Original Article

Canopy Characteristics Affect Reproductive Success of Golden-Cheeked Warblers

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ABSTRACT The golden-cheeked warbler (*Setophaga chrysoparia*), listed by the U.S. Fish and Wildlife Service as endangered in 1990 due primarily to habitat loss and fragmentation, is a Neotropical migrant songbird that breeds exclusively in mature juniper–oak (*Juniperus*–*Quercus*) woodlands in central Texas, USA. Previous studies suggested suitable breeding habitat consists of >35% canopy closure (with 50–70% cover optimal), and ≥10% oak composition. However, little is known about this species' habitat relationships at the southwestern edge of its breeding range. Therefore, within this portion of the species' breeding range, we investigated influences of canopy closure and tree species composition on pairing and reproductive success of golden-cheeked warblers during 2009 and 2010. We used remote sensing and ground sampling to acquire variables to describe habitat characteristics, and we estimated pairing for breeding and reproductive success by golden-cheeked warblers. We found successfully breeding pairs in areas with >20% canopy cover, 35% juniper composition, and only 3% oak composition. A logistic model for pairing success retained juniper, oak, and the interaction between these 2 variables, and the model for reproductive success retained juniper, canopy closure, study area, and the interaction between canopy closure and study area. Our results expand our knowledge of habitat conditions that warblers use for breeding, thus expanding the range of habitat management options available for this species during breeding season.

KEY WORDS abundance, endangered species, golden-cheeked warbler, habitat management, habitat use, *Setophaga chrysoparia*, Texas.

Due to widespread habitat loss and fragmentation (Reed 1995, Fahrig 1997, Donovan and Flather 2002), it is important to understand habitat variation throughout a species' range to effectively manage remaining habitat. Occasionally, land managers develop habitat management guidelines for a species from a few locations and then generalize across a species' breeding range (Campbell 2003). However, especially for wide-ranging species, habitat is generally not uniform throughout a species' breeding range, and, if this variation is not accounted for, habitat management guidelines might be less effective or even detrimental in portions of a species' range. In reference to forest songbirds, canopy closure and tree species composition are commonly used to describe breeding habitat (Lanham et al. 2002, Dalley et al. 2008, Newell and Rodewald 2011), although this can vary throughout a species' range (Nocera et al. 2007, Matsouka et al. 2010).

The golden-cheeked warbler (hereafter, warbler; *Setophaga chrysoparia*) is a Neotropical migratory passerine with a breeding range limited to central Texas, USA (USFWS 1992, Ladd and Gass 1999, DeBoer and Diamond 2006), which is generally characterized by Ashe juniper (*Juniperus ashei*) and mixed oak (*Quercus* spp.) woodlands. Ashe juniper is a necessary component of breeding habitat for this species because warblers construct nests from bark of mature trees and it provides foraging substrate. For unknown reasons, but possibly related to differing insect communities associated with different tree species (Seagle and Sturtevant 2005), breeding habitat must also consist of some proportion of oak or deciduous species (Campbell 2003, Marshall 2011). Canopy cover ≥50% (Dearborn and Sanchez 2001, USFWS 2003) is considered ideal to breeding habitat for warblers; it is selected by warblers possibly to conceal nests and, thus, reduce probability of nest predation and parasitism (Twedt et al. 2001). Ashe juniper distribution across Texas has become fragmented due to an increase in pasture land and development (Kroll 1980, Diamond 1997, Garriga et al. 1997), resulting in smaller patches of juniper–oak stands throughout central Texas (Pulich 1976, Wahl et al. 1990, Keddy-Hector et al. 1992). In 1990, the U.S. Fish and Wildlife Service (USFWS) listed the warbler as an endangered species, and provided habitat loss among the list of justifications (USFWS 1990).

