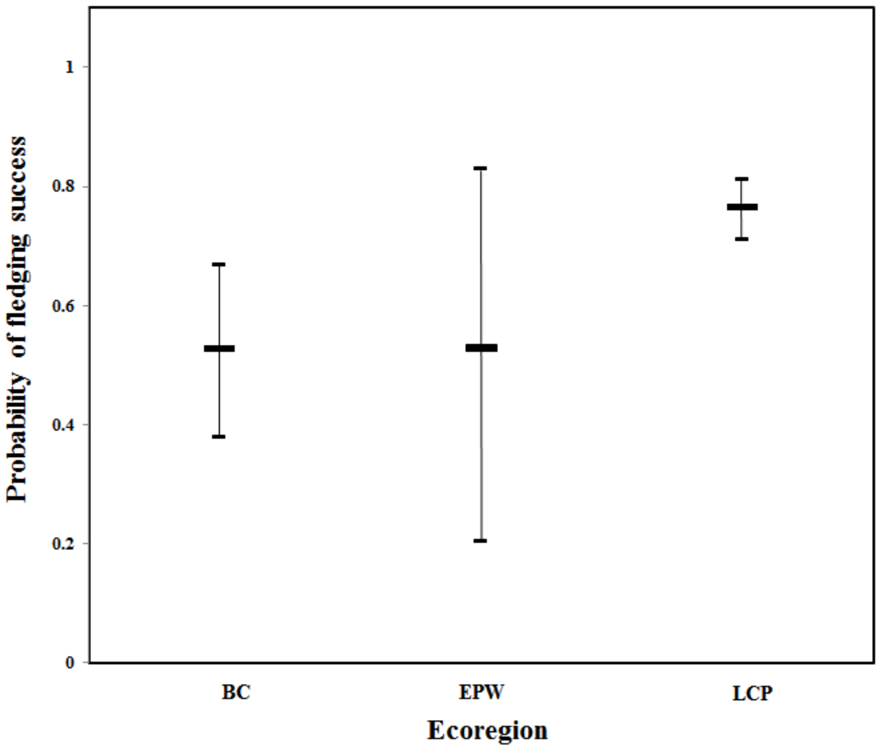

Figure 11. Predicted probability of golden-cheeked fledging success and the associated 95% confidence intervals (2011–2013). Territory cores delineated as 50% kernel isopleths (n = 486) were located across the 3 largest Level-4 Ecoregions within the warbler's breeding range in central Texas, USA (BC = Balcones Canyonlands, EPW = Edwards Plateau Woodland, and LCP = Limestone Cut Plain).

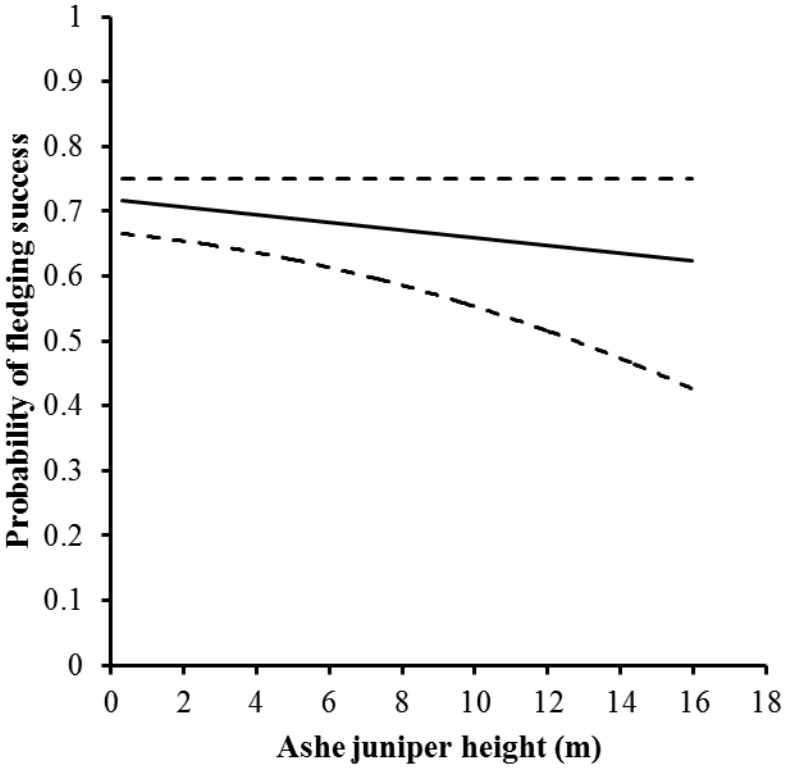

Figure 12. Predicted probability of golden-cheeked fledging success in relation to mean Ashe juniper height within the core territories and the associated 95% confidence interval (2011–2013). Territory cores delineated as 50% kernel isopleths (n = 486) were located across the 3 largest Level-4 Ecoregions within the warbler's breeding range in central Texas, USA.

