CANOPY CHARACTERISTICS AFFECTING AVIAN REPRODUCTIVE SUCCESS: THE GOLDEN-CHEEKED WARBLER

A Thesis

by

JESSICA ANNE KLASSEN

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

MASTER OF SCIENCE

May 2011

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	Michael L. Morrison
Committee Members,	Gary Voelker
	Gil G. Rosenthal
Head of Department,	Thomas E. Lacher

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ABSTRACT

Canopy Characteristics Affecting Avian Reproductive Success: The Golden-cheeked Warbler. (May 2011)

Jessica Anne Klassen, B.S.; B.A., The University of Minnesota-Twin Cities

Chair of Advisory Committee: Dr. Michael L. Morrison

Habitat disturbances play a major role in wildlife distribution. Disturbances such as loss of breeding habitat and fragmentation are of particular concern for Neotropical migrant songbird populations. Additionally, different avian species respond differently to the surrounding environment at different spatial scales. Thus, multi-scale studies on bird abundance and reproductive success is necessary for evaluating the effects of habitat alterations. The golden-cheeked warbler (*Dendroica chrysoparia*) is a Neotropical migrant songbird that breeds exclusively in central Texas. In 1990, the U.S. Fish and Wildlife Service listed the golden-cheeked warbler as endangered, providing habitat loss among the list of justifications. Habitat requirements for this species are known to include mature juniper-oak (*Juniperus-Quercus*) woodlands; however, relationships between habitat characteristics and golden-cheeked warbler reproductive success remain unclear. Whereas the majority of golden-cheeked warbler research has focused on areas in the center of the breeding range, little is known about interactions between warblers and the environment at the edge of the range. Therefore, it is important to understand these relationships for successful golden-cheeked warbler management.

I investigated relationships between golden-cheeked warbler reproductive success and habitat characteristics, including canopy closure and tree species composition, at the study site and territory scale. My study took place within Kickapoo Cavern State Park and surrounding private properties in Kinney and Edwards counties in the southwest corner of the golden-cheeked warbler breeding range. I derived habitat characteristics from satellite imagery from the US Geological Survey National Land Cover Dataset (NLCD) and from field sampling. The NLCD provided data on canopy closure and tree species composition at a 30 m resolution. Additionally, I used spherical densitometers and transect evaluations to ground-truth data and take more detailed measurements. I determined reproductive success by nest monitoring and the Vickery index when nests could not be found. I monitored 80 territories across six study sites in 2009 and 2010. Reproductive success was 39.5% in 2009 and 59.4% in 2010. I found statistically significant results at the study site scale, whereas golden-cheeked warbler abundance increased as the portion of woodland increased. Similarly, I found that golden-cheeked warbler reproductive success increased at the study site scale as canopy closure increased. I did not find correlations between reproductive success and canopy closure or tree species composition at the territory scale. Results suggest that golden-cheeked warblers utilize a wider variety of habitat composition than previously thought, and habitat composition as a whole may not be the driving factors influencing warbler reproductive success in this region.

ACKNOWLEDGEMENTS

I would like to thank my committee chair, Dr. Michael L. Morrison, and my committee members, Dr. Gary Voelker and Dr. Gil G. Rosenthal, for their guidance and support throughout the course of my graduate studies. I would like to thank the Texas Department of Transportation and the Texas Parks and Wildlife Department for funding this project. I would also like to thank the Institute of Renewable Natural Resources and the Land Information Systems Lab at Texas A&M University for providing logistical and technical support. Thanks also go to all private landowners who made this study possible and field technicians, A. Borowske, A. Densborn, D. Dessecker, L. Ketzler, D. Stumbaugh, and C. Montealegre for their hard work in data collection. Lastly, I would like to thank all my lab mates for their advice and support, as well as my friends and family for their love and encouragement.

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1. INTRODUCTION

1.1 Literature Review and Problem Statement

Habitat disturbances play a major role in wildlife distribution (Jones et al. 2001) with different species responding differently to the environment at different spatial scales (Böhning-Gaese 1997, MacFaden and Capen 2002). Additionally, the abundance and reproductive success of a species may reflect the integration of multiple environmental factors across spatial scales (Chalfoun and Martin 2007, Cornell and Donovan 2010). In regards to Neotropical migrant songbirds, disturbances such as loss of breeding habitat and fragmentation are believed to be the major cause of population declines in North America (Villard et al. 1995, Flather and Sauer 1996, Twedt et al. 2001). Landscapes are currently under disruption due to agricultural expansion, urbanization, and the construction of roadways and recreational areas. Such alterations have resulted in a fragmented landscape with the remaining forest patches intermixed with areas of human modification. Fragmented areas are characterized by a loss in tree species diversity and canopy cover (Trzcinski et al. 1999). Several studies found a positive correlation between canopy cover and nest success for forest songbirds (Martin and Roper 1988, Trzcinski et al. 1999, Twedt et al. 2001), whereby increased canopy cover provides concealment from predators and brood parasites such as the brown-headed cowbird (*Molothrus ater*). Additionally, tree species diversity is beneficial to avian species dependent on a variety of macroinvertebrates for food (Seagle and Sturtevent 2005).

This thesis follows the style of the Journal of Wildlife Management.

Habitat loss is a major concern for species conservation (Reed 1995), calling for the need to effectively manage remaining habitat (Fahrig 1997, Donovan and Flather 2002).

The golden-checked warbler (*Dendroica chrysoparia*) is a Neotropical migratory passerine with a breeding range limited to approximately 35 counties (< 90,000 square kilometers) in central Texas (Pulich 1976, Deboer and Diamond 2006, Magness et al. 2006). In 1990, the U.S. Fish and Wildlife Service listed the golden-cheeked warbler as an endangered species, providing habitat loss among the list of justifications. Ashe juniper (*Juniperus ashei*), as well as several species of oak (*Quercus fusiformis*, *Q. marilandica*, *Q. stellata*), were cited as essential for supporting reproductively successful populations of golden-cheeked warblers. In detail, Ashe juniper bark provides the majority of nesting material, while the insects found on Ashe juniper and oak species provide food for adults, nestlings, and fledglings (Pulich 1976, Kroll 1980, Magness et al. 2006). Canopy cover is also essential to conceal golden-cheeked warbler nests located in the mid-story to upper canopies of trees, thus reducing the probability of nest predation and parasitism (Reidy et al. 2008). Ashe juniper distribution across Texas has become fragmented due to an increase in pasture land and development (Kroll 1980, Diamond 1997, Garriga et al. 1997) resulting in smaller patches of juniper-oak stands throughout central Texas (Pulich 1976, Wahl et al. 1990, Keddy-Hector 1992). Additionally, fire suppression and human land use practices permitted a density increase of Ashe junipers within those remaining patches (Fulendorf et al. 1997, Allen et al. 2002). Therefore, increased understanding of the degree that habitat variability affects golden-cheeked warbler abundance and reproductive success is essential to the effective conservation and management of this species.

