EFFECTS OF HABITAT CHARACTERISTICS ON OCCUPANCY AND PRODUCTIVITY OF A FOREST-DEPENDENT SONGBIRD IN AN URBAN LANDSCAPE

A Thesis

by

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ABSTRACT

Habitat fragmentation and isolation can result in decreased occupancy and reproductive success within songbirds, particularly for species inhabiting urban environments where suitable habitat may be limited. The golden-cheeked warbler (*Setophaga chrysoparia*) is a federally endangered songbird that inhabits oak-juniper (*Quercus* spp.- *Juniperus* spp.) across central Texas. Past research on this warbler has indicated decreased patch occupancy near urban areas and negative reproductive effects associated with decreased distance to edge and decreased canopy cover. A rural study indicated warblers occupy patches ≥3 ha, and warblers in patches ≥20 ha are more likely to successfully fledge young. There are no thresholds yet identified for this warbler within urban environments, where effects of habitat fragmentation on reproductive success are more pronounced than within rural environments. I monitored patch occupancy, territory establishment, pairing success, and fledging success of warblers in an urban environment. I determined minimum patch-size thresholds for productivity measurements, and also monitored effects on productivity from canopy cover, woodland composition, distance to and size of the nearest habitat patch, and distance to the nearest habitat patch >100 ha. I compared my results to those from a similar study conducted in a rural system. I compared territory size and territory density between an urban and rural system. Warblers occupied 24% (n = 63) patches surveyed; the smallest patch occupied was 3.5 ha. The smallest patch with an established territory was 10.7 ha, and 10% (n = 63) of habitat patches had at least one established territory. Warblers successfully fledged young in 3 patches, the smallest of which was 26.5 ha. I found patch-size was predictive for territory establishment and pairing success with warblers requiring 13 ha (95% CI: 10.0 – 16.8 ha) and 19 ha (95% CI: 15.7 – 22.6 ha) habitat patches, respectively. I found a minimum threshold of approximately 66% canopy cover (95% CI: 65.2 – 66.4%) required for patch occupancy, and found no warblers established a territory in a habitat patch >25 m from the next nearest patch. I found higher minimum thresholds within an urban system for territory establishment and pairing success than those seen within a rural system. I suggest preserving warbler habitat patches >22 ha that are in close proximity to other habitat patches. This will help to enhance warbler habitat within urban areas and maintain reproductively viable habitat patches, while not halting development completely.

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Thanks goes to the over 400 private landowners who allowed me access to their property and made this research possible. I would like to thank the many field technicians for their hard work in data collection. I would also like to thank my friends and lab mates for their advice and support during the course of my graduate studies.

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INTRODUCTION

Literature Review and Problem Statement

Ecologists have been exploring wildlife-habitat relationships for many years (Grinnell 1917, Leopold 1970, Wiens et al. 1986, Morrison et al. 2008 pp. 1-35). In recent years ecologists have shown an increased interest in habitat fragmentation and isolation impacts on wildlife, in part due to the increase in urban living in the past 100 years and the expected increase in the next 50 years (Alig et al. 2004, Grimm et al. 2008, USEPA 2009). Loss of habitat not only results in fragmentation of habitat, it can also compound negative habitat effects, with wildlife impacted by decreasing habitat patch-size, increasing isolation from other habitat patches, and increasing edge effects (Temple and Cary 1986, Andrén 1994, Cox et al. 2012). In the Netherlands forest songbird occupancy and diversity decreased with decreased habitat patch-size and increasing habitat isolation within an agricultural landscape (van Dorp and Obdam 1987). Bayne and Hobson (2001) found decreased territory densities with increasing habitat fragmentation and decreasing distance from the edge. Many studies have found negative impacts on wildlife productivity from urbanization, transportation, and agricultural development (Collinge 1998, Miller and Cale 2000). Occupancy of neotropical migrants within Ontario and New England declined as distance to urban development decreased (Friesen et al. 1995, Kluza et al. 2000). Halfwerk et al. (2011) found great tit (*Parus major*) nest and post-fledging success decreased with increased traffic noise. Reijnen et al. (1995) witnessed decreasing territory densities with decreased distance to roads. Birds also adjust territory sizes based on resource availability (Smith and Shugart 1987), which may be limited in an urban system.

Andrén (1994) found that landscape's with highly fragmented habitat display a compounded effect from patch-size and isolation, where species loss will be greater with cumulative effects from habitat fragmentation and habitat loss, rather than from habitat loss alone. This idea has increased research on ecological thresholds, defined as a point or zone where a relatively rapid change occurs from one ecological state to another as a result of a small addition or change in one or more key factors (Groffman et al. 2006). These changes are often associated with habitat characteristics and requirements, such as the removal of habitat from an already fragmented landscape (Radford and Bennett 2004). However, the application of the ecological threshold concept is much more complex than a steady-state, equilibrium view of an ecosystem. The ecological threshold concept requires a non-linear relationship, often with multiple key drivers that may result in a threshold shift (Groffman et al. 2006). These key drivers may also operate on different time scales, resulting in a constantly shifting environment with no distinct threshold readily visible (Groffman et al. 2006). Some studies have found ecological thresholds within systems (Andrén 1994, Denoël and Ficetola 2007), whereas others have not (Lindenmayer et al. 2005). Radford et al. (2005) found strong evidence supporting a species-richness threshold response on a landscape level. Although the threshold varied based on patch isolation, Radford and Bennett (2004) determined minimum occupancy thresholds at 15% to 25% woodland cover for the white-browed treecreeper (*Climacteris affinis*).

Some ecologists have also looked at the linear relationship between limiting-factors and productivity. Burke and Nol (2000) found lower reproductive success in smaller habitat patch fragments for the ovenbird, wood thrush (*Hylocichla mustelina*), rose-breasted grosbeak (*Pheucticus ludovicianus*), and veery (*Catharus fuscens*). Rich et al. (1994) noticed occupancy and abundance was limited within interior forest bird communities by decreasing distance to the edge of habitat. Donnelly and Marzluff (2004) found an added emphasis from urbanization, with smaller habitat patches associated with urban areas had more limited species richness in Seattle, WA. Ecological thresholds and limiting factors are both useful in determining minimum habitat requirements for a species, and can result in added information available for improved management decisions (Swift and Hannon 2010). The ability to improve upon management decisions is particularly important for endangered or threatened species.

The golden-cheeked warbler (*Setophaga chrysoparia*, hereafter warbler), was listed as federally endangered in 1990 due to threats of habitat destruction and fragmentation (USFWS 1990, Beardmore et al. 1996, Groce et al. 2010). This warbler breeds in mature stands of Ashe juniper (*Juniperus ashei*) and oak (*Quercus* spp.) across the Edwards Plateau of central Texas (USFWS 1990). Numerous researchers have conducted studies on the warbler across both urban and rural landscapes (Benson 1990, Jette et al. 1998, Cooksey and Edwards 2008, Collier et al. 2012). The decision to list this warbler was partially due to the assumption that 67% of the breeding population occurred in counties on the eastern Edwards Plateau, where large amounts of urban development exists (Groce et al. 2010). Across the warbler breeding range, especially along the eastern border of the range, human population growth rates will continue to increase (Gaines 2008, Bierwagen et al. 2010). Previous research has indicated lower occupancy in habitat patches near urban areas, as well as a decrease in warbler reproductive success with increased habitat fragmentation and as distance to the edge of a habitat patch decreased (Coldren 1998, Maas 1998). Sperry (2007) compared different land use types adjacent to warbler habitat patches and found habitat patches adjacent to housing developments had lower warbler occupancy, in comparison to habitat patches adjacent to utility easements and woodland meadows. Coldren (1998) found warbler territory size decreased with improved reproductive success, a potential proxy for habitat productivity by way of habitat fragmentation or patch isolation.

There has also been research on impacts from potential limitations to productivity on smaller habitat patches in rural areas (Benson 1990, Arnold et al. 1996, Butcher et al 2010). Past research found warblers occupy patches as small as 0.66 ha (Benson 1990); however, other research suggests a minimum patch-size requirement of 10 ha for occupancy and a minimum patch-size requirement of 23 ha for fledging success (Arnold et al. 1996). Butcher et al. (2010) found minimum patch-size thresholds for warbler occupancy and territory establishment occurred at <3 ha, warbler pairing success occurred within patches ≥4 ha, and warbler fledging success occurred within patches ≥20 ha in a rural landscape in east-central Texas. No studies have examined warbler minimum thresholds within an urban system.