CONCLUSIONS

My broad-scale assessment of warbler habitat selection and productivity in relation to tree species composition reiterates that vegetation utilized by warblers is highly variable across their breeding range and that warblers successfully breed in areas with vegetation characteristics outside current descriptions of warbler breeding habitat (Tables 3–4). As others have suggested (Klassan et al. 2012), this variation should be included in state and federal definitions of warbler breeding habitat. Expanding the current definition of warbler breeding habitat could aid warbler management efforts and provide additional opportunities to conserve important breeding habitat for this species.

Acknowledging this variation exists is a positive step towards more effective conservation for priority species, but it is crucial we understand how spatial and temporal variation in environmental conditions and resources influence avian demographics. Warbler management guidelines indicate that mature, dense Ashe juniper cover is an attribute of high quality warbler breeding habitat (TPWD 1990, 2012; USFWS 1992), but few studies have examined warbler responses to Ashe juniper metrics across the continuum of vegetation types they inhabit. I analyzed a large data set (n = 899 territories and n = 486 territory cores) collected over a longer time frame-(2009–2013) and larger geographic extent (i.e., most of the warbler's breeding range in central Texas) than most avian habitat selection studies are able to consider, and the territories included in my analyses had substantial variation in vegetation characteristics (Tables 3–4). However, my results did not support most assumptions regarding warbler responses to Ashe juniper. This does not imply that mature Ashe juniper should be removed from occupied warbler habitat; the importance of this particular tree species to warblers is well established. However, prioritizing sites based on qualitative Ashe juniper metrics or managing sites to promote single-aged stands of mature Ashe juniper cover may not be the most effective strategy for this species.

Territories were larger when dominated by live, mixed, and post oak when compared to territories dominated by Lacey, shin, and Texas oak (Fig. 6). There is limited information regarding the mechanisms that might drive such patterns. However, live and post oak dominated warbler breeding habitat often occurs on dry, rocky, or clay-based upland soils (Diamond 1997, Campbell), while Texas and Lacey oak dominated warbler habitat typically occurs on mesic soils associated with slopes, canyons, and creek bottoms (Diamond 1997, Campbell 2003). Soil type (Catry et al. 2012), soil drainage capabilities (Stuen et al. 1988, Carroll et al. 2011), and soil nutrient availability (Tilgar et al. 1999) can contribute to tree species composition and the resulting arthropod community. Therefore, territory size may be larger and more comparable when males selected areas dominated by live or post oak due to similarities in food resource abundance across these particular vegetation types.

At a finer-scale, the size of the core area used by warblers was best predicted by variation in Ashe juniper height (Table 6) and the size of the core area used by male warblers generally increased with increasing variation in height across the dominant oak species categories (Fig. 9). The general direction of the relationships between core territory size and the characteristics of vegetation used by male warblers across the oak species categories is not unexpected. Territory size is a function of male warbler habitat selection decisions and male warblers use taller statured vegetation for singing perches and foraging substrates (Ladd and Gass 1999; Beardmore 1994); male warblers may defend a smaller area when the core portion of their territory includes less variable, more mature Ashe juniper. However, there was extreme overlap in 95% CIs for territory core size in relation to variation in Ashe juniper height within and across the dominant oak species categories, indicating that there is no statistically or biologically substantial relationship between these variables (Fig. 9).

Within territories, percent Ashe juniper cover was the best predictor of warbler pairing success. Similar to estimates for pairing success reported by warbler research groups working on prioritized study sites (Groce et al. 2010), warbler pairing success was high (89%) across all Ecoregions and vegetation types. Contrary to assumptions, I found little variation in pairing success with increasing percent Ashe juniper cover. In fact, the predicted probability of pairing success was essentially 1.0 for territories with >15% Ashe juniper cover (Fig. 7). This suggests that there is a minimum amount of Ashe juniper cover necessary for pairing success, which is expected given our knowledge of the general ecology of this species, but that level is much lower than one would predict based on current state and federal definitions of warbler breeding habitat.