The U.S. Fish and Wildlife Service (2003) categorized a forest as suitable golden-cheeked warbler habitat if it has at least 15 mature Ashe juniper stems (at least 4.5 m in height with a trunk diameter of at least 12.4 cm at 1.2 m above ground) per acre (38 mature Ashe juniper stems per hectare). Established guidelines provide a baseline for habitat requirements; however, variability within these guidelines, and how they may affect reproductive success across the breeding range, is not accounted for. Several studies relating habitat characteristics and golden-checked warbler reproductive success were conducted in Coryell County, Texas, on Fort Hood Military Reservation (Dearborn and Sanchez 2001, Anders and Dearborn 2004, Peak 2007). However, limited knowledge of golden-cheeked warbler activity is known outside of this area.

Additionally, studies outside the Fort Hood area involving tree species composition and canopy cover have arrived at different conclusions, thus perpetuating uncertainty for golden-cheeked warbler habitat needs. DeBoer and Diamond (2006) reported canopy cover was not correlated with occupancy, whereas Dearborn and Sanchez (2001) reported a canopy cover of at least 70% is required for reproductively successful populations. In contrast, the U.S. Fish and Wildlife Service (2003) stated that canopy closure of at least 50% is necessary for suitable golden-cheeked warbler habitat whereas Campbell (2003) stated that canopy closure could be as low as 35%.

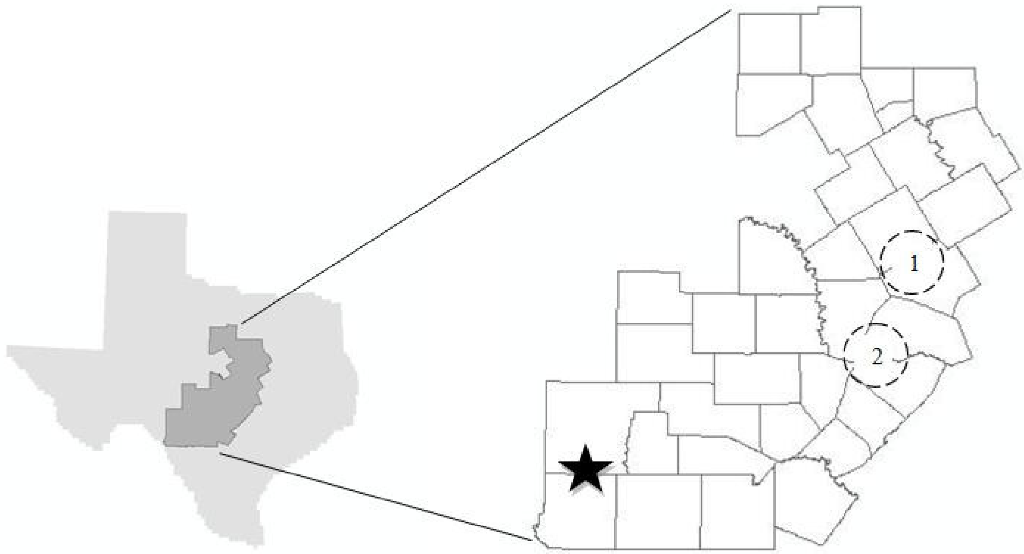

Figure 1. Map of the golden-cheeked warbler breeding range relative to the state of Texas, USA. The solid star indicates study location in Edwards and Kinney counties, whereas the dashed circles highlight areas of frequent warbler research (1 – Fort Hood; 2 – Austin).

My study addressed the relationships between habitat characteristics (canopy closure and tree species composition) and the abundance and reproductive success of golden-cheeked warblers at the southwestern edge of the breeding range (Figure 1). Since the golden-cheeked warbler is listed as a high priority species by the Texas Parks and Wildlife Department (TPWD; 2005), my research directly supports the interests laid out in the Texas Wildlife Action Plan (Texas Parks and Wildlife Department 2005) by addressing key problems facing warbler populations. In addition, my research will aid in developing appropriate management strategies to sustain optimal golden-cheeked warbler breeding habitat including 1) the degree of canopy closure and tree species that should remain during forest alterations, for either development or ranching purposes, to reduce negative impacts on golden-cheeked warblers, and 2) forest structure guidelines that will maximize reproductive success in areas managed for golden-cheeked warblers.

1.2 Study Objectives and Research Hypotheses

Objective 1**:** Determine the abundance of golden-cheeked warblers on study sites of differing habitat characteristics including canopy closure and tree species composition.

Research Hypothesis 1: Golden-cheeked warbler abundance will increase on study sites with higher canopy closure and in study sites with equal proportions of Ashe juniper and oak species.

Objective 2**:** Determine the reproductive success of golden-cheeked warblers on both the study site and territory scale of differing habitat characteristics including canopy closure and tree species composition.

Research Hypothesis 2a: Golden-cheeked warbler reproductive success, at both the study site and territory scale, will increase as canopy closure and proportions of Ashe juniper increases until reaching a threshold (Figure 2). This hypothesis is supported by golden-cheeked warblers utilizing Ashe juniper for both nesting material and foraging substrate (Pulich 1976, Kroll 1980, Magness et al. 2006). Additionally, previous research has found that increased vegetation provides increased nest concealment from predators and parasitic birds (Martin and Roper 1988, Trzcinski et al. 1999, Twedt et al. 2001).

Research Hypothesis 2b: Golden-cheeked warbler reproductive success, at both the study site and territory scale, will reach an optimum success rate in areas with equal proportions of Ashe juniper and oak species and intermediate canopy closure (Figure 2). This hypothesis is supported by golden-cheeked warblers utilizing both Ashe juniper and oak species for foraging substrates (Pulich 1976, Kroll 1980, Magness et al. 2006). Additionally, this hypothesis is supported by the natural history of the golden-cheeked warbler. Since Ashe juniper stands have increased in density over the past 100 years (Fuhlendorf et al. 1997), an intermediate level of canopy closure will mimic the habitat in which the golden-cheeked warbler originally evolved.

