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Original Article

Effects of a Forest Pathogen on Habitat Selection and Quality for the Endangered Golden-Cheeked Warbler

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ABSTRACT Oak wilt is a fatal forest disease caused by the fungus *Ceratocystis fagacearum*. Loss or degradation of habitat caused by oak wilt may negatively affect forest songbirds, including the federally endangered golden-cheeked warbler (*Setophaga chrysoparia*), a species that breeds exclusively in the Ashe juniper–oak woodlands (*Juniperus ashei*–*Quercus* spp.) of central Texas, USA. During 2010 and 2011, we investigated the influence of oak wilt on golden-cheeked warbler habitat selection and quality at 25 study sites that each contained forest affected by oak wilt and unaffected forest. We assessed habitat selection in terms of use versus availability at 2 scales: within the patch and within the territory. We also assessed post-breeding use of affected forest by comparing detection densities in affected and unaffected forest. To assess the influence of oak wilt on habitat quality, we compared the reproductive outcome of territories in unaffected and affected areas. We assessed within-patch habitat selection for 67 territories and found that golden-cheeked warblers used affected forest significantly less than its availability. We found use of affected forest to be variable within the 14 territories that contained affected forest in >10% of their area. Post-breeding use of affected forest was also variable. Pairing success was 27% lower for males whose territories contained >10% affected forest but fledging success was not affected. Our 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.

KEY WORDS endangered species, forest pathogen, golden-cheeked warbler, habitat quality, habitat selection, oak wilt, reproductive success, *Setophaga chrysoparia*.

Pathogen-induced changes to vegetation structure and composition may influence wildlife by altering nesting and roosting sites, availability of forage and foraging substrates, microclimatic conditions, predation risk, and the ability of an individual to attract a mate (Loo 2009). Although wildlife may sometimes benefit from the presence of a pathogen (Bell and Whitmore 1997, Garnett et al. 2004), diseases that occur in mature forest often cause shifts from forest interior species toward species found in earlier seral stages with more open vegetation structure (Kendeigh 1982, Rabenold et al. 1998, Tingley et al. 2002, Smith and Stephen 2005, Monahan and Koenig 2006). If the pathogen has a broad spatial distribution, the consequences for wildlife could be considerable (Castello et al. 1995).

Oak wilt is a broadly distributed forest disease found throughout the eastern and central portions of the United States as far south as Texas, USA (O'Brien et al. 2011). Changes to vegetation resulting from oak wilt may negatively affect the federally endangered golden-cheeked warbler (*Setophaga chrysoparia*), a migratory songbird that breeds exclusively in mature Ashe juniper–oak woodlands (*Juniperus ashei*–*Quercus* spp.) of central Texas (Wahl et al. 1990, Appel and Camilli 2010). Oak wilt is found throughout the range of the golden-cheeked warbler and may contribute to one of the primary threats to the species—loss and fragmentation of breeding habitat (Fig. 1; USFWS 1990, 1992, Texas Forest Service 2009).

Oak wilt is a frequently fatal disease of oaks caused by a fungus, *Ceratocystis fagacearum* (Gibbs and French 1980). Infection by *C. fagacearum* causes blockages to form in the vascular tissues of the host; the outcome of which varies by individual and species. Although oak wilt may occur in any oak species, its effects are most pronounced in red oaks

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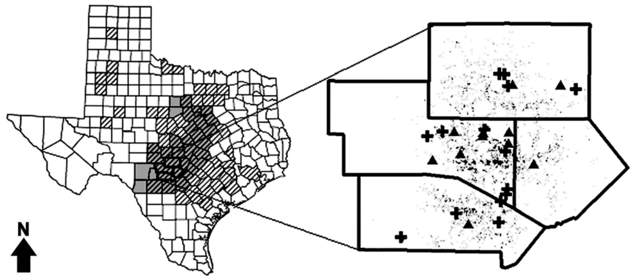

Figure 1. The breeding range of the golden-cheeked warbler (gray) and Texas (USA) counties with confirmed cases of oak wilt (slashed). We conducted this study in (clockwise from top) Gillespie, Kendall, Bandera, and Kerr counties (outlined in bold) in 2010 (triangles, $n = 11$) and 2011 (crosses, $n = 14$). Oak wilt (gray on close-up) is widespread in the central portion of our 4-county study region (J. Zhu, Texas Forest Service, unpublished data).

