AGE STRUCTURE OF GOLDEN-CHEEKED WARBLERS

IN AREAS OF LOW ABUNDANCE

A Thesis

by

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ABSTRACT

Understanding how habitat use and reproductive performance vary among age classes is important to understanding population structure and viability. Habitat conditions can affect occupancy and productivity of many songbirds, including golden-cheeked warblers (*Setophaga chrysoparia*). Thus, it is important to know which members of the population are using habitat of varying conditions. Existing demographic literature on golden-cheeked warblers focuses on populations where warblers occur in high abundance. I examined the age structure of golden-cheeked warblers in areas of low abundance to determine if there are patterns of differential habitat use based on age in this species. Over two breeding seasons, I monitored 13 low-density and 10 high-density study sites in central Texas for arrival dates and productivity. Males arrived to low density sites on average 6 days later (11 March) and those that established territories on those sites tended to be younger (62% Second-year, $n = 8$) than those males that established territories on high density sites (5 March, 32% SY, $n = 22$) although there were no differences in age structure by territory density. I aged 30 males on my study sites, 26 of which were territorial. Productivity did not vary between low and high-density sites; however, SY males had lower pairing and territory success than After Second-year (ASY) males. Understanding which portions of the warbler population are using patches of varying condition could lead to the detection of potential demographic drivers in habitat selection and could inform future management.

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INTRODUCTION

Migratory timing in birds is influenced by both age and sex and can subsequently influence reproductive success. Sex-based behavioral differences are common in many passerine species, for example, it is well documented that males migrate before females (Jones 1895; Lozano et al. 1996; Hopp et al. 1999; Swanson et al. 1999). Age-based behavioral differences are also supported by studies that suggest young males migrate later than older males, which may affect access to habitat (Francis and Cooke 1986; Stewart et al. 2002). Older birds also tend to exhibit higher reproductive success than their younger counterparts (Sæther 1990; Martin 1995; Lozano et al. 1996). Combined into a worst-case scenario, these differences could result in a proportion of the population that delays migration to the breeding grounds, only to end up in habitats where they have lower productivity.

Numerous studies have shown younger birds have decreased pairing and fledging success than older birds (Sæther 1990; Martin 1995; Lozano et al. 1996) and one possible explanation for this difference is delayed migration. Delayed migration of subadult males has been observed in many species (Francis and Cooke 1990; Lozano and Lemon 1999; Stewart et al. 2002) and has been explained in part by the following two hypotheses. The energetic constraint hypothesis posits that younger males delay migration as a result of interspecific competition on the wintering grounds. Young males are poor competitors and have limited access to food resources on the wintering grounds (Ekman 1990; Smith and Metcalfe 1997). As a result of their poor body condition they are not energetically able to migrate as early as their older (and better) competitors

(Marra et al. 1998; Stewart et al. 2002). The younger males and females also tend to migrate to the breeding grounds later when food resources are better (Francis and Cooke 1986; Stewart et al. 2002) suggesting that those individuals may delay migration to avoid potentially harsh springtime conditions. The second hypothesis, the reduced investment hypothesis, suggests that young males delay migration to the breeding grounds to avoid competition with established older males for breeding territories. Yearling males may have limited access to locations that have already been occupied by males that migrated earlier. Since second-year (SY) males typically migrate to breeding areas later than after second-year (ASY) males in most passerine species (Francis and Cooke 1986; Stewart et al. 2002) migration timing can have great effects on access to habitat at the beginning of the breeding season and subsequent reproductive success (Smith and Moore 2005). In a study on painted buntings (*Passerina ciris*) older males arrived to the breeding grounds earlier and occupied territories within higher quality habitat than the later-arriving young males (Lanyon and Thompson 1986). Also, those younger males that had established territories in higher quality habitat were later displaced by older males returning to territories they had occupied in previous years (Lanyon and Thompson 1986).

Older males may exclude younger males from habitats and force them into areas where they are less likely to attract females (Van Horne 1983; Breitwisch 1989; Sherry and Holmes 1989). Bayne (2000) found a higher proportion of SY male ovenbirds (*Seiurus aurocapillus*) than ASY males in relatively poorer, fragmented habitats lending strength to the theory that older males may prevent younger males from occupying habitat (Bayne 2000). This pattern also was observed at both local and landscape scales in black-throated blue warblers (*Setophaga caerulescens*, Holmes et al. 1996). Locally, it was observed that older male black-throated blue warblers typically produced more and higher quality young than SY males (Holmes et al. 1996). Additionally, the authors suggested that this was a result of older males establishing territories in higher quality habitat. Graves (1997) found that SY male black-throated blue warblers were found in proportionally higher abundance towards the margins of the breeding range implying that older males were saturating the high quality habitat and pushing the poor competitors to the fringes.

The golden-cheeked warbler (*Setophaga chrysoparia*, hereafter warbler) is a federally endangered insectivorous songbird that breeds exclusively in central Texas. Because warblers require the bark of mature Ashe juniper (*Juniperus ashei*) for nesting substrate, access to this bark is a limiting requirement for warblers (Pulich 1965; Ladd and Gass 1999). Warbler productivity is sensitive to habitat factors that determine breeding success. Marshall et al. (2013) showed that reproductive success varied with vegetation type. They examined food availability and tree species composition as the mechanism driving the differences in productivity. Small patches of habitat also typically have fewer birds in them and although warblers will pair in smaller patches, those males that do pair tend not to fledge young (Butcher et al. 2010). Research also suggests that warbler abundance increases with patch size (Coldren 1998; Baccus et al. 2007). Jette et al. (1998) found that SY male warblers may be less likely to pair than ASY males but once paired SY males were equally successful at fledging young as ASY males. Although it is well documented the occupancy and productivity of warblers are sensitive to habitat condition and patch size, little information exists regarding the potential demographic drivers of this discrepancy.

Studies regarding age structure of warbler populations have been conducted at locations within the warblers breeding range. One of the long-term study areas, the Fort Hood Military Reservation, hereafter Fort Hood, has been intensely monitored since 1992 (Peak and Thomas 2010). Of the territorial males identified in 2010, 27% were SY, 65% were ASY, and 8% were after hatch year (AHY); these numbers varied annually (Peak and Thomas 2010). Warbler abundance in this area is also high (96 territories/463 ha surveyed in 2010) and pairing success is typically ~90% each year (Peak and Thomas 2010).

Demographic information on warblers has also been collected in the Travis county area but for a more limited time period. Researchers for the City of Austin began banding on high-density sites in 2009 and expanded to include 18 study plots in 2013. In 2013 they were able to band 68% of the territorial males that they monitored across 18 sites of varying densities, averaging 35% SY, 64% ASY, and 1% AHY males (City of Austin [COA] 2013). The age structure varied across the sites such that the three sites with low densities of warblers (< 0.1 territory/ha) had a higher proportion of SY males than their higher density sites. The authors of this report suggested that this demographic relationship might indicate that something (perhaps habitat characteristics) may be influencing recruitment of young birds to sites. Overall pairing success across all sites was 87% in 2013 (consistent with previous years) and pairing success on the low density sites was similar albeit slightly lower (72%). Territory success, however, averaged 39% on the low-density sites compared to 72% on all sites combined (also similar to previous years' fledging estimates). To further examine demographics across a range of habitat conditions and qualities I included sites in both the Fort Hood area and the Travis county area.

