

THE IMPACT OF A FOREST PATHOGEN ON THE ENDANGERED  
GOLDEN-CHEEKED WARBLER

A Thesis

by

LAURA ROE STEWART

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 2012

Major Subject: Wildlife and Fisheries Sciences

The Impact of a Forest Pathogen on the Endangered Golden-cheeked Warbler

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Approved by:

Chair of Committee,	Michael Morrison
Committee Members,	David Appel
	Roel Lopez
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## ABSTRACT

The Impact of a Forest Pathogen on the Endangered Golden-cheeked Warbler.

(May 2012)

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Chair of Advisory Committee: Dr. Michael L. Morrison

Oak wilt is a fatal disease of oaks caused by the fungus *Ceratocystis fagacearum*. Loss or degradation of habitat due to the disease may negatively affect the federally endangered golden-cheeked warbler (*Setophaga chrysoparia*). To assess the impact of oak wilt on golden-cheeked warblers, I investigated its influence on habitat selection and quality. I used remote sensing to estimate the amount of potential golden-cheeked warbler habitat currently affected by oak wilt, to predict the amount of potential habitat likely to be affected in the near future, and to assess the current probability of warbler occupancy in areas affected by oak wilt historically. I also quantified vegetative characteristics to assess overstory vegetation and regeneration in areas affected by the disease. I found proportional occupancy and territory density in unaffected areas to be, respectively, 3.5 and 1.8 times that of affected areas. Pairing success was 27% lower for territories containing oak wilt but fledging success was not affected. I estimated that 6.9% of potential golden-cheeked warbler habitat and 7.7% of the total area within my study region was affected by oak wilt in 2008. By 2018, I predicted that 13.3% of potential golden-cheeked warbler habitat and 16.0% of the study region would be

affected by the disease. Using historical imagery, I found that areas affected by oak wilt in the past are less likely to be classified as current potential warbler habitat than areas never affected by the disease. I found no differences between the understory vegetation of affected and unaffected areas but that oaks were more common in the overstory than in the understory, suggesting that species composition in affected areas may shift in the years following an outbreak of the disease. My results suggest that the presence of oak wilt negatively influences habitat selection and quality for golden-cheeked warblers, likely due to reduced canopy cover in susceptible oak species. Additionally, oak wilt frequently occurs in golden-cheeked warbler habitat and will continue to spread into warbler habitat in the coming years. Future management efforts should address the threat oak wilt poses to golden-cheeked warblers by incorporating applicable preventative measures.

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## CHAPTER I

### INTRODUCTION

Forest pathogens can substantially modify the vegetative characteristics of forest stands. These changes can in turn alter the extent to which animal species utilize impacted areas (Castello et al. 1995). If the pathogen has the potential to occur across a broad spatial extent, the consequences for wildlife could be considerable. Monahan and Koenig (2006) predicted that the abundance of 5 oak-dependent avian species, acorn woodpecker (*Melanerpes formicivorus*), Nuttall's woodpecker (*Picoides nuttallii*), Hutton's vireo (*Vireo huttoni*), western scrub-jay (*Aphelocoma californica*), and oak titmouse (*Baeolophus inornatus*), would decline by 25 - 68% in response to loss of coastal live oak (*Quercus agrifolia*) due to sudden oak death in California. Such declines would be especially detrimental for any species whose range is restricted to areas impacted by similar forest pathogens.

Oak wilt is a forest pathogen with both a broad spatial distribution and a high potential to impact wildlife. The disease is caused by infection by a fungus, *Ceratocystis fagacearum* (Bretz) Hunt which causes blockages to form in the vascular tissues of the host (Gibbs and French 1980). While oak wilt can occur in all oak species (*Quercus* spp.), its effects are most pronounced in red oaks (subgenus *Erythrobalanus*) and live

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oak (*Quercus fusiformis*; Appel 1995). Oak wilt has been identified throughout the eastern and central portions of the United States as far south as Texas where it occurs throughout most the breeding range of the federally endangered golden-cheeked warbler (*Setophaga chrysoparia*; Texas Forest Service 2009).

The golden-cheeked warbler is a neotropical migrant endemic to the oak - Ashe juniper (*Quercus* spp. - *Juniperus ashei*) woodlands of central Texas during the breeding season (Ladd and Gass 1999). This species was placed on the endangered species list due to past and ongoing habitat loss (USFWS 1990). Because oaks are a necessary component of golden-cheeked warbler habitat, loss of live and red oaks caused by oak wilt could result in the destruction or degradation of warbler habitat. During the breeding season, golden-cheeked warblers are typically found in mixed oak - juniper woodlands with 50 - 100% canopy cover in the mid and upper layers (Ladd and Gass 1999).

Deciduous oaks are an important component of warbler habitat as their density has been found to be positively correlated with warbler density (Wahl et al. 1990). At the territory scale, oak wilt would likely reduce overall density and canopy cover of oaks resulting in a decrease in the availability of arthropod food, especially early in the breeding season when golden-cheeked warblers preferentially forage on this particular substrate (Wahl et al. 1990, Marshall 2011). At a larger scale, Magness et al. (2006) found that  $\geq 40\%$  of the surrounding landscape must be composed of woodland for golden-cheeked warblers to occur at a given location and that  $\geq 80\%$  must be woodland for the probability of occupancy to exceed 0.5. Collier et al. (2012) found woodland patch size and percent woodland composition of the surrounding landscape to be positively correlated with the

probability of occupancy by golden-cheeked warblers. Thus, the more open condition resulting from loss of oaks may negatively impact the suitability of large areas.

Similar to several other species that breed in mature forests (Marshall et al. 2003, Vitz and Rodewald 2006), post-breeding golden-cheeked warblers often disperse from their territories into habitats of a more open condition before migrating to the wintering grounds (Ladd and Gass 1999). In a study of post-breeding habitat use, golden-cheeked warblers were observed most frequently in patches with 0 – 25% canopy cover (M. Hutchinson, Texas A&M University, personal communication). Thus, areas that have lost many oaks to oak wilt may still provide habitat late in the season.

In addition to its immediate effects, the changes oak wilt produces in oak - juniper woodlands could last well into the future. Once the disease has moved through a stand, the stand may begin to regenerate. However, the density and species composition of the regenerating stand will likely be altered from pre-infection conditions. Menges and Loucks (1984) reported a strong possibility that oak wilt will cause stand composition to shift away from red oaks towards other species such as black cherry (*Prunus serotina*), sugar maple (*Acer saccharum*), and various species of white oak in Wisconsin. Alternatively, Tryon et al. (1984) found no significant change in stand composition post-oak wilt infection in West Virginia.

Though oak wilt has been confirmed in 29 of the 34 counties known to be occupied by golden-cheeked warblers (Texas Forest Service 2009), few studies have addressed the extent to which it occurs within warbler habitat. Appel and Camilli (2008) found that 18% of oak wilt disease centers in Coryell and Bell counties, located in the

north-central portion of the warbler's range, were located in golden-cheeked warbler habitat. Oak wilt also has been observed in golden-cheeked warbler habitat on Balcones Canyonlands National Wildlife Refuge, Travis county (C. Sexton, USFWS, personal communication), and at the former Kerrville State Recreation Area, Kerr county (Wahl et al. 1990).

To assess the potential impact of oak wilt on golden-cheeked warblers, I employed two approaches. First, I investigated the immediate impact of the disease by examining its influence warbler habitat selection and quality. Second, I used remote sensing to assess the historical, current, future distribution of the disease as it pertains to the warbler. I also quantified vegetative characteristics to assess overstory vegetation and regeneration in areas affected by the disease. Results of my study will inform us about the threat oak wilt poses to golden-cheeked warblers and will help determine the importance of oak wilt control to future management efforts.

## CHAPTER II

### THE EFFECT OF A FOREST PATHOGEN ON HABITAT QUALITY AND SELECTION BY THE ENDANGERED GOLDEN-CHEEKED WARBLER

#### **SYNOPSIS**

Oak wilt is a fatal disease of oaks caused by the fungus *Ceratocystis fagacearum*. Loss or degradation of habitat due to the disease may negatively affect the federally endangered golden-cheeked warbler (*Setophaga chrysoparia*). To assess the impact of oak wilt on golden-cheeked warblers, I investigated its influence on habitat selection by comparing proportional occupancy, territory density, and post-breeding warbler density between affected and unaffected portions of 25 study sites. I also assessed the influence of oak wilt on habitat quality by comparing the reproductive outcome of territories in unaffected and affected areas. I found proportional occupancy and territory density in unaffected areas to be, respectively, 3.5 and 1.8 times that of affected areas. Pairing success was 27% lower for territories containing oak wilt but fledging success was not affected. My results suggest that the presence of oak wilt negatively influences habitat selection and quality for golden-cheeked warblers, likely due to reduced canopy cover in susceptible oak species. Future management efforts should address the threat oak wilt poses to golden-cheeked warblers by incorporating applicable preventative measures.

#### **INTRODUCTION**

Pathogens can substantially modify the vegetative characteristics of forest stands. These changes can in turn alter the extent to which animals use impacted areas (Castello

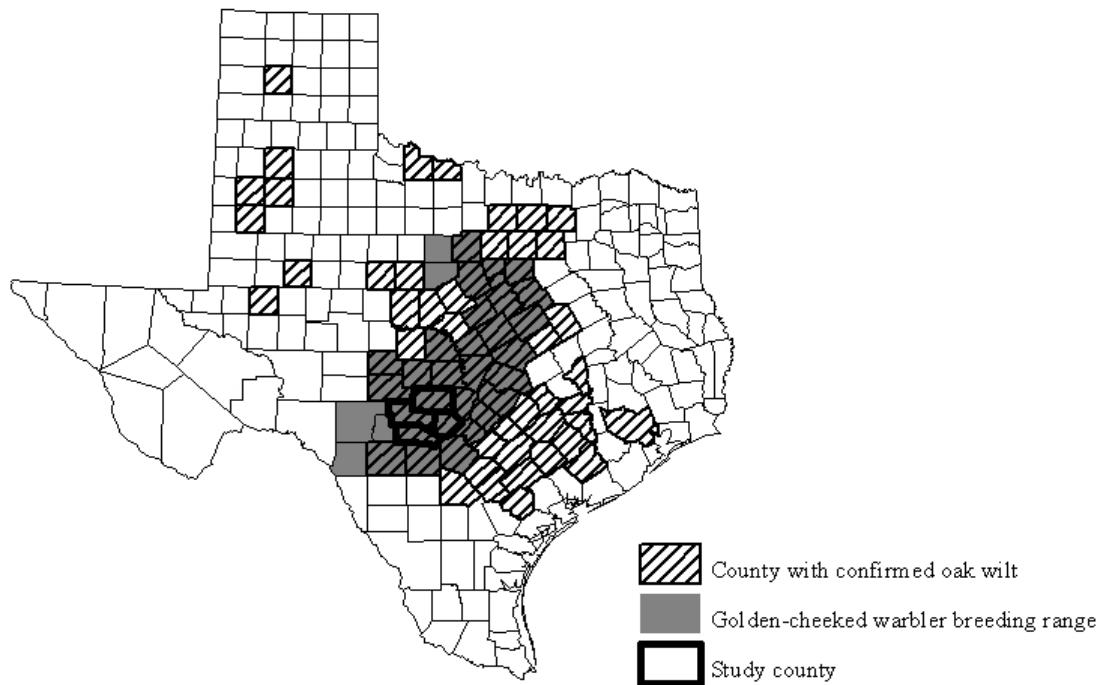


et al. 1995). Alterations may affect animals negatively (Bennetts et al. 1996, Garnett et al. 2004) or positively (Elkinton et al. 1996, Rabenold et al. 1998), by altering the availability of nesting and roosting sites, the availability of forage and foraging substrate, predation risk, ability to attract a mate, and microclimatic conditions (Loo 2009).

Oak wilt is a disease of oaks caused by infection by a fungus, *Ceratocystis fagacearum* (Bretz) Hunt (Gibbs and French 1980) that has a high potential to impact wildlife. Infection by *C. fagacearum* causes blockages to form in the vascular tissues of the host; the outcome of which varies by individual and species. While oak wilt may occur in all oak species (*Quercus* spp.), its effects are most pronounced in red oaks (subgenus *Erythrobalanus*) such as Texas red oak (*Q. texana*) and blackjack oak (*Q. marilandica*) and in live oaks such as Texas live oak (*Q. fusiformis*). These species are highly susceptible to the disease and usually experience mortality within 1 to 6 months post-infection (Appel 1995). Oak wilt centers form when fungal spores are transmitted overland by several species of nitidulid beetle (Gibbs and French 1980, Juzwick and French 1983). Once a new center of oak wilt infection has formed, the disease then begins to spread to adjacent trees via the roots. Centers of oak wilt can spread quickly (< 45 m per year) through otherwise healthy forest usually leaving < 20% of susceptible individuals alive (Appel et al. 1989).

The presence of oak wilt may have ramifications for the federally endangered golden-cheeked warbler (*Setophaga chrysoparia*), a migratory songbird restricted to the oak - Ashe juniper (*Juniperus ashei*) woodlands of central Texas during the breeding

season. This species was placed on the federal endangered species list in 1990 due to past and on-going loss of breeding habitat caused by urbanization and clearing of juniper for agricultural purposes (USFWS 1990, Keddy-Hector 1992). Oak wilt has frequently been cited as another potential threat to warbler habitat (Keddy-Hector 1992, Wahl et al. 1990, Carothers et al. 2008). Though oak wilt has been confirmed in 30 of the 35 counties known to be occupied by golden-cheeked warblers (Figure 1; Texas Forest Service 2009), few studies have addressed the extent to which it occurs within warbler habitat. Appel and Camilli (2008) found that 18% of oak wilt disease centers in Coryell and Bell Counties, located in the north-central portion of the warbler's range, were located in golden-cheeked warbler habitat. Oak wilt also has been observed in golden-cheeked warbler habitat on Balcones Canyonlands National Wildlife Refuge, Travis County (C. Sexton, USFWS, personal communication), and at the former Kerrville State Recreation Area, Kerr County (Wahl et al. 1990).