Management guidelines provide a baseline for defining breeding habitat likely to support warblers (e.g., USFWS 1992, Campbell 2003). Texas Parks and Wildlife

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Department (TPWD) defined warbler breeding habitat as ≥35% total canopy cover, with 10–30% of the canopy consisting of oak or deciduous trees, and high-quality breeding habitat as ≥50% total canopy cover (Campbell 2003). Ostensibly, these recommendations apply across the breeding range of the warbler. However, information used to develop these guidelines originated from studies located in few locations (Campbell 2003). Since federal listing, studies from Fort Hood Military Reservation, in Coryell and Bell counties, and locations in Travis County, Texas, USA have generated most of the data regarding breeding habitat use by warblers (e.g., Dearborn and Sanchez 2001; Fig. 1). Although many studies describe breeding habitat in terms of warbler occupancy, relatively few studies have established a link between reproductive success and habitat metrics cited as constituting high-quality breeding habitat for this species by TPWD (Coldren 1998, Baccus et al. 2007). Warbler activity outside of these areas, particularly in the southwestern portion of the species' range, is relatively unknown. An increased understanding of the degree to which breeding habitat variability affects warbler reproductive success is essential to range-wide species conservation and management.

Given the general lack of knowledge of breeding habitat for warblers at the fringe of their range, and the conservation