(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 particular species are highly susceptible to the disease and usually die within 1–6 months post-infection (Appel 1995). Oak wilt disease centers form when fungal spores are transmitted overland to a new host tree by one of several species of beetle in the Nitidulidae family (Gibbs and French 1980, Juzwick and French 1983). Once a host tree has become infected, the pathogen can spread to adjacent trees via interconnected root systems. A concentration of oaks destroyed by oak wilt and their actively infected neighbors are collectively referred to as an oak wilt center. Oak wilt centers can expand quickly (<45 m/yr) through otherwise healthy forest, usually leaving <20% of susceptible trees alive (Appel et al. 1989).

Loss of live and red oaks from otherwise suitable woodland due to oak wilt may negatively influence habitat selection by golden-cheeked warblers. During the breeding season, golden-cheeked warblers are typically found in Ashe juniper–mixed oak 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 because oak density has been found to be positively correlated with warbler density (Wahl et al. 1990). The presence of oak wilt may further influence habitat selection by increasing the amount of edge within a woodland patch, a feature previous studies have found to be negatively correlated with golden-cheeked warbler occupancy (DeBoer and Diamond 2006, Magness et al. 2006). We investigated the influence of oak wilt on golden-cheeked warbler habitat selection during the breeding season at 2 distinct spatial scales—within the patch (second-order selection; Johnson 1980) and within territory boundaries (third-order selection; Johnson 1980). Because golden-cheeked warbler habitat has been described in detail by previous studies (see Groce et al. 2010), we did not consider all potential vegetation types within our study area. Rather, we assessed use of oak wilt centers within areas of potential habitat (Ashe juniper–oak woodland). Additionally, we assessed the influence of oak wilt during the post-breeding period when warblers might alter their selection of habitat (USFWS 1992, Ladd and Gass 1999, M. R. Hutchinson, unpublished data). We predicted that golden-cheeked warblers would use oak wilt centers less than their availability within the patch and within the territory and that density of post-breeding detections would be lower in affected forest.

Preferential use of one habitat category over another does not necessarily indicate that use of the preferred habitat will confer increased fitness to an individual (Jones 2001). Changes to woodland composition and structure caused by oak wilt may result in modified thermal conditions, increased susceptibility to predation, and decreased availability of arthropod food (Wahl et al. 1990, Marshall et al. 2013); all of which may cause decreases in reproductive success. Therefore, we assessed the influence of oak wilt on habitat quality for golden-cheeked warblers in terms of pairing and fledging success. We predicted both measures would be lower in affected forest.

We hypothesized that the influence of oak wilt on habitat selection and quality would ultimately be driven by altered vegetation structure and composition in affected forest. Therefore, we assessed the vegetation of our study sites to quantify differences between forest affected by oak wilt and unaffected forest. We predicted that juniper–oak woodlands 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 for Ashe juniper or less susceptible (white) oaks (subgenus *Leucobalanus*).

STUDY AREA

We conducted our study in Bandera, Gillespie, Kendall, and Kerr counties, Texas, located in the southwestern portion of the golden-cheeked warbler's range (Fig. 1). Located on the Edward's Plateau, these counties were characterized by limestone hills separated by broad, flat valleys or canyons. The elevation in our study counties ranged from approximately 300 m to 750 m. Common vegetation communities included oak savanna and Ashe-juniper woodland (Diamond 1997). Collier et al. (2012) estimated that approximately 314,000 ha of golden-cheeked warbler habitat existed in these 4 counties. Oak wilt was widespread throughout the southern portion of Gillespie County, the western portion of Kendall County, and the eastern portions of Bandera and Kerr counties. The Texas Forest Service estimated that oak wilt had affected ≥32,030 ha in these 4 counties by 2009 (J. Zhu, Texas Forest Service, unpublished data).