I examined the proportion of the population that established territories in areas of predicted low abundance and compared these data with those collected in habitat predicted to have high abundance. It is important to determine what proportion of the warbler population is establishing territories in areas where there are few individuals and pairing success is lower because if warblers are using habitats differently according to age, this information could potentially alter the way we view habitat quality and manage warbler habitat.

A habitat model developed by Collier et al. (2012) assigned predicted patch occupancy values to all patches within the warbler's breeding range based on the associated patch size and landscape composition. According to the model, much of the identified potential habitat across the breeding range has low predicted occupancy. Using this and other previous studies, I selected study sites that I predicted to have high and low abundances of warblers, assuming that abundance is associated with habitat quality such that areas of high habitat quality will support more warblers (Marshall et al. 2013; Robinson 2013). I use the term "high quality" to describe habitats that have the conditions that lead to breeding success described in the *Methods: Site Selection* section below. By establishing the first date of arrival and the age structure of birds across my sites I was able to determine if younger birds established territories across a patch size gradient (i.e., equal proportion of younger and older birds on patches of various sizes) or if younger birds arrived, but did not establish territories, on larger patches. I then examined the age structure of male warblers in areas of low and high abundance to determine if there are patterns of differential habitat use based on age in warblers. I examined my predictions that study sites are of low or high habitat quality by determining pairing and reproductive success for all territorial males in sample units. Additionally, I examined my assumption that abundance is related to habitat quality. I did not expect to find a large effect size because I anticipated a limited sample size due to the difficulty of capturing warblers.

OBJECTIVES AND HYPOTHESES

Objective 1. Describe the age structure of male golden-cheeked warblers in areas predicted to have low golden-cheeked warbler abundance compared to areas predicted to have high warbler abundance.

Hypothesis 1. Older birds select areas that satisfy the conditions of high habitat quality, and thus high abundance, to establish territories and younger males are displaced to areas of relatively poorer conditions, and thus lower abundance.

Prediction 1. A higher proportion of SY males will occupy areas of low golden-cheeked warbler abundance than high abundance.

Objective 2. Compare the timing of golden-cheeked warbler arrivals in areas predicted to have low golden-cheeked warbler abundance with areas predicted to have high warbler abundance.

Hypothesis 2. Golden-cheeked warblers will establish territories in areas of varying abundance based on when they arrive to the breeding grounds.

Prediction 2. Areas of low golden-cheeked warbler abundance will be occupied later than areas of high abundance.

Objective 3. Examine the assumption that abundance of golden-cheeked warblers varies with habitat quality, defined by pairing success.

Hypothesis 3. Pairing success of golden-cheeked warblers is higher in areas of high abundance than areas of low abundance.

Prediction 3. A higher proportion of males will pair in areas of high golden-cheeked warbler abundance than low-abundance areas.

Objective 4. Describe the age structure of male golden-cheeked warblers that successfully pair in areas predicted to have low golden-cheeked warbler abundance compared to areas predicted to have high warbler abundance.

Hypothesis 4. Older males experience an advantage over young males regarding pairing success in areas of low warbler abundance.

Prediction 4a. A higher proportion of ASY males will pair than SY males in areas of low golden-cheeked warbler abundance.

Prediction 4b. A higher proportion of SY males will successfully pair in areas of high abundance than low abundance.

Objective 5. Describe the age structure of male golden-cheeked warblers that successfully reproduce (fledge young) in areas predicted to have low golden-cheeked warbler abundance compared to areas predicted to have high warbler abundance.

Hypothesis 5. Older males experience an advantage regarding reproductive success in areas of low warbler abundance.

Prediction 5a. A higher proportion of ASY males will successfully fledge young than SY males in areas of low abundance.

Prediction 5b. A higher proportion of SY males will successfully fledge young in areas of high abundance than low abundance.

METHODS

Study Area

I conducted my study in east-central Texas along the eastern portion of the golden-cheeked Warbler breeding range. In 2012 I located sites (see below) in Bell County, within the Cross Timbers and Prairies ecoregion, an area characterized by limestone-capped buttes and mesas interspersed with grassland savannahs and woodland (Butler 2014). Common species in these woodlands are Ashe juniper, Texas oak (*Quercus buckleyi*), live oak (*Q. virginiana*), and other various hardwoods (Hatch 2014). Mean temperatures during the breeding season (March-June) typically range from 14.8-26.7° C, and cumulative precipitation during this time averages 31.2 cm (NOAA 2014).

During the second year (2013) of my study, I located sites in Travis and Hays counties, TX, within the Edwards Plateau ecoregion, an area characterized by steep limestone hills and woodlands (Fig. 1). Woody vegetation on the Edwards Plateau is dominated by Ashe juniper, live oak, shin oak (*Q. sinuata*), and mesquite (*Prosopis glandulosa*) (Hatch 2014). During the breeding season mean temperatures in this region typically range from 15.2-26.3° C and precipitation totals 36.3 cm on average (NOAA 2014).

I selected different sites each year to increase the number of total study sites surveyed and decrease the influence of confounding patch-specific covariates not measured, such as vegetation variation, or predator assemblage. By surveying sites that encompass a broad spectrum of variables, I could potentially observe a wider range of responses from the warblers. I also spaced sites across two different portions of the warblers range to further limit covariates.

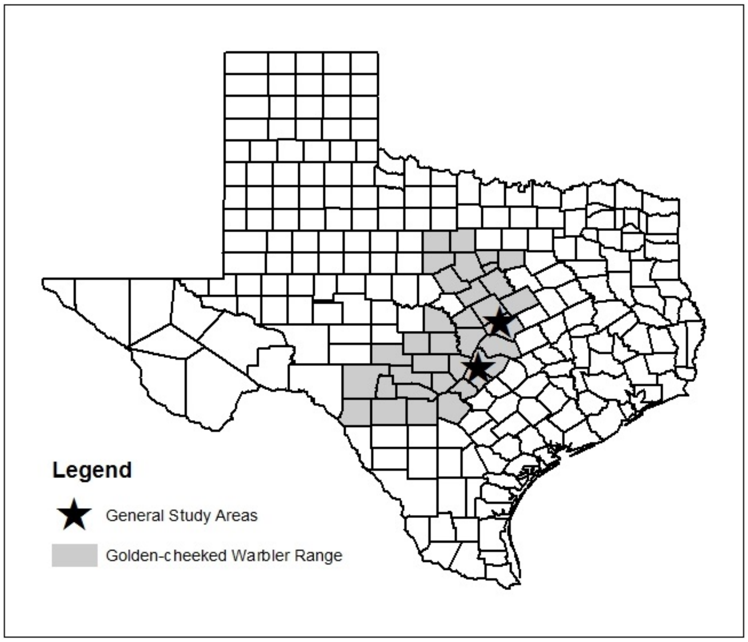

Figure 1. Golden-cheeked warbler breeding range by county in central Texas, USA (2012-2013).

Site Selection

Breeding warblers are predominantly found in oak-juniper woodlands (Wahl et al. 1990; Groce et al. 2010) so I first located habitat patches in my study areas that were dominated by this vegetation type using the predictive habitat model described in (Wahl et al. 1990; Groce et al. 2010); Collier et al. (2012). Baccus et al. (2007) found positive relationships associated with patch size and abundance, pairing success, and fledging success on Fort Hood; however, warblers were not territorial in patches smaller than

10.5 ha. Butcher et al. (2010) found that warblers exhibit a minimum patch size productivity threshold around 20 ha in such a way that warblers will not fledge young below this patch size. Thus, indicating that patch size can be a limiting factor to warbler occupancy and productivity. Proximity to occupied patches can also influence whether a patch is occupied or not; warblers are more likely to establish territories near other males and small patches are more likely to be occupied if they are close to larger occupied patches (U. S. Fish and Wildlife Service [USFWS] 1996; Peterson 2001; The Nature Conservancy [TNC] 2002; Campomizzi et al. 2008; Farrell et al. 2012; Mathewson et al. 2012). The approximate distance at which songs can be heard by conspecifics is 250m so I selected patches that were at least 250 m from a patch > 200 ha to limit potential influences of conspecific attraction (Naguib 1996; Forman 2000; Farrell et al. 2012).