The best-fit model for fledging success at the territory scale included the interaction between percent Ashe juniper cover and Ecoregion. Similar to pairing success, I found that fledging success was high across all Ecoregions and vegetation types. My estimates for fledging success within MCPs are comparable to other study sites located within the warbler’s breeding range (Groce et al. 2010). The probability of fledging success remained constant at ~0.70 across the continuum of percent Ashe juniper cover (Fig. 8). Campomizzi et al (2012) found that the direction of the relationships between fledging success and canopy cover depended on Ecoregion. However, I did not find a statistically or biologically relevant difference across the geographic locations included in my study.

At a finer-scale, Ecoregion was the best predictor of warbler pairing success for the territory cores (Table 6), but overlapping confidence intervals indicated no substantial statistical or biological differences in warbler pairing success across the geographic locations included in my study (Fig. 11). Again, this result likely reflects the high pairing success I observed across all study sites. The two plausible models for fledging success within the territory cores included Ecoregion and the quadratic trend for mean Ashe juniper height within the core area used by warblers (Table 6). The predicted probability of warbler fledging success was slightly higher in the LCP than in the BC. This may reflect differences in nest predator abundance or composition, which can vary over geographic extents (e.g., Chalfoun et al. 2002). The predicted probability of warbler fledging success generally decreased with increasing mean Ashe juniper height within the territory cores (Fig. 12). However, the decline in the predicted probability of fledging success in relation to mean Ashe juniper height was minimal and likely inconsequential. Most occupied warbler stands range between 4.5–7 m in height (Ladd and Gass 1999). The predicted probability of fledging success was constant when Ashe juniper was $\leq$8 m and variation around the predicted values from 0 to 8 m was small.

Overall, my results suggest that warbler management guidelines should be updated to reflect the substantial variation in this particular habitat component that exists across the warbler’s breeding range. This could aid warbler management efforts and provide additional opportunities to conserve important breeding habitat for this species. In addition, my results indicate that assumptions between Ashe juniper metrics and warbler habitat selection and productivity may be unfounded. Prioritizing sites based on qualitative Ashe juniper metrics or managing sites to promote single-aged stands of mature Ashe juniper cover may not be the most effective strategy for this species. Future studies that examine how variation in understory vegetation characteristics contributes to warbler productivity may prove beneficial. There is also need for manipulative experiments to directly examine warbler responses to forest management techniques (e.g., prescribed burning, thinning). Conducting this research across the geographic extent of the warbler's breeding range is necessary if our goal is to fully understand the ecology of this species and develop more effective site-specific warbler management and restoration strategies for this species of conservation concern.

CHAPTER IV

CONCLUSIONS

My broad-scale study quantitatively demonstrates that local vegetative characteristics of warbler habitat vary widely across the warbler's breeding range and that tree species composition within generically classified oak-juniper woodland stands influences the spatial distribution of warblers across habitats. Contrary to current management guidelines, which emphasize the importance of dense Ashe juniper in the canopy, warbler territory density did not increase with increasing percent Ashe juniper across all oak species categorizations. Similarly, dominate oak species, not percent Ashe juniper cover, was the best predictor of warbler territory size at both the woodland stand and territory scales. Management guidelines indicate that land managers and private landowners can remove Ashe juniper <4.5 m in height from warbler breeding habitat. Widespread juniper removal would have obvious consequences for this songbird. However, my results suggest that thinning in this manner would have less of an effect on the spatial distribution of warblers in some oak juniper woodland types than others. Lack of oak recruitment, drought, and disease may also have a weaker influence on the warbler territory density and warbler territory size in oak-juniper woodland dominated by certain oak species.

Within territories, percent Ashe juniper cover was the best predictor of warbler pairing success. However, warbler pairing success was high across all Ecoregions and vegetation types and the predicted probability of pairing success was essentially 1.0 for territories with >15% Ashe juniper cover. This suggests that there is a minimum amount of Ashe juniper cover necessary for pairing success, which is expected given our knowledge of the general ecology of this species, but that level is much lower than one would predict based on current state and federal definitions of warbler breeding habitat. I additionally found that fledging success was high across all Ecoregions and vegetation types. Management guidelines suggest a relationship between warbler habitat quality and Ashe juniper cover. However, the probability of fledging success remained constant at ~0.70 across the continuum of percent Ashe juniper cover included in my study.