METHODS

Study Site Selection

We collected data from 11 study sites in 2010 and 14 study sites in 2011, all located on private property (Fig. 1). We selected potential study sites using a Geographic Information System shapefile depicting oak wilt centers that the Texas Forest Service identified either during aerial surveys conducted in the mid-1990s or during ongoing opportunistic visits to private properties that began in 1991 (J. Zhu, unpublished data). We began by randomly selecting an oak wilt center from the shapefile. If the oak wilt center was large enough to accommodate at least one golden-cheeked warbler territory ($\geq$4 ha; Ladd and Gass 1999) and if it was bordered by a contiguous patch of unaffected forest $\geq$20 ha in size, the minimum patch size required for golden-cheeked warblers to successfully reproduce (Butcher et al. 2010), we accepted the location as a study site. If we rejected the location as a study site or if a landowner denied us access to their property, we randomly selected another oak wilt center for consideration. Because we replaced study sites that landowners denied us access to with others selected using identical criteria, we assumed inaccessible potential study sites to be missing at random (Stevens and Jensen 2007, Collier et al. 2012). We delineated the boundary of each study site to include the oak wilt center plus all unaffected forest within 400 m of the center's boundary, as permitted by private property lines. We selected a 400-m buffer because this distance allowed us to cover an area large enough to contain several golden-cheeked warbler territories. If a study site contained multiple oak wilt centers spaced <400 m from one another, we delineated the boundary of the site to encompass the centers, the unaffected forest between them, and unaffected forest within 400 m of the outermost centers.

Habitat Selection Within the Patch

To assess selection of habitat within the patch, we compared the proportion of each golden-cheeked warbler territory that contained affected forest (use) with the proportion of the corresponding study site that contained affected forest (available). First, we systematically placed transects every 200 m across each study site to locate additional oak wilt centers that the Texas Forest Service did not previously identify and to verify the location and extent of known oak wilt centers. We used the transects to survey for oak wilt centers 5 times at our 2010 study sites and 4 times at our 2011 study sites. We conducted our oak wilt surveys between 16 March and 1 June of each year in conjunction with our surveys for golden-cheeked warblers (see below). To ensure that we detected all oak wilt centers present at our study sites, we alternated transect placement for each survey round. Specifically, during the first round of surveys observers walked transects spaced 200 m apart on a latitudinal axis. On the second survey, we shifted the transects 100 m south, maintaining the 200-m spacing. Surveys 3 and 4 followed the same pattern on a longitudinal axis. Observers recorded the Global Positioning System locations of all oak wilt centers intercepted on surveys. Upon completion of each year's transect surveys, we returned to map the boundaries of the oak wilt centers we had encountered. For the purposes of our delineations, we defined an oak wilt center as an area with either foliar symptoms of active infection, such as veinal necrosis or vein banding, or as an area with $\geq$80% oak mortality (Appel and Maggio 1984, Appel et al. 1989). We marked the outer boundaries of each center using handheld Global Positioning System units and then used the points to create polygons in ArcMap 9.3.1 depicting the extent of each oak wilt center.

We located golden-cheeked warbler territories for subsequent mapping by conducting transect surveys at each study site in conjunction with our surveys for oak wilt centers. Observers covered each site by slowly walking transects spaced 200 m apart, a spacing determined by mean golden-cheeked warbler territory sizes of 1.72–4.15 ha found in previous studies (Ladd and Gass 1999). We alternated transect placement over the course of the breeding season as described previously. We surveyed our study sites 5 times (approx. once every 15 days) between 19 March and 1 June in 2010 and 4 times between 16 March and 17 May in 2011. The number of surveys we conducted exceeded the 3 recommended by MacKenzie and Royle (2005) for species with detection probabilities of 0.50–0.85 (Collier et al. 2010); we conducted these additional surveys to increase the likelihood that we detected all territories present within our study sites.

To define the spatial extent of territories, we returned to the location of each golden-cheeked warbler found during our transect surveys once every 4–10 days to conduct territory mapping. We conducted <60-min territory mapping sessions from 23 March to 30 June in 2010 and from 16 March to 21 June in 2011. We altered our territory mapping techniques between study years because we determined that the method used in 2010 was not appropriate for examining within-territory habitat selection (see below). In 2010, we used hand-held Global Positioning System units to mark 3–6 locations spaced >20 m apart/visit for each focal male. We obtained a mean of 16.6 points/territory (SD = 3.7), which exceeded the minimum number Anich et al. (2009) found necessary to accurately delineate the territories of Swainson's warblers (*Limnothlypis swainsonii*). In 2011, we recorded the location of the focal male every 2 min and obtained a mean of 50.8 points/territory (SD = 29.0). We used the point locations collected in both years 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 (Beyer 2004).