Because I shifted study areas between the two years of my study, I used characteristics that had been identified as influencing warbler productivity in those regions to identify potential study sites. In some instances, I did not survey the entire patch due to logistical constraints or sampling frame so I use the term "study site" to indicate the surveyed area within a patch. I located study sites in the first year of my study in Bell County, Texas. In this portion of the warbler's range Marshall et al. (2013) indicated that ecosite is a predictor of warbler productivity. Namely, those territories on Low Stony Hill ecosites had up to 30% higher productivity than territories established on Redlands ecosites. I used this habitat characteristic in 2012, in addition to the above stated patch characteristics, to select habitat patches where I would expect to find desired target abundances. In 2013, I located study sites in Travis and Hays counties, Texas.

Ecosite in these counties is less discrete than in Bell County so I used information on the presence and abundance of male warblers detected during previous studies (Pruett et al. 2013; Robinson 2013) to select patches I predicted would have varying abundances.

Low Abundance Sites: To select sites in 2012 with predicted low abundances, I used the predictive habitat model described in Collier et al. (2012) and information on ecosite from Natural Resource Conservation Service (NRCS) to locate patches occurring on targeted ecosite layers in ArcGIS 9.3 (ESRI 2012). In addition to identifying patches of oak-juniper woodland, the Collier et al. (2012) model ascribes each patch a probability of occupancy based on patch characteristics such as patch size and landscape composition. I identified all patches 20-100 ha that occurred on the Redlands ecosite and that had a predicted occupancy of at least 0.60 according to the Collier et al. (2012) model. I chose a minimum predicted occupancy of 0.60 because I wanted to limit my surveys to patches where warblers would likely occur but not necessarily occur in high numbers. I also limited my selection process to patches that were at least 250 m from a patch > 200 ha to limit the influence of conspecific attraction (Farrell et al. 2012). From these criteria, I identified ten possible study sites and I received permission to access four of those sites.

To select sites with predicted low abundances in 2013 I first identified patches of oak-juniper woodland that had been occupied by golden-cheeked warblers as determined by surveys conducted in previous years. I selected those patches that that were 20-100 ha in size and separated from patches > 200ha by at least 250 m. I identified 12 predicted low abundance sites across the two counties in 2013 and surveyed nine of them.

High Abundance Sites: There are often a large number of birds within large contiguous habitat patches. To sample patches with a high predicted abundance I established study plots within large warbler habitat patches (> 1000 ha) that I expected to be of high habitat quality. The size of each study plot was equal to the average size of the surveyed predicted low abundance plots for that year. To maximize factors affecting habitat quality I placed the plots ≥100m away from the edge of the patch because warblers are sensitive to edge effects (Peak 2007). I also placed the plots ≥ 250m apart to limit interactions between the study plots.

In 2012, using ecosite as a selection characteristic, I delineated four plots (81 ha) within large (> 1,000 ha) Low Stony Hill patches on Fort Hood. In 2013, I delineated seven predicted high abundance study plots (36 ha) within Barton Creek Habitat Preserve (> 1,600 ha), an area that has historically been of high habitat quality (Lopez et al. 2012). Warbler populations on both Fort Hood and Barton Creek Habitat Preserve had been monitored for at least three years prior to the start of my study and are sites with consistently high numbers of breeding warblers (Marshall et al. 2013; Pruett et al. 2013).

Occupancy and Arrival Date

To determine arrival date of warblers, trained observers surveyed each study site daily. The earliest documented arrival date was 28 Feb on Fort Hood so observers began surveys starting in the last week of February (Groce et al. 2010). Observers started surveys 29 February 2012, and 25 February 2013 by walking parallel transects spaced

~150 m apart through suitable habitat. Observers recorded the date that a warbler was first detected within the study site and ceased daily surveys after initial detection. We continued to survey sites every 5-7 days to locate individual warblers for banding attempts as well as territory mapping (see description of methods below). I described the site as occupied based on the presence of at least one male within the site detected during surveys. I considered the site unoccupied if a warbler was not detected after one month of daily surveys.

Banding

I began target netting male warblers upon initial detection of a warbler in a study site using a combination of territorial songs to attract males into the net. I rotated banding efforts between all occupied sites and ensured that all banding activities were conducted according to the North American Banding Council guidelines (TNABC 2001) . I attempted to capture individuals in each territory for no more than 30 minutes per territory as specified by USFWS permit regulations. I banded all birds with a USGS aluminum band and up to three colored plastic bands. Unique band color combinations facilitate identification of birds throughout the season and band combinations were coordinated through the research group at Fort Hood. I aged individuals in hand using plumage characteristics described by Pyle (1997). I continued banding until I had marked all birds in each study site or until 1 June when pre-basic molting begins. In high abundance survey plots that included partial territories, I attempted to band only territories that were > 50% within the plot.

Field-observed Aging

Due to the difficulty of mist netting all territorial warblers within my study sites, I implemented an experimental aging technique whereby experienced observers conducted extensive visual field observations of territorial warblers through binoculars to determine the age of the bird without the need to observe the bird in-hand. Observers aged adult male warblers to the following three age categories: second-year (SY), after second-year (ASY), or after hatch year (AHY). We used the AHY category only if observers were unable to determine a finer-scale age. Using binoculars, observers recorded observations of the warbler's chin and throat, cap and eyeline, and the outer rectrices. Observers then compared the bird's specific coloration to plumage criteria to age the individual (Table 1).

Table 1. Plumage criteria used to age adult male golden-cheeked warblers based on a visual assessment through binoculars on study sites in central Texas, USA (2012-2013).

	Second-Year (SY)	After Second-Year (ASY)
Chin and throat color	Chin white to yellowish with black mottling or black with light yellow mottling	Chin and throat all black with very little yellow mottling in spring
Cap color and eyeline	Cap is black with a green wash; eyeline olive with some black flecking	Cap and eyeline are completely black
Outer rectrix color and shape	Relatively abraded and tapered, dusky with little white (average more white in male)	Fresh and truncated, dusky with moderate amount of white (more white in male)

Each of the three locations was scored a value 1-4:

1. Plumage displays SY characteristics.
2. Adult plumage evident, but observer is unable to distinguish between SY and ASY criteria (i.e. not definitively one or the other).
3. Plumage displays ASY characteristics.
4. Unable to see the region (because the bird is obstructed from view), or observer is only able to get a brief, insufficient look.

I designated birds as SYs if one or more locations was scored as a "1" and if scores from multiple observations were not conflicting or ambiguous. I designated birds to be ASYs if one or more locations was scored as a "3" and if scores were not conflicting or ambiguous. If the observer recorded conflicting aging criteria for two or more locations, I recorded the bird as AHY for that visit. Observers attempted aging on all territorial males until 1 June when pre-basic molt begins (Pyle 1997). I implemented this protocol starting 1 May 2012 and throughout the 2013 field season. Observers also collected field-observed aging data on 3 banded and 30 unbanded males at Balcones National Wildlife Refuge in 2013.