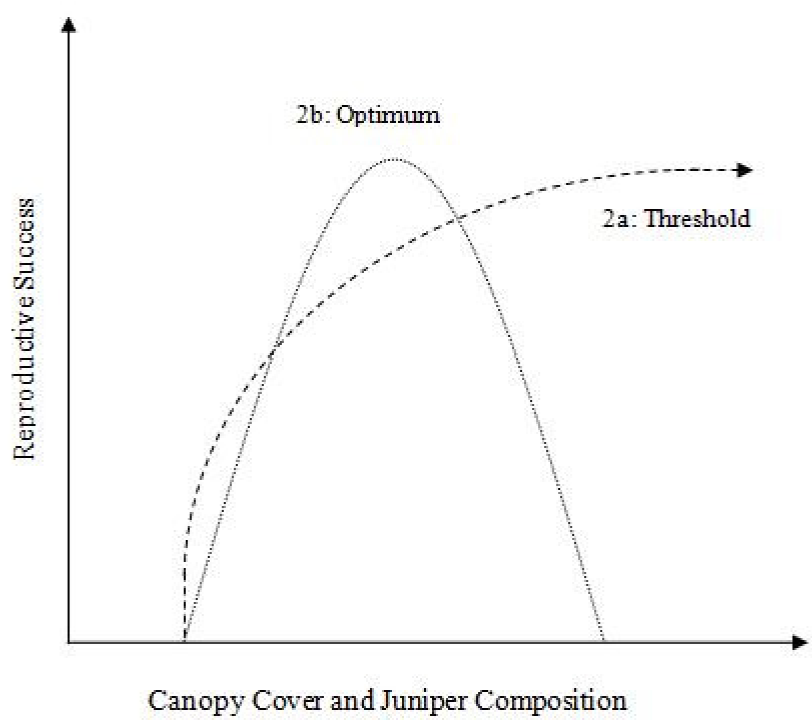

Figure 2: Hypothesized relationships between golden-cheeked warbler reproductive success and canopy closure and tree species composition. Hypothesis 2a: dashed line; Hypothesis 2b: solid line.

Objective 3**:** Develop effective and efficient forest management guidelines that would support golden-cheeked warbler breeding populations including 1) the degree of canopy closure and tree species that should remain during forest alterations, for either development or ranching purposes, to reduce negative impacts on golden-cheeked warbler reproductive success, and 2) forest structure guidelines that will maximize reproductive success in areas managed for golden-cheeked warblers.

2. METHODS

2.1 Study Area

My study took place in Edwards and Kinney counties located in southwestern Texas, USA. I selected this study region as part of an overall study of golden-cheeked warblers throughout their range, and because little research has been conducted in this area. This area is located within the Edward's Plateau ecoregion, characterized by steep canyons, narrow divides, and high-gradients (North American Regional Center of Endemism 2008). Elevation ranges from 250 to 800 meters (North American Regional Center of Endemism 2008). Mean annual precipitation is 35 cm and the mean annual temperature is 21^{o} C (North American Regional Center of Endemism 2008). During the golden-cheeked warbler breeding season (March through June), the mean precipitation is 5.4 cm and the mean temperature is 23.1^{o} C (National Oceanic and Atmospheric Administration 2010). During the course of this study, the mean precipitation and temperature during golden-cheeked warbler breeding season was 4.3 cm and 23^{o} C in 2009 and 7.6 cm and 22^{o} C in 2010 (National Oceanic and Atmospheric Administration 2010). Soil composition is mainly limestone bedrock and alkaline soils. Common tree species include Ashe juniper, live oak (*Quercus fusiformis*), and pinyon pine (*Pinus cembroides*) (North American Regional Center of Endemism 2008). Patches of mixed juniper-oak woodlands occur within rangeland used for cattle grazing. Most mature forests occur within canyons and along slopes leading up to mesas.

2.2 Patch Selection

I determined potential juniper-oak woodland patches using 1-m resolution digital orthophoto quadrangles (DOQs) taken in 2004. I defined a patch as a stand of juniper-oak forest at least 10 m from other such stands (Rich et al. 1994, Horne 2000, Butcher et al. 2010). I standardized patch size to approximately 250 ha to remove patch size as a confounding variable. This size is substantially larger than that shown to support breeding populations of warblers (i.e., > 20 ha; Butcher et al. 2010), but small enough to effectively survey in a field season (Collier et al. 2010). After I identified potential woodland patches, I overlaid canopy and landcover images from the 2001 US Geological Survey National Land Cover Dataset (Homer et al. 2007) to locate patches of different habitat characteristics. I randomly selected six patches based on the following parameters: at least two patches in two canopy closure categories (Category 1: 20%–29% closure, and Category 2: > 30% closure), and at least one patch in the three tree species composition categories (Category 1: 41–60% Ashe Juniper, Category 2: 61–70% Ashe juniper, and Category 3: 71–100% Ashe juniper). In the event I could not gain access to certain properties, I randomly selected an additional patch until I achieved access to six patches. Due to property boundaries, I was occasionally unable to gain access to the entire area of the patch. Therefore, I defined my study sites as the area of the patch in which I could access. Of the six study sites, I surveyed three in 2009 and the remaining three in 2010. I divided sampling between two years due to required sampling effort and private land availability, and labeled study sites A through F.

2.3 Territory Selection

Within the study sites, I monitored warbler territories based on the following parameters: canopy closure in three categories (Category 1: 20–30% closure, Category 2: 31–40% closure, and Category 3: > 41% closure) and tree species composition in three categories based on the percentage of Ashe juniper (Category 1: 41–60% Ashe juniper, Category 2: 61–70% Ashe juniper, and Category 3: 71–100% Ashe juniper). I studied at least 6 territories from each of the nine resulting categories, resulting in a minimum of 54 studied territories across the breeding seasons of 2009 and 2010. Since I studied different sites in 2009 and 2010, I studied different territories between the two years. I randomly selected a sub-sample of territories for statistical analysis, with the criterion that selected territories cannot be adjacent, to ensure independent sampling.