We used our oak wilt center polygons to calculate the proportion of each study site and the proportion of each territory's minimum convex polygon that contained forest affected by oak wilt. We used a 1-tailed Wilcoxon paired-sample test for non-normally distributed data (Zar 1996:167) to test whether the proportion of affected forest contained in each territory (use) was lower than the proportion of affected forest contained within the corresponding study site (available). We used analysis of variance to determine that year did not influence this response variable ($F_{1,65} = 0.700$, $P = 0.406$); therefore, we pooled the data from both years for our analysis.

Habitat Selection Within the Territory

We assessed within-territory–scale habitat selection only for territories that contained a substantial amount of affected forest defined as $\geq$10% of the total area. We did not include territories from 2010 in this assessment because our territory mapping methods in that year were only intended to delineate the boundaries of the territory and did not provide information on patterns of use within that boundary. In 2011, we recorded the location of the focal male every 2 min during territory mapping sessions. Because this sampling interval provided ample opportunity for an individual to traverse the length of its territory, we considered successive point locations to be biologically independent (Lair 1987, Barg et al. 2005). We used a 1-tailed paired-sample *t*-test for normally distributed data (Zar 1996:163) to test whether the proportion of each male's territory mapping locations that were within the boundaries of an oak wilt center (use) was lower than the proportion of his territory's minimum convex polygon that contained affected forest (available).

Post-Breeding Habitat Use

Because golden-cheeked warblers are less territorial during the post-breeding season, we could not delineate the spatial extent of areas used during this time period. Therefore, we assessed post-breeding habitat use as a function of detection density in oak wilt centers and in unaffected forest. To locate post-breeding warblers, we conducted additional late-season transect surveys at 10 sites where warblers held territories during the breeding season. We surveyed all areas within 400 m of a territorial boundary 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), we surveyed at a finer resolution than we did during our breeding surveys by decreasing the spacing of transects from 200 m to 100 m. We also conducted transect surveys once every 7 days instead of once every approximately 15 days. Each time we detected one or more warblers, we followed the first adult detected for one 5-min interval. If no adults were present, we followed the first fledgling detected. We noted the number, age, and sex of all individuals in the group and took a Global Positioning System point every time the focal individual changed substrate. We considered all points taken during each 5-min post-breeding observation period to be one detection event. We considered the detection event to have occurred within an oak wilt center if any of the points taken during the 5-min interval were located in affected forest.

For each study site, we calculated the mean density of detection events made in oak wilt centers and, separately, in unaffected forest across our 5 post-breeding surveys. To test for differences in density of post-breeding detections, we used 1-tailed paired-sample *t*-tests where detection densities in unaffected forest were paired with detection densities in affected forest by study site. We used analysis of variance to determine that year did not influence this response variable ($F_{1,8} = 2.043$, $P = 0.191$); therefore, we pooled the data from both years for our analysis.

Habitat Quality

We made behavioral observations using a modified version of methods described in Vickery et al. (1992) to determine index values for the final reproductive outcome of each territorial male. Though final 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 while avoiding biases associated with non-randomly collected nest data (Vickery et al. 1992). Christoferson and Morrison (2001) found that final Vickery index ranks correctly predicted 80–92% of territorial males' final reproductive outcomes determined from nest observations and several published studies of golden-cheeked warblers have utilized this technique (e.g., Butcher et al. 2010, Lackey et al. 2011, Farrell et al. 2012, Klassen et al. 2012, Marshall et al. 2013). We conducted behavioral observations from the time of the warblers' arrival on the breeding grounds, mid-March, until all territories had either fledged young or were no longer active. We visited each territory for <60 min once every 4–10 days to determine breeding status; this schedule allowed us to visit each territory at least once per nesting stage (Ladd and Gass 1999). If we could not access the full extent of a territory because of private property boundaries, we dropped that territory from our data set.