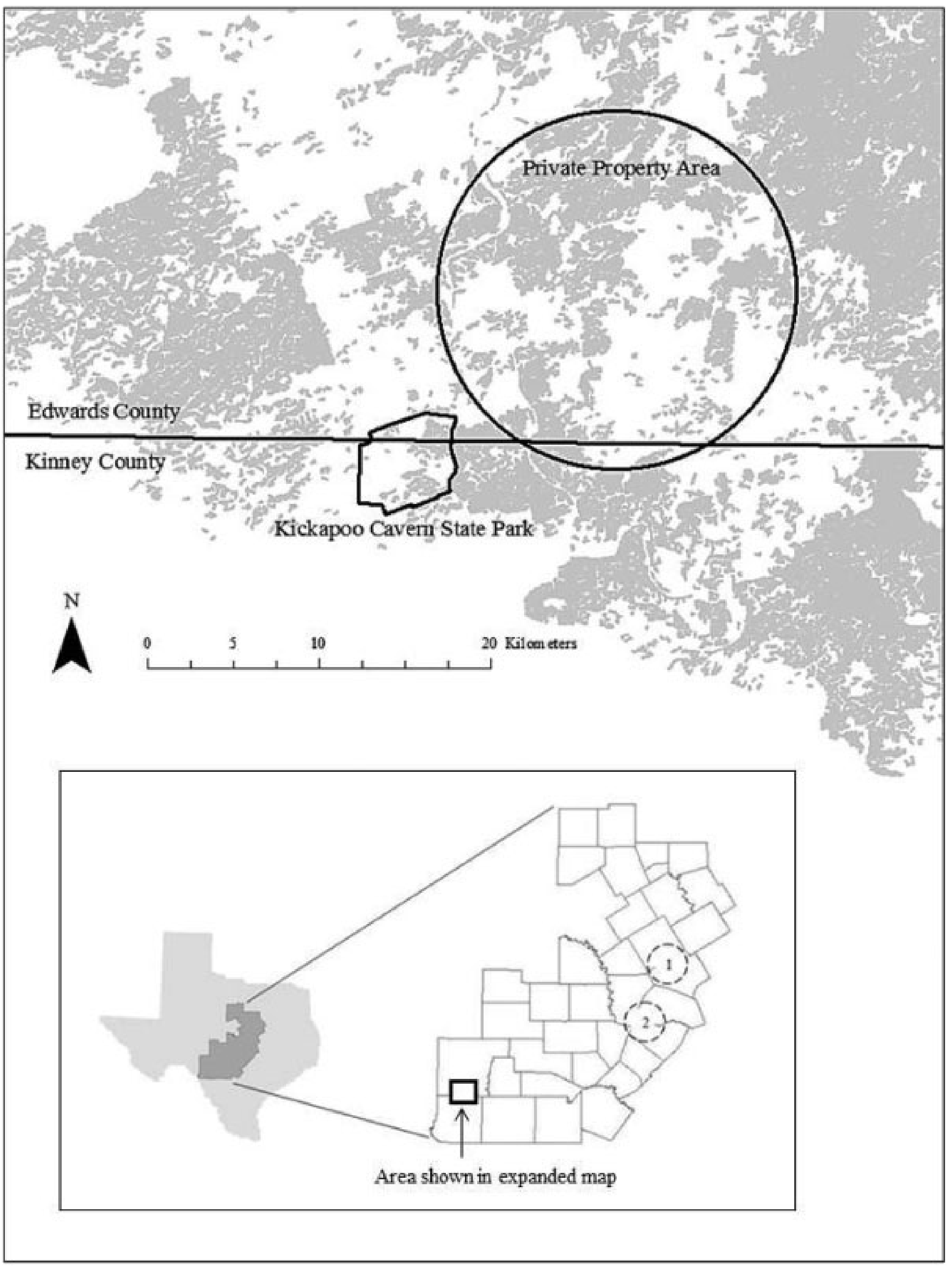

Figure 1. Map of golden-cheeked warbler breeding range relative to the state of Texas, USA, and study areas (Kickapoo Cavern State Park and private properties) for surveys conducted in 2009–2010. The dashed circles highlight areas of frequent warbler research (1 = Fort Hood; 2 = Austin). Grayed areas show potential juniper–oak woodland habitat. Due to confidentiality agreements with private landowners, only the general area of private property locations is indicated.

priority status for this species, our objective was to examine relationships between breeding habitat characteristics (canopy closure and tree species composition) and pairing and reproductive success of warblers at the southwestern edge of their breeding range. We predicted warbler pairing and territory success would increase with higher canopy closure and equal proportions of Ashe juniper and oak species at the territory scale. Additionally, we predicted that reproductive success would increase as canopy closure and proportions of Ashe juniper increase, or reproductive success will reach an optimum or threshold success rate in areas with equal proportions of Ashe juniper and oak species and intermediate canopy closure.

STUDY AREA

Our study occurred in Edwards and Kinney counties, southwestern Texas, USA (Fig. 1) during the 2009 and 2010 breeding season (Mar–Jun). We selected this study region as part of an overall study of warblers throughout their range and because little research has been conducted in this area. Our study area was located within the Edward's Plateau ecoregion, characterized by steep canyons and narrow divides at elevations ranging from 250 m to 800 m (North American Regional Center of Endemism 2008). During our study, mean precipitation and temperature during warbler breeding season was 4.3 cm and 23° C in 2009 and 7.6 cm and 22° C in 2010 (National Oceanic and Atmospheric Administration 2010). Soil composition was mainly limestone bedrock and alkaline soils. Common tree species included Ashe juniper, live oak (*Q. fusiformis*) and pinyon pine (*Pinus cembroides*). Patches of mixed juniper–oak woodlands occurred within scrub–shrub rangeland used for cattle grazing. Most mature forests occurred within canyons and along slopes leading up to mesas.

METHODS

Study Area Selection

We determined potential juniper–oak woodland patches in Edwards and Kinney counties using 1-m-resolution digital orthophoto quadrangles taken in 2004. Because Texas is >95% privately owned, our study areas were decided ultimately by landowner participation. In 2009, we sampled on Kickapoo Cavern State Park and surrounding private property in Edwards and Kinney counties. In 2010, we sampled on private properties in Edwards County approximately 15 km north and northeast of the properties surveyed in 2009. We divided sampling between 2 years due to required sampling effort and private land availability. Because properties we surveyed within each year were very close to one another (<3.5 km), we considered them in the same study area. Therefore, we had 2 study areas: one in 2009, the other in 2010. Both study areas were similar in size, but varied in their coverage of juniper–oak woodland. In 2010, our study area was 782 ha made up of 4 large patches of juniper–oak woodland (a patch is defined as continuous woodland ≥10 m away from another patch). In 2009, our study area was 860 ha and contained 28 smaller patches of juniper–oak woodland.

