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Postbreeding habitat use by Golden-cheeked Warblers (*Setophaga chrysoparia*)

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ABSTRACT.—The period following breeding but prior to migration is an important, though understudied, component of the avian annual life cycle. We quantified habitat use by endangered Golden-cheeked Warblers (*Setophaga chrysoparia*) during the postbreeding period in Golden-cheeked Warbler breeding habitat (i.e., oak-juniper [*Quercus-Juniperus*] woodlands) predominated by Texas oak (*Quercus buckleyi*) or post oak (*Q. stellata*), as well as in immediately adjacent oak woodland, oak savanna, and riparian vegetation not usually associated with breeding activity for this species. Most (87%) of the Golden-cheeked Warblers we detected were in oak-juniper woodlands, especially in Texas oak sites, but we also detected warblers in each of the other vegetation types we surveyed. Adults and family groups used breeding and nonbreeding habitat similarly, as did males and females, but juveniles used nonbreeding habitat more than adults did. Neither canopy cover nor territory density during the breeding season influenced postbreeding habitat use by warblers, regardless of vegetation type. We detected warblers 82% less often in post oak breeding habitat than in Texas oak breeding habitat despite similar densities of breeding territories, suggesting that warblers left post oak sites earlier during the postbreeding period. However, we found no evidence that warblers that bred in post oak sites were more likely to move into adjacent nonbreeding habitat than those that bred in Texas oak sites. Ashe juniper (*Juniperus ashei*) was the most consistently used woody substrate during the postbreeding period, regardless of warbler sex, warbler age, habitat type, or predominant oak species. Our results emphasize the continued importance of oak-juniper woodlands to Golden-cheeked Warblers during the postbreeding period but suggest that other vegetation types may also have conservation value for this species.

RESUMEN.—El período despues de la reproducción pero antes de la migración es un componente importante, pero poco estudiado del ciclo de vida anual de las aves. Cuantificamos uso del hábitat por las reinitas caridoradas (*Setophaga chrysoparia*), un especie en peligro de extinción, durante el período posterior a la reproducción en su hábitat reproductivo (i.e., bosques de roble-enebro [*Quercus-Juniperus*]), predominado por *Quercus buckleyi* o *Q. stellata* así como en bosques inmediatamente adyacentes de roble, sabana dominada por robles, y vegetación ribereña usualmente no asociada con la actividad de reproducción de esta especie. La mayoría (87%) de las reinitas caridoradas que detectamos estuvieron en bosques de roble con enebro, especialmente en sitios predominados por *Q. buckleyi,* pero también detectamos reinitas en cada uno de los otros tipos de vegetación que muestreamos. Los adultos y los grupos familiares utilizaron el hábitat de reproducción y no reproductivo de manera similar, al igual que los machos y las hembras, pero los juveniles utilizaron el hábitat no reproductivo más que los adultos. Ni la cobertura del dosel ni la densidad del territorios durante la época reproductiva influyeron en las tasas medias de detección durante el período posterior a la reproducción, independientemente del tipo de vegetación. Detectamos a las reinitas caridoradas 82% menos frecuente en sitios predominados por roble *Q. stellata,* en comparación con el hábitat de reproducción predominado por *Q. buckleyi,* a pesar las densidades de territorios de reproducción fueron similares, lo que sugiere que las reinitas caridoradas dejaron los sitios predominados por *Q. stellata* más temprano durante el período posterior a la reproducción. Sin embargo, no encontramos evidencia que mostrara si las reinitas que anidado en sitios predominados por *Q. stellata* tuvieran más probabilidades de mudarse a un hábitat adyacente no reproductivo que las que anidado en los sitios predominados por *Q. buckleyi.* Enebro de Ashe (*Juniperus ashei*) fue el sustrato leñoso utilizado más consistentemente durante el período posterior a la reproducción, independientemente del sexo o la edad de la reinita, el tipo de hábitat o las especies de robles predominantes. Nuestros resultados enfatizan la continua importancia de los bosques de junípero con roble para las reinitas caridoradas durante el período posterior a la reproducción pero sugieren que otros tipos de vegetación también pueden tener valor de conservación para esta especie.