We used 2 metrics to assess reproductive success: pairing success and fledging success. We considered a male to be successfully paired if we observed a female within his territory for ≥ 4 weeks. We considered a territory to have successfully fledged if we observed either adult with a fledgling. We calculated percent pairing success as the number of paired territories relative to the total number of territories and percent fledging success as the number of territories that fledged relative to the total number of paired territories. Consistent with our analysis of within-territory–scale habitat selection, we considered a territory to be located in affected forest if $\geq 10\%$ of its area overlapped an oak wilt center. Overall pairing success was 83% in both 2010 ($n = 12$) and 2011 ($n = 54$). We used chi-square goodness-of-fit to test for inter-annual variation in fledging success ($\chi^2_1 = 1.184$, $P = 0.175$; Zar 1996:457). Because year did not influence these response variables, we pooled the data from both years for subsequent analyses. We used chi-square goodness-of-fit to test for differences in pairing and fledging success between affected and unaffected forest.

Vegetation Measurements

To quantify differences in vegetation between affected and unaffected forest, we used a tubular densiometer to measure total canopy cover >3 m height at 150 randomly selected points in oak wilt centers and at 150 randomly selected points in unaffected forest at each study site. We also used the tubular densiometer to record percent canopy cover of each oak species and of Ashe juniper at each point. To avoid measuring vegetation at multiple locations containing the same individual trees, we spaced points ≥ 20 m from one another (Gilman and Watson 1994, Jennings et al. 1999).

We calculated the mean total percent canopy cover as well as the mean percent canopy cover in highly susceptible oaks (live and red oaks), Ashe juniper, and less susceptible oaks (white oaks) for the affected and unaffected portions of each study site. For our analyses, we paired areas of unaffected forest to areas of affected forest by study site to control for potential variation in vegetation characteristics between study sites. We used 1-tailed paired-sample *t*-tests to test our predictions that total canopy cover and canopy cover in species highly susceptible to oak wilt would be lower in affected forest and to test our predictions that canopy cover in less susceptible oak species and canopy cover in Ashe juniper would not be lower in affected forest. We excluded 5 study sites from our analysis of canopy cover in less susceptible oaks because white oaks were not present at these locations.

RESULTS

We 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. We mapped 188 total individual oak wilt centers, 77 in 2010 and 111 in 2011. We located golden-cheeked warblers on 13 of 25 sites and territories overlapped with oak wilt centers on 5 study sites. Golden-cheeked warblers occupied 16 ha (2.7%) of the 606 total ha of affected forest we surveyed and 167 ha (6.1%) of the 2,732 ha of unaffected forest we surveyed.

Habitat Selection Within the Patch

We mapped 13 golden-cheeked warbler territories on 4 study sites in 2010 and 54 territories on 9 study sites in 2011. Forty-six territories (68.7%, $n = 67$) did not overlap with oak wilt centers. Fourteen territories (20.9%) contained affected forest in $\geq$10% of their total area and occurred on 4 of the 13 occupied study sites; these territories were all located in 2011. Three territories contained affected forest in >50% of their area; no territories were located entirely within an oak wilt center (Fig. 2). The mean proportion of each territory containing affected forest (use) was lower than the proportion of the corresponding study site containing affected forest (available; $\bar{x} = -0.052$, SD $= 0.174$, $S_{66} = 585$, $P = <0.001$).

Habitat Selection Within the Territory

Of the 14 territories with $\geq$10% of their area within oak wilt centers, 7 used oak wilt centers more than expected based on availability and 7 used affected forest less than expected (Fig. 3). The mean proportion of warbler locations in affected forest ($\bar{x} = 0.373$, SD $= 0.263$) was not statistically lower than the proportion available ($\bar{x} = 0.379$, SD $= 0.210$, $t_{13} = 0.128$, $P = 0.450$), and the proportion of locations in affected forest varied widely by territory. This variability does not appear to be related to differences between study sites because we observed no consistent usage patterns within the 3 sites that contained >1 territory in affected forest.

Post-Breeding Habitat Use

We detected golden-cheeked warblers 110 times on 8 of 10 study sites surveyed during the post-breeding season (Table 1). Seventy-three detections (66%, $n = 110$) occurred completely outside of breeding season territories. Nine (8.2%, $n = 110$) detections occurred in affected forest. We located warblers within oak wilt centers at 2 study sites where affected areas were unused during the breeding season. Although mean post-breeding density was 2.1 times greater in unaffected forest, the difference was not statistically significant (Table 1; $t_9 = 1.263$, $P = 0.120$).