Territory Mapping

We located warblers by conducting transect surveys across selected juniper–oak woodland patches within our study areas. We conducted transect surveys throughout March (when warblers arrive on breeding grounds), and walked each transect at least once per week for 4 weeks. Each transect was 100 m apart, with placement of the first transect chosen randomly and subsequent points spaced 50 m apart (Buckland 2006). We spent 7 min at each point and recorded estimated distance (m) and cardinal direction of all detected singing male warblers with a Global Positioning System (GPS) unit. We continuously surveyed for warblers while walking between points along transects, noting direction and distance to the warbler. We surveyed when songbirds are most vocally active, beginning at sunrise and continuing for 4 hours (Buckland 2006). Once we detected males during transect surveys, we mapped territories by marking a minimum of 3 GPS locations, per visit, of singing perches, with each location separated by ≥15 m. We defined a territory as presence of a singing male in a general area for >4 weeks. We visited each territory for a minimum of 30 min every 4–5 days during duration of the breeding season (Mar–Jun) for a minimum of 15 visits. This study design exceeded recommendations by MacKenzie and Royle (2005) to accurately determine occupancy.

We used minimum convex polygons in ArcMap™ 9.3 to determine territory area and placement. We removed outlying points because those points may be due to measurement error or rare movement events. We considered outliers to be points in which a bird was located >200 m outside of the primary survey area on only 1 occasion during the breeding season.

Reproductive Index

We conducted behavioral surveys in each territory using a modified version of the Vickery index (Vickery et al. 1992) to determine an index of territory reproductive success, specifically male pairing success and fledging success. The Vickery index is a method of estimating reproductive success that avoids potential biases associated with nonrandomly collected nest data, and it does not disrupt nests, which is critically important when studying rare or endangered species (Vickery et al. 1992). Numerical ranks (1–5) were associated with each territory, and correlated with a specific reproductive behavior (Rank 1 = territorial M; Rank 2 = pair present; Rank 3 = nest material carry observed; Rank 4 = food carry by ad; Rank 5 = fledgling sighted).

Effectiveness of the index has been independently tested on many songbird species and shown to predict the correct level of reproductive activity 61–79% of the time (Christoferson and Morrison 2001, Rivers et al. 2003). More importantly, Christoferson and Morrison (2001) were able to correctly predict the breeding outcome of a pair 80–92% of the time. Because this was a short-term study, we could not expend the effort necessary to color-band a large proportion of breeding pairs, which is the case for most studies of songbird–habitat relationships (e.g., Bonifait et al. 2006, Cooper et al. 2009, Cox and Martin 2009). Additionally, we have been successfully using the methods described herein with the golden-cheeked warbler in other locations (e.g., Butcher et al. 2010, Lackey et al. 2011, Marshall 2011). We took care to ensure that we properly linked breeding outcome with a specific territory by repeatedly (i.e., daily) visiting each territory near our estimated time of fledging. The concept of the territory means there is a defended area, which, in turn, means the territory holders concentrate activities within a confined area. The fact that there can be overlap around edges of territories and incursions of neighboring birds into adjacent territories does not negatively impact our ability to link nesting outcome to that territory. If we could not determine breeding status of a territory, we dropped that territory from the data set. In both 2009 and 2010, we dropped <5% of territories from the data set because we were able to link specific fledglings with a specific territory. Additionally, because we are comparing locations (and not individual territories) with structurally different vegetation, we were confident in assuming that any error in assigning reproductive outcome to territories was similar between comparisons.

We considered a male successfully paired if we detected a female within his territory for ≥4 weeks. We considered a territory reproductively successful if ≥1 fledgling was located within a territory. We calculated territory success as the number of territories with ≥1 fledgling relative to total number of territories with confirmed females.

Breeding Habitat Characteristics

We used ArcMap 9.3 to systematically lay a grid of points with 20-m spacing within territory boundaries defined by our territory mapping protocol. This procedure allowed for randomization (through the random placement of the first point) and interspersion (through the systematic placement of subsequent points; Johansson 1985, Jennings et al. 1999). We measured canopy closure with a spherical densiometer facing 4 cardinal directions while standing at the center of each grid point (Strickler 1959), which we then averaged to obtain mean canopy closure at that point. We averaged all canopy-closure values for each point to estimate mean territory canopy closure. At each point, we also recorded all tree species (woody stem ≥2 m tall; Wilder et al. 1999) that had a portion of their trunk or canopy within the frame of view of the spherical densitometer (approx. 3 m^2). Due to low tree species diversity in our study areas, we were able to accurately determine tree species from the frame of view of the densitometer. Ashe juniper and oak tree species accounted for >85% of the tree composition; therefore, we eliminated other tree species from our analyses.