Overall, my results suggest that prioritizing oak-juniper woodland stands based on qualitative Ashe juniper metrics or managing sites to promote single-aged stands of mature Ashe juniper cover may not be the most effective strategy for golden-cheeked warblers. Instead, warbler conservation efforts may be more effective if tailored to local vegetation characteristics associated with tree species composition. Future studies should examine how variation in understory vegetation characteristics contributes to patterns of warbler abundance and productivity. There is also need for manipulative experiments to directly examine warbler responses to forest management techniques (e.g., prescribed burning, thinning). Conducting this research across the geographic extent of the warbler’s breeding range is necessary if our goals are to fully understand the ecology of this species and to develop more effective site-specific warbler management and restoration strategies for this species of conservation concern.

LITERATURE CITED

Atuo, F. A. and S. A. Manu. 2013. Territory size and habitat selection of cinnamon breasted rock bunting *Emberiza tahapisi* in Nigeria. Ostrich 84:71-78.

Baccus J. T., M. E. Toller, 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.

Balda, R. P. 1969. Foliage use by birds of oak-juniper woodland and ponderosa pine forest in southeastern arizona. Condor 71:399-412.

Barber, D. R., T. E. Martin, M. A. Melchiors, R. E. Thill, and T. B. Wigley. 2001. Nesting success of birds in different silvicultural treatments in southeastern US pine forests. Conservation Biology 15:96-207.

Barg, J. J., J. Jones, and R. J. Robertson. 2005. Describing breeding territories of migratory passerines: Suggestions for sampling, choice of estimator, and delineation of core areas. Journal of Animal Ecology 74:139-149.

Beardmore, C. J. 1994. Habitat use of golden-cheeked warblers in Travis County, Texas. Thesis, Texas A&M University, College Station, Texas, USA.

Bersier, L., and D. Meyer. 1994. Bird assemblages in mosaic forests: the relative importance of vegetation structure and florisitic composition along the successional gradient. Acta Ecologica 15:561-576.

Betts, M. G, J. G. Forbes, and A. W. Diamond. 2007. Thresholds in songbird occurrence in relation to landscape structure. Conservation Biology 21:1046-1058.

Blake, J. G., and W. G. Hoppes. 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. Auk:328-340.

Block, W., and L. Brennan. 1993. The habitat concept in ornithology. Pages 35-91 *in* D. Power, editor. Current ornithology. Plenum Press, New York, New York.

Block, W. M., M. L. Morrison, J. Verner, and P. N. Manley. 1994. Assessing wildlife habitat relationships models - a case-study with california oak woodlands. Wildlife Society Bulletin 22:549-561.

Bohm, S. M., and E. K. V. Kalko. 2009. Patterns of resource use in an assemblage of birds in the canopy of a temperate alluvial forest. Journal of Ornithology 150:799-814.

Bock, C. E., and Z. F. Jones. 2004. Avian habitat evaluation: should counting birds count? Frontiers in Ecology and the Environment 2:403-410.

Bonebrake, T. C., J. Christensen, C. L. Boggs, and P. R. Ehrlich. 2010. Population decline assessment, historical baselines, and conservation. Conservation Letters 3:371-378.

Bonnot, T. W., J. J. Millspaugh, and M. A. Rumble. 2009. Multi-scale nest-site selection by black-backed woodpeckers in outbreaks of mountain pine beetles. Forest Ecology and Management 259:220-228.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference. Springer-Verlag, New York, New York.

Butcher, J. A., M. L. Morrison, J. Ransom, D., 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.

Campbell, L. 2003. Endangered and threatened animals of Texas: their life history and management. Texas Parks and Wildlife Department, Austin, USA.

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.

Carroll, M. J., P. D., J. W. Pearce-Higgins, and C. D. Thomas. Maintaining northern peatland ecosystems in a changing climate: effects of soil moisture, drainage and drain blocking on craneflies. Global Change Biology 17:2991-3001.

Catry, F. X., F. Moreira, E. Cardillo, and J. G. Pausas. 2012. Post-fire management of cork oak forests. Pages 195-222 *in* Post-Fire Management and Restoration of Southern European Forests. Springer, Netherlands.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215-244.

Chalfoun, A. D., M. J. Ratnaswamy, and F. R. Thompson. 2002. Songbird nest predators in forest-pasture edge and forest interior in a fragmented landscape. Ecological Applications 12:858-867.

Christoferson, L. L., and M. L. Morrison. 2001. Integrating methods to determine breeding and nesting status of 3 western songbirds. Wilson Society Bulletin 29:688-696.