Reproductive Success

We obtained measures of reproductive success for 66 territories, 13 of which contained affected forest in >10% of their minimum convex polygon. Overall pairing success was 83% (55 of 66). Pairing success was 27% lower for males whose territories were in affected areas: 62% (8 of 13) of territories in affected forest paired successfully compared with 89% (47 of 53) of territories in unaffected areas ($\chi^2_1 = 5.537$, $P = 0.019$). None of the 3 males whose territories contained >50% affected forest paired. Of the 55 males that paired, 75% (6 of 8) of those in affected forest fledged young and 72% (34 of 47) of those in unaffected areas fledged young ($\chi^2_1 = 0.024$, $P = 0.876$).

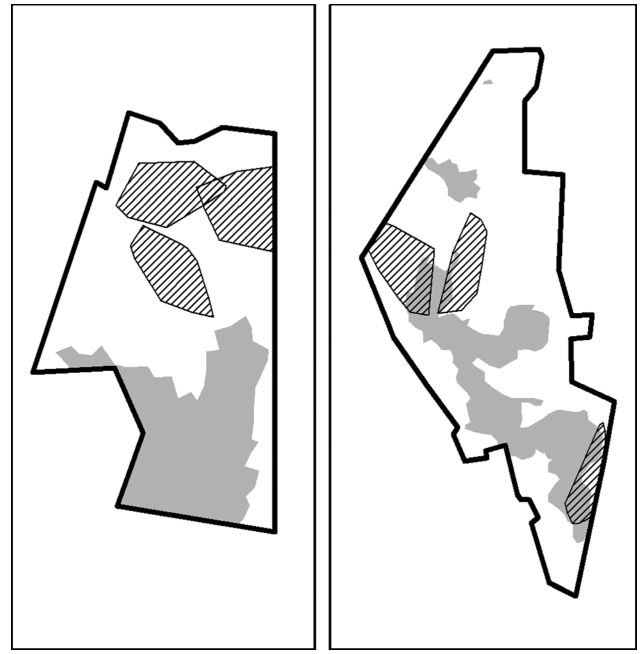

Figure 2. Example of the arrangement of golden-cheeked warbler territories (slashed) within a study site where territories did not overlap oak wilt centers (gray; left) and within a study site where overlap occurred (right) in Texas, USA, during 2010 and 2011. Oak wilt centers were often irregularly shaped and no territories were located completely within an affected area.

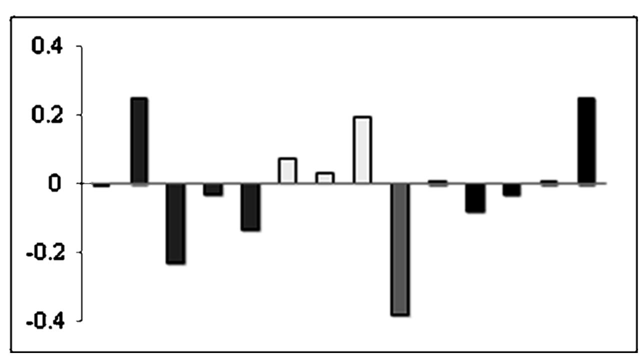

Figure 3. Difference between the proportion of golden-cheeked warbler locations in affected forest (use) and the proportion of the corresponding territory that contained affected forest (available) for 14 territories that contained affected forest in >10% of their area in Texas, USA, during 2010 and 2011. Positive values denote greater usage of affected forest than expected based on availability. Selection of affected forest at the within-territory–scale was variable both overall and within study sites (color corresponds to study site).

Table 1. Golden-cheeked warblers observed during post-breeding detection events in Texas, USA, during 2010 and 2011. Most warblers observed ($n = 110$) were either family groups or single males. We classified a detection event as "unknown" if the observer could not verify the number, age, and/or sex of individuals present. Group composition did not appear to influence whether the group utilized forest affected by oak wilt as compared to unaffected forest.