Objectives and Research Hypotheses

Objective 1: Within an urban system, examine evidence for minimum patch-size thresholds in patch occupancy, territory establishment, pairing success, and fledging success.

Research Hypothesis 1: I hypothesize golden-cheeked warblers will exhibit a minimum patch-size threshold for each productivity measurement.

Objective 2: In addition to individual effects from patch-size, examine possible effects on patch occupancy, territory establishment, pairing success, and fledging success from a other habitat predictor variables (canopy cover, woodland composition, distance to the nearest patch, size of the nearest patch, distance to the nearest patch >100 ha).

Research Hypothesis 2: I hypothesize that other habitat characteristics in addition to patch-size will affect warbler productivity.

Objective 3: Examine possible effects on territory size and territory density from habitat characteristics of interest (patch-size, canopy cover, woodland composition, distance to the nearest patch, size of the nearest patch, distance to the nearest patch >100 ha).

Research Hypothesis 3: I hypothesize that territory size and territory density will vary based on different habitat characteristics associated with specific habitat patches.

Objective 4: Compare my results of warbler threshold responses within an urban environment to a recent study (Butcher et al. 2010) in a rural environment.

Research Hypothesis 4: I hypothesize that warbler minimum thresholds will be higher within an urban environment than a rural environment due to added activity and fragmentation within the urban environment.

Answering these questions will increase understanding of the breeding ecology of warblers, refine management strategies utilized across the breeding range, and allow for more effective management of warbler breeding habitat within urban areas.

METHODS

Study Area

I conducted my research on >400 public and private properties during the breeding seasons, 14 March to 10 June in 2011, and 12 March to 1 June in 2012 in Travis and Hays counties, Texas (Fig. 1). As of 1 July in 2011, Austin had received cumulative rainfall of 18.9 cm, and as of 1 July in 2012, Austin received 48 cm of cumulative rainfall. Approximately 65% of my study area was comprised of developed commercial and residential areas, with some cropland and other vegetation types interspersed (Homer et al. 2007). I selected my study sites from the remaining 35% of the landscape, comprised of potential habitat patches using habitat patch delineations from Collier et al. (2012). The habitat patches associated with these patch delineations were comprised of habitat patches of mature oak-juniper woodlands.

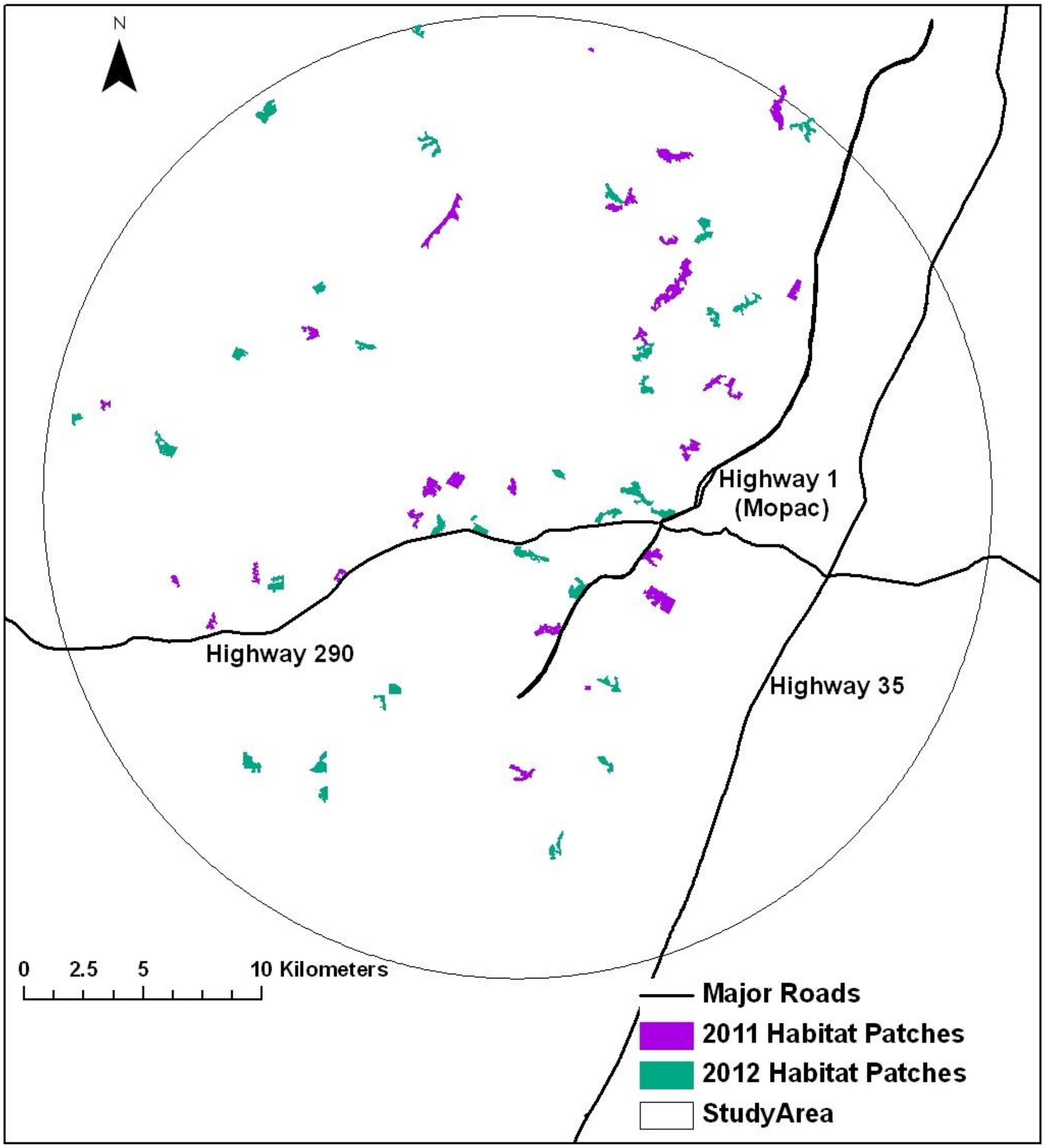

Figure 1. Golden-cheeked warbler habitat patches monitored around Austin, TX, within Travis and Hays counties, Texas, USA, 2011-2012.

Patch Definition

I used 6 different criteria to select potential study sites (habitat patches): habitat patch delineations, proximity to urban areas, edge:area ratio, patch canopy cover, patch-size, and woodland composition of the patch.

Collier et al. (2012) delineated warbler habitat patches with LANDSAT imagery, using an unsupervised classification of woodland types and the 2001 National Land-Cover Database ((NLCD), and creating breaks between patches using the Texas strategic mapping program (STRATMAP). I used patch delineations from Collier et al. (2012) to select potential study sites of mature oak-juniper woodlands and ground-truthed patch boundaries during the field season.

Coldren (1998) and Sperry (2007) documented decreases in warbler occupancy with decreasing distance to urban areas, and Maas (1998) documented a decrease in warbler reproductive success as distance to the edge of a habitat patch decreased. The 2001 NLCD created a 30 m resolution land cover data layer across the United States that can identify land cover classes, canopy cover (i.e., the percent canopy cover of all trees >2 m in height) and urban imperviousness. I used the 2001 NLCD and the buffering tool in ArcGIS 9.3.1 to select patches where ≥25% of the patch edge was within 50 m of residential areas, to ensure all potential habitat patches had a possible effect from residential areas.

Although warblers occupy and utilize habitat edge (Kroll 1980, Magness et al. 2006), Peak (2007) found that edge effects negatively impacted nest success. Sperry (2007) found that occupancy decreased with decreased distance to edge, and DeBoer and

Diamond (2006) observed lower occupancy in patches with more edge (e.g., higher edge:area ratio). Therefore, I chose patches with an edge:area ratio <0.035; this low edge:area ratio also removed potential habitat patches with lower core areas, such as long, narrow patches.

Texas Parks and Wildlife defined golden-cheeked warbler habitat as ≥35% canopy cover (Campbell 2003). Although DeBoer and Diamond (2006) found that canopy cover was not predictive of occupancy, Klassen et al. (2012) found fledging success in territories with ≥20% canopy cover, and Dearborn and Sanchez (2001) found >70% canopy cover accounted for successful nest sites when compared to non-use sites. I used 2010 National Agricultural Imagery Program color infrared digital imagery at 1 m resolution and the Zonal Statistics tool in ArcGIS 9.3.1 to determine the mean percent canopy cover for each delineated habitat patch. I selected habitat patches of mature oak-juniper woodland with ≥35% canopy cover.