Analysis

We used forward stepwise logistic regression (Ott and Longnecker 2001:701–708) in SAS 9.2 to test the hypotheses that canopy closure, Ashe juniper composition, and oak composition affected pairing (paired or not-paired response variable) or reproductive success (successful or not-successful response variable) of warblers. We considered a territory successfully paired if we detected a female once within a territory during breeding season. We considered a territory reproductively successful if we detected fledglings at least once within a territory. Additionally, we included an interaction term between Ashe juniper and oak composition. Because our study areas varied slightly in location (>3.5 km apart) between 2009 and 2010, we added study area–year and the interaction terms between study area–year with canopy closure, Ashe juniper composition and oak composition, as covariates in both sets of logistic models. We did not account for modeling biases due to multicollinearity because none of our variables were correlated with an $R^2 \geq 0.50$ (Graham 2003). Not all territories acquire females; therefore, we excluded territories where we did not detect females in the reproductive success models. With this method, we could test probability of a territory becoming reproductively successful independent of whether the territory acquired a female. In both stepwise procedures, we set the significance level for a variable to enter the model at 0.25 and significance for a variable to stay in the model at 0.1.

RESULTS

We monitored 48 territories in 2009 and 32 territories in 2010. In 2009, 42 (87.5%) territories paired, of which 19 (45%) successfully fledged young. In 2010, 24 (75%) territories paired, of which 19 (79%) successfully fledged young. Of the 80 total territories for both years, 66 territories paired and 38 successfully fledged young. Across all territories in 2009, we found a mean canopy closure of 35% (SD = 9), a mean of 70% Ashe juniper composition (SD = 10), and a mean of 20% oak composition (SD = 10). Similarly, we found a mean canopy closure of 40% (SD = 13), a mean of 60% Ashe juniper composition (SD = 12), and a mean of 20% oak composition (SD = 8) within territories studied in 2010. Pairs formed in territories with as little as 15% canopy closure and successfully bred in those with ≥17% canopy closure and 3% oak composition (Table 1).

Oak composition and an interaction between Ashe juniper and oak composition, predicted pairing success of warbler territories ($\chi^2 = 13.2$, df = 3, $P = 0.004$; Table 2). When juniper composition was low (e.g., 35%), males were more likely to acquire a female if the oak composition also was low (e.g., 5%). Similarly, when juniper composition was high (e.g., 80%), males were more likely to acquire a female if the oak composition was high (e.g., >20%). Canopy closure, juniper composition, and study area–year effects were not related to pairing success. Reproductive success was related to an interaction between study area–year and canopy closure ($\chi^2 = 14.5$, df = 4, $P = 0.006$; Table 2). At the study sites in 2010, reproductive success increased with increasing canopy closure, but this effect was opposite for the study sites in 2009.

DISCUSSION

Reproductive success of a songbird territory hinges on 2 events: acquisition of a female and successful output of fledglings. It is important to note that our study was based primarily on vegetative traits of the territory alone. Traits of

Table 1. Vegetative characteristics (mean, standard deviation [SD], median, range) of golden-cheeked warbler territories studied in south-central Texas, USA, 2009 and 2010, separated by pairing and reproductive success.

Vegetative characteristic	Territory status	Mean (%)	SD	Median	Min.	Max.
Canopy closure	Unpaired ($n = 14$)	41	15	42	21	74
	Paired ($n = 66$)	37	11	39	15	70
	Unsuccessful ($n = 42$)	35	10	39	15	51
	Successful ($n = 38$)	38	11	39	17	70
Ashe juniper	Unpaired ($n = 14$)	60	15	56	40	84
	Paired ($n = 66$)	65	12	66	35	86
	Unsuccessful ($n = 42$)	65	11	64	35	84
	Successful ($n = 38$)	65	13	65	38	86
Oak	Unpaired ($n = 14$)	16	9	17	5	30
	Paired ($n = 66$)	20	9	20	3	43
	Unsuccessful ($n = 42$)	21	9	19	8	40
	Successful ($n = 38$)	20	10	21	3	43

Table 2. Estimated coefficients of models generated from stepwise logistic regression analyses for predicting pairing and reproductive success of golden-cheeked warblers in south-central Texas, USA, 2009–2010. Sample size for pairing success and reproductive success was 80 and 66, respectively.