Cody, M. L. 1981. Habitat selection in birds - the roles of vegetation structure, competitors, and productivity. Bioscience 31:107-113.

Collier, B. A. 2012. Avian kernel density. R package biRdkern, version 1.0.

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.

Danchin, E., T. Boulinier, and M. Massot. 1998. Conspecific reproductive success and breeding habitat selection: Implications for the study of coloniality. Ecology 79:2415-2428.

Danchin, E., L. A. Giraldeau, T. J. Valone, and R. H. Wagner. 2004. Public information: from nosy neighbors to cultural evolution. Science 305:487–491.

DeBoer, T. S., and D. D. Diamond. 2006. Predicting presence-absence of the endangered golden-cheeked warbler (*Dendroica chrysoparia*). Southwestern Naturalist 51:181-190.

Diamond, D. D. 1997. An old-growth definition for western juniper woodlands: Texas ash juniper dominated or codominated communities. U.S. Department of Agriculture, Forest Service, Southern Research Station. Report SRS-15.

Driscoll, M. J. L, T. Donovan, R. Mickey, A. Howard, and K. K. Fleming. 2005. Determinants of wood thrush nest success: a multi-scale, model selection approach. Journal of Wildlife Management 69:699-709.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65:169-175.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology Evolution and Systematics 34:487-515.

Farrell, S. L., M. L. Morrison, A. J. Campomizzi, and R. N. Wilkins. 2012. Conspecific cues and breeding habitat selection in an endangered woodland warbler. Journal of Animal Ecology 81:1056-1064.

Forsman, J. T., M. Monkkonen, P. Helle, and J. Inkeroinen. 1998. Heterospecific attraction and food resources in migrants' breeding patch selection in northern boreal forest. Oecologia 115:278-286.

Franzreb, K. E. 1978. Tree species used by birds in logged and un-logged mixed-coniferous forests. Wilson Bulletin 90:221-238.

Fretwell, S. D., and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16-36.

Griffith, G. E., S. A. Bryce, J. A. Comstock, A. C. Rogers, B. Harrison, S. L. Hatch, and D. Bezanson. 2004. Ecoregions of texas (color poster with map, descriptive text, and photographs) *in* U. S. G. Survey, editor., Reston, VA, USA.

Groce, J. E., H. A. Mathewson, M. L. Morrison, and R. N. Wilkins. 2010. Scientific evaluation for the 5-year status review of the golden-cheeked warbler. Texas A&M University, Institute of Renewable Natural Resources.

Haché, S., M. Villard, and E. M. Bayne. 2013. Experimental evidence for an ideal free distribution in a breeding population of a territorial songbird. Ecology 94:861-869.

Harris, S., W. J. Cresswell, P. G. Forde, W. J. Trewhella, T. Woollard, and S. Wray. 1990. Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. Mammal Review 20:97-123.

Heilbrun, R. D., N. Lake, A. Arnold, and D. Hisler. 2009. Habitat suitability model for evaluating City of San Antonio land donation for golden-cheeked warblers. Texas Parks & Wildlife Department PWD W7000-1685. Austin, TX, USA.

Hildén, O. 1965. Habitat selection in birds. Annales Zoologici Fennici 2:53-75.

Holmes, R. T., and S. K. Robinson. 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. Oecologia 48:31-35.

Huggett, A. J. 2005. The concept and utility of ‘ecological thresholds’ in biodiversity conservation. Biological Conservation 124:301–310.

Hutto, R. 1985. Habitat selection by nonbreeding, migratory land birds. Pages 455-476 *in* M. L. Cody, editor. Habitat selection in birds. Academic Press, San Diego, CA.

James, F. C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bulletin 83:215-236.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk 118:557-562.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Johnson, M. D. 2007. Measuring habitat quality: a review. Condor 109:489-504.

Keane, J. J., and M. L. Morrison. 1999. Temporal variation in resource use by black-throated gray warblers. Condor 101:67-75.

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.

Ladd, C., and L. Gass. 1999. Golden-cheeked Warbler (*Setophaga chrysoparia*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology.

Lundquist, R., and D. Manuwal. 1990. Seasonal differences in foraging habitat of cavity-nesting birds in the southern washington cascades. Studies in Avian Biology 13.

Magness, D. R., R. N. Wilkins, and S. J. Hejl. 2006. Quantitative relationships among golden-cheeked warbler occurrence and landscape size, composition, and structure. Wildlife Society Bulletin 34:473–479.