Butcher et al. (2010) suggested a 2.9 ha minimum patch-size occupancy threshold and a 15-20 ha minimum patch-size threshold for reproductive success in a rural environment. Arnold et al. (1996) found warblers did not occur in patches <6 ha, and were not reproductively successful in patches <23 ha in an urban environment. Therefore, I selected patches 2-75 ha to encompass previously observed occupancy and reproductive success thresholds.

Although warblers are found in habitat patches with lower woodland composition (i.e., the average percent of landscape within 400 m of a pixel composed of oak-juniper woodlands), Magness et al. (2006) found that warblers were not present within patches with <40% woodland cover, and probability of occupancy was >0.5 when woodland cover was >80%. Based on this information, I used the landscape composition metric from Collier et al. (2012) to determine oak-juniper woodland composition within habitat patches and only surveyed patches with >40% oak-juniper woodland composition. Collier et al. (2012) used ArcGIS 10 to find the mean percentage of woodlands within a 400-m radius circle (Magness et al. 2006) around a given pixel, and used this percentage as the landscape composition estimate.

Habitat Characteristics

I measured 6 habitat characteristic variables that were most likely to determine occupancy and productivity in golden-cheeked warblers: patch-size, patch canopy cover, woodland composition, size of and distance to the nearest habitat patch, and size of the next nearest habitat patch >100 ha. I used patch-size, canopy cover, and woodland composition of each habitat patch, as described above (See Patch Delineations). I determined size of and distance to the nearest habitat patch in ArcGIS 9.3.1 using patch delineations from Collier et al. (2012). I determined distance to the nearest habitat patch >100 ha using the Buffer tool in ArcGIS 9.3.1.

Patch Occupancy

I determined occupancy for 63 potential habitat patches ranging in size from 2 to 73 ha, during the 2011 and 2012 breeding seasons (Fig. 1). Because I was interested in general warbler use of the habitat patch, including use by both migrating and breeding warblers, I defined patch occupancy as ≥1 warbler detected in the habitat patch at any point during occupancy surveys. My occupancy definition incorporated any golden-cheeked warblers detected within a habitat patch, regardless of length of stay. I visited each patch 6 times starting mid-March (MacKenzie and Royle 2005, Collier et al. 2012) with 7 days between each visit over a 6 week time period, concluded in late-April and well into the warbler breeding season (Campbell 2003). This survey length allowed for a higher potential of warbler detections across the breeding season. If I located a warbler only once in a patch I considered that patch occupied for the purpose of my study. If I did not locate a warbler after 6 visits I assumed migrating and breeding warbler movement between patches stopped, and considered the survey patch unoccupied. I did not visit the patch again that season for additional monitoring surveys. I surveyed along parallel transects systematically established ~150 m apart. Number of transects per study site and length of transect varied by patch-size. Observers walked along each transect, stopping for 2-3 minutes at points located every 100 m to listen for warblers. Observers recorded the GPS coordinates of any warblers seen or heard at any point during these initial surveys (Morrison et al. 2008).

Territory Reproductive Success

I determined territory establishment, defined as a male actively defending a territory for >4 weeks, for all occupied patches of the original 63. I determined pairing and fledging success for all established territories using a method based on Vickery et al. (1992). This is a reliable system used successfully in previous studies on territorial songbirds (Christoferson and Morrison 2001) including the golden-cheeked warbler (Butcher et al. 2010, Lackey et al. 2011, Klassen et al. 2012). I defined pairing success as a territorial male with a female detected during at least 2 separate visits and defined fledging success as a paired, territorial male with ≥ one fledgling located at least once, within the first 7 days of fledging. The Vickery method assigns a rank to male or female behavior to determine the reproductive activity for each territory. This ranking system helped to determine reproductive success for the territory, while not disrupting nests of an endangered species. The ranks below are based on Vickery et al. (1992):

1. Territorial male present ≥4 weeks
2. Territorial male present ≥4 weeks and female present with male in at least 2 visits
3. Evidence of nest in territory (female carrying nest material; active nest located)
4. Evidence of nestlings (adult carrying food to nest; nestlings at nest)
5. Evidence of fledglings (single or double brood)

Starting on 14 March 2011 and 12 March 2012, I delineated territories, gathering one point every 2 minutes for a maximum of one hour. I searched each territory to determine pairing and fledging success until 10 June 2011 and 1 June 2012, to account for the entire breeding period (Gass 1996).

Territory Density and Territory Size

I created minimum convex polygons in ArcGIS 9.3.1 using all territory points collected throughout the field season to determine utilized area for all territorial male warblers. I calculated territory density by dividing the number of territories in each habitat patch with at least one established territory by the size of the patch to determine territories/ha for each habitat patch (Robinson et al. 2012).

STATISTICAL ANALYSES

I used logistic regression (Ott and Longnecker 2001, pp. 675-683) in JMP Pro 10.0.0 to determine predictive potential of patch-size for each of my 4 response variables (patch occupancy, territory establishment, pairing success, and fledging success). I then determined probability of occurrence for each response variable (MacKenzie et al. 2006, pp. 83-131) in Presence 4.9. With the predicted probabilities from the logistic regression model, I used segmented regression (Muggeo 2003) in R 2.15.1 to find a minimum threshold (i.e., breaking point) and corresponding slopes before and after the threshold for the response variables and patch-size. I report the breaking point from segmented regression ± the 95% confidence interval for that point. Segmented regression is similar to standard linear regression, except with the ability to determine multiple regression parameters, in this case the slopes of multiple lines (Betts et al. 2007). Numerous studies have used segmented regression to determine the breaking point at which species vary in habitat requirements (Betts et al. 2007, Rhodes et al. 2008, Vanak et al. 2010). To determine no lack of fit between the two slopes from segmented regression, I used a goodness of fit test (Muggeo 2008).

To test the assumption of no interannual variation between study years for my 6 selected predictor variables (habitat patch-size, canopy cover, woodland composition, distance to the nearest habitat patch, size of the nearest habitat patch, and distance to the nearest habitat patch >100 ha) for each monitored patch, I used logistic regression. To test correlations between my predictor variables, I ran a multivariate covariance correlation (Ott and Longnecker 2001, pp. 646-657) in JMP Pro 10.0.0 for all 6 predictor variables mentioned above. I used forward stepwise logistic regression (Ott and Longnecker 2001, pp. 717-720) in JMP Pro 10.0.0 to determine the best individual predictor variable for each response variable. I set the significance level for a variable to enter the model at 0.25 and significance for a variable to stay in the model at 0.05. Although it is possible that an interaction between multiple predictor variables may better predict my response variables, I was interested in the primary effect from any given habitat characteristic, and thus did not look at any interactive models. I used the best predictive model to estimate probability of occurrence for response variables. I used segmented regression to find the minimum threshold and corresponding slopes before and after the threshold for patch occupancy and the best predictor variable. To determine no lack of fit between the two slopes from segmented regression, I used a goodness of fit test.

I used an analysis of variance (ANOVA; Ott and Longnecker 2001, pp. 853-878) to determine any changes in territory density or territory size in relation to reproductive success. I ran forward stepwise logistic regression to determine the single best predictor variable for territory size.

For my comparison between rural and urban systems, I used descriptive statistics to compare minimum threshold values for the habitat characteristics mentioned above (habitat patch-size, canopy cover, woodland composition, distance to the nearest habitat patch, size of the nearest habitat patch, and distance to the nearest habitat patch) by patch occupancy, territory establishment, pairing success, and fledging success (Butcher et al.

2010). I compared territory size and territory density using an ANOVA to determine any differences between the rural and urban systems.

RESULTS

I contacted over 1,000 private landowners across both years, to request access to their property. Over 400 private and public landowners granted me access to their properties, composing a total of 63 habitat patches suitable for my study. I surveyed 30 patches in 2011 and 33 in 2012, ranging in size from 1.8 – 73 ha. Canopy cover across all surveyed patches ranged from 46 – 83%, and woodland composition ranged from 39 – 70%. Surveyed patches ranged from 10 – 225 m from the nearest neighboring patch, with the neighboring patch ranging in size from 2 to 2,800 ha. Distance to the nearest patch >100 ha ranged from 50 m to 1.1 km. There was no difference between years for patch-size, woodland composition, canopy cover, distance to nearest patch, size of nearest patch, or distance to the nearest patch >100 ha ($\chi^2 = 9.24$, df = 6, $P = 0.161$). This showed my randomized patch selection was not significantly different between years.