**Figure 1.** The breeding range of the golden-cheeked warbler and Texas counties with confirmed cases of oak wilt (Texas Forest Service 2009). Oak wilt has been confirmed in 30 of the 35 counties where golden-cheeked warblers breed. My study was conducted in (clockwise from top) Gillespie, Kendall, Bandera, and Kerr Counties, TX.

At this time, no previous studies have addressed the effects on oak wilt on avian species but similar forest pathogens have been found to negatively impact other forest birds. Observed impacts include declines in density (Tingley 2002, Monahan et al. 2006) and reproductive success (Allen 2009). Loss of live and red oaks from golden-cheeked warbler breeding habitat could affect the birds in several ways. During the breeding season, golden-cheeked warblers are typically found in mixed oak - juniper woodlands with 50 - 100% canopy cover in the mid and upper layers (Ladd and Gass 1999). Deciduous oaks are also an important component of warbler habitat as their density has

been found to be positively correlated with warbler density (Wahl et al. 1990). At the territory scale, oak wilt would likely reduce overall density and canopy cover of oak trees resulting in a decrease in the availability of arthropod food, especially early in the breeding season when golden-cheeked warblers preferentially forage on this particular substrate (Wahl et al. 1990, Marshall 2011). Loss of oaks also may result in reduced availability of suitable nest locations, modified thermal conditions, and altered predator assemblages, all of which may affect warbler reproductive success. At a larger scale, Magness et al. (2006) found that  $\geq 40\%$  of the surrounding landscape must be composed of woodland for golden-cheeked warblers to occur at a given location and that  $\geq 80\%$  must be woodland for the probability of occupancy to exceed 0.5. Collier et al. (2012) found woodland patch size and percent woodland composition of the surrounding landscape to be positively correlated with the probability of occupancy by golden-cheeked warblers. Thus, the more open condition resulting from loss of oaks may negatively impact the suitability of large areas. In the worst case scenario, presence of oak wilt may cause complete abandonment of affected patches. Wahl et al. (1990) cited oak wilt as one possible reason golden-cheeked warblers are no longer found at the former Kerrville State Recreation Area. If oak wilt does cause golden-cheeked warblers to abandon affected areas, its presence on the landscape could lead to fragmentation and increased isolation of remaining woodland thus reducing the probability of occupancy of otherwise unaffected areas (Coldren 1998, Collier et al. 2012).

Similar to several other species that breed in mature forests (Marshall et al. 2003, Vitz and Rodewald 2006), post-breeding golden-cheeked warblers often disperse from

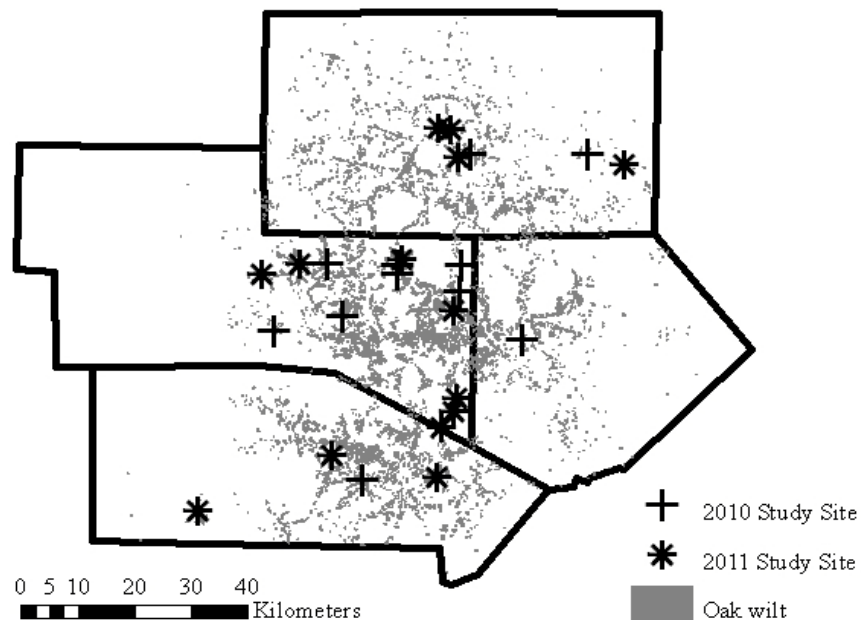
their territories into habitats of a more open condition before migrating to the wintering grounds (Ladd and Gass 1999). In a study of post-breeding habitat use, golden-cheeked warblers were observed most frequently in patches with 0 – 25% canopy cover (M. Hutchinson, Texas A&M University, personal communication). Thus, areas that have lost many oaks to oak wilt may still provide habitat late in the season. However, Vitz and Rodewald (2006) found that post-breeding mature-forest birds tended to avoid large regenerating clearcuts in favor of smaller clearcuts. Similarly, large areas impacted by oak wilt may be of less use to post-breeding golden-cheeked warblers than small oak wilt centers surrounded by unaffected breeding habitat.

To determine whether oak wilt impacts golden-cheeked warblers, I assessed its influence on habitat selection by comparing the proportion of forest occupied by warblers, the density of warbler territories, and the density of post-breeding detections between affected and unaffected areas. I also assessed the effect of oak wilt on habitat quality by comparing rates of reproductive success between affected and unaffected areas. I predicted that if oak wilt impacted golden-cheeked warblers, I would observe lower proportional occupancy, territory density, use within territories, post-breeding density, and reproductive success in forest affected by the disease. I measured vegetative characteristics to quantify differences between affected and unaffected forest. I predicted that areas where oak wilt has occurred would have lower total canopy cover and lower canopy cover in susceptible oak species but that there would be no difference in Ashe juniper or white oak canopy cover. Results of my study will inform us about the threat

oak wilt poses to golden-cheeked warblers and will help determine the importance of oak wilt control to future management efforts.

## STUDY LOCATIONS

I conducted my study in Bandera, Gillespie, Kendall, and Kerr counties, Texas, from March through June of 2010 and 2011. Collier et al. (2012) estimated just under 314,000 ha of golden-cheeked warbler habitat exist in these 4 counties. Oak wilt is widespread throughout the southern portion of Gillespie County, the western portion of Kendall County, and the eastern portions of Bandera and Kerr Counties (Figure 2). At least 32,026 ha in these 4 counties are known to have been impacted by the disease by 2009 (J. Zhu, Texas Forest Service, unpublished data).



**Figure 2.** Confirmed oak wilt centers and study sites in (clockwise from top) Gillespie, Kendall, Bandera, and Kerr Counties, TX. Oak wilt locations courtesy of the Texas Forest Service (J. Zhu, unpublished data).

I collected data from 25 study sites located within my study region, 11 in 2010 and 14 in 2011 (Figure 2). I selected my study sites using a GIS shapefile depicting oak wilt centers identified by the Texas Forest Service during either aerial surveys conducted in the mid-1990s or during opportunistic visits to private properties beginning in 1991 (J. Zhu, Texas Forest Service, unpublished data). I randomly selected an oak wilt center, then accepted or rejected the location as a study site based on the requirement that the oak wilt center was  $\geq 4$  ha and that it was bordered by a contiguous patch of unaffected forest  $\geq 20$  ha, the minimum patch size required for golden-cheeked warblers to successfully reproduce (Butcher et al. 2010). If I rejected the potential study site, I randomly selected another oak wilt center for consideration. I accepted or rejected potential study sites in this manner until I obtained my desired number of sites for that year. Site selection was constrained by my ability to obtain access to private land but since study sites I could not gain access to were replaced with other sites selected using identical criteria, I assumed inaccessible properties to be missing at random (Stevens and Jenson 2007, Collier et al. 2012). As permitted by private property boundaries, I considered each study site to include the oak wilt center plus all unaffected forest within 400 m of the center's boundary allowing me to cover an area large enough to contain several warbler territories. Several of my study sites contained multiple oak wilt centers spaced  $< 400$  m from one another; at these locations I surveyed all unaffected forest between the oak wilt centers plus all unaffected forest within 400 m of the boundary of the outermost centers.

## METHODS

### *Territory and oak wilt center location*

I conducted transect surveys to locate golden-cheeked warblers for subsequent territory mapping and behavioral observations, and to update the locations of oak wilt centers. Because the probability of detecting a target species present at a location on a single survey is usually less than one (MacKenzie et al. 2002), I surveyed each study site multiple times during the breeding season to locate golden-cheeked warblers. Collier et al. (2010) found that across the golden-cheeked warbler's range in central Texas, detection probabilities ranged from 0.50 to 0.85 when surveys were completed by 15 May. Based on the recommendations of MacKenzie and Royle (2005), I surveyed each study site 5 times between 19 March and 1 June in 2010. I located golden-cheeked warblers at 4 of my 11 study sites in 2010, giving me an occupancy probability of 0.36. Based on this probability, I surveyed each study site 4 times between 16 March and 17 May in 2011.

Based on the average size of a golden-cheeked warbler territory (Ladd and Gass 1999), observers covered each study site by walking transects spaced 200 m apart. To ensure that we detected all oak wilt centers present at my study sites, I effectively reduced the spacing of my survey transects to 100 m when searching for oak wilt by alternating transect placement for each survey round. For example, during the first survey round observers walked transects spaced 200 m apart on a latitudinal axis. For the second survey, I shifted the transects 100 m south. Surveys three and four followed the same pattern on a north-south axis. This allowed me to survey for oak wilt of a finer



scale than a 200 m transect spacing would otherwise allow. Observers recorded the GPS locations of all golden-cheeked warblers detected and of the inner and outer edges of all oak wilt centers passed through on surveys. I compiled warbler detection locations and oak wilt locations into separate shapefiles using ArcMap 9.3.1.

#### *Oak wilt delineations*

I used oak wilt locations marked during surveys to map the boundaries of centers on each of my study sites. I mapped centers between 18 May and 22 June in both study years. I defined oak wilt centers as areas with either signs of active infection such as veinal necrosis or vein banding or as areas with at least 80% mortality of susceptible species (Appel and Maggio 1984, Appel et al. 1989). I walked the circumference of each center, marking my location every 25 m, then used these points to create polygons in ArcMap 9.3.1 depicting the extent of each oak wilt center.

#### *Territory mapping*

I used locations of warblers detected during surveys to relocate individuals for territory mapping during subsequent visits. I visited each territory for up to 60 minutes once every 7 - 10 days. In 2010, I used hand-held GPS units to mark 3 – 6 locations spaced < 20 m apart per visit for each focal male. I obtained a mean of 16.6 (SD = 3.7) points per territory which exceeded the minimum number Anich et al. (2009) found to be necessary to accurately delineate the territories of Swainson's warblers (*Limnothlypis swainsonii*). In 2011, I took a point every 2 minutes throughout each visit which enabled me to compare each individual's use of oak wilt to the amount of oak wilt available within the territorial boundary. Because my 2-minute sampling interval provided ample

opportunity for an individual to traverse the length of its territory, I considered successive point locations to be biologically independent (Barg et al. 2005, Lair 1987). I obtained a mean of 51.0 (SD = 29.0) points per territory in 2011. I used the point locations to create minimum convex polygons delineating the maximum extent of each territory (i.e. the area utilized by each focal male) using Hawth's Tools for ArcGIS. Although kernel density estimation is considered to provide a more robust delineation of animal home ranges (Laver and Kelley 2008), minimum convex polygons were more appropriate for my particular study for two reasons. First, the process of kernel density estimation uses known locations to delineate the area where a focal individual is likely to occur, effectually placing a buffer around the individual's documented locations. In both 2010 and 2011, I had a number of territories where the male was observed at the border of an oak wilt center but never within the center. In such situations, kernel density estimation would result in the oak wilt center being included within the territory boundary even though the bird was never actually observed in oak wilt. Second, minimum convex polygons return a representation of the entire area an individual has used whereas kernel estimators return an area the bird is likely to occur in. As such, minimum convex polygons provided a better representation of the area available to the bird at the territory scale, one of my metrics of interest.

### *Reproductive success*

I made behavioral observations according to the method described by Vickery et al. (1992) to determine final reproductive outcome for each territorial male. Though reproductive outcome is not synonymous with the frequently used metric of nest success,

it provides a reliable alternative to nest monitoring for sensitive species and species whose nests are difficult to locate. The effectiveness of the Vickery method was tested by Christoferson and Morrison (2001), who used it to correctly predict the reproductive outcome for 80% of painted redstarts (*Myioborus pictus*), 90% of plumbeous vireos (*Vireo plumbeus*), and 92% western wood-pewees (*Contopus sordidulus*) monitored. I conducted behavioral observations from the time of the warblers' arrival on the breeding grounds, mid-March, through the end of June when all territories had either fledged young or were no longer active. I visited each territory for < 60 minutes once every 7 – 10 days to determine breeding status; this was usually done in conjunction with territory mapping. As recommended by Vickery et al. (1992), this schedule allowed me to visit each territory at least once per nesting stage (Ladd and Gass 1999). Using this method, I determined which birds successfully fledged young, which birds were paired but unsuccessful, and which birds remained unpaired throughout the breeding season.

#### *Post-breeding*

To determine if golden-cheeked warblers used oak wilt centers post-breeding, I conducted additional transect surveys at sites where warblers held territories during the breeding season. I surveyed both the areas used for breeding and the areas where territories had not been present at each post-breeding study site 5 times between 24 May and 12 July, at which time most golden-cheeked warblers had concluded breeding. Because golden-cheeked warbler detection probabilities are known to decrease as the season progresses (Collier et al. 2010), I surveyed at a finer resolution than I did previously by decreasing the spacing of transects from the 200 m to 100 m. I also

conducted transect surveys more frequently, once every 7 days instead of once every approximately 15 days. Each time I detected one or more warblers, I followed the first adult I detected for one 5-minute interval. If no adults were present, I followed the first fledging detected. If the focal individual moved from an unaffected area into oak wilt or vice versa, I continued to follow it for the remainder of the observation period. I noted the number, age, and sex of all individuals in the group and took a GPS location every time the focal individual changed substrate.

#### *Vegetation measurements*

To quantify differences in vegetation between those portions of my study sites affected by oak wilt and those that were not, I used a tubular densiometer to measure total canopy cover  $> 3$  m at 150 randomly selected points in each portion of each study site. I also used the tubular densiometer to record all canopy species present and their percent canopy cover at each point. To avoid measuring vegetation at multiple locations containing the same individuals, I spaced points  $\geq 20$  m from one another (Gilman and Watson 1994, Jennings et al. 1999).