Marshall, M. R., and R. J. Cooper. 2004. Territory size of a migratory songbird in response to catapillar density and foliage structure. Ecology 85:432-445.

Marshall, M. E., M. L. Morrison, and R. N.Wilkins. Tree species composition and food availability affect productivity of an endangered species: the golden-cheeked warbler. Condor 115:882-892.

Martin, T. E. 1993. Nest predation and nest sites: new perspectives on old patterns. Bioscience 43:523-532.

Mathewson, H. A., J. E. Groce, T. M. Mcfarland, M. L. Morrison, J. 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.

Mazerolle, M. 2013. Model selection and multimodel inference based on (Q)AIC(c). R package AICcmodavg, version 1.35.

Moilanen, A., and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. Ecology 83:1131-1145.

Morrison, M. L., I. C. Timossi, K. A. With, and P. N. Manley. 1985. Use of tree species by forest birds during winter and summer. Journal of Wildlife Management 49:1098-1102.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 2006. Wildlife-habitat relationships: concepts and applications. 3rd edition. Island Press, Washington, D. C., USA.

Morse, D. H. 1978. Populations of bay-breasted and cape-may warblers during an outbreak of spruce budworm. Wilson Bulletin 90:404-413.

Nagy, L. R., and R. T. Holmes. 2004. Factors influencing fecundity in migratory songbirds: is nest predation the most important? Journal of Avian Biology 35:487-491.

Newton, I. 1998. Population limitation in birds. Academic Press, San Diego, California, USA.

National Oceanic and Atmospheric Association [NOAA]. 2014. National Climate Data Center Reports. <http://www.ncdc.noaa.gov/ >

Omernik, J. M. 1987. Ecoregions of the conterminous United States. Annals of the Association of American Geographers 77:118-125.

Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137:S29-S49.

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.

Petit, L. J., and D. R. Petit. 1996. Factors governing habitat selection by prothonotary warblers: field tests of the fretwell-lucas models. Ecological Monographs 66:367-387.

Pulich, W. M. 1976. The golden-cheeked warbler: a bioecological study. Austin, Texas, USA.

Radford J. Q., and A. F. Bennett. 2004. Thresholds in landscape parameters: occurrence of the white-browed treecreeper *Climacteris affinis* in Victoria, Australia. Biological Conservation 117:375-391.

R Core Development Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Reemts, C. M., C. Picinich, D. Cimprich, and R. G. Peak. 2008. Vegetation studies of black-capped vireo and golden-cheeked warbler habitat. Chapter 9 *in* Endangered species monitoring and management at Fort Hood, Texas: 2008 annual report. The Nature Conservancy, Fort Hood Project, Fort Hood, Texas, USA.

Reidy, J. L., F. R. Thompson, III., and R. G. Peak. 2009. Factors affecting golden-cheeked warbler nest survival in urban and rural landscapes. Journal of Wildlife Management 73:407-413.

Robinson, D. H. 2013. Effects of habitat characteristics on occupancy and productivity of a forest-dependent songbird in an urban landscape. Thesis, Texas A&M University, College Station, TX, USA.

Robinson, S. K., and R. T. Holmes. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. Ecology 63:1918-1931.

Rodenhouse, N. L., and R. T. Holmes. 1992. Results of experimental and natural food reductions for breeding black-throated blue warblers. Ecology 73:357-372.

Rotenberry, J. T. 1985. The role of habitat in avian community composition - physiognomy or floristics. Oecologia 67:213-217.

Silverman, B. W. 1986. Density estimation for statistics and data analysis. Chapman & Hall, New York, New York, USA.

Sisk, T. D., N. M. Haddad, and P. R. Ehrlich. 1997. Bird assemblages in patchy woodlands: Modeling the effects of edge and matrix habitats. Ecological Applications 7:1170-1180.

Smith, T. M., and H. H. Shugart. 1987. Territory size variation in the Ovenbird: the role of habitat structure. Ecology 68:695–704.

Staake, M. M. 2003. Golden-cheeked warbler nest predators and factors affecting nest predation. Thesis, University of Missouri, Columbia, Missouri, USA.

Stewart, L. R., M. L. Morrison, M. R. Hutchinson, D. N. Appel, and R. N. Wilkins. 2014. Effects of a forest pathogen on habitat selection and quality for the endangered golden-cheeked warbler. Wildlife Society Bulletin 38:279-287.

Strode, P. K. 2009. Spring tree species use by migrating yellow-rumped warblers in relation to phenology and food availability. Wilson Journal of Ornithology 121:457-468.