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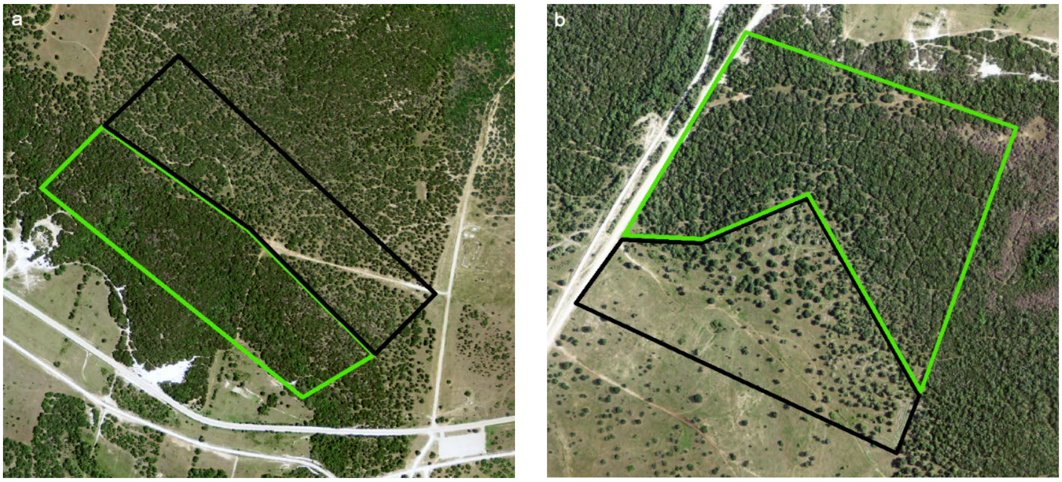
The postbreeding period (i.e., time between nesting and fledging and the onset of migration) is a portion of the avian life cycle about which we know very little (Pärt 1990, Morton 1991, Baker 1993). During this period, adults and fledglings of many species are difficult to follow (Nolan 1978, Haas 1995) because they become more secretive, disperse far from the breeding grounds, or inhabit vegetation not typically associated with the species' breeding ecology (e.g., Anders et al. 1998, Pagen et al. 2000, Vitz and Rodewald 2006, Akresh et al. 2009). For instance, adults and juveniles of several upland forest-breeding species become more abundant in early successional or riparian habitats during the postbreeding period (Pagen et al. 2000, Akresh et al. 2009). Differences in postbreeding habitat use by sex or age class can further complicate our understanding of species' needs during this period (Vega Rivera 1998, 1999, Bartelt et al. 2004, Skórka et al. 2016). Despite these limitations, research suggests that some migratory bird species experience high mortality during the postbreeding period (Dhondt 1979, Anders et al. 1997, Thompson et al. 1999, Pagen et al. 2000), and information on habitat use during this stage may be necessary for identifying management actions that can improve annual survival for species of conservation concern.

The Golden-cheeked Warbler (*Setophaga chrysoparia*) is an endangered Neotropical songbird that breeds exclusively in central Texas and winters from southern Mexico (Chiapas) through Central America to Nicaragua (Ladd and Gass 1999). Though habitat variation exists across the species' breeding range (e.g., Klassen et al. 2012, Long 2014, Long et al. 2016), breeding habitat is typically characterized by oak-juniper (*Quercus-Juniperus*) woodlands with ≥50% canopy cover (Dearborn and Sanchez 2001, USFWS 2003). Ashe juniper (*Juniperus ashei*) is a core component of Golden-cheeked Warbler breeding habitat. Warblers use Ashe juniper for foraging (Marshall et al. 2013, Smith-Hicks et al. 2016) and nesting (Ladd and Gass 1999), but the oak component is also important, because the species of oak present in the canopy can influence habitat quality. Previous research has shown that Golden-cheeked Warblers maintain larger territories and have lower productivity in oak-juniper woodlands predominated by post oak (*Quercus stellata*) compared to those predominated by Texas oak (*Q. buckleyi;* Marshall et al. 2013, Long 2014). There have been no formal studies that quantify habitat use by adult Golden-cheeked Warblers during the postbreeding period (but see Farrell et al. 2012, Smith-Hicks et al. 2016), though Trumbo (2019) tracked dependent juveniles for several weeks after fledging and others have observed independent juveniles in aggregations (Keddy-Hector 1993) or mixed-species flocks (Ladd and Gass 1999) in areas that are more open than typical breeding habitat.