#### *Analyses*

I calculated descriptive statistics for all variables measured. I obtained the proportion of affected and unaffected forest occupied by warblers by dividing the area within territories by the area outside territories separately for each portion of each site. I used analysis of variance to test for an effect of year on the difference in proportion occupied between affected and unaffected areas (Zar 1996; 235). I used a one-tailed Wilcoxon paired-sample test for non-normally distributed data (Zar 1996:167) to test my

prediction that oak wilt would be used less by golden-cheeked warblers than unaffected forest.

I assessed how oak wilt affected territory placement by calculating the density of territories overlapping oak wilt centers and the density of territories outside of oak wilt centers at each study site where I detected golden-cheeked warblers. I considered a territory to be in oak wilt if  $\geq 10\%$  of its area overlapped with an infection center. I used analysis of variance to test for an effect of year on the difference in territory density between affected and unaffected areas. I used a two-tailed paired sample  $t$ -test to test my hypothesis that density of golden-cheeked warbler territories is different between oak wilt centers and unaffected forest (Zar 1996; 163). To determine whether differences in vegetation between the affected portions of my study sites influenced whether or not warblers placed their territories in oak wilt, I used analysis of variance (Zar 1996; 179) to test whether total canopy cover, canopy cover in susceptible oaks, canopy cover in less susceptible oaks, and canopy cover in Ashe juniper differed between the affected portions of sites where warbler territories overlapped with oak wilt and the affected portions of occupied sites where territories did not overlap oak wilt.

To assess warbler use of oak wilt within territories, for each oak wilt territory I calculated the proportion of warbler locations in oak wilt and matched this to the proportion of the territory's area affected by oak wilt. I used a two-tailed paired sample  $t$ -test to test my hypothesis that golden-cheeked warblers would use oak wilt disproportionate to its availability at the territory scale.

I used two metrics to assess reproductive success: pairing success and fledging success. I considered a male to be successfully paired if he was observed with a female or fledgling at least once over the course of the breeding season. I considered a territory to have successfully fledged if either adult was observed with at least one fledgling. I calculated percent pairing success as the number of paired territories/the total number of territories and percent fledging success as the number of territories that fledged/the total number of paired territories. As with territory density, I considered a territory to be in oak wilt if  $\geq 10\%$  of its area overlapped with a disease center. For both pairing and fledging success, I used chi-square goodness of fit (Zar 1996; 457) to test my prediction that reproductive success would be lower in territories placed in oak wilt. I also used chi-square goodness of fit to test for inter-annual variation.

To assess post-breeding use of oak wilt, I calculated the mean density of post-breeding detections per survey in oak wilt and in unaffected forest for each study site. I considered all points taken during a given 5-minute observation period to be part of one detection event. If any of the point locations were within an oak wilt center, I considered that detection to be in oak wilt. I used analysis of variance to test for inter-annual variation in the difference in post-breeding density between affected and unaffected portions of my study sites. I used a one-tailed paired sample *t*-test to test my prediction that post-breeding warbler density would be lower within oak wilt centers.

To quantify differences in vegetation between affected and unaffected forest, I used a one-tailed paired sample *t*-test to test my prediction that total canopy cover and canopy cover in species highly susceptible to oak wilt (live and red oaks) would be

lower in affected areas. I also tested my prediction that canopy cover in less susceptible oak species (white oaks) and canopy cover in Ashe juniper would not be affected by the presence of oak wilt. I excluded 4 study sites from my analysis of canopy cover in less susceptible oaks because white oaks were present in neither the oak wilt nor the unaffected portion of the site.

## RESULTS

### *Occupancy*

I surveyed 189 ha of affected forest and 775 ha of adjacent unaffected forest on 11 study sites in 2010 and 417 ha of affected forest and 1,957 ha of unaffected forest on 14 study sites in 2011 (Table 1). I mapped a total of 188 individual oak wilt centers, 77 in 2010 and 111 in 2011. I located golden-cheeked warblers on 13 of my 25 study sites; territories overlapped with oak wilt on 5 study sites. I found year to have no effect on the difference in proportion occupied between affected and unaffected portions of sites ( $F_{1,23} = 0.794$ ,  $P = 0.435$ ). The mean proportion of unaffected forest that was occupied ( $\bar{x} = 0.042$ ,  $SD = 0.069$ ) was 3.5 times the mean proportion of oak wilt occupied by golden-cheeked warblers ( $\bar{x} = 0.013$ ,  $SD = 0.033$ ,  $S_{24} = 33.50$ ,  $P = 0.009$ ; Table 1).

**Table 1.** Total area (ha), area occupied, and % of total area occupied for oak wilt and unaffected forest at each study site, 2010 – 2011.

Site	Oak wilt affected			Unaffected		
	Total	occupied	%	Total	occupied	%
<b>2010</b>						
A	5.5	0	0	18.8	0	0
B	21.4	0.03	0.1	116.9	10.7	9.1
C	6.7	0	0	60.4	0	0
D	9.2	0	0	82.3	2.3	2.8
E	2.5	0	0	55.2	0	0
F	7.0	0	0	157.7	13.9	8.8
G	20.6	0	0	70.7	0.5	0.7
H	6.1	0	0	50.7	0	0
I	79.3	0	0	34.1	0	0
J	16.3	0	0	64.8	0	0
K	14.7	0	0	63.1	0	0
<b>2011</b>						
L	85.5	7.6	8.9	490.1	84.8	17.3
M	6.5	0	0	15.7	4.4	27.9
N	4.0	0	0	69.7	1.5	2.1
O	24.9	3.0	12.2	69.4	6.6	9.5
P	47.2	1.3	2.8	186.2	1.9	1.0
Q	83.2	0	0	264.5	0	0
R	10.6	0	0	49.6	0	0
S	71.6	0	0	66.0	0	0
T	7.2	0.0	0	34.4	0	0
U	5.9	0	0	71.7	4.9	6.9
V	5.8	0	0	71.7	9.9	13.8
W	55.0	4.3	7.9	318.8	14.3	4.5
X	4.9	0	0	184.2	11.1	6.0
Y	4.4	0	0	64.8	0	0
<b>Total</b>	606.1	16.3	2.7	2731.5	166.8	6.1

### *Territory density*

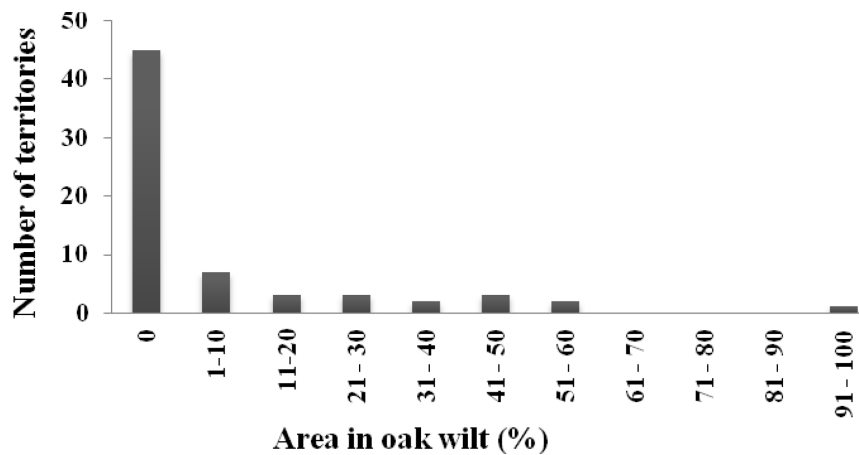
I located 13 golden-cheeked warbler territories on 4 study sites in 2010 and 56 territories on 9 study sites in 2011. Forty-four (68.2%) territories did not overlap with oak wilt centers, 7 territories (10.6%) overlapped with oak wilt for  $> 0$  but  $< 10\%$  of their total area. Fourteen (21.2%) territories had oak wilt in  $\geq 10\%$  of their total area and occurred on 4 of the 13 occupied study sites; these territories were all located in 2011, no



territories located in 2010 overlapped with oak wilt for  $\geq 10\%$  of their total area (Figure 3). Though higher proportions of oak wilt in territories may be prevented in part by the irregular shape of some of the oak wilt centers, of the 14 territories I categorized as oak wilt territories, only 3 had more than 50% of their area in oak wilt. Only 1 territory contained oak wilt in  $< 60\%$  of its total area and no territories were located entirely within an oak wilt center (Figure 4). I found year to have no effect on the difference in territory density between affected and unaffected portions of sites ( $F_{1,11} = 0.066$ ,  $P = 0.802$ ). Territory density was not significantly different between oak wilt and unaffected forest ( $t_{12} = 0.833$ ,  $P = 0.421$ ). Golden-cheeked warblers did not place their territories in oak wilt at 69% ( $n = 13$ ) of the study sites where they were present, but territory density was greater in oak wilt than unaffected areas at the 4 sites where oak wilt was used (Table 2). I found no significant differences in total canopy cover ( $F_{1,11} = 0.231$ ,  $P = 0.640$ ), canopy cover in susceptible oaks ( $F_{1,11} = 0.079$ ,  $P = 0.784$ ), canopy cover in less susceptible oaks ( $F_{1,11} = 1.672$ ,  $P = 0.222$ ), or canopy cover in Ashe juniper ( $F_{1,11} < 0.001$ ,  $P = 0.998$ ), between the affected portions of sites where territories overlapped with oak wilt and the affected portions of sites where territories did not overlap with oak wilt.



**Figure 3.** Arrangement of golden-cheeked warbler (GCWA) territories at a study site where territories did not overlap oak wilt (left) and at a study site where territories and oak wilt overlapped (right).



**Figure 4.** Proportion of total territory area comprised of oak wilt for territories mapped 2010 – 2011 ( $n = 66$ ).

**Table 2.** Density of golden-cheeked warbler territories (number/ha) with  $\geq 10\%$  of their area in oak wilt and unaffected forest with the difference between the two calculated as density in oak wilt – density in unaffected.

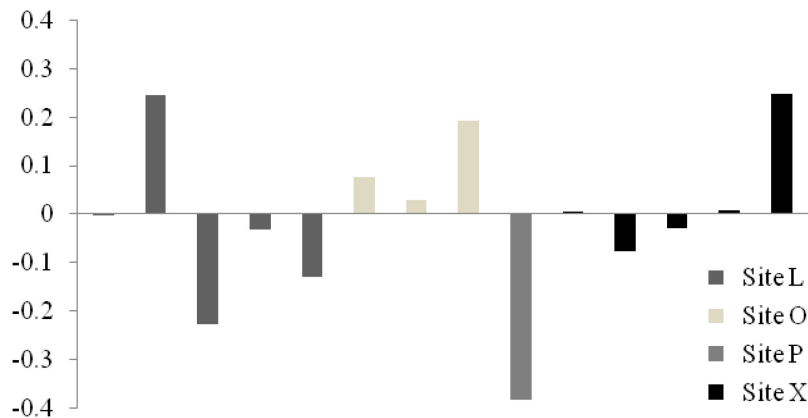
Site	Density in oak wilt	Density in unaffected	Difference
<b>2010</b>			
B	0	0.026	-0.026
D	0	0.012	-0.012
F	0	0.051	-0.051
G	0	0.014	-0.014
<b>2011</b>			
L	0.058	0.045	0.014
M	0	0.191	-0.191
N	0	0.014	-0.014
O	0.120	0	0.120
P	0.021	0	0.021
U	0	0.070	-0.070
V	0	0.070	-0.070
W	0.091	0.013	0.078
X	0	0.011	-0.011
<b>Mean</b>	0.022	0.040	-0.017

#### *Use within territories*

Of the 14 territories with  $\geq 10\%$  of their area in oak wilt, 7 had more warbler locations in oak wilt more than expected based on oak wilt availability and 7 used oak wilt less than expected (Table 3, Figure 5). The mean proportion of warbler locations in oak wilt was very similar to the mean proportion available, 0.373 (SD = 0.263) and 0.379 (SD = 0.210), respectively, but the proportion of locations in oak wilt varied widely by territory. This variability does not appear to be related to differences between study sites because I observed no consistent usage patterns within each of the 3 sites that contained  $> 1$  oak wilt territory. I found no significant difference between proportion of locations in oak wilt and area of oak wilt available ( $t_{13} = 0.833$ ,  $P = 0.789$ ).

**Table 3.** Proportion of warbler locations in oak wilt and proportion of area in oak wilt for each warbler territory with >10% of its total area in oak wilt, 2010 – 2011.

Study Site	Locations in oak wilt (% of total)	Area in oak wilt (% of total)
<b>L</b>	0.418	0.420
	0.405	0.159
	0.053	0.282
	0.222	0.254
	0.222	0.353
<b>O</b>	0.319	0.243
	0.167	0.137
	0.755	0.562
<b>P</b>	0.000	0.384
<b>X</b>	0.548	0.544
	0.846	0.923
	0.123	0.153
	0.483	0.476
	0.667	0.420

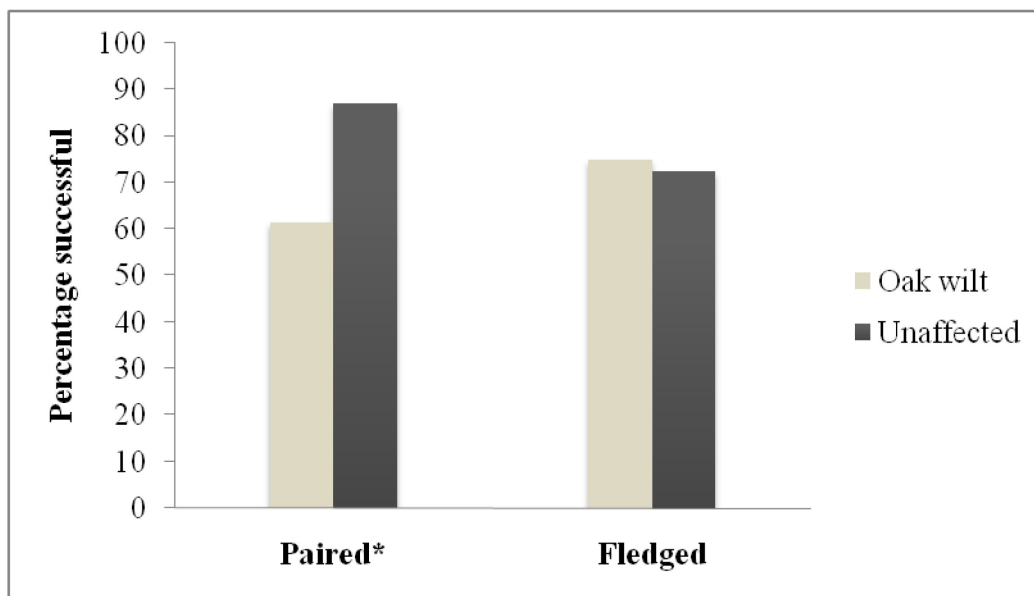


**Figure 5.** Difference between observed proportion of warbler locations in oak wilt and expected proportion of locations in oak wilt by territory. Positive values denote greater usage of oak wilt than expected based on availability.