Warblers occupied 25% of the patches surveyed ($n = 63$; Fig. 2), with the smallest patch occupied at 3.5 ha. The smallest patch with an established territory was 10.7 ha, and 10% ($n = 63$) of the habitat patches had at least one established territory (Fig. 3). The smallest patch where warblers successfully paired or fledged young was 26.5 ha (Fig. 4). Of the 4 patches where warblers successfully paired, 3 warbler pairs also successfully fledged. I delineated 16 warbler territories, 44% ($n = 16$) of which paired and 71% ($n = 7$) of the paired territories successfully fledged.

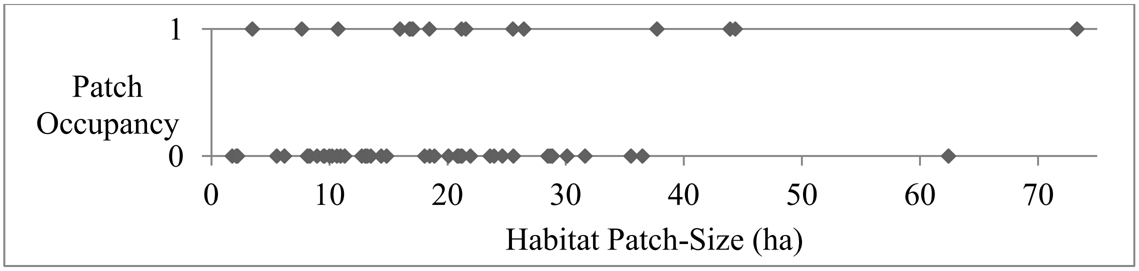

Figure 2: Habitat patch occupancy relative to habitat patch-size for golden-cheeked warblers within Hays and Travis counties, Texas, USA, 2011-2012.
Patch occupancy of zero signifies no warbler detected in the habitat patch at any point during occupancy surveys. Patch occupancy of one signifies ≥1 warbler detected in the habitat patch at any point during occupancy surveys.

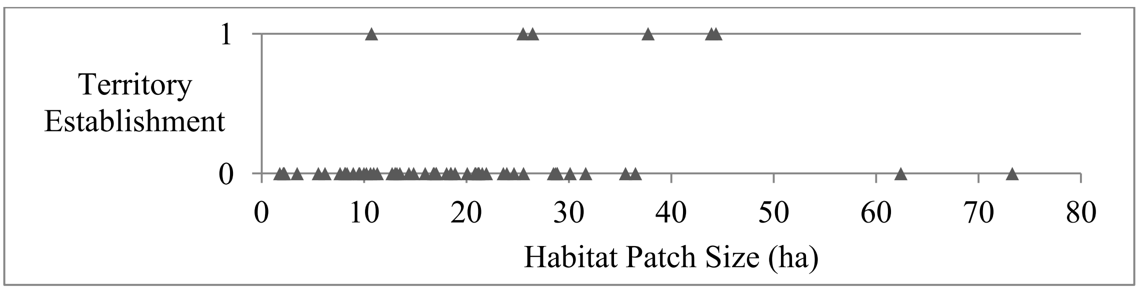

Figure 3: Territory establishment by habitat patch-size for golden-cheeked warbler within Hays and Travis counties, Texas, USA, 2011-2012.
Territory establishment of zero signifies no male actively defending a territory for >4 weeks. Territory establishment of one signifies a male actively defending a territory for >4 weeks.

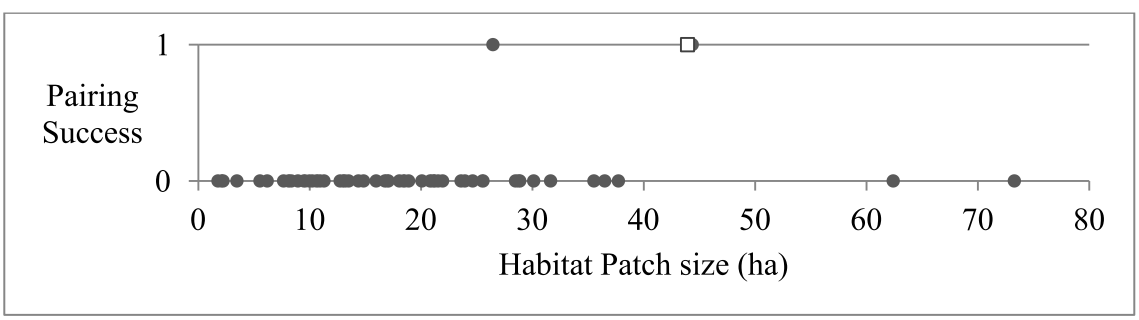

Figure 4: Pairing success by habitat patch-size for golden-cheeked warbler within Hays and Travis counties, Texas, USA, 2011-2012. White square signifies the single habitat patch where no warblers successfully fledged.
Pairing success of zero signifies no female present in 2 separate visits with a territorial male. Pairing success of one signifies at least one female present in 2 separate visits with a territorial male within the patch.

Patch Size

Patch-size was not predictive of patch occupancy ($\chi^2 = 3.15$, df = 1, $P = 0.076$) or fledging success ($\chi^2 = 3.37$, df = 1, $P = 0.066$); however, patch-size was predictive of territory establishment ($\chi^2 = 4.13$, df = 1, $P = 0.042$) and pairing success ($\chi^2 = 5.76$, df = 1, $P = 0.016$). Using the predicted probabilities of territory establishment with patch-size, I fit 2 lines to my data using segmented regression. I found a minimum breaking point (threshold) for territory establishment at 13.4 ha (95% CI: 10.0 – 16.8 ha, Figure 5). Slope of the regression line before the breaking point was 0.004; slope of the regression line after the breaking point was 0.017. These 2 regression lines were not statistically different enough to account for any random deviance ($\chi^2 = 4.07$, df = 3, $P = 0.254$, Fig. 6).

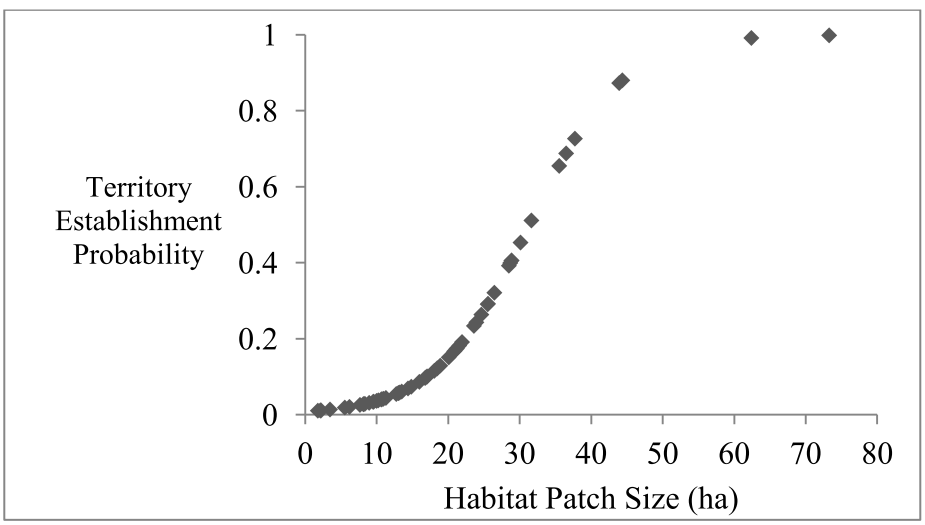

Figure 5: Probability of territory establishment for golden-cheeked warblers by habitat patch-size (ha) of each habitat patch for study sites in Hays and Travis counties, Texas, USA, 2011-2012.