2.4 Territory Mapping

Within each study site, I conducted point-transect surveys in order to locate golden-cheeked warblers. Each transect was 100 m apart, with the placement of the first transect chosen randomly. I positioned survey points 50 m apart on each transect. This spacing is described by Buckland (2006) as effective for surveying forest song birds and allows for randomization (through the random placement of the first transect) as well as interspersion (through the systematic placement of subsequent transects). I conducted surveys when songbirds are most vocally active, beginning at sunrise and continuing for 4 hours (Buckland 2006). I spent a total of 7 minutes at each point. The first minute allowed for birds to resume normal activity after my arrival (Martin and Geupel 1993, Buckland 2006). During the following 6 minutes, I recorded estimated distance and direction of all detected singing male golden-cheeked warblers with a GPS unit. Once males were detected, I mapped out territories by marking GPS locations of singing perches where I detected a male. I defined a territory as the presence of a singing male in a general area for over 4 weeks. In order to construct a territory, I took a minimum of 10 GPS locations over the course of 3 or more days (Butcher 2008). I visited each territory once every 4–5 days during the duration of the breeding season (March through June).

Mackenzie and Royle (2005) suggested surveying a sample unit a minimum of 3 times throughout a study for species of high detection probability (> 0.5) in order to accurately determine occupancy. The detection probability of golden-cheeked warblers is between 0.6 and 0.8 for point counts that last for 5 minutes and are visited at least 6 times throughout the season (Collier et al. 2010). These requirements are met by my study's protocol.

I used minimum convex polygons in ArcMap™ 9.2 to determine territory size and placement. I removed outlying points because those points may be due to measurement error or rare movement events. I considered outliers to be points in which a bird was located over 200 m outside of the primary survey area on only 1 occasion during the breeding season.

2.5 Reproductive Index

Once I mapped territories, I used active nest searching, as well as a reproductive index developed by Vickery et al. (1992) to determine the level of golden-cheeked warbler reproductive activity. I followed the nest searching protocols established by Martin and Geupel (1993). While in a territory, I watched for behavioral cues that indicated an active nest. Such behaviors include copulation events and nest material carries. Since females generally spend more time near the nest site, I gave more attention to female location and behavior during nest searching. I spent at least 30 minutes within a territory every 4–5 days until I found a nest to maximize detection probability, but reduce stress upon the bird (Martin and Geupel 1993). Once I located a nest, I used a camera system to record nest activity. This system consisted of a weatherproof bullet camera with a 1/3" (8.5 mm), 3.6 mm lens and infrared lighting (Rainbow, Costa Mesa, CA) to record night events. I placed the cameras 1–2 m away from the nest in order to capture all nest activities, but minimize nest disturbance. A 15 m cable connected the camera to a digital video recorder ([DVR], Detection Dynamics, Austin, TX) and a 12v 26ah battery (Batteries Plus, Hartland, WI). I also used solar panels (Suntech, San Francisco, CA) to supplement battery power. I used 8 GB SD memory cards and a time-lapsed recording of 5 frames per second to maximize data storage on the DVR. I checked the camera system biweekly to change data cards and to check nest activity. The camera system remained in place until a nest fledged or failed. Since golden-cheeked warblers nest in canopies, I was not able to access each nest visually or for camera set-up. In this case, the behaviors used for the Vickery index (described below) provided an accurate estimate of nest activity.

The Vickery index (VI) was developed in order to record reproductive activity levels (Table 1) based on the behavior exhibited by birds, without requiring visual access to nest contents, known location of the nest, or disturbance to the birds themselves. Whereas direct nest monitoring is preferred, the VI is able to supplement reproductive data in the event that a nest cannot be found. However, noting the behaviors required to assign a VI rank mirror the behaviors Martin and Geupel (1993) layout as essential to locating a nest. Therefore, active nest searching and observing bird behaviors to assign a VI rank can occur simultaneously. Studies by Christoferson and Morrison (2001) and Rivers et al. (2003) tested the effectiveness of this index and were able to predict the correct level of reproductive activity 61 – 79% of the time. Birds assigned an incorrect VI in these studies were usually given a rank that underestimated their reproductive activity. For the purposes of this study, underestimating reproductive activity is preferable to overestimating in order to avoid exaggerated claims on reproductive success.

Table 1. Vickery reproductive index used to determine reproductive success of golden-cheeked warblers.

Vickery Rank	Description
1	Territorial male present ≥ 4 weeks
2	Female observed in territory during ≥ 1 survey
3	Evidence of nest building; male observed carrying food to presumed female on nest; female observed laying or incubating eggs
4	Female observed carrying food to presumed nestlings; male observed feeding nestlings
5	≥ 1 fledgling of the same species as the parent observed with the pair

Either by nest monitoring, or by implementation of the VI, I was able to detect which territories successfully fledged young. Fledglings were easy to detect because they often vocally food-beg to nearby foraging adults (personal observation). Fledglings also tend to stay within their natal territories for two weeks after fledging (Butcher 2008), which lowers the odds of counting fledgling groups more than once.

2.6 Habitat Characteristics

2.6.1 Canopy Closure

I defined canopy closure as the proportion of the sky obscured by vegetation when viewed from a single point (Jennings et al. 1999). Due to the natural variation of the landscape, canopy closure is best determined from randomly stratified points within the area of interest (Johansson 1985, Jennings et al. 1999). Therefore, I used ArcMap 9.2 to systematically lay a grid of points across each study site so that each point was 20 m away from all other points. This protocol allowed for randomization (through the random placement of the first point) as well as interspersion (through the systematic placement of subsequent points). For the territory scale, I took canopy closure measurements at every point that fell within the territory boundaries delineated by territory mapping. For the study site scale, I randomly choose which point outside a territory to measure first, and then took canopy closure measurements at every fourth point. I also took canopy closure measurements at located nest sites.

I measured canopy closure with a spherical densitometer while facing in four cardinal directions at each point as prescribed by Stickler (1959). I averaged the resulting four measurements to get the recorded canopy closure at the point of interest. Once I completed measurements for all points, I could calculate the average canopy closure for each territory and study site.

2.6.2 Tree Species Composition

I used DOQs provided by the Institute of Renewable Natural Resources at Texas A&M University to determine juniper-oak composition at a 1x1 m resolution. I ground-truthed these data at the systematic points described in the canopy closure section: measuring every point within a territory, and every fourth point within a study site. At each point, I recorded all tree species that had a portion of their trunk or canopy within the frame of view of the spherical densiometer. I defined a tree as a woody stem at least 2 m tall (Wilder et al. 1999).