### *Reproductive success*

I obtained measures of reproductive success for 66 territories, 13 in oak wilt and 53 in unaffected areas. Overall pairing success was 83% in both 2010 ( $n = 12$ ) and 2011 ( $n = 54$ ). Pairing success was 27% lower for males whose territories were in oak wilt,

62% ( $n = 13$ ) of oak wilt territories paired successfully compared to 89% ( $n = 53$ ) of territories in unaffected areas ( $\chi^2_1 = 5.547$ ,  $P = 0.019$ ; Figure 6). None of the 3 males whose territories contained more than 50% oak wilt paired. Of the 55 males that successfully paired, 75% ( $n = 8$ ) successfully fledged young in oak wilt and 72% ( $n = 47$ ) fledged young in unaffected areas ( $\chi^2_1 = 0.024$ ,  $P = 0.876$ ; Figure 6). Overall fledging success was 90% ( $n = 10$ ) in 2010, higher than the 69% fledging success observed in 2011, however, the difference was not statistically significant ( $\chi^2_1 = 1.184$ ,  $P = 0.175$ ).



\* denotes significance at  $\alpha = 0.05$ .

**Figure 6.** Pairing and fledging success for territories in oak wilt and territories in unaffected areas.

### *Post-breeding density*

I detected golden-cheeked warblers 110 times on 8 of 10 study sites surveyed during the post-breeding season. Single males or family groups comprised 39.1 and 43.6% of detections, respectively (Table 4). I classified 3 detections as “unknown”; these were situations where the observer could not verify the whether or not more than one warbler was present. Seventy-three detections (66%,  $n = 110$ ) occurred completely outside of breeding season territories. Nine (8.2%,  $n = 110$ ) detections occurred in oak wilt. I located warblers in oak wilt at two study sites where they did not use it during the breeding season. The difference in post-breeding density between affected and unaffected areas did not vary significantly with year ( $F_{1,8} = 2.043$ ,  $P = 0.191$ ). Although the mean density of post-breeding detections was 2.1 times greater in unaffected forest (0.017 detections/ha) than it was in oak wilt (0.008 detections/ha), the difference was not statistically significant ( $t_9 = 1.263$ ,  $P = 0.120$ ; Table 5). Mean post-breeding density was greater in oak wilt at 3 study sites and was greater in unaffected forest at 5 study sites.

**Table 4.** Composition of groups observed during post-breeding detection events, number of detections where each composition was observed, and proportion of all detections each composition comprised.

<b>Individuals detected</b>	<b>Number</b>	<b>%</b>
Single Female	7	6.4
Single Male	43	39.1
Multiple Adults	43	2.7
Family Group	57	43.6
Fledges only	3	5.5
Unknown	3	2.7

**Table 5.** Mean density (number/ha) of post-breeding golden-cheeked warbler detections in oak wilt and unaffected forest at each survey site. The difference between the two was calculated as density in oak wilt – density in unaffected.

Site	Mean density in oak wilt	Mean density in unaffected	Difference
<b>2010</b>			
B	0.019	0	0.019
D	0	0	0
F	0	0.008	-0.008
G	0	0	0
<b>2011</b>			
L	0.007	0.030	-0.023
M	0.031	0.089	-0.058
O	0.010	0	0.010
U	0	0.011	-0.011
V	0	0.024	-0.024
W	0.010	0.003	0.007
<b>Total</b>	0.008	0.017	-0.009

### *Vegetation measurements*

Total canopy cover ranged from 5 to 38% ( $n = 25$ ,  $\bar{x} = 17$ ,  $SD = 9$ ) in the affected portions of my study sites and from 6 to 36% ( $n = 25$ ,  $\bar{x} = 21$ ,  $SD = 8$ ) in the unaffected portions of my study sites. Mean total canopy cover was 15% lower in areas with oak wilt relative to unaffected forest ( $t_{24} = 2.272$ ,  $P = 0.016$ ). See Appendix A for all canopy species recorded at my study sites.

Canopy cover in oak species susceptible to oak wilt ranged from 1 to 25% ( $n = 25$ ,  $\bar{x} = 6$ ,  $SD = 6$ ) in portions of my study sites with oak wilt and from 1 to 25% ( $n = 25$ ,  $\bar{x} = 8$ ,  $SD = 5$ ) in unaffected forest. Canopy cover in susceptible oaks was 23% lower in areas with oak wilt relative to unaffected forest ( $t_{24} = 3.015$ ,  $P = 0.003$ ). I detected 3

species of susceptible oaks at my study sites: live oak, Texas oak, and blackjack oak.

The mean canopy cover for each species of susceptible oak was lower in oak wilt than in unaffected forest; the greatest relative difference was seen in Texas oak which had 64% less canopy cover in areas affected by oak wilt (Table 6).

Canopy cover in less susceptible oak species (white oaks) ranged from 0 to 8% ( $n = 21$ ,  $\bar{x} = 1$ ,  $SD = 2$ ) in oak wilt and from 0 to 5% ( $n = 21$ ,  $\bar{x} = 2$ ,  $SD = 2$ ) in unaffected forest. Of the 21 sites where white oaks were present, canopy cover in white oaks was not significantly lower in areas with oak wilt ( $t_{20} = 0.830$ ,  $P = 0.208$ ).

Canopy cover in Ashe juniper ranged from 0 to 31% ( $n = 25$ ,  $\bar{x} = 7$ ,  $SD = 8$ ) in oak wilt and from 0 to 20% ( $n = 25$ ,  $\bar{x} = 7$ ,  $SD = 6$ ) in unaffected forest. Though percent canopy cover in Ashe juniper was lower in oak wilt than unaffected forest, the difference was not statistically significant ( $t_{24} = 0.836$ ,  $P = 0.206$ ).

**Table 6.** Mean % canopy cover in susceptible oak species in oak wilt and unaffected forest. The difference between the two was calculated as mean canopy cover in oak wilt – mean canopy cover in unaffected forest.

	<b>Oak wilt</b>		<b>Unaffected</b>		<b>Difference</b>
	Mean	SD	Mean	SD	
<b>Live Oak</b>	5	4	6	5	-1
<b>Texas Oak</b>	< 1	1	2	2	-1
<b>Blackjack Oak</b>	< 1	2	1	2	-1 < n < 0

## DISCUSSION

I located golden-cheeked warblers on just over half of my study sites and found oak wilt within active territories at 5 locations. These results are consistent with previous observations of oak wilt in golden-cheeked warbler habitat within my study region



(Wahl et al. 1990). I found affected areas to be vegetationally similar between sites where warblers used oak wilt and sites where they did not, indicating that variable use of oak wilt among sites was not due to differences in vegetation. One possible explanation for why warbler territories were located in oak wilt at some sites but not at others is conspecific attraction. Farrell (2011) found that golden-cheeked warblers maintain territories in areas where they perceive other warblers to be present, even if those areas had previously gone unoccupied. Ten of the 14 oak wilt territories were located at the two sites with the highest and second highest absolute number of golden-cheeked warbler territories. Conspecific attraction might have influenced birds to settle in areas affected by oak wilt at these locations but additional data would be necessary to draw any firm conclusions.

Of the 69 territories I mapped, only 3 contained oak wilt for > 50% of their area, suggesting that the presence of oak wilt negatively influences habitat selection by male warblers. Males whose territories were located in oak wilt for > 10% of their area had significantly lower pairing success than those in unaffected forest and none of the males with > 50% of their territory in oak wilt paired. However, males using oak wilt that did pair fledged young as successfully as those who only used unaffected forest. Similar results were observed by Allen et al. (2009) who found pair density of Acadian flycatchers (*Empidonax virescens*) to be negatively associated with defoliation caused by hemlock woolly adelgids (*Adelges tsugae* Annand) but that nest survival was unaffected. Tye (1992) found that vegetative characteristics may be used by birds as an indicator of habitat quality but that this assessment is not always correct. Females may

have used vegetative characteristics such as percent canopy cover to assess the quality of a male's territory but, in the end, females that chose territories in oak wilt fledged young just as successfully as those in unaffected areas. However, because no females chose to pair with males whose territories were >50% oak wilt, I could not assess rates of fledging success for territories mostly in oak wilt. Despite this, my data indicate that habitat quality is lower in areas affected by oak wilt for males because those that use oak wilt are less likely to pair and thus are less likely to fledge young. The combination of lower mean territory density and lower pairing success suggests that areas affected by oak wilt have a lower overall reproductive output than unaffected forest.

My comparisons of canopy cover between oak wilt and unaffected forest supported my predictions that total canopy cover and canopy cover in susceptible oaks would be lower in areas with oak wilt and that canopy cover in less susceptible oaks and Ashe juniper would not differ significantly. Though mean total canopy was only 3% lower in oak wilt than in unaffected forest, this difference represents a relative difference of 15%. Golden-cheeked warblers are typically found in areas with high canopy cover during the breeding season (Ladd and Gass 1999). Because canopy cover was no greater than 38% at any of my study sites, a 15% relative loss could substantially reduce an area's perceived suitability. Alternatively, Klassen (2011) found no effect of total canopy closure on territory density but did find a positive relationship between the proportion of oak per study site and territory density. The difference I observed in total canopy cover was mainly due to a decrease in canopy cover in susceptible oaks. I observed the greatest difference in Texas oak which was 63% lower in oak wilt relative

to unaffected forest. This result is likely due to its high susceptibility to oak wilt and the rapid rate at which it succumbs to the disease. Loss of Texas oak from golden-cheeked warbler habitat may be especially detrimental to the bird as compared to the loss of other oak species. Marshall (2011) found that golden-cheeked warblers in areas dominated by red oaks had higher reproductive success than warblers in areas dominated by blackjack and post oak. This indicates that golden-cheeked warbler habitat with high canopy cover in red oaks may simultaneously be the best quality and the most likely to be substantially changed by oak wilt.

Though not statistically significant, mean warbler density in unaffected areas was 2.1 times greater than in oak wilt during the post-breeding season. My results indicate that post-breeding warblers are more commonly found in unaffected forest than in oak wilt but that movement from unaffected forest to oak wilt does occur. Marshall (2011) found that though golden-cheeked warblers forage on Ashe juniper more frequently than oak late in the season, they still use oaks as a foraging substrate during this time. Thus, lower oak canopy cover in affected areas could cause the birds to forage preferentially in unaffected areas during the post-breeding season.

## **MANAGEMENT IMPLICATIONS**

My results suggest that the presence of oak wilt negatively influences habitat selection and quality for golden-cheeked warblers. Because oak wilt is not only widespread throughout my study region but also occurs in varying intensities in all but 5 of the counties where golden-cheeked warblers are known to breed, the disease should be considered as a factor when evaluating the status of threats to the species. Several

techniques such as trenching and chemical control may be employed to stop or slow local spread of the disease (Appel 1995), I recommend these methods be used where managers wish to halt the spread of oak wilt at a specific location such as a state park or a private property managed for golden-cheeked warblers. To control oak wilt on a larger scale, management efforts should focus on preventing the formation of new infection centers. To this end, programs designed to educate the public on proper pruning and wound treatment for susceptible oaks, and the establishment of a diverse assortment of tree species may be an effective approach (Billings 2008). Future management efforts should address the threat oak wilt poses to golden-cheeked warblers by incorporating applicable preventative measures.

### CHAPTER III

#### AN ESTIMATION OF THE CURRENT AND FUTURE DISTRIBUTION OF OAK WILT AS IT PERTAINS TO THE ENDANGERED GOLDEN-CHEEKED WARBLER

##### SYNOPSIS

Oak wilt is a fatal disease of oaks caused by the fungus *Ceratocystis fagacearum*. Loss or degradation of habitat due to the disease may negatively impact the federally endangered golden-cheeked warbler (*Setophaga chrysoparia*). I used remote sensing to estimate the amount of potential golden-cheeked warbler habitat affected by oak wilt in 2008, to predict the amount of potential habitat likely to be affected by 2018, and to assess the current probability of warbler occupancy in areas affected by oak wilt historically. I also quantified vegetative characteristics to assess regeneration in areas affected by the disease. My results indicate that oak wilt frequently occurs in golden-cheeked warbler habitat and will continue to spread into warbler habitat in the coming years. I estimated that 6.9% of potential golden-cheeked warbler habitat and 7.7% of the total area within my study region was affected by oak wilt in 2008. By 2018, I predicted that 13.3% of potential golden-cheeked warbler habitat and 16.0% of the study region would be affected by the disease. Using historical imagery, I found that areas affected by oak wilt in the past are less likely to be classified as current potential warbler habitat than areas never affected by the disease. I found no differences between the understory vegetation of affected and unaffected areas but that oaks were more common in the overstory than in the understory, suggesting that species composition in affected areas

may shift in the years following an outbreak of the disease. Future management efforts should address the threat oak wilt poses to golden-cheeked warblers by incorporating applicable preventative measures.

## INTRODUCTION

Forest pathogens can substantially modify the vegetative characteristics of forest stands. These changes can in turn alter the extent to which animal species utilize impacted areas (Castello et al. 1995). If the pathogen has the potential to occur across a broad spatial extent, the consequences for wildlife could be considerable. Monahan and Koenig (2006) predicted that the abundance of 5 oak-dependent avian species, acorn woodpecker (*Melanerpes formicivorus*), Nuttall's woodpecker (*Picoides nuttallii*), Hutton's vireo (*Vireo huttoni*), western scrub-jay (*Aphelocoma californica*), and oak titmouse (*Baeolophus inornatus*), would decline by 25 - 68% in response to loss of coastal live oak (*Quercus agrifolia*) due to sudden oak death in California. Such declines would be especially detrimental for any species whose range is restricted to areas impacted by similar forest pathogens.