Stuen, O. H., and T. K. Spids. 1988. Invertebrate abundance in different forest habitats as animal food available to capercaillie *Tetrao urogallus* chicks. Scandinavian Journal of Forest Research 3:527-532.

Sugiura, N. 1978. Further analysts of the data by akaike's information criterion and the finite corrections: further analysts of the data by Akaike's. Communications in Statistics-Theory and Methods 7:13-26.

Svardson, G. 1949. Competition and habitat selection in birds. Oikos 1:157-174.

Tear, T. H., J. M. Scott, P. H. Hayward, and B. Griffith. 1995. Recovery plans and the Endangered Species Act: are criticisms supported by data? Conservation Biology 9:182–195.

Tilgar, V., R. Mänd, and A. Leivits. 1999. Effect of calcium availability and habitat quality on reproduction in Pied Flycatcher Ficedula hypoleuca and Great Tit Parus major. Journal of Avian Biology 30:383-391.

Thompson III, F. R., and E. K. Fritzell. 1989. Habitat use, home range, and survival of territorial male ruffed grouse. Journal of Wildlife Management 53:15-21.

Thompson, W. L., G. C. White, and C. Gowan. 1998. Basic concepts. Pages 1–43 *in* Monitoring vertebrate populations. Academic Press, San Diego, CA, USA.

Texas Parks and Wildlife Department [TPWD]. 1990. Golden-cheeked warbler. <http://www.tpwd.state.tx.us/publications/ pwdpubs/media/pwd_bk_w7000_0013_golden_cheeked_warbler.pdf>.

Texas Parks and Wildlife Department [TPWD]. 2012. Management guidelines for the golden-cheeked warbler in rural landscapes. <http://www.tpwd.state.tx.us/ publications/ pwdpubs /media/pwd_bk_w7000_0013_golden_cheeked _warbler_mgmt.pdf>.

Thériault, S., M. A. Villard, and S. Hache´. 2012. Habitat selection in site-faithful ovenbirds and recruits in the absence of experimental attraction. Behavioral Ecology 23:1289–1295.

Tremblay, J. P., E. J. Solberg, B. E. Sæther, and M. Heim. 2007. Fidelity to calving areas in moose (*Alces alces*) in the absence of natural predators. Canadian Journal of Zoology 85:902–908.

U.S. Fish and Wildlife Service [USFWS]. 1990. Endangered and threatened wildlife and plants; emergency rule to list the golden-cheeked warbler as endangered. Federal Register 55:18844-18845.

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

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Vickery, P. D., J. Hunter, M. L., and J. V. Wells. 1992. Use of a new reproductive index to evaluate relationship between habitat quality and breeding success. Auk 109:697-705.

Village, A. 1982. The home range and density of kestrels in relation to vole abundance. Journal of Animal Ecology 51:413-428.

Wahl, R., D. Diamond, and D. Shaw. 1990. The golden-cheeked warbler: a status review. Fort Worth, TX, USA.

Wiens, J. 1969. An approach to the study of ecological relationships among grassland birds. Ornithological Monographs 8:1-93.

With, K. A., and T. O. Crist. 1994. Critical thresholds in species' responses to landscape structure. Ecology 76:2446-2459.

Wolf, L. L., and F. R. Hainsworth. 1971. Time and energy budgets of territorial hummingbirds. Ecology 52:980-988.

Zar, J. H. 1999. Biostatistical analysis. Prentice-Hall, Upper Saddle River, NJ, USA.