Abundance Estimate

To support my assumption that abundance is related to habitat quality, I first needed to establish that the habitat characteristics I used to select sites in 2012 influence productivity. I did so by examining overall productivity on each of my sites; this established my measure of quality since "quality" refers to the reproductive success of the species. I then related that measure of quality to the abundance of warblers on each site. I determined the number of birds in each of my study plots (estimated abundance in 2012, exact abundance in 2013) and related that to productivity estimates for each study site.

In 2012, I conducted four single-observer point counts over a four-week period. I evenly distributed point count stations across each of the study sites so they were ≥350 m apart and at least 100 m from the edge of the patch (Collier et al. 2010). I did not conduct point counts in 2013 because I was able to count (and monitor) all males in each of my study plots making estimates of abundance unnecessary. I mapped and monitored territories at each study site (see *Territory Mapping* and *Productivity Estimate* below) to determine breeding status and then examined the overall productivity of each study site type.

Territory Mapping

I began territory mapping in mid-March once behavioral observations indicated that males were establishing territories. Trained observers visited each territory ≥6 times (MacKenzie and Royle 2005; Collier et al. 2010), with 7-10 days between each visit. In 2012, I monitored all males identified in all low abundance study sites and subsampled territories in my high abundance study sites due to logistical constraints. I randomly selected a quarter of the total number of territories identified during transect surveys in each of my high abundance sites to monitor. In 2013, I elected to monitor all males identified on all study sites. For each of the monitored territories, observers collected spatial data to delineate territories using a spot-mapping approach. Once observers located the warbler, he or she recorded the GPS location of the bird every two minutes for as long as visual contact was maintained for a maximum of 30 minutes. I considered locations that remained occupied for > 4 weeks to be established territories (Vickery et al. 1992). I ceased mapping when ≥ 1 fledgling was observed with an adult in the territory because this event signals the disintegration of territory boundaries.

Productivity Estimate

In conjunction with territory mapping I conducted surveys to determine the reproductive status of the territory using the methods described by Vickery et al. (1992). This method uses male and female behavioral cues to infer the pairing and reproductive status of the territory and also limits disturbance of nests of endangered species (Maas 1998; Christopherson and Morrison 2001). This method has been used in previous studies to accurately predict reproductive status of songbirds (Christopherson and Morrison 2001; Butcher et al. 2010; Marshall et al. 2013). I also opportunistically searched for nests in each territory to supplement these behavioral observations.

I described a male as paired if I observed a female with the male within an established territory or if I observed evidence of nest building (i.e., food carry or nest material carry by either sex). I confirmed territory boundaries of male warblers through repeated observations of color-banded birds. I determined success of the territory based on the observation of ≥1 fledgling within the territory at least once. Productivity definitions are from Vickery et al. (1992). I assigned each territory a rank based on predicted reproductive status as follows: (1) occupancy; (2) territory formation; (3) evidence of nest building; (4) evidence of nestlings; (5) evidence of fledglings.

Data Analysis

For analyses I analyzed both 2012 and 2013 together because I assumed that if a pattern of differential sorting by age existed then it would be evident regardless of temporal or spatial variations between the two study areas. Also, although weather patterns varied from historical weather patterns for the study areas they did not occur outside the normal range of conditions. I used Fisher's exact test to test for a difference between the observed proportion of SY to ASY males in each predicted habitat quality category and the expected proportion of equal likelihood in each category (Zar 1999: 543-555) . I used Fisher's exact test over chi-square analyses because it works better with low sample sizes, and because it calculates an exact p-value rather than an approximate p-value as would result from a chi-square analysis.

I determined whether I could incorporate data from my field-observed aging first by examining visual ages ascribed to birds of known age. This category included only those birds that were aged in-hand during banding. I determined whether this visual aging method worked for golden-cheeked warblers by calculating the proportion of correct field-based observations for each age category (SY/ASY) of known aged birds. If male warblers were correctly aged 75% of the time, I would then incorporate field-observed ages into further analyses with birds of known ages.

I used a *t*-test to compare the mean arrival dates in sites predicted to have high abundance and sites predicted to have low abundance (Zar 1999:122-129). I converted all calendar dates to Julian dates for comparison. I did not examine age or sex of the first arrivers to study sites because it was logistically unfeasible to age every bird as it arrived and I did not have information on individual birds beforehand. I have no information on arrival date of females because all initial detections were aural and therefore male warblers.

To test my assumption that abundance varies with predicted habitat quality, I calculated the density of male warblers at each point count location across the 2012 season by dividing the number of birds observed per visit by the area of the point count survey (3.14 ha or a 100m radius circle). I then averaged the density of each point count location within the study site to determine the estimated density of the site. I determined an estimated abundance at each of my study sites by multiplying this number by the total area of the site. I analyzed my measures of abundance separately by year since the data are not directly comparable; 2012 being an estimate of abundance and 2013 being an absolute measure. In 2013, I calculated the site abundance by identifying all territorial males observed at each site. I established habitat quality for both years by determining pairing success of each territorial male and the overall territory success of each site including both banded and unbanded warblers. I calculated pairing success but dividing the number of territorial males observed with a female by the total number of territories at that site. Territory success was calculated by dividing the number of territories that fledged young by the total number of territories at that site. I compared the mean territory density in low versus high quality habitat using a *t*-test (Zar 1999:122-129). This test compared the mean territory densities of each predicted habitat quality.

To compare measures of productivity between high and low abundance areas, I conducted analyses using Fisher's exact test examining the influence of age (SY or ASY) on pairing success and fledging success for each of the monitored territories (Zar 1999:543-555). I compared the observed number of SY males and ASY males that paired (or fledged young) to expected values of equal likelihood of pairing (or fledging young) regardless of age.

Finally, I developed *a priori* models using variables I hypothesized could influence pairing and reproductive success. I included bird age because research suggests that older males have higher productivity. Large patches have also been shown to have higher reproductive success than small patches so I included patch size in my models. Because I conducted my study in different study areas each year, I included year as my final variable as a way to examine regional variation between study sites. I used a generalized linear model approach and Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Akaike 1973) to evaluate candidate models for reproductive success. I considered models with $\Delta AIC_c < 2$ to be competitive models (Burnham and Anderson 2002). I used the AIC_w to indicate the strength of each model given the set of candidate models. I constructed 6 models examining the main effects of bird age, patch size, and variation between study years as well as the additive combinations of those variables on pairing and territory success (table on p. 35). Because patch size and year were correlated, I did not include the additive model of those variables in my model evaluation. I set $\alpha = 0.05$ and ran all analyses in R statistical software (R Core Team 2013).

RESULTS

Weather Analyses

Temperatures in 2012 were on average 3.4° warmer, ranging from 19-29.4° C (NOAA 2014; Fig. 2) . In 2012, precipitation in March (20.5 cm) was 3 times higher than the average rainfall (5.1 cm) for that month over the past 67 years, and April was drier than observed in historical records (NOAA 2014, Fig. 3). Overall, this area received an additional 8 cm of rain during the 2012 breeding season than historic averages during these months (NOAA 2014). In 2013, temperatures were 1.6° C warmer than previously observed averages (17.2-29.7° C; Figure 2); however, precipitation in 2013 was much less than expected for the region, averaged only 28.8 cm during the breeding season 8.1 cm below average (NOAA 2014; Fig. 3).