Oak wilt is a forest pathogen with both a broad spatial distribution and a high potential to impact wildlife. The disease is caused by infection by a fungus, *Ceratocystis fagacearum* (Bretz) Hunt which causes blockages to form in the vascular tissues of the host (Gibbs and French 1980). While oak wilt can occur in all oak species (*Quercus* spp.), its effects are most pronounced in red oaks (subgenus *Erythrobalanus*) including Texas red oak (*Q. texana*) and blackjack oak (*Q. marilandica*) and live oaks such as Texas live oak (*Q. fusiformis*). These species are highly susceptible to the disease and

usually experience mortality within 1 to 6 months of infection (Appel 1995). Oak wilt has been identified throughout the eastern and central portions of the United States as far south as Texas where it occurs throughout most the breeding range of the federally endangered golden-cheeked warbler (*Setophaga chrysoparia*; Texas Forest Service 2009).

The golden-cheeked warbler is a neotropical migrant endemic to the oak - Ashe juniper (*Quercus* spp. - *Juniperus ashei*) woodlands of central Texas during the breeding season (Ladd and Gass 1999). This species was placed on the endangered species list due to past and ongoing habitat loss (USFWS 1990). Because oaks are a necessary component of golden-cheeked warbler habitat, loss of live and red oaks caused by oak wilt could result in the destruction or degradation of warbler habitat. My study of golden-cheeked warbler habitat selection and quality described in Chapter 2 addresses this possibility; its results supported my hypotheses that golden-cheeked warblers would use oak wilt less than unaffected forest and those that do use oak wilt would experience lower rates of reproductive success. However, additional data examining the current and future extent of oak wilt within golden-cheeked warbler habitat is necessary to assess the full scope of the problem. Oak wilt has been confirmed in 30 of the 35 counties known to be occupied by golden-cheeked warblers (Figure 8, Texas Forest Service 2009), but few studies have addressed the extent to which it occurs within warbler habitat. Appel and Camilli (2008) found that 18% of oak wilt disease centers in Coryell and Bell counties were located in golden-cheeked warbler habitat. Oak wilt also has been observed in golden-cheeked warbler habitat on Balcones Canyonlands National Wildlife

Refuge, Travis County (C. Sexton, USFWS, personal communication), and at the former Kerrville State Recreation Area, Kerr County (Wahl et al. 1990). There is some debate concerning the origin of oak wilt but the available evidence suggests that its incidence has increased considerably within Texas since the 1910s likely due to altered species composition, increased density, and decreased isolation of forest stands caused by changing land management practices (Appel 1995, Juzwick 2008).

In addition to its immediate effects, the changes oak wilt produces in oak - juniper woodlands could last well into the future. Once the disease has moved through a stand, the stand may begin to regenerate. However, the density and species composition of the regenerating stand will likely be altered from pre-infection conditions. Menges and Loucks (1984) reported a strong possibility that oak wilt will cause stand composition to shift away from red oaks towards other species such as black cherry (*Prunus serotina*), sugar maple (*Acer saccharum*), and various species of white oak in Wisconsin. This tendency has been documented in stands affected by other pathogens such as chestnut blight, white pine blister rust, beech bark disease and various fungal root infections (Castello 1995). Alternatively, Tryon et al. (1984) found no significant change in stand composition post-oak wilt infection in West Virginia.

Several factors may prevent the regeneration of oaks in areas affected by oak wilt. First, regeneration may be prevented by lingering infection in the stand working in conjunction with low rates of root sprouting. Sprouts originating from trees destroyed by oak wilt often become infected which could provide a source of inoculum for seed sprouts within the stand (Bruhn 1991). Additionally, trees destroyed by oak wilt do not



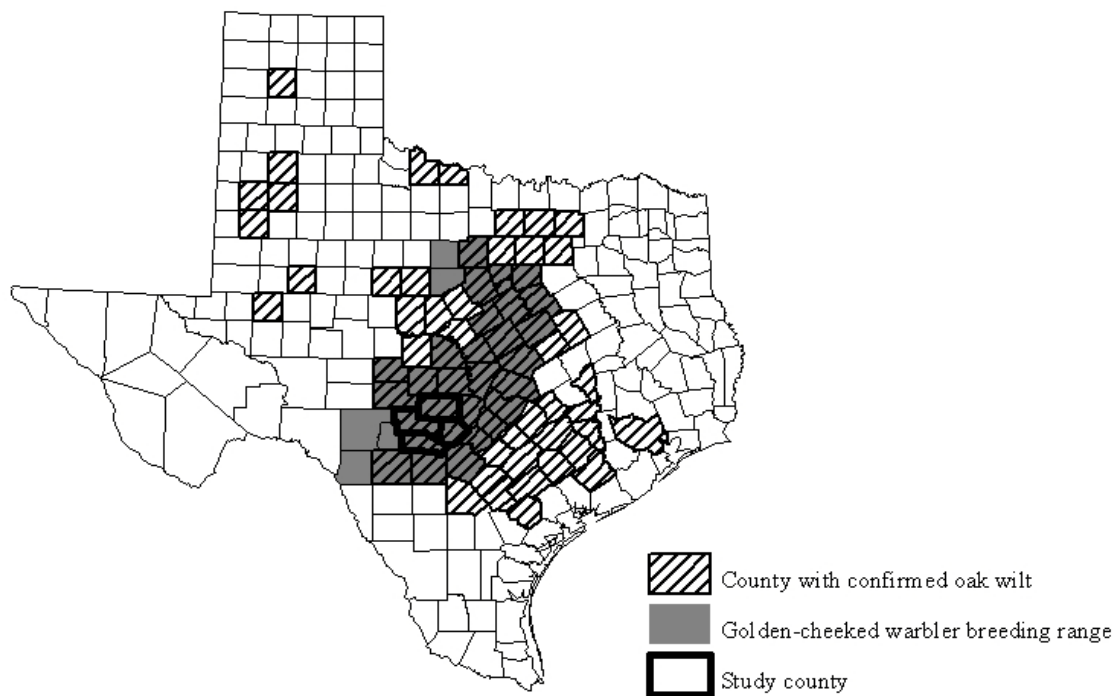
develop new sprouts as successfully as oaks affected by other disturbances such as fire (Menges and Loucks 1984); low sprout rates might allow oaks to be replaced by other species. Browsing by deer, cattle, and small mammals can also prevent recruitment of oaks, further altering stand density and composition (Keddy-Hector 1992, MacDougall et al. 2010). Therefore, the value of regenerated stands likely differs from pre-infection conditions, potentially affecting golden-cheeked warblers over the long term.

I used remote sensing to estimate the amount of potential golden-cheeked warbler habitat affected by oak wilt in 2008, to predict the amount of potential golden-cheeked warbler habitat likely to be affected by oak wilt by 2018, and to assess the current probability of warbler occupancy in areas affected by oak wilt historically. I used an assessment of vegetative characteristics to quantify the abundance of all woody vegetation, susceptible oaks, less susceptible (white) oaks, and Ashe juniper regenerating in areas affected by oak wilt compared to unaffected forest. I predicted that areas affected by oak wilt in the early 1980s would currently contain a lower proportion of warbler habitat than unaffected forest. Additionally, I predicted that the understory of areas where oak wilt has occurred would consist of a more open condition with fewer susceptible oaks and more Ashe juniper and white oaks than the understory of unaffected forest.

## **STUDY LOCATIONS**

I conducted my study in Bandera, Gillespie, Kendall, and Kerr counties, Texas, located in the southern portion of the golden-cheeked warbler's range (Figure 8). Collier et al. (2012) estimated just under 314,000 ha of potential golden-cheeked warbler habitat

exist in these 4 counties. Oak wilt is widespread throughout the southern portion of Gillespie County, the western portion of Kendall County, and the eastern portions of Bandera and Kerr Counties (Figure 7). At least 32,026 ha in these 4 counties are known to have been impacted by the disease by 2009 (J. Zhu, Texas Forest Service, unpublished data).



**Figure 7.** The breeding range of the golden-cheeked warbler, Texas counties with confirmed cases of oak wilt (Texas Forest Service 2009), and study region encompassing (clockwise from top) Gillespie, Kendall, Bandera, and Kerr counties, TX. Oak wilt has been confirmed in 30 of the 35 counties where golden-cheeked warblers breed.

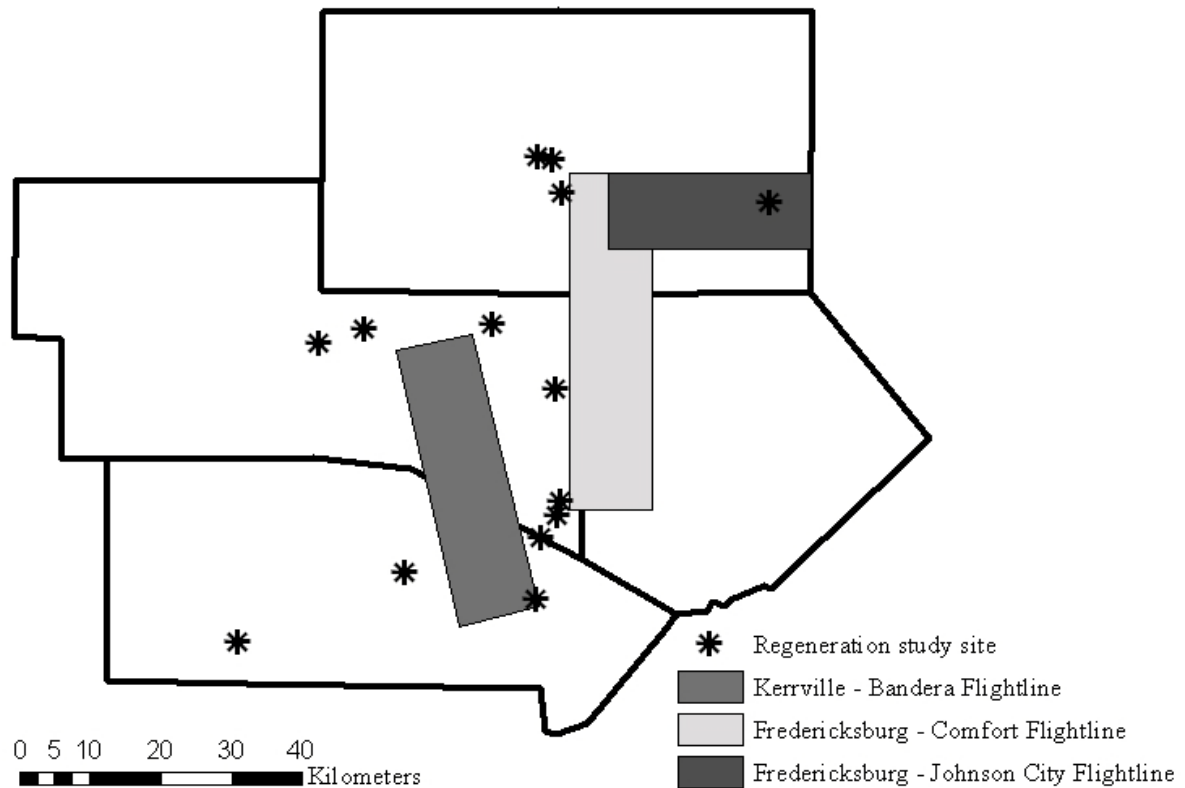
To determine the current and future extent of oak wilt present in potential golden-cheeked warbler habitat, I used ArcMap 9.3.1 to set up a grid of 1-km<sup>2</sup> blocks

covering my 4-county study region. I randomly selected my first square then selected every 10<sup>th</sup> square thereafter. Using this method, I selected 96 1-km<sup>2</sup> sample squares for analysis.

I used a similar protocol to identify the sample locations used to assess the current occupancy probability of areas affected by oak wilt historically. I obtained color infrared aerial photography taken below three flight lines: Kerrville to Bandera, TX, taken on 27 and 28 July 1982, Fredericksburg to Johnson City, TX, taken on 27 July 1982, and Fredericksburg to Comfort, TX, taken on 26 July 1982 and 21 August 1983 (Figure 8). Within the area photographed during each flight, I used ArcMap 9.3.1 to set up a grid of 1-km<sup>2</sup> blocks. I randomly selected the first square then selected every 5<sup>th</sup> square thereafter. Using this method, I selected a total of 46 1-km<sup>2</sup> sample squares for analysis.

To assess the regeneration of vegetation within oak wilt centers, I collected data from 14 study sites in conjunction with my study of golden-cheeked warbler habitat selection and quality (see Chapter 2) in May and June of 2011 (Figure 8). I selected study sites using a GIS shapefile depicting oak wilt centers identified by the Texas Forest Service during either aerial surveys conducted in the mid-1990s or during opportunistic visits to private properties beginning in 1991 (J. Zhu, Texas Forest Service, unpublished data). I randomly selected an oak wilt center then accepted or rejected the location as a study site based on two criteria. First, the oak wilt center had to be  $\geq 4$  ha in size. Appel et al. (1989) observed mean oak wilt spread rates of 11 – 16 m/year in my study region. Thus, a center  $\geq 4$  ha in size is likely to have been present for  $> 6$  years,

allowing time for regeneration to begin. The second criterion was that each oak wilt center was adjacent to  $\geq 20$  ha of unaffected forest, the minimum patch size required for golden-cheeked warblers to successfully reproduce. It should be noted that aside from the size of the forested area, the potential for golden-cheeked occupancy did not influence whether I accepted a potential site. If I rejected a potential study site, I randomly selected another oak wilt center for consideration. I accepted or rejected potential study sites in this manner until I obtained my desired number of sites. Site selection was constrained by my ability to obtain access to private land but because I replaced study sites that I could not gain access to with other sites selected using identical criteria, I assumed inaccessible properties to be missing at random (Stevens and Jenson 2007, Collier et al. 2012). As permitted by private property boundaries, I considered each regeneration study site to include the oak wilt center plus all adjacent unaffected forest within 400 m of the center's boundary allowing me to cover an area large enough to contain several warbler territories. Most of my study sites contained multiple oak wilt centers spaced  $< 400$  m from one another; at these locations I considered the study site to include all unaffected forest between the oak wilt centers plus all unaffected forest within 400 m of the boundary of the outermost centers.