Reproductive status	Variable	Estimate	SE	z-Value	P-value
Pairing success	Intercept	5.04	3.439	1.47	0.14
	Juniper	−0.08	0.051	−1.47	0.14
	Oak	−0.43	0.201	−2.15	0.03
	Juniper × oak	0.01	0.003	2.50	0.01
Reproductive success	Intercept	1.03	3.67	0.28	0.78
	Study area–year	−2.62	2.23	−1.18	0.24
	Canopy	−0.17	0.09	−1.89	0.06
	Juniper	0.04	0.03	1.54	0.13
	Study area–year × canopy	0.13	0.06	2.04	0.04

the male, other than his ability to occupy and defend a territory, cannot be inferred. Based on our final model, oak composition and the interaction between juniper and oak compositions predicted pairing success. From a biological perspective, this model supports the observation that golden-cheeked warblers rely both on Ashe juniper and oak tree species during breeding season, whether for food or nest construction. The interaction term suggests that more equal proportions of both tree species increase likelihood of a male acquiring a female, because pairing success increased as both Ashe juniper and oak increased or decreased. Warbler dependency on both tree species throughout the breeding season may be due to oak species' influence on temporal macroinvertebrate food availability, particularly at the beginning of the breeding season (Mar–Apr), whereas Ashe juniper is the primary foraging substrate later in the breeding season (May–Jun; Ladd and Gass 1999, Marshall 2011).

Our final model for reproductive success included study area, canopy closure, Ashe juniper composition, and the interaction term between study area and canopy closure. The only statistically significant term within this model was the study area–year and canopy-closure interaction term. In 2009, an increase in canopy closure led to a decrease in reproductive success. However, in 2010, an increase in canopy closure led to an increase in reproductive success. These contrary findings suggest that there may be other biotic (e.g., predation) or abiotic (e.g., rainfall) factors contributing differently to reproductive success at the 2 study areas across 2009 and 2010. For instance, rat snakes (*Elaphe obsoleta lindheimeri*), a documented predator of golden-cheeked warbler nests (Stake 2001, Reidy et al. 2008), are a common arboreal snake in Texas. Mansfield and Jayne (2011) found that rat snakes preferred to move within trees that are close together, thus facilitating transportation from one tree to another. In a patchy landscape, warbler nests may benefit from lower canopy closure due to reduced predation risk by rat snakes in 2009. However, higher canopy closure may have protected warbler nests from the heavy and increased rainfall in 2010.

Our most interesting finding was the wide range of characteristics in which we found breeding warblers, and this perhaps has greater implication than the particular vegetative characteristics we found within territory locations. Although warbler-breeding habitat is typically characterized as continuous juniper–oak woodland, we found territories comprised varying degrees of juniper–oak woodlands and scrub–shrub vegetation with several canopy openings. The mean canopy closure on our study sites (approx. 35%) greatly contrasts with the study on Fort Hood Military Reservation by Dearborn and Sanchez (2001; >75%), the only other study we are aware of that related warbler reproductive success to canopy characteristics. This disparity stresses importance of multiple studies across a species' range to accurately define used habitat.

MANAGEMENT IMPLICATIONS

Based on vegetative composition and habitat structure of breeding warblers in Edwards and Kinney counties, the current descriptions of golden-cheeked warbler breeding habitat used by management agencies and other land managers will need to expand to include areas of lower canopy closure and oak composition. TPWD guidelines describe warbler-breeding habitat as exceeding 35% canopy closure, with much higher (>50–70%) canopy closure considered optimal; oak species comprising ≥10% of tree composition is also advised (Campbell 2003). Our findings, however, indicate that warblers will occupy and successfully reproduce in areas with canopy closure as low as 15% and only 3% oak composition.

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