3. ANALYSIS

3.1 Density of Golden-cheeked Warbler Territories

I calculated territory density for each study site by dividing the total number of territories within a study site by the area within a study site. Since my study sites had several openings of scrub/shrub vegetation within the woodland vegetation, often representing over 40% of the study area, I also calculated territory density by dividing the number of territories within a study site by the area of woodland present within a study site. I used scatter plots to explore the relationships between canopy closure, Ashe juniper composition, and oak composition against golden-cheeked warbler territory density at the study site scale. Because of small sample sizes, I could not assume the data were normally distributed, so I used a Spearman's correlation (Zar 1984:318–320) to identify relationships between golden-cheeked warbler territory density and vegetative characteristics. I examined the relationships between golden-cheeked warbler territory density and (1) canopy closure, (2) Ashe juniper composition, and (3) oak composition ($\alpha = 0.05$).

3.2 Reproductive Success

I used scatter plots to explore the relationships between canopy closure, Ashe juniper composition, and oak composition against golden-cheeked warbler pairing success and reproductive success, at both the study site and territory scale. I compared the mean pairing and territory success percentages at the study site scale between all six study sites. I considered territories successful if adults were seen with fledglings at least once throughout the field season. I considered a male paired if a female was observed at least once within the territory, and unpaired if a female was never detected.

I randomly selected a sub-sample of territories for statistical analysis at the territory scale, with the criterion that selected territories cannot be adjacent, to ensure independent sampling. Since the largest number of territories that satisfied these criteria was 42, I used these territories in the analysis in order to maximize sample size. With these 42 territories, I performed a logistic regression (Ott and Longnecker 2001:701–708) analysis ($\alpha = 0.05$) with pairing success and territory success (yes/no) as the dependent variables. I entered the independent variables – canopy closure, Ashe juniper composition, and oak composition – as all possible subsets.

4. RESULTS

4.1 Density of Golden-cheeked Warbler Territories

Canopy closure ranged from 25% to 35% within a study site and the standard deviation ranged from 17 to 43. Ashe juniper composition ranged from 52% to 78%, whereas oak composition ranged from 11% to 20% within study sites. Golden-cheeked warbler territory density within study areas ranged from 0.03 territories/ha to 0.07 territories/ha. However, territory density was larger when only considering areas of woodland rather than total study area, with territory density ranging from 0.07 territories/ha of woodland to 0.10 territories/ha of woodland (Table 2).

Table 2. Density of golden-cheeked warbler territories in six study sites with differing canopy closure, tree species composition, and area.

Study Site	% Canopy Closure	Canopy Closure Standard Deviation	% Ashe Juniper[1]	% Oak[1]	Study Site Area (ha)	Area of Woodland Vegetation (ha)	Total Number of Territories	Study Site Density[2]	Woodland Area Density[3]
A	25	28	71	11	311	208	15	0.05	0.07
B	25	28	68	13	241	141	10	0.04	0.07
C	35	28	78	20	309	275	23	0.07	0.08
D	35	29	55	17	250	177	18	0.07	0.10
E	26	30	52	13	262	128	9	0.03	0.07
F	32	33	71	12	137	74	5	0.04	0.07

[1]Other tree species were present within the study sights, but are not shown due to their low (< 5%) total percentage within the study sites
[2]Study site density=total number of territories/area surveyed
[3]Woodland habitat area density=total number of territories/area of woodland present within study area

Whereas I did not find a statistical relationship between golden-cheeked warbler study area territory density and canopy closure (r^2 =0.618, df = 5, P = 0.191), I found that woodland area territory density was positively correlated with canopy closure (r^2

=0.845, df = 5, P = 0.034) (Figure 3). I did not find a pattern between the proportion of Ashe juniper and study area territory density (r^2 =0.530, df = 5, P = 0.280) or woodland territory density (r^2 =0.068, df = 5, P = 0.899). I found a positive relationship between the proportion of oak and study area territory density (r^2 =0.874, df = 5, P = 0.023). Although not significant at 0.05, woodland territory density showed a nearly significant relationship with oak composition (r^2 =0.778, df = 5, P = 0.069) (Figure 4). Lastly, I found a strong positive correlation between density of golden-cheeked warbler territories and the amount of woodland habitat present within a study site (r^2 =0.971, df = 5, P = 0.001) (Figure 5).

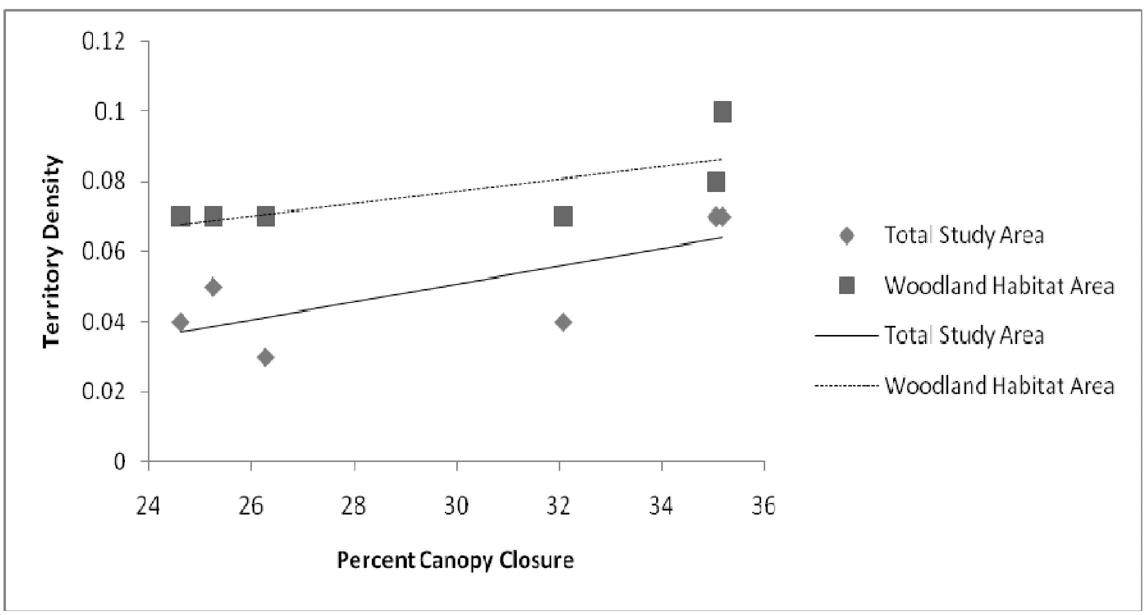

Figure 3. Density of golden-cheeked warbler territories in study sites of different canopy closure. Density calculated in two methods: one using the total study area (P = 0.191), and the other using only the area consisting of woodland (P = 0.034).