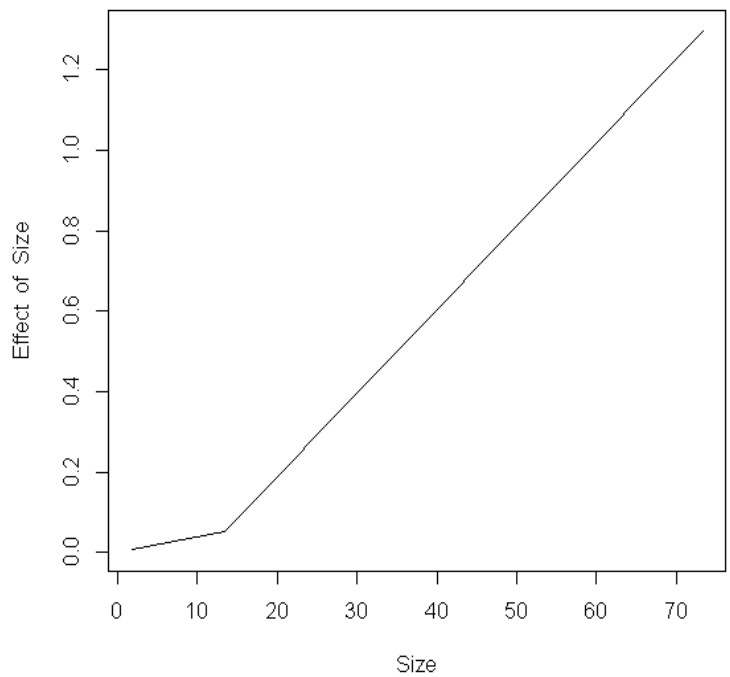

Figure 6: Regression lines (2) and minimum breaking point for probability of territory establishment (Effect of Size) using segmented regression for golden-cheeked warbler habitat patch-size (Size) for study sites in Travis and Hays counties, Texas, USA, 2011-2012.

Using the predicted probabilities of pairing success with patch-size, I fit 2 lines to my data using segmented regression. I found a minimum breaking point (threshold) for pairing success at 19.2 ha (95% CI: 15.7 – 22.6 ha, Figure 7). Slope of the regression line before the breaking point was 0.0005; slope of the regression line after the breaking point was 0.025. These 2 regression lines were not statistically different enough to account for any random deviance (χ^2 = 4.74, df = 3, P = 0.192, Fig. 8).

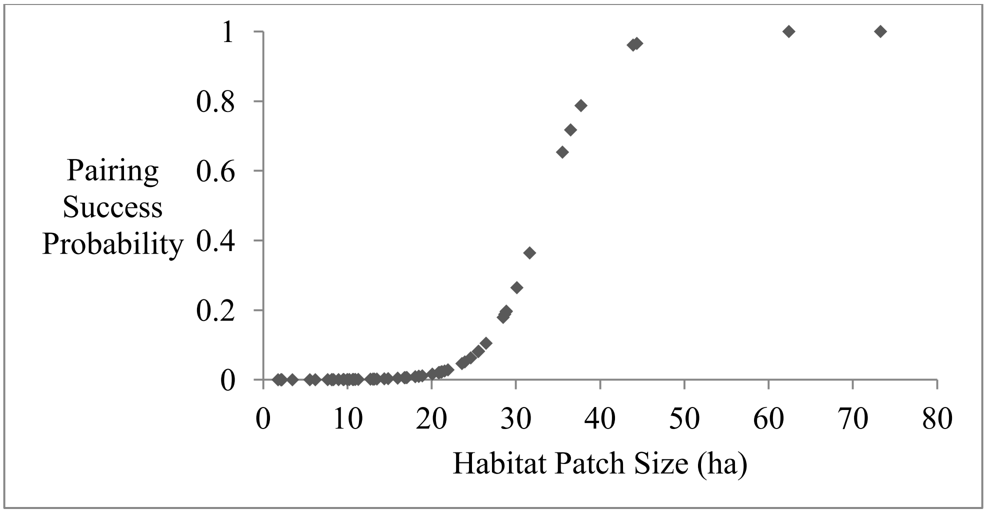

Figure 7: Probability of pairing success for golden-cheeked warblers by habitat patch-size (ha) of each habitat patch for study sites in Hays and Travis counties, Texas, USA, 2011-2012.

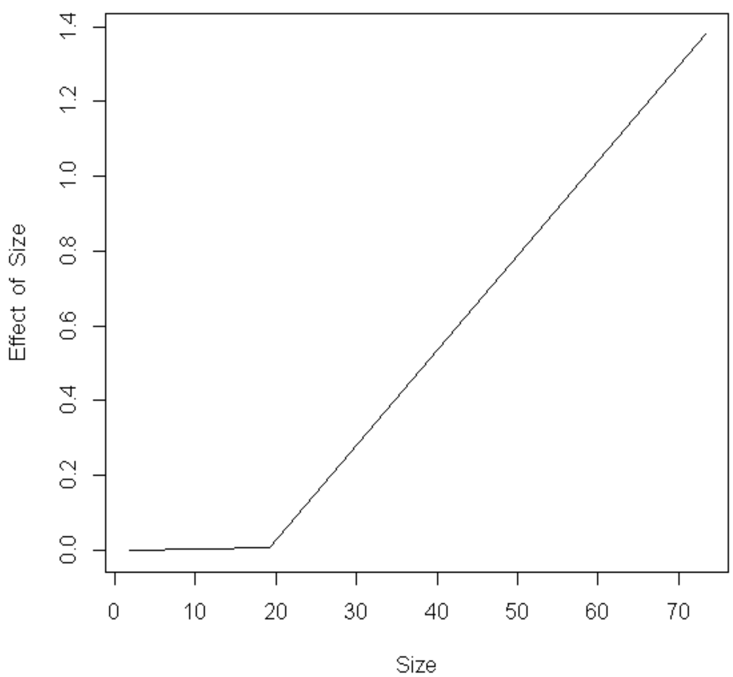

Figure 8: Regression lines (2) and minimum breaking point for probability of pairing success (Effect of Size) using segmented regression for golden-cheeked warbler habitat patch-size (Size) for study sites in Travis and Hays counties, Texas, USA, 2011-2012.

Patch Occupancy

I ran forward stepwise logistic regression with the 6 habitat characteristics (patch-size, canopy cover, woodland composition, size of the nearest patch, distance to the nearest patch, distance to the nearest patch >100 ha), and found canopy cover was the best predictor of patch occupancy (χ^2 = 11.66, df = 1, P < 0.001). I determined probability of patch occupancy using canopy cover as the site covariate and predicted this probability based on the estimated values of canopy cover (Fig. 9). Using the predicted probabilities of patch occupancy with canopy cover, I fit 2 lines to my data using segmented regression. I found a minimum breaking point (threshold) for habitat patch occupancy at 66% canopy cover (95% CI: 65.2 – 66.4%). Slope of the regression line before the breaking point was 0.007; slope of the regression line after the breaking point was 0.019. These 2 regression lines were not statistically different enough to account for any random deviance (χ^2= 2.11, df = 3, P = 0.552, Fig. 10).

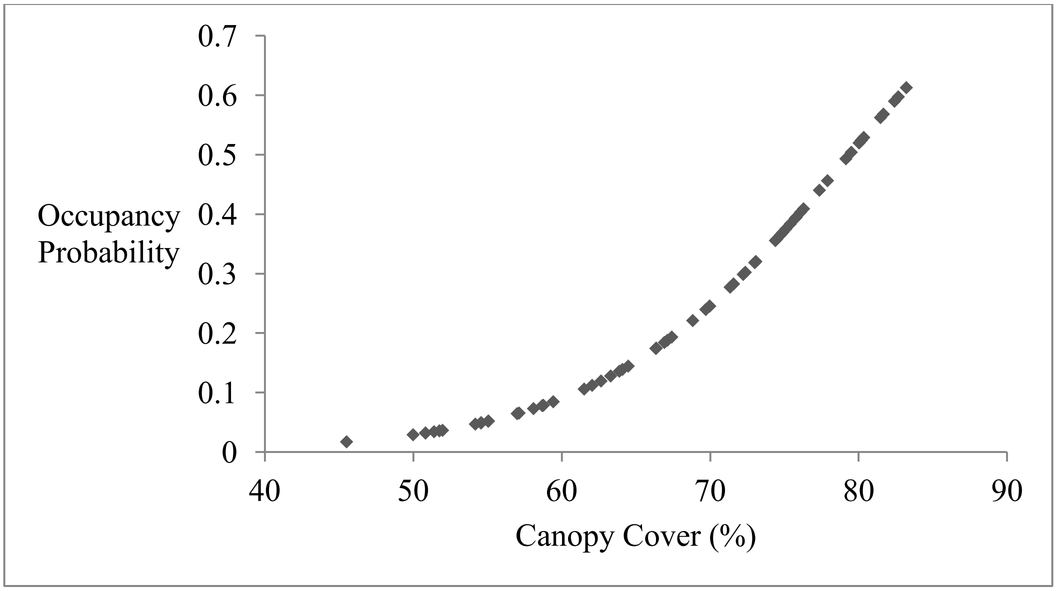

Figure 9: Probability of habitat patch occupancy for golden-cheeked warblers by percent canopy cover of each habitat patch for study sites in Hays and Travis counties, Texas, USA, 2011-2012.