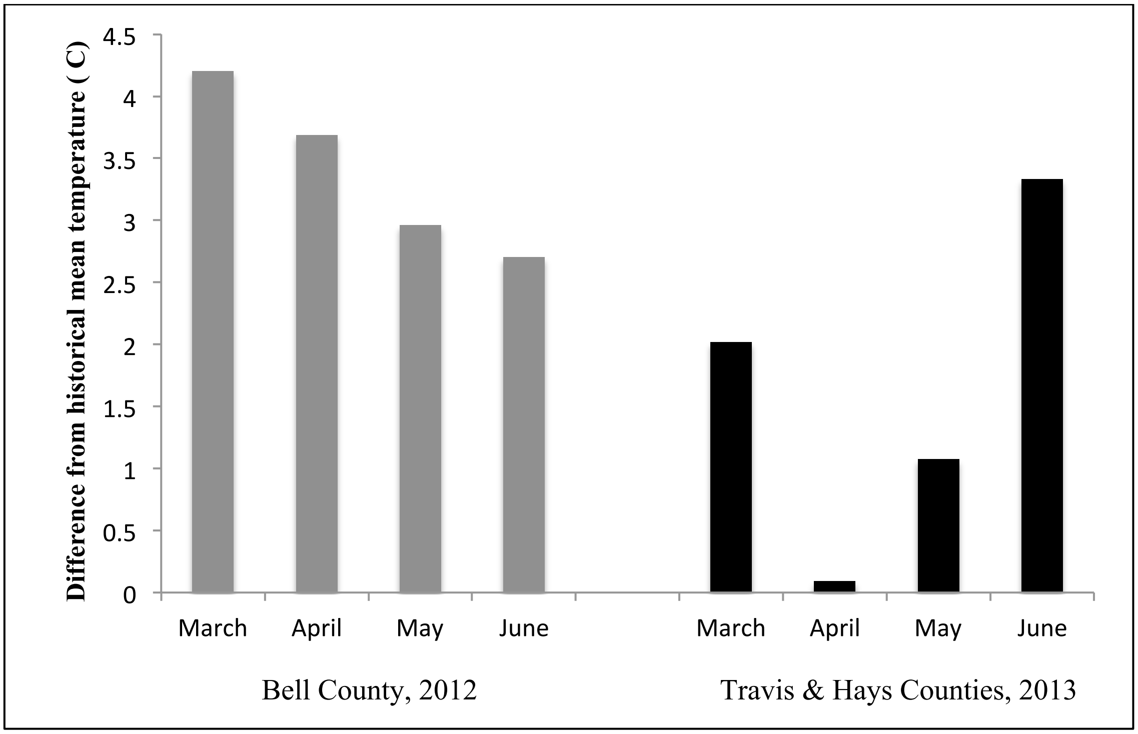

Figure 2. Differences in breeding season temperatures from the historical mean by month for two study regions in central Texas, USA (2012-2013).

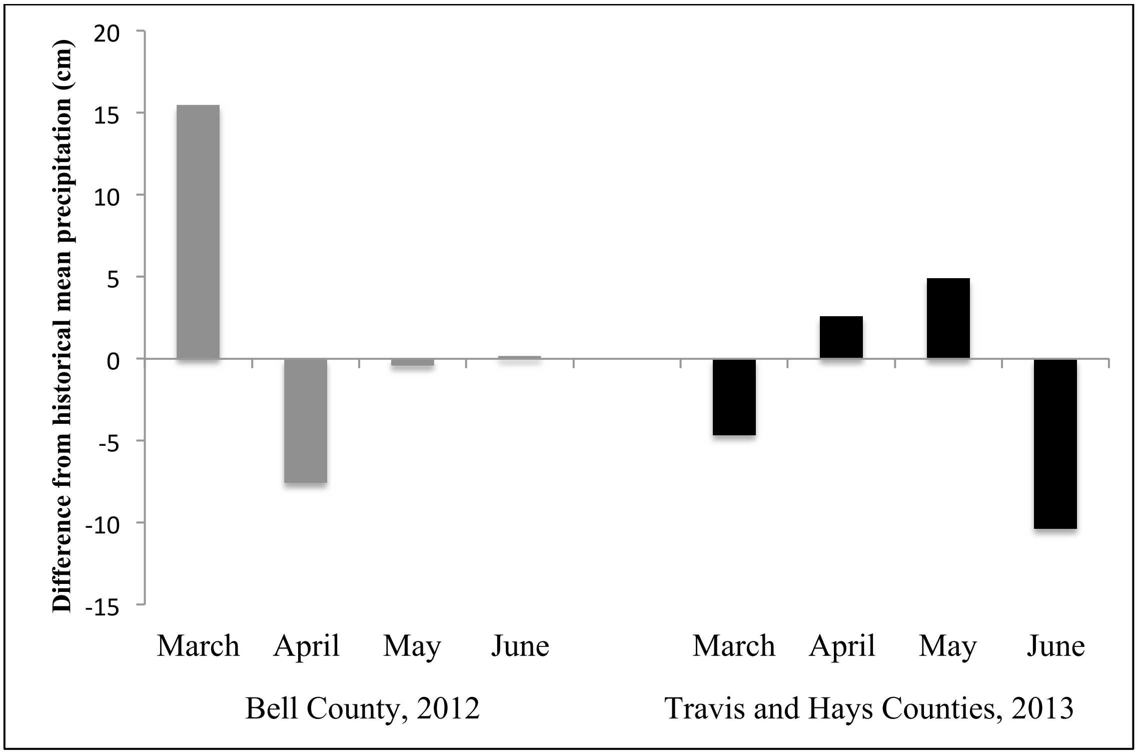

Figure 3. Differences in breeding season precipitation (cm) from the historical mean for two study regions in central Texas, USA (2012-2013).

Site Selection

In 2012, my site selection criteria accurately identified sites with various abundances; however, 3 of my predicted low abundance sites did not have territorial warblers. In 2013, although my criteria resulted in sites of various abundances they were not good predictors of abundance. Three of the seven predicted high abundance plots exhibited low abundances of birds (< 5 territories), and two sites I expected to have low abundances exhibited high abundances. I subsequently categorized sites as high or low abundance site based on their actual abundance rather than the abundance I had predicted. I surveyed a total of 10 predicted high abundance sites, and 13 predicted low abundance sites across both years.

Aging

I aged and banded 18 male warblers as ASY (7 in 2012/11 in 2013; Table 2), and 12 male warblers as SY (7 in 2012, 5 in 2013). I caught most birds (73%, n = 30) on sites with high abundances and the remaining birds on low abundance sites. There was no significant difference in the proportion of SY to ASY males among sites of differing abundances (P = 0.21).

Table 2. Age distribution of banded male golden-cheeked warblers in predicted low and high abundance survey plots in central Texas, USA (2012-2013).

	Low Abundance (n = 8)		High Abundance (n = 22)	
	SY	ASY	SY	ASY
2012 (n = 14)	3	0	4	7
2013 (n = 16)	2	3	3	8

Field-observed Aging

I tested my field-observed aging protocol on 22 banded male warblers field-aged 1 - 4 times (46 total observations recorded). I separated my accuracy analyses into 2 categories: observations made before banding (n = 20), and observations made after banding (n = 26) to examine the possibility of biased observations. Before banding, observers aged 12 males and documented a total of 20 observations. Observers correctly aged the warbler only half of the time (11 out of 20 aging attempts). In nine instances, the observer incorrectly aged the bird, either recording a SY male as an ASY (n = 5) or, in four cases, the observer saw only enough of the bird to call it an AHY. Males aged using the field-observation method after banding showed a similar pattern of accuracy. Observers correctly aged the male 18 times, and the 8 incorrect observations were a result of 4 birds identified only to AHY and 4 observations of SY males incorrectly identified as ASYs.