**Figure 8.** Study region encompassing (clockwise from top) Gillespie, Kendall, Bandera, and Kerr counties, TX, including flightlines where aerial photographs were taken 1982 - 1983 and locations of regeneration study sites, 2011.

## METHODS

### *Present and future extent of oak wilt*

To determine the amount of potential golden-cheeked warbler habitat currently affected by oak wilt, I used the most recent high resolution imagery available, 2008 leaf-on color infrared 0.5-m digital orthoimagery acquired from the Texas Orthoimagery Program, to visually delineate the boundaries of mortality centers within my sample squares using ArcMap 9.3.1. I defined a mortality center as an area containing  $\geq 3$  dead or dying trees spaced  $\leq 20$  m apart (Appel et al. 1989). For each mortality center I

identified, I used 2010 color infrared 1-m digital orthoimagery to filter areas with temporary defoliation from areas with true mortality.

I ground-truthed 14% ( $n = 96$ ) of my sample squares in June 2010 to confirm the presence and cause of mortality and to mark the boundaries of any oak wilt centers that I did not identify using the remote imagery. I used veinal necrosis or vein banding as an indicator of active infection and  $\geq 80\%$  mortality of susceptible species as an indicator of past infection by *C. fagacearum* (Appel and Maggio 1984, Appel et al. 1989).

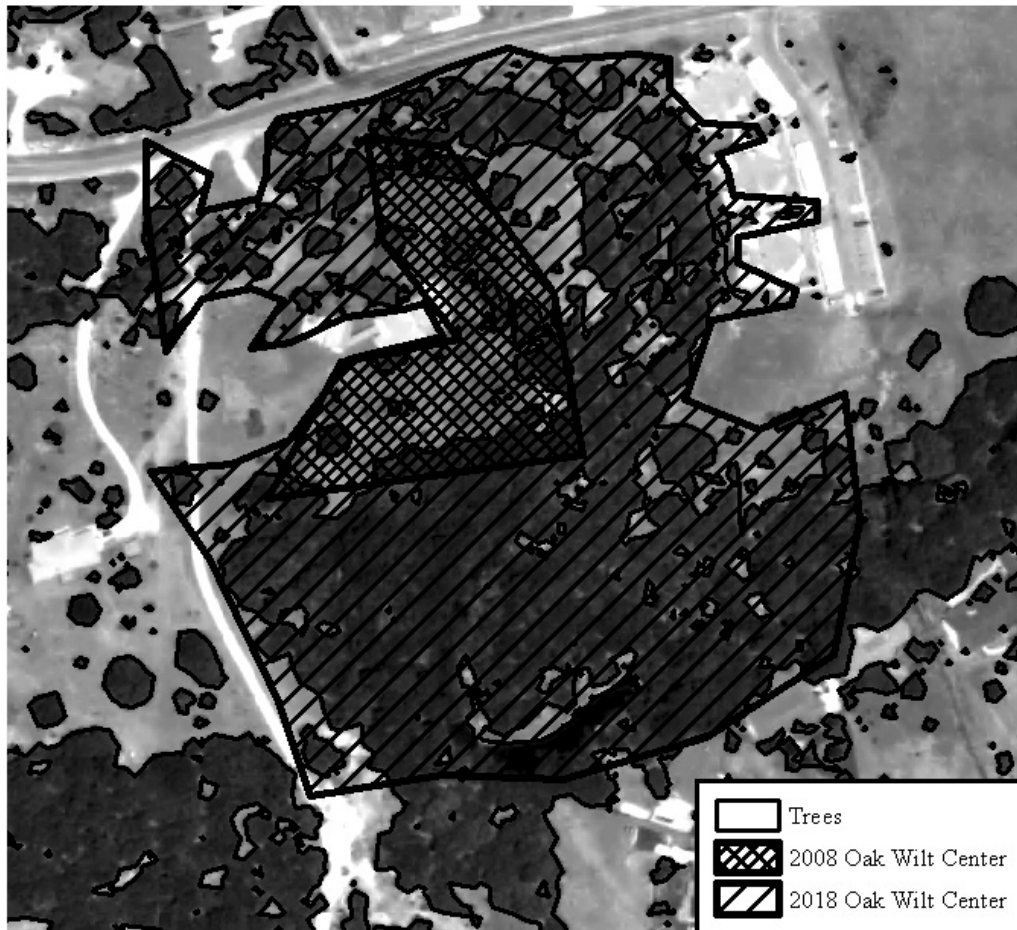
To identify areas of potential golden-cheeked warbler habitat, I used an occupancy model described by Collier et al. (2012) which identified patches of potential golden-cheeked warbler habitat across the range of the species, then assigned a probability of occupancy to each patch based on characteristics including size and surrounding percent woodland composition. Using ArcMap 9.3.1, I identified all potential habitat within my sample squares that was affected by oak wilt in 2008.

I used the oak wilt centers delineated on the 2008 imagery to create a spatial model predicting the amount of potential golden-cheeked warbler habitat at risk of being affected by oak wilt by 2018. I chose a 10-year timeframe because it was long enough to show change over time but short enough to provide an estimate relevant to current management efforts. I ran a supervised classification on 2008 natural color 0.5-m orthoimagery using ArcMap 9.3.1 which identified all areas potentially susceptible to oak wilt (i.e., areas with trees) within each sample square. To ensure a high degree of accuracy, I manually deleted all areas classified as trees that were actually another land cover type such as grassy fields or water. Local spread of oak wilt occurs via

transmission through grafted roots (Gibbs and French 1980) or via the shared root system of clonally propagating live oaks (Appel 1995) resulting in ever-widening centers of disease. Based on average oak wilt spread rates of 11 - 16 m/year observed by Appel et al. (1989) within my study region, I placed a conservative 10 m buffer around each oak wilt center identified within my study squares then removed all areas composed of a land cover other than trees. I completed 10 iterations of this procedure to simulate 10 years of oak wilt spread. To account for any oak wilt that may spread into my sample squares from areas immediately adjacent to them within my 10-year timeframe, I completed the same procedure for all areas within 100 m of each sample square. Following the same criteria I used to delineate oak wilt centers initially, I used my final model to delineate the boundaries of the areas within my sample squares likely to be affected by oak wilt by 2018 (Figure 9). To identify areas of potential golden-cheeked warbler habitat at risk of being affected by oak wilt by 2018, I calculated the amount of potential habitat identified by Collier et al. (2012) that overlapped with areas containing oak wilt at the end of my simulation.

Because the probability of occupancy for any given patch is dependent on its size and the percent woodland composition of the surrounding landscape, fragmentation of potential habitat caused by oak wilt could decrease the suitability of areas not directly affected by the disease (Coldren 1998, Collier et al. 2012). To account for the effects of fragmentation, I reran the Collier et al. (2012) model twice with the assumption that all areas affected by oak wilt no longer represent potential habitat (see Chapter 2). The first run assessed the amount of potential habitat present excluding areas affected by oak wilt

in 2008, the second assessed the amount of potential habitat remaining excluding areas predicted be affected by 2018.



**Figure 9.** Example of an oak wilt center delineated from 2008 digital orthoimagery and the predicted boundaries of the same oak wilt center in 2018. Oak wilt does not spread across agricultural fields and other land cover types without trees.

#### *The effect of historical oak wilt on current occupancy probability*

To assess the effect of historical oak wilt on current occupancy probability, I obtained the oldest high resolution imagery available to me: color infrared aerial



photography taken in 1982 and 1983 on the three flightlines described previously (Figure 8). Using this imagery, I identified areas affected by oak wilt by visually delineating the boundaries of mortality centers within my sample squares. Consistent with the oak wilt delineations I did across my entire 4-county study region, I defined a mortality center as an area containing  $\geq 3$  dead or dying trees spaced  $\leq 20$  m apart (Appel et al. 1989). Appel and Maggio (1984) delineated oak wilt centers on this imagery using a similar protocol; oak wilt was the likely cause of mortality for 86% ( $n = 37$ ) of centers they ground-truthed in September 1983. I also identified all unaffected forest present in my sample squares in 1982 and 1983 which I used as a reference to draw comparisons between historically affected and unaffected areas. I removed all areas with oak wilt visible on 2008 0.5 m color infrared orthoimagery from these forested areas, leaving me with a representation of historical forest with no past or recent evidence of oak wilt. I then calculated the proportion of historically affected and unaffected forest identified as potential warbler habitat by Collier et al. (2012) for each sample square where oak wilt was present in 1982-3.

#### *Effects on future stand composition*

To assess the regeneration of vegetation within oak wilt centers, I took measurements at 150 randomly selected points each portion of each study site. I spaced points  $\geq 20$  m from one another to avoid measuring vegetation at multiple locations containing the same individuals (Gilman and Watson 1994, Jennings et al. 1999). At each point, I recorded all species present within 1 m with height  $< 3$  m, enabling me to draw comparisons between the understory vegetation of affected and unaffected areas. I

also recorded all species present within 1 m of the point with height  $> 3$  m in order to compare the vegetation of the understory to that of the overstory.

### *Analyses*

I calculated descriptive statistics for all variables measured. For my assessment of the current and future extent of oak wilt within warbler habitat, I broke the potential habitat up into 3 categories of low ( $> 0 - < 25\%$ ), medium ( $\geq 25\% - < 75\%$ ) and high ( $\geq 75\%$ ) probability of occupancy. I defined these categories based on the probability of occupancy of patches where I located territories (see Chapter 2). No occupied patches ( $n=24$ ) had a probability of occupancy  $< 25\%$ , 33% had a probability of occupancy between 25 and 75%, and 67% had an occupancy probability  $\geq 75\%$ . To obtain the amount of potential habitat affected by oak wilt across my study region, I multiplied the area of potential habitat within my sample squares by 98.3 (total ha in sample squares/total ha in study region). I applied the percent of potential habitat within my sample squares that was affected in 2008 and, separately, the percent my simulation predicted would be affected by 2018 to the amount of potential habitat in the study region to obtain the estimated amount of affected habitat. I completed this procedure for each category of potential habitat.

To assess the effect of historical oak wilt on current probability of occupancy, I broke areas of potential habitat identified by Collier et al. (2012) into 3 categories: all potential habitat,  $\geq 25\%$  occupancy probability, and  $\geq 75\%$  occupancy probability. Because my data was not normally distributed, I used a two-tailed Wilcoxon paired-sample test to evaluate my hypothesis that the proportion of area currently identified as

potential golden-cheeked warbler habitat differs between historically affected and unaffected forest (Zar 1996:167). I used a one-tailed Wilcoxon paired-sample test for non-normally distributed data to test my prediction that the proportion of area with occupancy probabilities  $\geq 25\%$  and, separately,  $\geq 75\%$  is less in areas affected by oak wilt than in unaffected forest.

To assess the regeneration of vegetation within oak wilt centers, I used a two-tailed Wilcoxon paired sample test to evaluate my hypotheses that the proportion of points with, separately, woody vegetation, susceptible oaks, less susceptible oaks, and Ashe juniper in the understory would differ between affected and unaffected forest. I also used a one-tailed Wilcoxon paired sample test to test for differences in the proportion of points with understory and overstory vegetation in affected and unaffected forest.

## RESULTS

### *Present and future extent of oak wilt*

I identified 158 mortality centers in 54% ( $n = 96$ ) of my sample squares. For sample squares containing oak wilt centers, mean area affected by oak wilt was 14.3 ha ( $n = 52$ , SD = 21.7 ha). Of the total area within my sample squares, 7.7% ( $n = 9,613$  ha) was affected by oak wilt. I applied this proportion to my entire study region and found that 73,091 ha were likely to have been affected by oak wilt by 2008. My simulation predicted that by 2018, 16.0% of the area inside my sample squares would be affected by oak wilt, an increase of 207% (77,921 ha) across my study region.

I ground-truthed 26 mortality centers located on 53% ( $n = 13$ ) of the squares I visited. I confirmed mortality at 100% of centers and attributed 96% of mortality centers to oak wilt. I identified 66% ( $n = 32$ ) of oak wilt centers present, only one of the missed centers ( $n = 13$ ) was located in a sample square with no other areas predicted to be oak wilt. Of the centers I missed, 92% ( $n = 13$ ) were  $< 0.4$  ha in size; 43% of all ground-truthed centers were  $< 0.4$  ha in size.

In 2008, 3,299 ha of potential golden-cheeked warbler habitat were present within my sample squares, 6.9% of which was affected by oak wilt. My simulation predicted that by 2018, 13.3% of potential habitat would be affected by oak wilt, a change of 193%. I found that 22,326 ha of potential habitat were likely to have been affected by oak wilt in 2008 and an additional 20,847 ha are at risk of being affected by 2018. My simulation predicted the largest percent increase in affected area would occur in potential habitat with a low probability of occupancy ( $0 < p < 25\%$ ). Potential habitat with high probability of occupancy ( $\geq 75\%$ ) was predicted to have the lowest percent increase by 2018 but since areas with high probability of occupancy comprised 51% all affected potential habitat in 2008, these areas contained the highest total number of hectares at risk (Table 7).

When I accounted for fragmentation of potential habitat caused by the presence of oak wilt on the landscape, I found that 21,234 ha of potential golden-cheeked warbler habitat were at risk of being affected between 2008 and 2018, 0.7% more total habitat than predicted to contain oak wilt alone (Table 8). The greatest absolute loss occurred in

areas with high probability of occupancy ( $\geq 75\%$ ) and the greatest percent loss occurred in areas with an intermediate probability of occupancy ( $25 < p < 75\%$ ).

**Table 7.** Percent of potential golden-cheeked warbler habitat containing oak wilt within sample squares and the area my model identifies as containing oak wilt across Bandera, Kendall, Kerr and Gillespie counties, TX, in 2008 and by 2018.