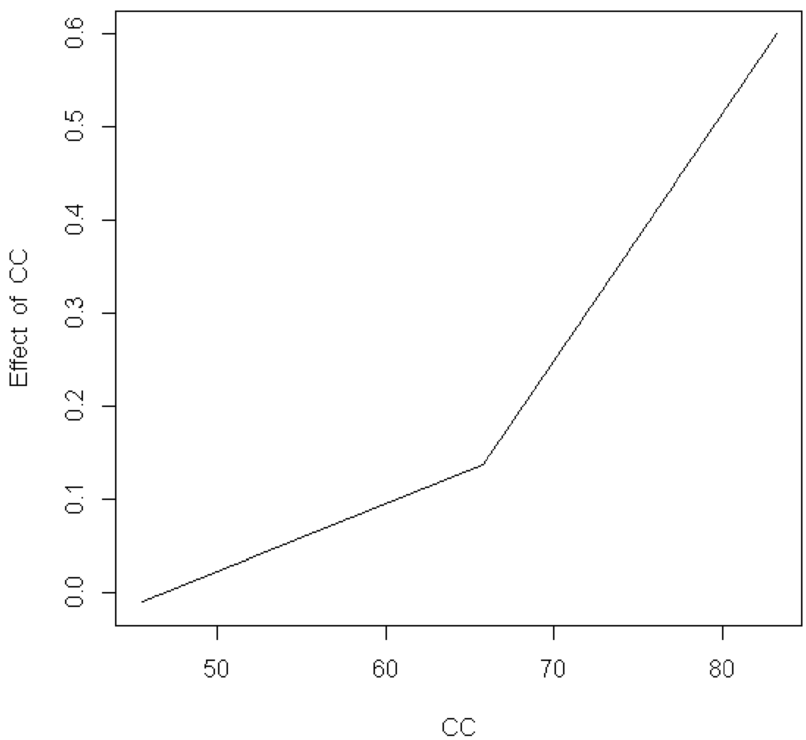

Figure 10: Regression lines (2) and breaking point for probability of patch occupancy (effect of CC) using segmented regression for golden-cheeked warblers by percent canopy cover (CC) for study sites in Travis and Hays counties, Texas, USA, 2011-2012.

Territory Reproductive Success

I ran stepwise regression with the 6 habitat characteristics (patch-size, canopy cover, woodland composition, size of the nearest patch, distance to the nearest patch, distance to the nearest patch >100 ha), and found distance to the nearest habitat patch was the best predictor of territory establishment (χ^2 = 6.72, df = 1, P = 0.01). Because I had so few habitat patches that had at least one established territory, I was not able to determine probability of territory establishment or the minimum threshold associated with territory establishment (Figure 11). All patches with ≥1 territorial male were within 25 m of the nearest habitat patch.

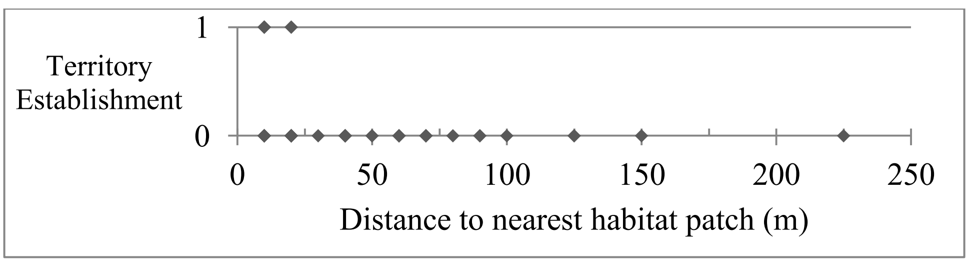

Figure 11: Territory establishment by distance from the breeding patch to the next nearest habitat patch (m) for golden-cheeked warblers within Hays and Travis counties, Texas, USA, 2011-2012. Territory establishment of zero signifies no male actively defending a territory for >4 weeks. Territory establishment of one signifies a male actively defending a territory for >4 weeks.

I found that size of the nearest habitat patch was the best predictor for pairing success (χ^2 = 9.7, df = 1, P = 0.002), however an examination of the data showed a large gap in data points between 1,116 ha and 2,405 ha (Fig. 12). Removal of outlying points >2,405 ha resulted in a non-significant relationship between pairing success and size of the nearest habitat patch (χ^2 = 2.0, df = 1, P = 0.158). When size of the nearest habitat patch was not included in stepwise regression, patch size was the best predictor of pairing success (Fig. 7, 8).

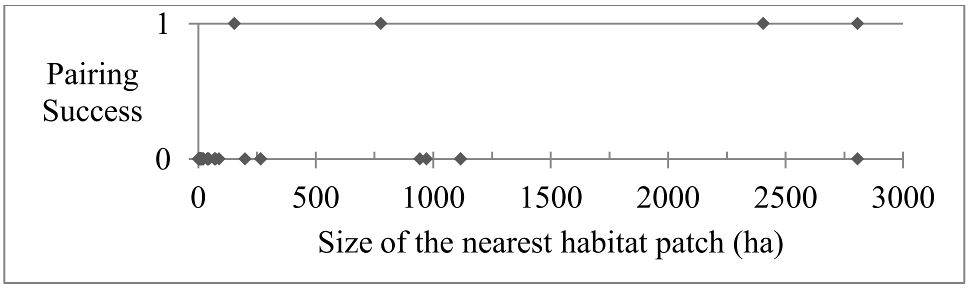

Figure 12: Pairing success by size of the nearest habitat patch for golden-cheeked warblers within Hays and Travis counties, Texas, USA, 2011-2012.
Pairing success of zero signifies no female present in 2 separate visits with a territorial male. Pairing success of one signifies at least one female present in 2 separate visits with a territorial male within the patch.

I found that size of the nearest habitat patch was the best predictor for fledging success (χ^2 =4.43, df = 1, P = 0.03), however an examination of the data showed a large gap in data points between 1,116 ha and 2,405 ha (Fig. 13). Removal of those outlying points >2,405 ha resulted in a non-significant relationship between pairing success and size of the nearest habitat patch (χ^2 = 2.0, df = 1, P = 0.158). When size of the nearest habitat patch was not included in stepwise regression, patch size was the best predictor for fledging success, although it was not a significant predictor (χ^2= 3.37, df = 1, P = 0.066). A visual inspection of my fledging success data (Fig. 4) shows only 2 patches where ≥1 warbler successfully fledged, with a large gap in patch-size data at 40-80 ha.

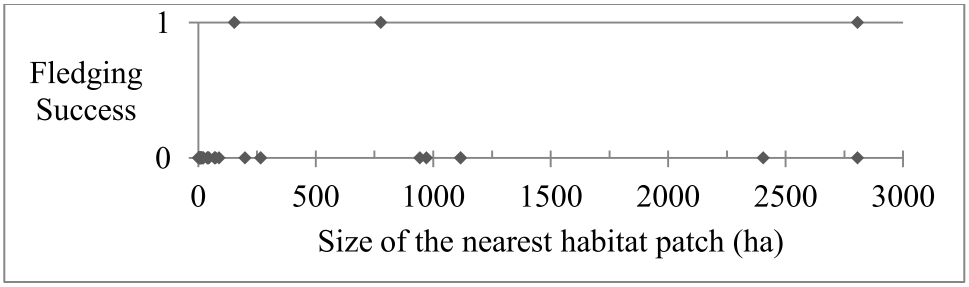

Figure 13: Fledging success by size of the nearest habitat patch for golden-cheeked warblers within Hays and Travis counties, Texas, USA, 2011-2012.
Fledging success of zero signifies no fledglings present within a paired territory. Fledging success of one signifies at least one fledging located within 7 days of estimated fledge date within a paired territory.

Territory Density and Territory Size

As mentioned previously, I monitored a total of 16 territories across all habitat patches (Table 2). The average territory size was 2.39 ha (SD = 1.43, n = 16). Average territory density for the 6 habitat patches with ≥1 territory was 0.09 birds/ha (SD = 0.01, n = 6). There was no statistically significant difference between territory size and year ($F_{4,12}$ = 1.54, df = 4, P = 0.491) or productivity ($F_{4,12}$ = 1.54, df = 4, P = 0.166). I ran stepwise regression for territory size, and found that woodland composition best predicted territory size, although the relationship was not significant ($F_{1,14}$ = 0.52, df = 1, P = 0.723). There was no statistically significant difference between territory density and year ($F_{4,1}$ = 0.25, df = 4, P = 0.930) or reproductive success ($F_{1,4}$ = 0.08, df = 4, P = 0.704). Territory density did not appear to vary based on any of the predictor variables I measured (Table 1).