Because the data show similar trends of inaccuracy regardless of when the bird was field-aged relative to banding, I combined all observations into a single group. Within this group, trained observers correctly aged the male 63% of the time (n = 46) and observers correctly identified SY males in three instances. Of the incorrect aging attempts, SY birds were incorrectly identified as ASY eight times and in nine instances the bird was aged only to AHY (Table 3).

Table 3. Accuracy of experimental aging observations of adult male golden-cheeked warblers. Second-year warblers were more frequently aged incorrectly regardless of field-aging observation relative to banding date at survey plots in central Texas, USA (2012-2013).

		Correct[1]		Incorrect[1]		Total
		n	(%)	*n*	(%)	*n*
	Pre	9	69	4	31	13
ASY	Post	17	89	2	11	19
	Total	26	81	6	19	32
	Pre	2	29	5	71	7
SY	Post	1	14	6	86	7
	Total	3	21	11	79	14
Combined	Total	29	63	17	37	46

[1] Correctness based on observation relative to the bird age as determined at time of banding in-hand.

Arrival Date

I detected warblers on 20 of the 23 study sites I surveyed. On average, warblers arrived to high abundance study sites on 5 March and to low abundance sites on 11 March. In both years, observers detected warblers on high abundance sites before they were detected on low abundance sites (2 March 2012, 28 Feb. 2013). Observers first detected warblers on low abundance sites on 7 March 2012 and 6 March 2013. Warblers arrived to high abundance plots on average six days earlier than low abundance plots; this difference was significant (t = 3.96, df = 16.43, P = 0.001; Fig. 4).

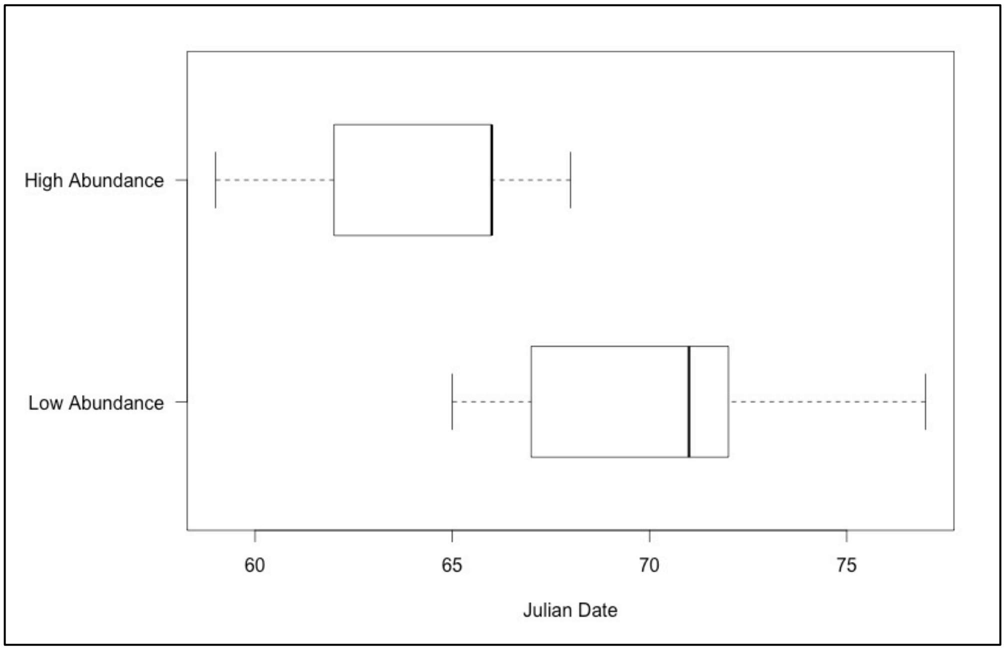

Figure 4. Mean arrival dates of golden-cheeked warblers to sites of high and low abundances. Warblers arrived to high abundance study plots 6 days earlier than low abundance study plots in central Texas, USA (2012-2013).

Abundance Estimate

In 2012, estimated abundances at study sites I predicted to be high ranged from 24-37 male warblers (Fig. 5). Estimated abundances at low abundance sites were between 0 and 4 warblers. Two sites with zero warblers remained unoccupied for the duration of the season and warblers were detected on a third site although they did not establish territories. Only one low-abundance site supported territorial warblers. Mean estimated territory density in 2012 was 95% higher on predicted high abundance plots ($\bar{x}$ = 0.37 territories/ha) than low abundance plots ($\bar{x}$ = 0.02 territories/ha; t = 8.74, df = 4.73, P < 0.001). In 2013, absolute abundances at high abundance sites ranged from five to seven warbler territories, and low abundance sites ranged from zero to four territories

(Fig. 6). Mean territory density in 2013 was 71% higher on predicted high abundance sites ($\bar{x}$ = 0.17 territories/ha) than predicted low abundance sites ($\bar{x}$ = 0.05 territories/ha; t = 7.65, df = 12.14, P < 0.001).

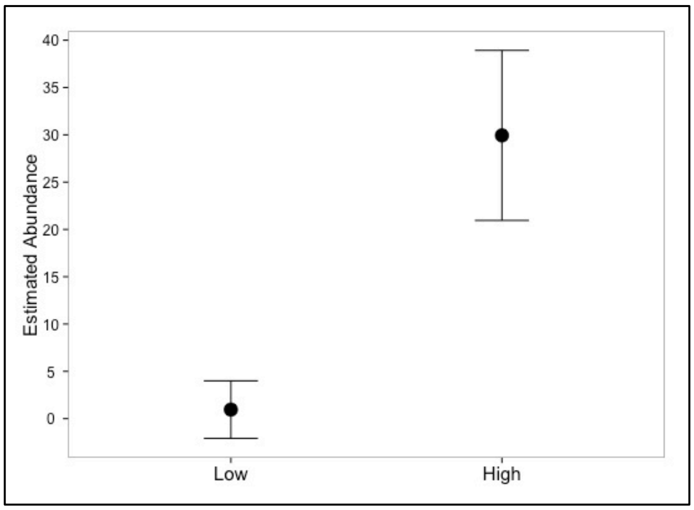

Figure 5. Estimated mean abundance and 95% Confidence Intervals of territorial male golden-cheeked warblers on survey plots of varying abundance (n = 8) in central Texas, USA. Data were collected during 4 single-observer point counts conducted during the month of April 2012.

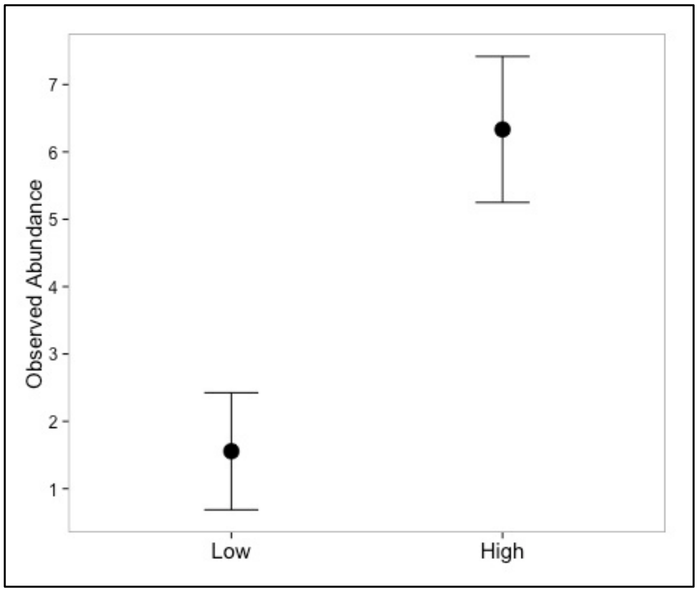

Figure 6. Mean abundance and 95% Confidence Intervals of territorial male golden-cheeked warblers at predicted high and low abundance study plots (n = 14) in central Texas in 2013.