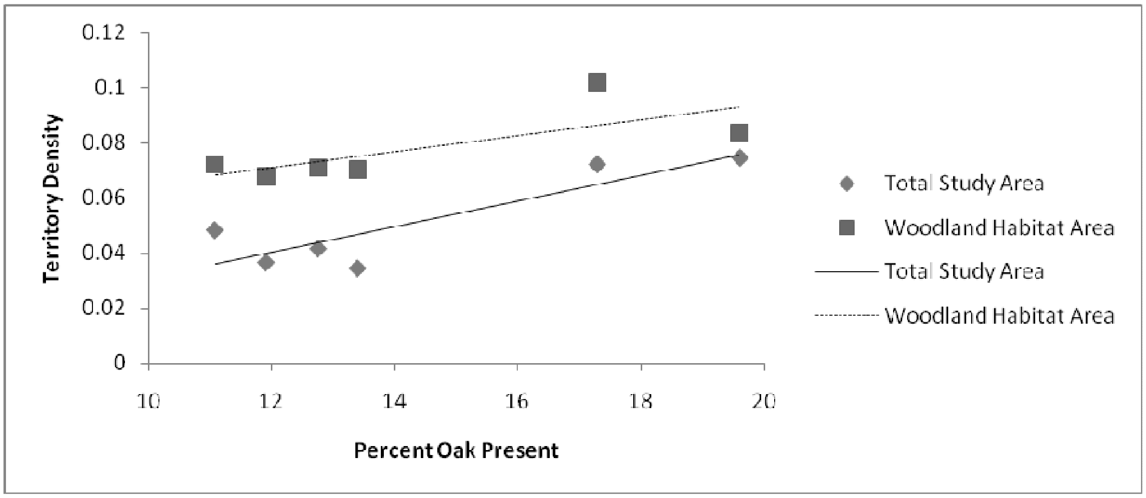

Figure 4. Density of golden-cheeked warbler territories in study sites of different oak compositions. Density calculated in two methods: one using the total study area (*P* = 0.023), and the other using only the area consisting woodland (*P* = 0.069).

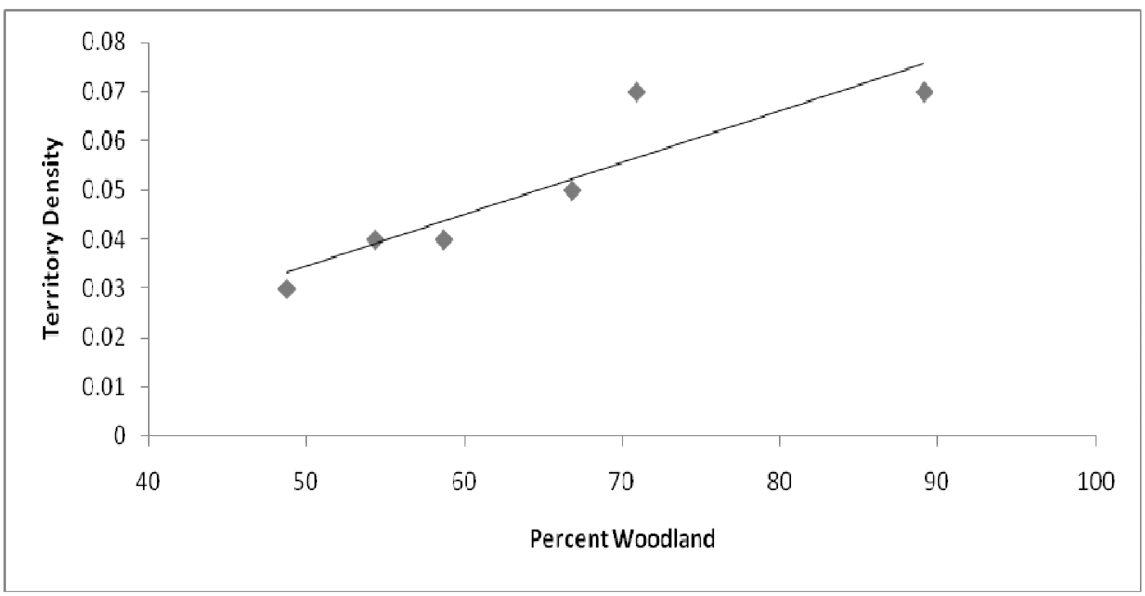

Figure 5. Density of golden-cheeked warbler territories in study sites with different proportions of woodland habitat (*P* = 0.001).

4.2 Reproductive Success

I monitored 80 territories across six study sites during the 2009 and 2010 field seasons. Overall pairing success across the six study sites for 2009 and 2010 was 82.5% (n = 80). Reproductive success across both 2009 and 2010 was 47.5% (n = 80), but increased to 57.6% if only looking at the reproductive success of territories with paired males (n = 66). At the study site scale, I did not find significant correlations between canopy closure (r^2 =0.200, df = 5, P = 0.704), Ashe juniper (r^2 =0.200, df = 5, P = 0.704) or oak (r^2 =0.543, df = 5, P = 0.266) composition, or presence of woodland (r^2 =0.371, df = 5, P = 0.468) with pairing success. Similarly, I did not find a significant correlation between Ashe juniper (r^2 = -0.086, df = 5, P = 0.872) or oak (r^2 =0.429, df = 5, P = 0.397) composition or presence of woodland (r^2 =0.257, df = 5, P = 0.623) with reproductive success at the study site scale. However, I found a statistically significant positive relationship at the study site scale between canopy closure and reproductive success (r^2 =0.943, df = 5, P = 0.005) (Figure 6).