Occupancy probability (p)	Sample squares (%)	Study region (ha)	Sample squares (%)	Study region (ha)	Change (%)	Study region at risk (ha)
	2008		2018		2008 to 2018	
$0 < p < 25$	9.6	4,012	22.7	9,432	235	5,419
$25 \leq p < 75$	14.7	6,996	30.4	14,491	207	7,496
$p \geq 75$	4.8	11,318	8.1	19,250	170	7,932
All habitat	6.9	22,326	13.3	43,173	193	20,847

**Table 8.** Area (ha) of potential habitat not containing oak wilt within my sample squares and across Bandera, Kendall, Kerr, and Gillespie Counties, TX, in 2008 and by 2018. Changes to the amount of potential habitat are attributed both to the actual presence of oak wilt and to fragmentation of otherwise unaffected habitat.

Occupancy probability (p)	Sample squares (ha)	Study region (ha)	Sample squares (ha)	Study region (ha)	Area lost (ha)	Area lost (%)
	2008		2018		2008 to 2018	
$0 < p < 25$	410	40,287	371	36,432	3,855	9.6
$25 \leq p < 75$	398	39,134	322	31,616	7,517	19.2
$p \geq 75$	2,246	220,864	2,146	211,004	9,861	4.5
All habitat	3,054	300,285	2,838	279,052	21,234	7.1

### *The effect of historical oak wilt on current occupancy probability*

Using the 1982 - 1983 aerial imagery, I identified 51 oak wilt centers on 48% ( $n = 46$ ) of my samples squares. For sample squares containing oak wilt centers, mean area

affected was 2.6 ha ( $n = 22$ ,  $SD = 5.2$  ha). Of the area inside my sample squares, 1.2% ( $n = 4,603$  ha) was affected by oak wilt. Using the 2008 imagery, I located 72 oak wilt centers on 63% ( $n = 46$ ) of my sample squares. The mean area affected in sample squares containing oak wilt was 6.4 ha ( $n = 29$ ,  $SD = 9.1$  ha). 4.1% ( $n = 4,604$  ha) of the area inside the sample squares was affected by oak wilt, a 329% change from 1982-1983. The change in area affected by oak wilt varied by flightline (Table 9). The flightline with the least oak wilt in 1982-3, Fredericksburg to Johnson City, experienced the highest percent increase, 16,064%, while the Fredericksburg to Comfort flightline, experienced a more moderate, but still substantial, increase of 2,821%. The amount of visible oak wilt on the flightline with the highest incidence in 1982, Kerrville to Bandera, decreased by 63%. Of the sample squares where oak wilt occurred in 1982-3, 77.3% ( $n = 22$ ) contained oak wilt in 2008; 13.7% ( $n = 51$ ) of the individual centers were still visible. Of the squares where I located oak wilt in 2008, 37.9% ( $n = 29$ ) did not contain oak wilt in the early 1980s.

**Table 9.** Percent of squares containing oak wilt centers in 1982-3 and in 2008, percent of total area within sample squares containing oak wilt in 1982-3 and in 2008, and percent change in area with oak wilt between 1982-3 and 2008 for each flightline, Fredericksburg to Johnson City (F – JC), Fredericksburg to Comfort (F – C) and Kerrville to Bandera (K – B) and for all three flightlines combined (all).

Flightline	Squares with oak wilt (%)		$n$	Area with oak wilt (%)		$n$ (ha)	Change (%)
	1982-3	2008		1982-3	2008		
F - JC	8.3	50.0	12	<0.001	1.1	1200	16,064
F - C	52.9	82.4	17	0.3	9.1	1701	2,821
K- B	70.6	52.9	17	3.0	1.1	1702	37
All	47.8	63.0	46	1.2	4.1	4603	329

I found no difference in the proportion of area composed of all potential habitat ( $n = 22$ ,  $S_{21} = 21$ ,  $P = 0.452$ ) between affected and unaffected areas but found the proportion of area composed of potential habitat with  $\geq 25\%$  occupancy probability ( $n = 22$ ,  $S_{21} = 40.5$ ,  $P = 0.004$ ) was 71% less in affected areas. I found no difference in the proportion of area composed of potential habitat with  $\geq 75\%$  occupancy probability ( $n = 22$ ,  $S_{21} = 10$ ,  $P = 0.098$ ) between affected and unaffected areas (Table 10).

**Table 10.** Mean proportion of affected and unaffected forest containing potential golden-cheeked warbler habitat with  $> 0\%$ ,  $\geq 25\%$ , and  $\geq 75\%$  probability of occupancy, the mean and standard deviation of the difference between the two calculated as proportion habitat in affected – proportion habitat in unaffected, and results of Wilcoxon paired sample tests.

Occupancy probability (%)	Proportion of affected	Proportion of unaffected	Mean difference	SD difference	$S$	$P$
All	0.30	0.21	0.09	0.72	21.0	0.452
$\geq 25$	0.05	0.17	-0.12	0.20	40.5	0.004
$\geq 75$	0.03	0.07	-0.04	0.21	10.0	0.098

#### *Effects on future stand composition*

Ashe juniper was the most common overstory and understory species in both affected and unaffected forest. I found no difference in the proportion of points with understory vegetation between areas affected by oak wilt and areas that were not ( $S_{13} = 1.5$ ,  $P = 0.952$ ). I also found no difference in the proportion of points with less susceptible oaks ( $S_{13} = 4.5$ ,  $P = 0.695$ ) or Ashe juniper ( $S_{13} = 10.5$ ,  $P = 0.542$ ) in the understory between affected and unaffected forest. The mean proportion of points with susceptible oaks in affected areas was 1.6 times that of unaffected areas but this difference was not statistically significant ( $S_{13} = 20.5$ ,  $P = 0.217$ ; Table 11).

The proportion of points with susceptible oaks in the overstory was 3.4 times that of the understory in affected areas ( $S = 41.5$ ,  $P = 0.007$ ) and 6.7 times that of the understory in unaffected areas ( $S = 52.5$ ,  $P = 0.0001$ ; Table 12). Similarly, the proportion of points with less susceptible oaks in the overstory was 5.2 times that of the understory in affected areas ( $S = 33.0$ ,  $P = 0.007$ ) and 6.6 times that of the understory in unaffected areas ( $S = 43.5$ ,  $P = 0.004$ ). I found no statistical difference in the proportion of points with Ashe juniper between the overstory and understory in affected ( $S = 7.5$ ,  $P = 0.636$ ) and unaffected areas ( $S = 2.5$ ,  $P = 0.903$ ). I also found no significant difference in the proportion of points with woody vegetation between the overstory and understory in affected areas ( $S = 24.5$ ,  $P = 0.135$ ) but found the proportion of points with woody vegetation was 163% higher in the overstory than the understory in unaffected areas ( $S = 44.5$ ,  $P = 0.003$ ). See Appendix B for all understory and overstory species recorded at my study sites.

**Table 11.** Mean proportion of points with susceptible oak species, less susceptible oak species, Ashe juniper and all vegetative species < 3 m in height, the mean and standard deviation of the difference between the two calculated as the proportion of points in affected areas minus the proportion of points in unaffected areas with, and results of paired sample  $t$ -tests.

Species	Proportion of affected	Proportion of unaffected	Mean difference	SD	$S$	$P$
Susceptible oaks	0.04	0.03	-0.01	0.05	20.5	0.217
Less susceptible oaks	0.007	0.008	-0.001	0.01	4.5	0.695
Ashe juniper	0.18	0.22	0.04	0.14	10.5	0.542
All vegetation	0.31	0.30	-0.01	0.14	1.5	0.952



**Table 12.** Mean proportion of points with susceptible oak species, less susceptible oak species, Ashe juniper and all woody species in the understory (< 3 m in height) and the overstory (> 3 m in height), the mean and standard deviation of the difference between the two calculated as the proportion of understory points minus the proportion of overstory points, and results of Wilcoxon paired-sample tests for affected and unaffected portions of study sites.

Species	Proportion of understory	Proportion of overstory	Mean difference	SD	<i>S</i>	<i>P</i>
<b>Affected</b>						
Susceptible oaks	0.04	0.14	-0.10	0.10	41.5	0.007
Less susceptible oaks	0.007	0.036	-0.030	0.043	33.0	0.007
Ashe juniper	0.18	0.17	0.01	0.17	-7.5	0.636
All vegetation	0.31	0.41	-0.10	0.19	24.5	0.135
<b>Unaffected</b>						
Susceptible oaks	0.03	0.17	-0.15	0.06	52.5	<0.001
Less susceptible oaks	0.008	0.053	-0.045	0.050	43.5	0.004
Ashe juniper	0.22	0.27	-0.05	0.16	2.5	0.903
All vegetation	0.30	0.49	-0.19	0.19	44.5	0.003

## DISCUSSION

The model I developed is the first to estimate the area affected by oak wilt within my study region at a single point in time using systematic methodology; its results suggest that over twice as much area has been affected by oak wilt than previously anticipated (J. Zhu, Texas Forest Service, unpublished data). My model showed oak wilt occurred in potential golden-cheeked warbler habitat nearly as often as it occurred in all forest; 22,326 ha or 6.9% of potential warbler habitat was affected by oak wilt in 2008. By 2018, the model predicted 43,163 ha or 13.3% of potential warbler habitat would be directly affected by the disease, a 193% change, with the greatest increase occurring in the areas with the highest probability of occupancy. When I accounted for the additional effect of fragmentation, less potential habitat was lost from the  $0 < p < 25\%$  category and more potential habitat was lost from patches with high probability of occupancy

( $\geq 75\%$ ). This outcome was likely caused by a downward shift in occupancy probability in patches fragmented by oak wilt. Because many patches of potential habitat were not completely contained within my sample squares, oak wilt may have caused additional fragmentation not accounted for in my estimates. Thus, the losses I attributed to fragmentation should be considered to be a minimum effect. As discussed in the second chapter of this manuscript, golden-cheeked warblers use areas affected by oak wilt significantly less than unaffected forest and those that do place their territories in oak wilt have lower reproductive success. Previous studies have suggested that urbanization and agricultural practices are the main causes of loss and degradation of warbler habitat (Wahl et al. 1990); my data suggest that oak wilt may be a third contributing factor.

Several factors may influence the rate of oak wilt spread and, thus, the amount of warbler habitat potentially impacted by the disease, that I could not account for in my simulation. In instances where specific information was lacking, I went with the most conservative option. First, my model assumes that oak wilt spreads locally at a constant rate of 10 m per year. Appel et al. (1989) observed mean expansion rates of 11 – 16 m per year with a maximum of 45 m per year in central Texas. Therefore, it is likely that more total area and thus more warbler habitat will be affected by oak wilt over the next 10 years than my model predicts. A second assumption in my model is that oak wilt only spreads locally via interconnected root systems. However, oak wilt can also be vectored over longer distances by several species of nitidulid beetle which transport fungal spores (Gibbs and French 1980, Juzwick and French 1983). Vectored spread always initiates with an infected red oak as *C. fagacearum* does not form reproductive mats on live or

white oaks (Appel 1995). Appel (1995) described the relationship between *C. fagacearum* and its vector as inefficient, leading to low rates of new center formation. Once a new center of oak wilt infection has formed, the disease then begins to spread to adjacent trees via the roots. In Chapter 2, I found canopy cover in live oaks in both oak wilt centers and in adjacent unaffected forest to be > 5 times that of canopy cover in species susceptible to fungal mat formation (Texas red oak and blackjack oak). Given the relative abundance of live oaks within my study sites and oak wilt's inefficient relationship with its vector, I assumed the amount of forest affected by vectored spread would be negligible over the 10-year period of my simulation. One assumption that could have resulted in an overestimation of oak wilt spread was that all trees identified by supervised classification were susceptible species oak wilt could spread through. The supervised classification successfully distinguished between areas with trees and those without trees but did not differentiate between tree species. Thus, some forested areas composed of unsuitable species such as Ashe juniper or mesquite (*Prosopis* spp.) may have been incorrectly predicted to contain oak wilt by 2018.

I found that how habitat was categorized influenced whether there was a difference in the proportion of potential habitat currently present between historically affected and unaffected areas. The tendency of oak wilt to reduce the total number of trees but to infrequently remove all trees may provide an explanation. Because not all trees are susceptible to oak wilt, areas affected by the disease are often still forested so are likely to have been identified as warbler habitat despite historical infection. However, areas where oak wilt occurred historically are likely to be more fragmented

and contain fewer trees than unaffected areas. Because previous studies have found a positive correlation between patch size, surrounding percent woodland composition, and the probability of warbler occupancy, the more open condition resulting from loss of oaks may work to decrease the occupancy probability of areas affected by oak wilt resulting in the variation I observed (Magness et al. 2006, Collier et al. 2012).

I found no differences in understory vegetation between affected and unaffected portions of my study sites. However, I did find that understory oaks were rather uncommon in general while Ashe juniper was the most frequently observed species. Oaks were 3.4 – 6.7 times more common in the overstory than the understory while the proportion of points with Ashe juniper was not significantly different between the two. This suggests that as mature oaks are removed from the forest by a variety of factors, of which only one is oak wilt, the species composition will shift towards Ashe juniper. Because golden-cheeked warblers forage preferentially on oak early in the breeding season, a reduction in oaks over time may increase foraging effort and decrease reproductive success (Marshall 2011).

The results from my assessment of historical oak wilt and my assessment of understory vegetation suggest that once oaks are removed from an area, new oaks are unlikely to replace them. Therefore, it is unlikely that oak wilt would occur in the same place more than once. This suggests that within a bounded area the percent of susceptible trees affected by oak wilt will increase quickly at first then taper off once a level of saturation has been reached. The rates of expansion I observed between 1982-3 and 2008 lend support to this hypothesis because the greatest increases occurred in areas

with the least historical oak wilt and vice versa. The amount of visible oak wilt on the flightline with the highest incidence in 1982, Kerrville to Bandera, actually decreased by 63%, suggesting that the saturation point may have been reached. Future studies within these study areas could provide valuable information concerning how oak wilt expands through a system.