APPENDIX A

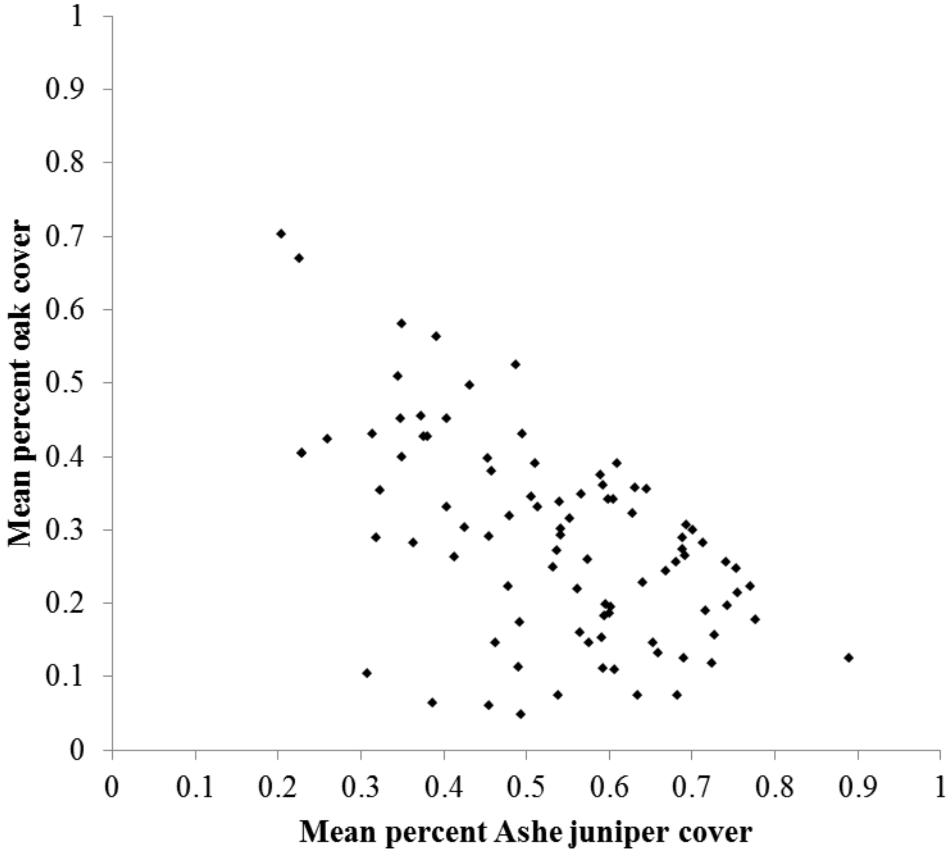

Figure 13. Statistically significant relationship ($F_{1,88}$ = 38.50, P < 0.01) between mean percent Ashe juniper cover and mean percent oak cover at 90 golden-cheeked warbler study sites located across the 3 largest Level-4 Ecoregions within the warbler's breeding range in central Texas, USA.

APPENDIX B

There were statistically significant ($P < 0.05$) correlations between the following variables included in *a priori* models for warbler territory size, pairing success, and fledging success ($n = 899$ territories as delineated by MCPs): Ecoregion and dominant oak species ($\chi_{12}^2 = 318.94$, $P \leq 0.01$), Ecoregion and mean Ashe juniper height ($F_{2,914} = 60.12$, $P \leq 0.01$), Ecoregion and variation in Ashe juniper height ($F_{2,914} = 27.71$, $P \leq 0.01$), mean percent Ashe juniper cover and mean Ashe juniper height ($\rho = 0.44$, $P \leq 0.01$), mean percent Ashe juniper cover and variation in Ashe juniper height ($\rho = -0.10$, $P \leq 0.01$), mean Ashe juniper height and variation in Ashe juniper height ($\rho = 0.37$, $P \leq 0.01$), dominant oak species and mean percent Ashe juniper cover ($F_{6,910} = 13.63$, $P \leq 0.01$), dominant oak species and mean Ashe juniper height ($F_{6,910} = 4.58$, $P \leq 0.01$), and dominant oak species and variation in Ashe juniper height ($F_{6,910} = 4.34$, $P \leq 0.01$). As such, these interaction models were excluded from analyses.

There were statistically significant ($P < 0.05$) correlations between the following variables included in *a priori* models for warbler core territory size, pairing success, and fledging success ($n = 486$ core territories as delineated by 50% kernel isopleths): Ecoregion and dominant oak species ($\chi_{12}^2 = 232.95$, $P \leq 0.01$), Ecoregion and mean percent Ashe juniper cover ($F_{2,511} = 8.75$, $P \leq 0.01$), Ecoregion and mean Ashe juniper height ($F_{2,511} = 6.19$, $P \leq 0.01$), Ecoregion and variation in Ashe juniper height ($F_{2,511} = 11.96$, $P \leq 0.01$), mean percent Ashe juniper cover and mean Ashe juniper height ($\rho = 0.44$, $P \leq 0.01$), mean percent Ashe juniper cover and variation in Ashe juniper height (ρ

$= -0.10$, $P \leq 0.01$), mean Ashe juniper height and variation in Ashe juniper height ($\rho = 0.25$, $P \leq 0.01$), and dominant oak species and mean percent Ashe juniper cover ($F_{6,507} = 13.27$, $P \leq 0.01$). As such, these interaction models were excluded from analyses.