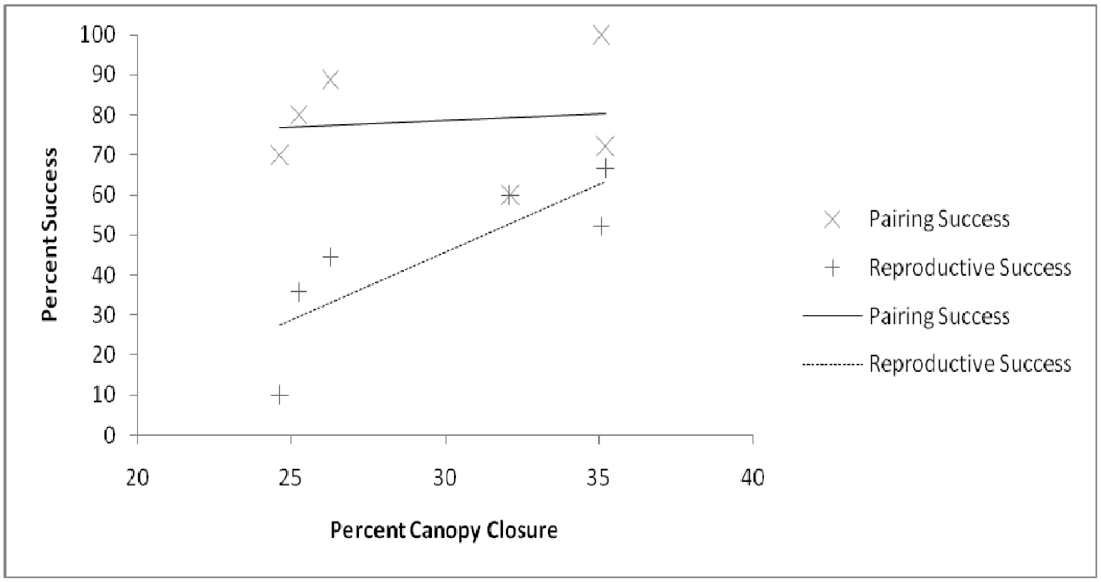

Figure 6. Golden-cheeked warbler pairing (P = 0.841) and reproductive success (P = 0.042) with increasing canopy closure at the study site scale.

At the territory scale, canopy closure ranged from 16% to 74%. Ashe juniper composition ranged from 36% to 86%, whereas oak composition ranged from 3% to 43% within territories (Table 3). Logistic regression analyses showed insignificant results between canopy closure, Ashe juniper composition, and oak composition with pairing success (χ^2 = 5.63, df = 3, P = 0.131) and reproductive success (χ^2 = 1.32, df = 3, P = 0.725). Territories that paired had 10% less canopy closure than territories that did not pair, whereas territories that successfully fledged young had 3% more canopy closure than territories that did not fledge young. Territories that paired had 8% more Ashe juniper than territories that did not pair, whereas territories that successfully fledged young had 3% more Ashe juniper than territories that did not fledge young. Territories that paired had 22% more oak than territories that did not pair, whereas territories that successfully fledged young had 5% more oak than territories that did not fledge young.

Table 3. Summary statistics of the vegetative characteristics found within the 80 studied territories.

	Mean	**Standard Deviation**	**Minimum**	**Maximum**
% Canopy Closure	38	11	16	73
% Ashe Juniper	64	12	36	86
% Oak	20	9	3	43
% Woodland[1]	76	23	23	100
Territory Size (ha)	3.30	2	0.49	8.15
Tree Height (m)	4.5	1	3	7

[1]Percent woodland is defined at the proportion of trees taller than 2 m comprising a territory.

I also did not find a significant relationship between territory size and pairing (χ^2 = 0.58, df = 2, *P* = 0.5616) or reproductive success (χ^2 = 0.02, df = 2, *P* = 0.9863), or the amount of woodland present with pairing (χ^2 = 0.27, df = 2, *P* = 0.7914) or reproductive success (χ^2 = -.029, df = 2, *P* = 0.7694). Territories that paired were 9% larger than territories that did not pair, whereas territories that successfully fledged young were 1% larger than territories that did not fledge young. Territories that paired had 1% more woodland than territories that did not pair, whereas territories that successfully fledged young had 2% less woodland than territories that did not fledge young.

4.3 Nest Site Descriptions

I located six nests during the 2009 and 2010 field seasons. Five nests were located within similar habitat with canopy closure about 60% in trees taller than 3 m. However, one nest was located in scrub/shrub habitat in a tree 2 m tall. Since this nest was located at the top of an isolated tree, it had no concealment from high or neighboring branches and was recorded to have 0% canopy closure. This nest successfully fledged young. I was able to install cameras on three nests; two of these nests failed due to depredation by a western scrub-jay (*Aphelocoma californica*) (Table 4).

Table 4. Nest success, vegetative characteristics, and camera placement of nests located during the 2009–2010 field seasons.

Nest	Substrate Height (m)	Nest Height (m)	% Canopy Closure	Camera Installed (Y/N)	Fledge (Y/N)
1	5	3.5	55	Y	Y
2	5.5	5	67.5	Y	N
3	2	1.8	0	N	Y
4	4	3.5	60	Y	N
5	6	5.5	62.5	N	Y
6	4	3.5	67.5	N	Y

5. DISCUSSION

My first objective was to determine the abundance of golden-cheeked warblers on study sites of different canopy closure and tree species density at the edge of the breeding range. I hypothesized that warbler density would increase with canopy closure and with more equal proportions of Ashe juniper and oak species, but my results did not support these relationships. Whereas golden-cheeked warblers are usually associated with canopy closure of 50% or greater (Wahl et al. 1990, Dearborn and Sanchez 2001, Campbell 2003), I found established territories the successfully fledged young in study sites with as low as 24% canopy closure. These findings expand our knowledge of the vegetation types in which golden-cheeked warblers will occupy. However, the territory density within my area is about six fold less than density measures in areas with higher canopy closure in neighboring counties (e.g. Lackey 2010), suggesting that the vegetative composition within Edwards and Kinney counties is unable to support higher densities of breeding birds, possibly because of limited habitat or food availability.