Table 1. Landscape information, territory size, and territory density for each established territory in Hays and Travis counties, Texas, USA, for 2011-2012. All patches were within 20 m of the nearest habitat patch, so I did not show this information in the table.

Territory Success	Territory Size (ha)	Territory Density (birds/ha)	Patch-size (ha)	Woodland Composition (%)	Canopy Cover (%)	Size of Nearest Patch (ha)	Distance (m) to Nearest Patch >100 ha
Unpaired	1.637	0.093	11	51	80	15	1125
Unpaired	2.239	0.078	26	58	75	3	70
Unpaired	3.194						
Fledged	4.837	0.076	26	64	80	2806	200
Fledged	1.627						
Unpaired	4.393	0.106	38	62	80	777	500
Paired	1.353						
Fledged	2.750						
Fledged	2.566						
Unpaired	0.535	0.068	44	50	81	2405	20
Unpaired	0.874						
Unpaired	2.039						
Unpaired	1.307	0.090	44	40	66	154	300
Unpaired	1.216						
Paired	5.258						
Fledged	1.145						

Urban/Rural Comparison

Of the 12 rural patches surveyed by Butcher et al. (2010), 92% (*n* = 12) were occupied with at least one warbler. Of those occupied patches, all had canopy cover ≥60%, although only 45% (*n* = 11) had canopy cover ≥66% (Table 2). Of the 17 territories Butcher et al. (2010) located, 88% (*n* = 17) had paired warblers and 86% (*n* = 15) of the paired warblers fledged ≥1 young. All patches where warblers established ≥1 territory and ≥1 warbler paired were ≥3 ha and were within 10 m of another habitat patch. All patches where ≥1 paired warbler successfully fledged were ≥20 ha. The only patch where warblers were not present was 15 ha in size. Average territory size within a rural system was 1.86 (SD = 0.78) and average territory density within a rural system was 0.186 (SD = 0.09).

Table 2: Landscape information and reproductive success information for habitat patches with established territories across study sites in Coryell and Hamilton counties, Texas, USA, 2006-2007 (Butcher et al. 2010).
Dash (-) signifies data not obtained due to lack of information from the previous column.

Pairing Success	**Fledging Success**	**Patch-size (ha)**	**Canopy Cover (%)**
Yes	No	2.9	60.1
Yes	No	3.2	61.2
No	-	4.1	61.2
No	-	4.4	60.1
Yes	No	8.9	65.9
No	-	10.8	64.2
Yes	No	11.9	72.9
Yes	Yes	20.1	70.3
Yes	Yes	21.1	67.5
Yes	Yes	22.2	72.9
Yes	Yes	27.7	70.3

Butcher et al. (2010) found a minimum patch-size threshold of 20 ha for fledging success, and that patch occupancy, territory establishment, or pairing success did not reliably indicate this minimum requirement for reproductive success (Table 3). Rather, patch occupancy, territory establishment, and pairing success occurred regardless of the size of the patch. I also found that patch occupancy was not predicted by patch-size; however I found that territory establishment, pairing success, and fledging success were predicted based on patch-size. Golden-cheeked warblers within an urban system generally required a larger patch-size than warblers within a rural system for territory establishment and pairing success (Table 3). I was not able to determine a minimum threshold for fledging success, and thus can only assume the minimum patch-size threshold for fledging success is greater than the minimum threshold for pairing success. Territory size was not significantly different between rural (Butcher et al. 2010) and urban sites ($F_{1,43} = 2.60$, df = 1, $P = 0.114$). When I compared rural territory density to urban territory density, rural territory density was 120% larger than density within the urban sites ($F_{1,14} = 7.52$, df = 1, $P = 0.016$).

Table 3. Comparison of patch-size requirements between a rural system based in Coryell and Hamilton counties, Texas, USA, 2006-2007 (Butcher et al. 2010) and an urban system in Travis and Hays counties, Texas, USA, 2011-2012.
n/a: signifies value not available based on dataset.

	Urban	Rural
Patch occupancy	3 ha	3 ha
Territory establishment	13 ha	3 ha
Pairing success	19 ha	4 ha
Fledging success	n/a	15-20 ha

DISCUSSION AND SUMMARY

Summary

My first objective was to determine if there was a minimum patch-size threshold for patch occupancy, territory establishment, pairing success, or fledging success. Patch-size did not predict habitat patch occupancy, and thus I did not find a minimum patch-size threshold for habitat patch occupancy. I did find a minimum patch-size threshold for territory establishment and pairing success. Patch-size was the best predictor for fledging success; however it was not a significant predictor. This is likely due to the small number of habitat patches where ≥1 warbler successfully fledged.

Patch occupancy as I defined it (≥1 warbler detected in the habitat patch at any point during occupancy surveys) required only the presence of warblers and the measure was not necessarily associated with reproductive success. The lack of a relationship between patch occupancy and patch-size suggests warblers may visit a habitat patch at least once regardless of size. However, my patch occupancy measure does not include measures of reproductive success for warblers. Stopover sites are common during spring and fall migration, and allow for songbirds to rest and refuel after energy expenditures during migration (Schwilch et al. 2002, Wikelski et al. 2003). Thus, it is possible warblers are stopping at habitat patches regardless of specific patch characteristics for rest and refueling, before moving on to other patches for breeding objectives. Additionally, researchers commonly see songbirds select habitat early in the season based on presence of conspecifics, not necessarily based on habitat characteristics (Arlt and Part 2007, Farrell et al. 2012). The lack of a minimum patch-size requirement for patch occupancy is a consistent finding in other golden-cheeked warbler research (Benson 1990, Arnold et al. 1996, Butcher et al. 2010), and suggests warblers do not require a minimum habitat patch-size to successfully occupy a patch.

I found a minimum patch-size threshold of 13.4 ha and 19.7 ha where territory establishment and pairing success occurred, respectively, although these minimum thresholds were non-significant. Muggeo (2003) states it is often difficult to distinguish a breaking-point between 2 slopes with smaller samples, which may have resulted in the non-predictive nature of my data. Although I was not able to determine a solid breaking-point for territory establishment and pairing success, small confidence intervals for territory establishment and pairing success (± 3.35, ±3.47, respectively) suggest the breaking point for territory establishment is 10-17 ha and the breaking point for pairing success is 16-23 ha.

Because territory establishment is associated with the goal of obtaining a female and fledging young for most songbirds, the minimum patch-size requirement for territory establishment demonstrated in this study suggests warblers select habitat patches for breeding purposes based on patch-size. Farrell et al. (2012) experimentally added warbler vocalizations to habitat patches and found golden-cheeked warblers displayed significantly higher territory density within treatment sites with conspecific vocalizations broadcast than within control sites without conspecific broadcasts. This trend was consistent within habitat patches previously unoccupied and deemed less suitable (i.e., low quality), suggesting territory selection was in part due to proximity of other warblers. I found a higher minimum patch-size threshold for pairing success than for territory establishment, suggesting that selection of habitat patches for breeding purposes was not consistent between males and females. Female golden-cheeked warblers are the primary selectors for nest-sites, and thus are more likely to cue in to habitat characteristics that males may not, such as potential for nest predation, forage availability, and competition (Fontaine and Martin 2006).

I also found that patch-size was the best predictor for fledging success, although patch-size was not a significant predictor of fledging success. I found a minimum patch-size threshold of 15.9 ha for fledging success; however because of the small number of habitat patches I surveyed where ≥1 warbler successfully fledged young, this threshold is likely not representative of an urban environment. Based on a visual inspection of my data, I monitored very few patches 40 – 80 ha in size, and it is possible that this may be the patch-size range where warblers begin to fledge young. I suggest future researchers monitor more patches 40 – 80 ha in urban areas, to determine a minimum patch-size threshold for fledging success.

My second objective was to determine if any other habitat characteristics predicted habitat patch occupancy, territory establishment, pairing success, or fledging success. I found that canopy cover was the best predictor for patch occupancy, and distance to the nearest patch was the best predictor for territory establishment. Patch-size was the best predictor for pairing success and fledging success. I found a minimum canopy cover threshold of approximately 66% where patch occupancy began to occur. Other research that looked at the effects of canopy cover on warblers across the range determined that canopy cover does not relate to warbler occupancy (DeBoer and

Diamond 2006, Campomizzi et al. 2012). Federal requirements (USFWS 1990) state a minimum of 35% canopy cover is necessary for an area to be considered warbler habitat, and Campbell (2003) determined high-quality warbler habitat requires a minimum of 50% canopy cover. Within an urban environment, my study suggests that warblers require a higher minimum threshold for canopy cover to occupy a patch.