Productivity Estimate

I monitored 86 warbler territories across 19 study plots. Seventeen territories were established on predicted low abundance sites and 69 territories were established on predicted high abundance sites (Table 4). Overall productivity was not significantly different between predicted high and low sites in regards to pairing success (P = 0.21, Table 4) or fledging success (P = 1.0).

Table 4. Pairing and fledging success of territorial male golden-cheeked warblers at 20 predicted high and low abundance survey plots in central Texas, USA (2012-2013).

	Monitored Territories	Pairing Success		Territory Success[1]	
	n	*n*	(%)	*n*	(%)
Low	17	11	65	10	59
High	69	55	80	41	59
Total	86	66	77	51	59

[1] Territory success is calculated out of total number of monitored territories.

Of the 86 territories I monitored, I determined ages for 26 territorial males when I banded them. When I evaluated productivity of only those territories with males of known age, there was a significant difference in the proportion of territories that paired among age classes (P = 0.028; Table 5) as well as in territory success based on age (P = 0.038).

Table 5. Pairing and fledging success of banded territorial male golden-cheeked warblers. Second-year territorial males were less likely to pair than ASY males at survey plots in central Texas, USA (2012-2013).

	Monitored Territories	Pairing Success		Territory Success[1]	
	n	*n*	(%)	*n*	(%)
SY	9	4	44	2	22
ASY	17	15	88	12	71
Total	26	19	73	14	54

[1] Territory success is calculated out of total number of monitored territories.

Of the 26 aged territorial males, I further examined productivity by predicted abundance categories (Table 6, Fig. 7). None of the SY males (*n* = 4, Fig. 7) on low abundance sites paired, all ASY males (*n* = 3) on those sites paired, and two of the three ASY males that paired on low abundance sites fledged young. Pairing success was much higher for SY males (80%, *n* = 5) on sites with high abundance but only two of those territories fledged young (40%, *n* = 5). Eighty-six percent of ASY males (*n* = 14) paired on high abundance sites and 71% of those males fledged young (*n* = 14).

Table 6. Pairing and fledging success of territorial male golden-cheeked warblers of known age split by site type at survey plots in central Texas, USA (2012 - 2013). ASY males on low abundance plots were more likely to pair than SY males on the same plots. SY males were more likely to pair and fledge on high abundance plots.

		Monitored Territories	Pairing Success		Territory Success[1]	
		n	*n*	(%)	*n*	(%)
Low Abundance	SY	4	0	0	0	0
	ASY	3	3	100	2	67
High Abundance	SY	5	4	80	2	40
	ASY	14	12	86	10	71

[1] Territory success is calculated out of total number of monitored territories.

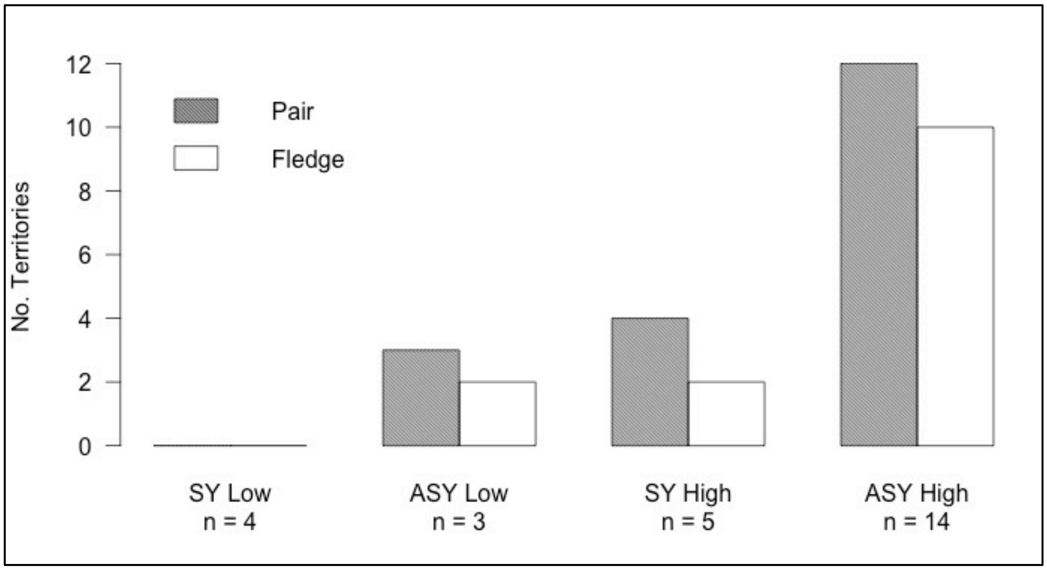

Figure 7. Pairing and fledging success of territorial male golden-cheeked warblers of known age split by site type at survey plots in central Texas, USA (2012-2013). ASY males on low abundance plots were more likely to pair than SY males on the same plots. SY males were more likely to pair and fledge on high abundance plots.

Generalized Linear Modeling

There were two best-fit models for pairing success occurring within 2 ΔAIC_c of the top model: the main effect of bird age, and the additive model of age and patch size (Table 7). A significant amount of variation in the additive model was accounted for by age so I considered the most parsimonious of the models, the main effect model of age, to be my best-fit model. There was a similar trend in the models for territory success. The top models for territory success included the additive models of age with patch size and year, as well as the main effect of age (Table 7). The top model for territory success was the additive model of age and patch size, which indicates that patch size influences territory success, however, the age variable was consistent in all of the models within 2

ΔAIC_c of the top model. Although age has a strong influence over territory success, the additional variables of patch size and year also predict territory success.

Table 7. Candidate models for pairing success, and territory success for 26 golden-cheeked warbler territories monitored on 15 study plots located within the breeding range of the golden-cheeked warbler in central Texas, USA (2012-2013).

Response	**Model**[1]	***K***[2]	**Log likelihood**	**AIC_c**[3]	**ΔAIC_c**[4]	**w_i**[5]
Pairing						
	Age	2	-12.34	29.2	0	0.47
	Age + Patch Size	3	-11.9	30.88	1.68	0.2
	Age + Year	3	-12.34	31.77	2.56	0.13
	Constant	1	-15.14	32.46	3.25	0.09
	Patch Size	2	-14.32	33.17	3.96	0.07
	Year	2	-15.11	34.73	5.53	0.03
Territory						
	Age + Patch Size	3	-12.97	33.04	0	0.4
	Age + Year	3	-13.44	33.98	0.94	0.25
	Age	2	-15.07	34.65	1.61	0.18
	Patch Size	2	-15.42	35.36	2.32	0.12
	Constant	1	-17.94	38.06	5.02	0.03
	Year	2	-17.07	38.67	5.63	0.02

[1] Explanatory variable abbreviations are as follows: Constant = null model, Age = age of bird (SY/ASY), Patch Size = size in ha of the patch, Year = survey year, also refers to regional variation between years.
[2] Number of parameters in the model
[3] Akaike's Information Criteria corrected for small sample sizes
[4] AIC_c relative to the best-fit model
[5] Model weight

SUMMARY AND CONCLUSIONS

Discussion

Golden-cheeked warblers are similar to other passerine species that show differences in reproductive success by age. I found that older males had higher productivity measures than their younger counterparts. Additionally, the territory density of the study site influenced the productivity of warblers based on their age. In areas of low abundance, I found that young males experienced a disadvantage regarding pairing success and it was only the older males that successfully paired. Furthermore, if a SY male established a territory in an area with a high density of conspecifics, the male was able to reproduce; therefore, they may require patches that can support high densities of warblers to provide them with the opportunity to attempt to pair during the breeding season. However, although SY males were not reproducing on low-density patches, males of both age classes inhabited these patches during the breeding season.