Group composition	No. detected	%	No. in affected	%
Single female	7	6.4	1	14.3
Single male	43	39.1	3	7.0
Multiple adults	3	2.7	0	0.0
Family group	48	43.6	4	8.3
Fledglings only	6	5.5	1	16.7
Unknown	3	2.7	0	0.0

Vegetation Measurements

Total canopy cover ranged from 5% to 38% ($\bar{x} = 17$, SD = 9, $n = 25$) in the affected portions of our study sites and from 6% to 36% ($\bar{x} = 21$, SD = 8, $n = 25$) in the unaffected portions. Mean total canopy cover was 15% lower in affected areas relative to unaffected forest ($t_{24} = 2.270$, $P = 0.016$).

Canopy cover in species susceptible to oak wilt ranged from 1% to 25% ($\bar{x} = 6$, SD = 5, $n = 25$) in affected areas and from 1% to 25% ($\bar{x} = 8$, SD = 6, $n = 25$) in unaffected forest. Canopy cover in susceptible oaks was 23% lower in areas affected by oak wilt relative to unaffected forest ($t_{24} = 3.015$, $P = 0.003$). We detected 3 species of susceptible oaks at our study sites: live oak, Texas oak, and blackjack oak. Live oak was the most common of the 3 species, with canopy cover ranging from <1% to 15% ($\bar{x} = 5$, SD = 4, $n = 25$) in affected areas and from <1% to 17% ($\bar{x} = 6$, SD = 5, $n = 25$) in unaffected forest. Although mean percent canopy cover in Texas oak was low, we observed the greatest relative difference between treatments for Texas oak, which had 63% less canopy cover in affected areas (range = 0–3%, $\bar{x} = 0.6$, SD = 0.9, $n = 25$) relative to unaffected forest (range = 0–5%, $\bar{x} = 1.6$, SD = 1.7, $n = 25$). We observed little difference in canopy cover in blackjack oak, which ranged from 0% to 10% ($\bar{x} = 1$, SD = 2, $n = 25$) in affected areas and 0% to 8% ($\bar{x} = 1$, SD = 2, $n = 25$) in unaffected forest.

Of the 20 sites where they were present, canopy cover in less susceptible oak species (white oaks) ranged from 0% to 8% ($\bar{x} = 2$, SD = 2, $n = 20$) in affected forest and from 0% to 6% ($\bar{x} = 2$, SD = 2, $n = 20$) in unaffected forest. Canopy cover in white oaks was not significantly lower in areas affected by oak wilt ($t_{19} = 0.830$, $P = 0.208$).

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

DISCUSSION

We found that golden-cheeked warblers avoided establishing territories within affected forest. Though the irregular shape of some of the oak wilt centers may have prevented golden-cheeked warbler territories from containing a larger proportion of affected forest, few territories contained affected forest in a substantial portion of their area. Most (88%, $n = 60$) oak wilt centers located by Appel and Camilli (2010) at the Fort Hood Military Reservation occurred outside of designated golden-cheeked warbler habitat. However, preliminary data also collected on the Fort Hood Military Reservation suggests that golden-cheeked warblers may avoid utilizing oak wilt centers when they occur within occupied areas (Hammer 2011). Golden-cheeked warblers at our study sites did not completely avoid oak wilt within the patch. A possible explanation may be use of conspecific cues as an indicator of habitat quality by individuals selecting breeding habitat (Tye 1992, Danchin et al. 1998, Forbes and Kaiser 1994, Arlt and Part 2007). A recent study by Farrell et al. (2012) found that simulated conspecific vocalizations can induce golden-cheeked warblers to settle in previously unoccupied areas. Ten of our 14 territories that contained affected forest were located at the 2 sites with the highest and second highest absolute number of golden-cheeked warbler territories. The presence of conspecifics might have influenced warblers to settle at these locations such that their territories contained a small amount of affected forest.

We found that use of affected forest was variable compared with its availability for territories that contained affected forest in ≥10% of their minimum convex polygon. This variability occurred among territories located within the same study site, suggesting that differences in vegetation between study sites are not the cause. Non-habitat related phenomena may have influenced individual warblers' use of oak wilt centers at this scale (Jones 2001). Factors such as conspicuous singing perches, proximity to the boundaries of rival males' territories, and local patterns of food abundance may have exerted a stronger influence on within-territory habitat selection. Additionally, there may have been little reason for individual warblers to display a clear pattern of preference or avoidance of oak wilt centers at this scale because few territories contained a large affected area.