I found warblers did not establish territories within a patch unless that habitat patch was within 25 m of the next nearest habitat patch. Other research on songbirds has found significant negative effects on productivity from larger distances between habitat patches and habitat patch isolation, particularly within urban areas (van Dorp and Obdam 1987, Bergin et al. 2000, Bayne and Hobson 2001). However, Coldren (1998) found no effects on pairing or fledging success of golden-cheeked warblers from increased distance between habitat patches. My results suggest that within an urban environment, patch isolation in relation to distance between habitat patches may affect establishment of warbler territories.

My third objective was to determine if territory size or territory density varied based on the habitat characteristics I measured (patch-size, canopy cover, woodland composition, size of the nearest habitat patch, distance to the nearest habitat patch, and distance to the nearest habitat patch >100 ha). I found that neither territory size nor territory density varied significantly based on any of these habitat characteristics. Birds adjust territory size and territory density based on resource availability and food density (Smith and Shugart 1987). Butcher et al. (2010) found no change in arthropod biomass based on patch-size, and other researchers have found similar results for canopydwelling arthropods (Nour et al. 1998, Buehler et al. 2002), a major food source for golden-cheeked warblers (Pulich 1976). My results suggest that some driver other than food might be a limiting factor for warblers in an urban environment.

My final objective was to compare results in an urban environment to those in a rural environment. I found that neither habitat patches in a rural nor urban environment require a minimum patch-size for patch occupancy. I found warblers in an urban environment required a larger minimum patch-size threshold for pairing success than warblers in a rural environment. Research on other species has found negative effects on songbirds in close proximity to urban areas, possibly as a result of increased predation, decreased food availability, or increased habitat fragmentation and habitat continuity (Friesen et al. 1995, Kluza et al. 2000, Halfwerk et al. 2011). I was not able to compare fledging success minimum patch-size requirements between a rural and urban system, because I was not able to determine a minimum patch-size threshold for fledging success in an urban environment. However, because the minimum patch-size threshold for pairing success in an urban environment is approximately equivalent to the minimum patch-size threshold for fledging success in a rural environment, it is likely that warblers require a larger habitat patch to successfully fledge in an urban environment than a rural environment. These results emphasize the difference between the minimum threshold requirements for rural and urban systems that land managers must account for when managing for this endangered species.

Territory density was higher in a rural system than an urban system. This could be due to a higher minimum patch-size threshold within an urban system than a rural system, as I showed with my comparison to Butcher et al. (2010). This increased territory density could also be the result of warbler avoidance of edge within an urban area. Sperry (2007) found warblers were less likely to occupy the edge of a patch if that edge was near high intensity urban development, such as housing developments, when compared to areas of low-intensity or no urban development, such as a utility easement or woodland meadow. Warblers are likely to avoid placing a territory near the edge of a habitat patch within an urban area, thus minimizing the number territories that pack into a single habitat patch (Farrell et al. 2012). Although I found no significant difference in territory size between a rural and an urban environment, I did notice a larger average territory size at my study sites when compared to other warbler territories in rural and urban areas (Butcher et al. 2010, Locatelli et al. 2012, Robinson et al. 2012). I and other researchers have observed single males defending territories much more vigorously than paired males in my study sites and other, more reproductively successful sites (H. Pruett pers. comm.), possibly because they have more time available for territory defense, with no female or nesting responsibilities. Because so few of my warblers successfully paired and fledged, it seems possible territories were larger in my study sites when compared to other areas because more warblers had time to spare defending a territory.

Conclusion

Researchers expect the Texas human population to increase from 24.6 million to 33.3 million in the next 20 years, the equivalent of adding another Dallas-Fort Worth, Austin, Houston, and Corpus Christi (Gaines 2008). Within the golden-cheeked warbler range, researchers expect human population to increase by at least 50% in 6 of the 8 warbler recovery regions by 2060 (Fig. 14), specifically in the central part of the range (USEPA 2009, Bierwagen et al. 2010). This increase in population will likely increase urban development and sprawl, which may in turn result in smaller habitat patches and greater habitat isolation, a detriment to warbler occupancy and reproductive success. My research shows that golden-cheeked warblers require habitat patches ≥23 ha within an urban system to successfully pair and reproduce, whereas Butcher et al. (2010) found warblers within a rural system required habitat patches 15-20 ha in size to successfully reproduce. I suggest managing for warblers in an urban environment by preserving warbler habitat patches ≥23 ha in size that are also within 25 m of the next nearest habitat patch. I also suggest looking further at fledging success in patches 40-80 ha in size, to determine the urban minimum patch-size threshold for fledging success. This will help to enhance warbler habitat within urban areas and maintain reproductively viable habitat patches, while not halting development completely.

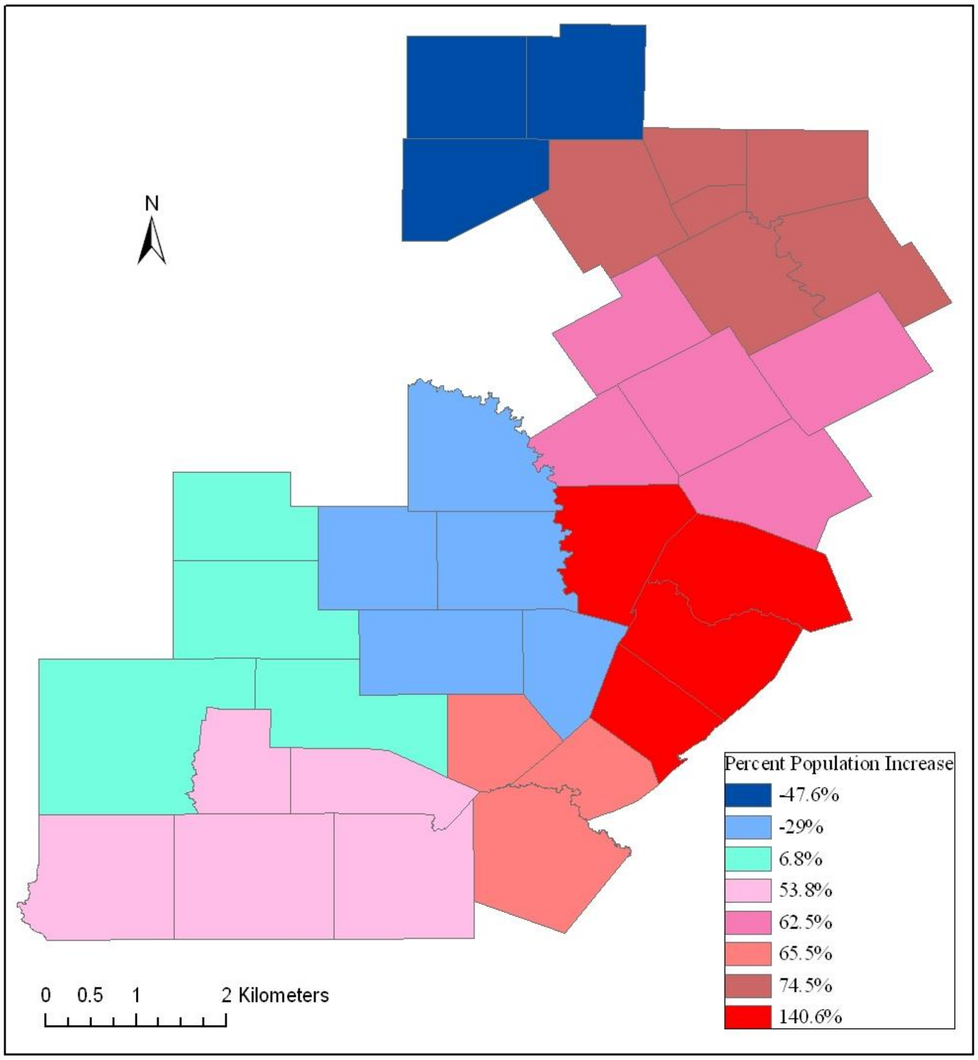

Figure 14. Expected population increase by 2060 for each recovery region within the golden-cheeked warbler range across Texas, USA.

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