Although I did not find patterns between the amount of Ashe juniper and territory density, territory density did increase as the amount of oak species within a study site increased. New research suggests that oak species play a role in temporal macroinvertebrate food availability (Texas A&M University, unpublished data), particularly at the beginning of the breeding season (March through April), whereas Ashe juniper is the primary foraging substrate later in the breeding season (May through June; Ladd and Gass 1999; Texas A&M University, unpublished data). Since the oak composition within my study sites was rather low (ranging only 11–20% of the total tree composition) in comparison to other portions of the breeding range (Heilbrun et al. 2009), it is possible that oak species are a limiting resource in the Edward and Kinney counties portion of the golden-cheeked warbler breeding range, and thus, more warblers would occupy areas of greater oak densities. However, my small number of study sites may not have been sufficient to fully examine these relationships. Further studies encompassing a greater number of study areas will reveal detailed patterns in golden-cheeked warbler territory density and habitat characteristics.

My second objective was to determine the reproductive success of golden-cheeked warblers on both the study site and territory scale of different canopy closure and tree species composition. For this objective, I had two competing hypotheses: reproductive success would increase with canopy closure and Ashe juniper composition until reaching an optimum level, or threshold relationship would exist. Reproductive success at the study site scale increased as canopy closure increased, matching previous songbird studies (Martin and Roper 1988, Trzcinski et al. 1999, Twedt et al. 2001) and suggesting canopy closure aides in concealment from predatory species or protection from harsh weather, such as intense sun or rain. At the territory scale however, my results did not support either hypothesis or suggest any other discernable pattern. This lack of correlation suggests that canopy closure and tree species composition are not the primary factors influencing golden-cheeked warbler reproductive success at this scale in this portion of their breeding range.

Perhaps my most interesting finding was not necessarily the particular vegetative characteristics of territory locations, but rather the range of characteristics in which I found breeding warblers. Whereas typical golden-cheeked warbler habitat is characterized as continuous juniper-oak woodlands, I found territories comprised of varying degrees of juniper-oak woodlands and scrub/shrub vegetation. Most notable is that the scrub/shrub vegetation is used by warblers during foraging and singing activities (personal observation), and even used as successful nesting locations.

My study took place at the edge of typical breeding range, where the juniper-oak woodlands of central Texas transition to the scrub/shrub grasslands of south Texas. At such range peripheries, we would expect certain relationships between golden-cheeked warbler productivity and habitat composition. Kirkpatrick and Barton (1997) discussed that deleterious effects of gene flow are often present at the peripheries of a species range. This follows the assumption that peripheral populations receive gene flow from the center of the species' range, and that these genes are suitable for conditions found only at the center of the range, but inhibit adaptation in peripheral regions due to a lack of genetic diversity. Whereas it has been hypothesized that areas within the center of golden-cheeked warbler breeding habitat function as source populations for the rest of the range (Anders and Dearborn 2004), other research suggests otherwise. Ladd and Gass (1999) reported high levels of philopatry, with adults usually dispersing < 1 km from their location the previous year. Additionally, natal dispersal is about 9 km for males and 3 km for females (Ladd and Gass 1999), making dispersal from center populations to areas at the edge of the breeding range unlikely. With this pattern of low dispersal rates and increased habitat fragmentation, concern has been expressed regarding the genetic isolation of breeding populations (U.S. Fish and Wildlife Service 1992). However, Lindsey et al. (2008) assessed genotypes throughout the golden-cheeked warbler breeding range and found no evidence of isolated lineages or bottlenecks.

If a lack of genetic adaptive ability was present at the peripheries of golden-cheeked warbler breeding range, we would expect low levels of reproductive success and decreasing abundance in localized populations. Whereas the duration of my study does not allow for long-term population estimates, reproductive success rates can serve as an indication of population growth or decline. I found the reproductive success within Edwards and Kinney counties to be about 20–40% lower in comparison to other parts of the breeding range during 2009 and 2010 (Texas A&M University, unpublished data). However, the reproductive success rate was in my study region was still comparable to the reproductive success rates of other forest songbirds (Vickery et al. 1992, Christoferson and Morrison 2001, Twedt et al. 2001). This suggests that, while my study area on the periphery of the breeding range may be lower in comparison to the rest of the range, it is not low enough to indicate regional population declines. As stated by Sagarin et al. (2006), the range of a species is based on several factors that interact in complex ways across geographic areas and through time. Therefore, I would suggest caution when making broad generalizations about the abundance and reproductive success of species based on its location within the known range.

I propose that golden-cheeked warbler occupancy and reproductive success in my study region is not a function of local adaptation, but rather conditions the warbler is already pre-adapted to inhabit. Historically, it is thought that golden-cheeked warblers bred in landscapes that were naturally patchy, and juniper-oak woodlands were not very extensive (Pulich 1976, Kroll 1980). Therefore, the golden-cheeked warbler must have had various successional stages available throughout its breeding range, similar to the landscapes in Edwards and Kinney counties. Increased reproductive success in larger woodland patches with higher canopy closure could be attributed to a decrease in predation rates. Previous studies have correlated increased predation rates with increases in woodland edge (Peak 2007, Reidy et al. 2009). Additionally, nest predation by corvids is also reported to be greater in more fragmented landscapes (Rich et al. 1994, Donovan et al. 1997), which is supported by the two western scrub-jay predations I documented with nest cameras. I suggest further research in the predator assemblage and predation rates in this portion of the golden-cheeked warbler breeding range to fully understand these dynamics. Whereas golden-cheeked warbler reproduction may have benefited by the growth of larger woodland stands, it should not be surprising that golden-cheeked warbler populations occupy and successfully reproduce in less dense habitat.

6. CONCLUSION

The Texas Parks and Wildlife (TPWD) service guidelines describe golden-cheeked warbler habitat as containing Ashe junipers at least 4.5 m tall with an average canopy height of at least 6 meters (Campbell 2003). Overall canopy cover exceeds 35%, with oak species comprising at least 10% of the canopy cover. I consistently found successfully breeding warblers in areas study areas with as low as 25% canopy closure, and in territories with as low as 20% canopy closure. Additionally, the canopy height within Edwards and Kinney counties is about 4.5 m, falling 1.5 meters shorter than TPWD guidelines. Whereas study areas contained more than 10% oak species, several successful territories contained as low as 3% oak composition.

Based on the vegetative composition and structure of breeding golden-cheeked warbler populations in Edwards and Kinney counties, the current descriptions of golden-cheeked warbler breeding habitat requirements used by management agencies and other land managers will need to expand to include areas of lower canopy cover, canopy height, and oak composition.

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