We observed no patterns in post-breeding density that would indicate a preference or avoidance of oak wilt centers late in the season. However, we frequently located post-breeding warblers in areas outside of breeding season territories. This may be a product of the tendency for the home ranges of post-breeding birds to be larger than breeding season territories (Vitz and Rodewald 2010, Vormwald et al. 2011). Movements of juvenile birds from the nest site often occur gradually and increase with age (Vitz and Rodewald 2010, Rush and Stutchbury 2008, Vormwald et al. 2011). This may have confounded our ability to quantify dispersal of post-breeding birds from the nest site, especially because we detected few fledglings that were not associated with an adult (i.e., fledglings that had reached independence). Previous studies have documented dispersal of forest-dwelling birds to areas with greater structural diversity post-breeding (Pagen et al. 2000, Marshall et al. 2003, King et al. 2006, Vitz and Rodewald 2006, Rush and Stutchbury 2008). Possible explanations for this shift in habitat use include predator avoidance and increased food availability (Anders et al. 1998, Yackel Adams et al. 2006, Mitchell et al. 2010). The presence of oak wilt may not have influenced post-breeding habitat use by golden-cheeked warblers because it did not affect these factors.

We observed a lower rate of pairing success for males that used affected forest; however, males that used affected forest who did pair fledged young as successfully as paired males who only used unaffected forest. Similar results were observed by Allen et al. (2009), who found approximately 70% fewer Acadian flycatcher (*Empidonax virescens*) pairs in forest defoliated by hemlock woolley adelgids (*Adelges tsugae*) but no differences in nest survival rates. These authors suggested that the lower observed pair densities may have resulted from a loss of potential nest sites in affected areas. Tye (1992) found that vegetation characteristics may be used by birds as an indicator of habitat quality, but that this assessment is not always accurate. Females may have used vegetation characteristics such as percent canopy cover to assess the quality of a male's territory but, in the end, females that chose territories placed in oak wilt centers fledged young just as successfully as those in unaffected areas. Alternatively, it is possible that territories containing very high percentages of affected forest would have had lower rates of fledging success. However, only 3 males placed their territories in such a way that they contained affected forest in >50% of their area and none of these males paired. Therefore, our data indicate that habitat quality is lower in areas affected by oak wilt because males that use affected forest are less likely to pair and thus are less likely to fledge young.

Our comparisons of canopy cover between affected and unaffected forest support our predictions that total canopy cover and canopy cover in susceptible oaks would be lower in areas affected by oak wilt and that canopy cover in less susceptible oaks and Ashe juniper would not differ significantly. Most of the oak wilt centers assessed by Appel and Camilli (2010) occurred in forest with lower overall stand density and greater live oak density than forest without oak wilt. Our vegetation assessment is not directly comparable to that study because we did not collect data from stands where oak wilt does not occur. However, the lack of a difference in Ashe juniper and less susceptible oaks suggests that the vegetation characteristics of affected and the unaffected portions of our study sites were likely to have been comparable prior to infection. Though mean total canopy cover was only 3% lower in affected 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 absolute canopy cover was not >38% at any of our study sites, a 15% relative loss could substantially reduce an area's perceived suitability. Alternatively, Klassen et al. (2012) found that territory density was not affected by total canopy closure. Instead, these authors identified a positive relationship between the proportion of oak per study site and territory density. The difference we observed in total canopy cover was mainly due to a decrease in canopy cover in susceptible oaks, with the greatest difference occurring for Texas oak. Loss of Texas oak from habitat may be especially detrimental to golden-cheeked warblers as compared to the loss of other oak species. Marshall et al. (2013) found that golden-cheeked warblers using areas dominated by red oaks had higher reproductive success than did warblers using areas dominated by blackjack and post-oak. This suggests that golden-cheeked warbler habitat with high canopy cover in red oaks may be of the highest quality and, at the same time, the most likely to be substantially changed by oak wilt.

MANAGEMENT IMPLICATIONS

Our 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 our 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. Additionally, the presence of oak wilt should be taken into account when assessing the size, quality, and connectivity of patches of potential habitat. Such assessments should consider the current presence of oak wilt as well as the potential for oak wilt to spread from nearby forests. Measures designed to control the spread of oak wilt at the local level, such as trenching, may be beneficial within areas known to be inhabited by golden-cheeked warblers.

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