Warblers, like most bird species, display bi-parental care of young (Gass 1996) and passerine nests with higher male involvement have higher fledging success (Møller 2000). Lozano et al. (1996) suggested that the lower productivity of SY males was due to their lack of local knowledge to assist in territory placement. Because they are arriving to the breeding grounds later, SY males are initiating nesting behaviors later and this therefore reduces the number of possible nesting attempts (Lozano et al. 1996). Other studies have also suggested that productivity might improve by age due to overall improvements such as foraging efficiency, intraspecific competition, or predator avoidance (Nol and Smith 1987; Daunt et al. 2007) that then enables the male to expend energy on attending to nestlings. Additionally, my data show, that ASY males were equally capable of successfully pairing on low-density sites suggesting that ASY males are not limited to breeding exclusively in high-density areas. This suggests a pattern of decreased pairing success for young males on sites with low abundance indicating that it is not only the age of the male, but also where the male establishes a territory that can determine whether his breeding season is successful.

I also found a similar advantage for older males regarding fledging success in areas of low warbler abundance. Older males did equally well regardless of the territory density of the study site, but SY males did not fledge young on low-density sites (because they also did not attract a female). Second-year males only contributed to the next generation when they established territories on high abundance sites.

The best-fit model for pairing success included the main effect of bird age; however, the weight of this model was only 0.47, a relatively low weight for a top model. This suggests that either there were additional variables such as vegetation types, predator assemblages, or female characteristics, besides those included in my candidate models that better predict pairing success on my sites or that each candidate model is equally good at predicting pairing success. Nevertheless, among the variables I tested, age was a better predictor than patch size or the sampled region.

I also found age to be a major component in the three top models for territory success. Patch size and year were each part of the top two additive models, and the main effect of age was the third best model; however, neither of those variables of patch size or year individually contributed to the significance of the model. Age was the dominant variable that was consistent in all three of the top models predicting territory success. The weights associated with these models also indicate that these models are weak predictors of territory success. However, because older males are more experienced than those in their first breeding season, one would expect ASY males to have higher reproductive success than their younger counterparts. This is a similar result to the model-selection results for pairing success because the datasets were very similar. I examined only a few variables in my study but overall, I had high levels of productivity in both high and low-density sites.

Although male age influenced the success of each breeding attempt, the age of the female may also influence productivity. Females may use criteria independent from males, such as potential for nest predation, forage availability, or competition, to select breeding sites, which could subsequently influence the pairing success of male birds (Fontaine and Martin 2006). Female golden-cheeked warblers select the nesting sites within the territories (Ladd and Gass 1999) and the experience of the female may influence her nest placement decisions. Each nest placement would be subjected to different levels of vulnerability to predation, which would lower productivity, or proximity to foraging substrate, which may increase the birds' productivity. Female selection decisions are not well studied due to the low detection rates of female warblers (Hayden and Tazik. 1991; Jette et al. 1998); however, this information is likely relevant to all productivity measures for the species.

I found no differences in the age structure of golden-cheeked warblers between my study sites. SY males were found equally on both high and low-density sites and not predominantly on low-density sites as I had predicted. My attempt to supplement my bird age data with field-observations did not provide accurate data regarding bird age; this result did not influence my overall results. Plumage differences between ages, although apparent in some individual warblers (HLP, pers. obs.), are not consistently reliable across the species when the bird is not in-hand. Although some passerine species such as the American redstart (*Setophaga ruticilla*) display delayed plumage maturation during which it is easy to distinguish between SY and ASY males (Francis and Cooke 1986, 1990), this is not the case with golden-cheeked warblers. For my study, it was important to be able to differentiate SY birds from their older counterparts and in order to do so accurately, the bird must be observed in-hand. Ideally, it would be best to band all birds before the pre-basic molt at the end of their first breeding season (as SY males or younger) to know the exact age of each bird as they return in subsequent years to breed.

The observed arrival date of warblers to my study sites was characteristic of previously documented patterns of warbler arrival. Early-arriving warblers have been observed as early as 28 Feb. on Fort Hood but usually arrive in early to mid-March (Groce et al. 2010). However, I additionally observed that warblers arrived to high-density sites before they were observed on low-density sites. This indicates that a particular suite of site characteristics made those sites more attractive to male warblers than low-density sites that were occupied later in the season. This could be for a number of reasons. Local knowledge may play a role in male settlement decisions since ASY males typically display high site fidelity and have been observed returning to the same breeding areas as previous years (Maas 1998; City of Austin [COA] 2013) but SY males have been observed dispersing long distances away from their HY sites (Jette et al. 1998; Maas 1998; City of Austin [COA] 2013). Because productivity increases with increasing patch size (Coldren 1998; Butcher et al. 2010) large patches may be occupied first. Maas (1998) found that AHY birds are more likely to return to large patches (> 700 ha) although there is no information on whether previous years' breeding success influences future settlement decisions (Groce et al. 2010). Conspecific attraction may also play a role in male site selection (Farrell et al. 2012) as males tend to settle near other males so high-density sites may be more likely to attract additional males than an empty patch of potential habitat.

Rockwell et al. (2012) cited numerous studies that reported a negative relationship between delayed arrival and reproductive success. Although I did not collect data on the age of the first bird to arrive to each study site, I did find differences in arrival based on territory density within the study site. I did not find differences in reproductive success though, which suggests that despite delayed arrival to the low-density sites, productivity was not influenced by that delay. Lozano et al. (1996) found that male American Redstarts that arrived early to the breeding grounds tended to have higher breeding success than later arrivals, independent of age. They suggested that this pattern may be explained by the fact that these birds not only had a longer breeding season but also access to the best territories. However, they suggested that this difference in reproductive success and age may be because of experience and local knowledge more than arrival time itself.

Golden-cheeked warblers have shown variation in productivity based on differences in patch size and habitat condition, a characteristic pattern within the central portion of the warbler's range (Butcher et al. 2010; Marshall et al. 2013; Robinson 2013); however, I did not find that abundance of golden-cheeked warblers varied with habitat quality. Although I did not find a statistically significant difference, pairing success was 15% lower on low abundance sites, thus indicating that additional research is warranted.

Management Implications

Roughly 90% of the patches in the warbler's breeding range have a low predicted occupancy (Collier et al. 2012) and many of these patches are relatively small. Typically, it's recommended to maintain large patches of habitat to support sustainable breeding populations of warblers, however, warblers are not restricted from breeding on smaller patches (Butcher et al. 2010). My research indicates that older males have similar territory success regardless of differences in territory density. In places where older males established territories, they were able to successfully breed. So, although it is important to maintain large tracts of potential habitat, smaller patches are also utilized by breeding warblers.

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