## **MANAGEMENT IMPLICATIONS**

My results indicate that oak wilt is widespread throughout my study region and frequently occurs in golden-cheeked warbler habitat. Additionally, the disease has experienced high rates of expansion over the past 30 years and will continue to spread into golden-cheeked warbler habitat in the future. Because oak wilt is present in varying intensities throughout most of the warbler's breeding range, additional research in other areas would broaden our understanding of its impact on the species as a whole. Several techniques such as trenching and chemical control may be employed to stop or slow local spread of the disease (Appel 1995), I recommend these methods be used where managers wish to halt the spread of oak wilt at a specific location such as a state park or a private property managed for golden-cheeked warblers. To control oak wilt on a larger scale, management efforts should focus on preventing the formation of new infection centers. To this end, programs designed to educate the public on proper pruning and wound treatment for susceptible oaks, and the establishment of a diverse assortment of tree species may be an effective approach (Billings 2008). Future management efforts should address the threat oak wilt poses to golden-cheeked warblers by incorporating applicable preventative measures.

## CHAPTER IV

### SUMMARY

I located golden-cheeked warblers on just over half of my study sites and found oak wilt within active territories at 5 locations. These results are consistent with previous observations of oak wilt in golden-cheeked warbler habitat within my study region (Wahl et al. 1990). I found affected areas to be vegetationally similar between sites where warblers used oak wilt and sites where they did not, indicating that variable use of oak wilt among sites was not due to differences in vegetation. One possible explanation for why warbler territories were located in oak wilt at some sites but not at others is conspecific attraction. Farrell (2011) found that golden-cheeked warblers maintain territories in areas where they perceive other warblers to be present, even if those areas had previously gone unoccupied. Ten of the 14 oak wilt territories were located at the two sites with the highest and second highest absolute number of golden-cheeked warbler territories. Conspecific attraction might have influenced birds to settle in areas affected by oak wilt at these locations but additional data would be necessary to draw any firm conclusions.

Of the 69 territories I mapped, only 3 contained oak wilt for > 50% of their area, suggesting that the presence of oak wilt negatively influences habitat selection by male warblers. Males whose territories were located in oak wilt for > 10% of their area had significantly lower pairing success than those in unaffected forest and none of the males with > 50% of their territory in oak wilt paired. However, males using oak wilt that did

pair fledged young as successfully as those who only used unaffected forest. Similar results were observed by Allen et al. (2009) who found pair density of Acadian flycatchers (*Empidonax virescens*) to be negatively associated with defoliation caused by hemlock woolley adelgids (*Adelges tsugae* Annand) but that nest survival was unaffected. Tye (1992) found that vegetative characteristics may be used by birds as an indicator of habitat quality but that this assessment is not always correct. Females may have used vegetative characteristics such as percent canopy cover to assess the quality of a male's territory but, in the end, females that chose territories in oak wilt fledged young just as successfully as those in unaffected areas. However, because no females chose to pair with males whose territories were >50% oak wilt, I could not assess rates of fledging success for territories mostly in oak wilt. Despite this, my data indicate that the habitat quality is lower in areas affected by oak wilt for males because those that use oak wilt are less likely to pair and thus are less likely to fledge young. The combination of lower mean territory density and lower pairing success suggests that areas affected by oak wilt have a lower overall reproductive output than unaffected forest.

My comparisons of canopy cover between oak wilt and unaffected forest supported my predictions that total canopy cover and canopy cover in susceptible oaks would be lower in areas with oak wilt and that canopy cover in less susceptible oaks and Ashe juniper would not differ significantly. Though mean total canopy was only 3.1% lower in oak wilt than in unaffected forest, this difference represents a relative difference of 15.2%. Golden-cheeked warblers are typically found in areas with high canopy cover during the breeding season (Ladd and Gass 1999). Because canopy cover was no greater

than 38% at any of my study sites, a 15% relative loss could substantially reduce an area's perceived suitability. Alternatively, Klassen (2011) found no effect of total canopy closure on territory density but did find a positive relationship between the proportion of oak per study site and territory density. The difference I observed in total canopy cover was mainly due to a decrease in canopy cover in susceptible oaks. I observed the greatest difference in Texas oak which was 62.5% lower in oak wilt relative to unaffected forest. This result is likely due to its high susceptibility to oak wilt and the rapid rate at which it succumbs to the disease. Loss of Texas oak from golden-cheeked warbler habitat may be especially detrimental to the bird as compared to the loss of other oak species. Marshall (2011) found that golden-cheeked warblers in areas dominated by red oaks had higher reproductive success than warblers in areas dominated by blackjack and post oak. This indicates that golden-cheeked warbler habitat with high canopy cover in red oaks may simultaneously be the best quality and the most likely to be substantially changed by oak wilt.

Though not statistically significant, mean warbler density in unaffected areas was 2.1 times greater than in oak wilt during the post-breeding season. My results indicate that post-breeding warblers are more commonly found in unaffected forest than in oak wilt but that movement from unaffected forest to oak wilt does occur. Marshall (2011) found that though golden-cheeked warblers forage on Ashe juniper more frequently than oak late in the season, they still use oaks as a foraging substrate during this time. Thus, lower oak canopy cover in affected areas could cause the birds to forage preferentially in unaffected areas during the post-breeding season.



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The results from my assessment of historical oak wilt and my assessment of understory vegetation suggest that once oaks are removed from an area, new oaks are unlikely to replace them. Therefore, it is unlikely that oak wilt would occur in the same place more than once. This suggests that within a bounded area the percent of susceptible trees affected by oak wilt will increase quickly at first then taper off once a level of saturation has been reached. The rates of expansion I observed between 1982-3 and 2008 lend support to this hypothesis because the greatest increases occurred in areas with the least historical oak wilt and vice versa. The amount of visible oak wilt on the flightline with the highest incidence in 1982, Kerrville to Bandera, actually decreased by 63%, suggesting that the saturation point may have been reached. Future studies within these study areas could provide valuable information concerning how oak wilt expands through a system.

My results suggest that oak wilt negatively influences golden-cheeked warbler habitat selection and quality. Additionally, frequently occurs in warbler habitat and will continue to spread into it in the near future. Because oak wilt is present in varying intensities throughout most of the warbler's breeding range, additional research in other areas would broaden our understanding of its impact on the species as a whole. Several techniques such as trenching and chemical control may be employed to stop or slow local spread of the disease (Appel 1995), I recommend these methods be used where managers wish to halt the spread of oak wilt at a specific location such as a state park or a private property managed for golden-cheeked warblers. To control oak wilt on a larger scale, management efforts should focus on preventing the formation of new infection

centers. To this end, programs designed to educate the public on proper pruning and wound treatment for susceptible oaks, and the establishment of a diverse assortment of tree species may be an effective approach (Billings 2008). Future management efforts should address the threat oak wilt poses to golden-cheeked warblers by incorporating applicable preventative measures.

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## APPENDIX A

**Table A-1.** Mean and standard deviation of the percent canopy cover for each woody species in areas affected by oak wilt and in unaffected forest, 2010 and 2011.

Species	No. Sites	Mean % canopy cover oak wilt	SD	Mean % canopy cover unaffected	SD
<i>Carya illinoensis</i>	3	0	-	< 1	-
<i>Celtis spp.</i>	15	2	1	< 1	1
<i>Cornus drummondii</i>	1	0	-	< 1	-
<i>Diospyros texana</i>	13	< 1	< 1	< 1	< 1
<i>Ehretia anacua</i>	2	< 1	< 1	< 1	< 1
<i>Fraxinus spp.</i>	7	< 1	< 1	< 1	< 1
<i>Ilex decidua</i>	1	< 1	-	0	-
<i>Juglans microcarpa</i>	17	< 1	< 1	1	1
<i>Juniperus ashei</i>	23	7	8	8	6
<i>Melia azedarach</i>	2	0	-	< 1	< 1
<i>Mimosa spp.</i>	1	0	-	< 1	-
<i>Morus microphylla</i>	1	< 1	-	0	-
<i>Platanus occidentalis</i>	6	< 1	< 1	< 1	< 1
<i>Prosopis glandulosa</i>	5	< 1	< 1	< 1	< 1
<i>Prunus serotina</i>	5	0	-	< 1	< 1
<i>Quercus fusiformis</i>	25	5	4	6	5
<i>Quercus buckleyi</i>	20	< 1	1	2	2
<i>Quercus laceyi</i>	8	< 1	1	1	< 1
<i>Quercus marilandica</i>	14	1	3	2	2
<i>Quercus sinuata</i>	13	< 1	1	< 1	< 1
<i>Quercus stellata</i>	19	< 1	1	< 1	1
<i>Rhus spp.</i>	1	0	-	< 1	-
<i>Salix nigra</i>	1	0	-	< 1	-
<i>Sideroxylon lanuginosum</i>	2	< 1	< 1	< 1	< 1
<i>Tilia spp.</i>	1	< 1	-	0	-
<i>Ulmus crassifolia</i>	16	2	3	2	3
<i>Ulmus spp.</i>	3	< 1	< 1	< 1	< 1

## APPENDIX B

**Table B-1.** Mean and standard deviation of the proportion of points with each woody species present in the understory (< 3 m in height) and the overstory (> 3 m in height) in areas affected by oak wilt, 2011. I considered a study site to contain a given species if that species was present in any portion of the site regardless of treatment (affected versus unaffected).

Species	No. Sites	Mean Proportion of Understory	SD	Mean Proportion of Overstory	SD
<i>Acacia spp.</i>	1	0	-	0	-
<i>Arbutus xalapensis</i>	2	0	-	0	-
<i>Baccharis spp.</i>	6	0.02	0.04	0	-
<i>Berberis trifoliata</i>	13	0.05	0.05	0	-
<i>Celtis spp.</i>	8	< 0.01	0.01	0.02	0.02
<i>Diospyros texana</i>	13	0.10	0.09	0.03	0.03
<i>Ehretia anacua</i>	2	0	-	0.03	0.05
<i>Fraxinus spp.</i>	6	< 0.01	0.01	< 0.01	< 0.01
<i>Ilex decidua</i>	6	< 0.01	< 0.01	< 0.01	< 0.01
<i>Juglans microcarpa</i>	11	< 0.01	< 0.01	0.02	0.02
<i>Juniperus ashei</i>	14	0.18	0.12	0.17	0.18
<i>Mimosa spp.</i>	1	0	-	0	-
<i>Platanus occidentalis</i>	4	< 0.01	< 0.01	< 0.01	< 0.01
<i>Prosopis glandulosa</i>	7	0.02	0.04	< 0.01	< 0.01
<i>Prunus serotina</i>	3	0	-	< 0.01	< 0.01
<i>Ptelea trifoliata</i>	1	0	-	0	-
<i>Quercus fusiformis</i>	14	0.04	0.05	0.12	0.08
<i>Quercus buckleyi</i>	12	< 0.01	< 0.01	0.02	0.03
<i>Quercus laceyi</i>	7	0	-	0.01	0.02
<i>Quercus marilandica</i>	5	0	-	0.01	0.01
<i>Quercus sinuata</i>	12	< 0.01	< 0.01	0.01	0.02
<i>Quercus stellata</i>	10	< 0.01	< 0.01	0.03	0.03
<i>Rhus spp.</i>	1	0	-	0	-
<i>Salix nigra</i>	1	0	-	0	-
<i>Sideroxylon lanuginosum</i>	2	0.01	0.02	0.02	0.03
<i>Sophora secundiflora</i>	4	< 0.01	< 0.01	0	-
<i>Ulmus crassifolia</i>	11	< 0.01	0.01	0.04	0.07
<i>Ulmus spp.</i>	1	0	-	0	-
<i>Ungnadia speciosa</i>	1	0	-	< 0.01	-
<i>Zanthoxylum hirsutum</i>	1	< 0.01	-	0	-

**Table B-2.** Mean and standard deviation of the proportion of points with each woody species present in the understory (< 3 m in height) or the overstory (> 3 m in height) in areas not affected by oak wilt, 2011. I considered a study site to contain a given species if that species was present in any portion of the site regardless of treatment (affected versus unaffected).

Species	No. Sites	Mean Proportion of Understory	SD	Mean Proportion of Overstory	SD
<i>Acacia spp.</i>	1	0.01	-	0	-
<i>Arbutus xalapensis</i>	2	0.02	0.01	0	0
<i>Baccharis spp.</i>	6	0.02	0.02	< 0.01	< 0.01
<i>Berberis trifoliata</i>	13	0.03	0.04	0	0
<i>Celtis spp.</i>	8	< 0.01	< 0.01	0.01	0.02
<i>Diospyros texana</i>	13	0.05	0.05	0.01	0.02
<i>Ehretia anacua</i>	2	0	0	0.04	0.05
<i>Fraxinus spp.</i>	6	< 0.01	< 0.01	0.02	0.01
<i>Ilex decidua</i>	6	< 0.01	< 0.01	0	0
<i>Juglans microcarpa</i>	11	< 0.01	< 0.01	0.02	0.02
<i>Juniperus ashei</i>	14	0.22	0.11	0.27	0.17
<i>Mimosa spp.</i>	1	0	-	< 0.01	-
<i>Platanus occidentalis</i>	4	< 0.01	0.01	< 0.01	< 0.01
<i>Prosopis glandulosa</i>	7	0.01	< 0.01	< 0.01	< 0.01
<i>Prunus serotina</i>	3	< 0.01	< 0.01	0.01	0.01
<i>Ptelea trifoliata</i>	1	< 0.01	-	0	-
<i>Quercus fusiformis</i>	14	0.02	0.02	0.11	0.06
<i>Quercus buckleyi</i>	12	< 0.01	< 0.01	0.05	0.04
<i>Quercus laceyi</i>	7	< 0.01	< 0.01	0.04	0.03
<i>Quercus marilandica</i>	5	n	n	0.01	0.01
<i>Quercus sinuata</i>	12	< 0.01	< 0.01	0.02	0.02
<i>Quercus stellata</i>	10	< 0.01	< 0.01	0.02	0.02
<i>Rhus spp.</i>	1	< 0.01	-	< 0.01	-
<i>Salix nigra</i>	1	0	-	< 0.01	-
<i>Sideroxylon lanuginosum</i>	2	0	0	< 0.01	< 0.01
<i>Sophora secundiflora</i>	4	0.03	0.05	< 0.01	< 0.01
<i>Ulmus crassifolia</i>	11	< 0.01	< 0.01	0.03	0.06
<i>Ulmus spp.</i>	1	0	-	0.01	-
<i>Ungnadia speciosa</i>	1	0	-	0	-
<i>Zanthoxylum hirsutum</i>	1	0	-	0	-

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