We examined postbreeding habitat use by adult and juvenile Golden-cheeked Warblers in 2 study areas from 2010 to 2012. We conducted surveys in both oak-juniper woodlands and adjacent areas with vegetation types not usually associated with breeding for this species—specifically oak woodlands, oak savannas, and riparian vegetation. We tested for differential use of habitat by group composition and among age and sex classes. Such differential use could have implications for survival and, ultimately, population persistence (Bowers 1994). Because age-related dominance behavior can influence habitat use in *Setophaga* species (Sherry and Holmes 1989, Holmes et al. 1996), we predicted higher detection rates of juveniles compared to adults outside oak-juniper woodlands. We also examined the influences of canopy cover, territory density, and predominant oak species on detection frequency in- and outside of oak-juniper woodlands. We predicted a positive relationship with canopy cover, given the importance often placed on this vegetation characteristic during the breeding season (Dearborn and Sanchez 2001, Campbell 2003, DeBoer and Diamond 2006). We also expected a positive relationship between breeding season territory density and competition among individuals during the postbreeding period, which we hypothesized would manifest in greater detections of Golden-cheeked Warblers in nonbreeding vegetation types adjacent to oak-juniper woodlands with the highest territory densities. Similarly, we anticipated that lower habitat quality during the breeding season would result in more warblers occupying nonbreeding vegetation adjacent to oak-juniper woodlands predominated by post oak compared to those predominated by Texas oak.



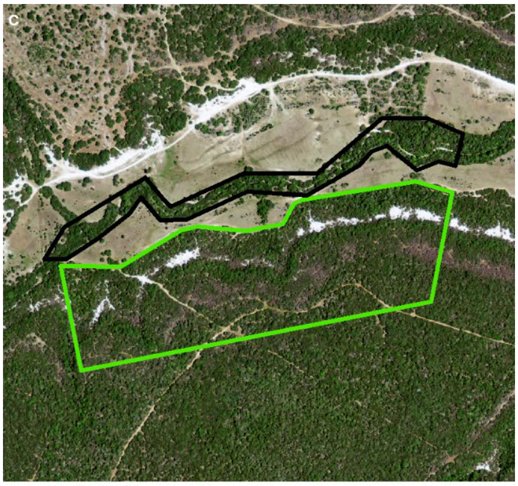


Fig. 1. Examples of study sites for Golden-cheeked Warblers (*Setophaga chrysoparia*) during postbreeding periods (late May–August) in 2010, 2011, and 2012 in central Texas. Each study site comprised 2 plots—a breeding plot (green outline) composed of typical Golden-cheeked Warbler breeding habitat (i.e., oak-juniper woodlands [*Quercus-Juniperus*]) and a nonbreeding plot (black outline) characterized by (a) oak woodland, (b) oak savanna, or (c) riparian strip vegetation not typically associated with Golden-cheeked Warbler breeding activity.

METHODS

Study Area

We surveyed 1463 ha across 2 study areas in central Texas: Fort Hood Military Reservation (hereafter Fort Hood) in Bell and Coryell Counties, and Big Springs Ranch for Children (hereafter Big Springs RC) in Real County. Common woody plants in both study areas include Ashe juniper, black cherry (*Prunus serotina*), Carolina buckthorn (*Frangula caroliniana*), cedar elm (*Ulmus crassifolia*), elbowbush (*Forestiera pubescens*), green ash (*Fraxinus pennsylvanica*), gum bumelia (*Sideroxylon lanuginosum*), Lacey oak (*Q. laceyi*), little walnut (*Juglans microcarpa*), live oak (*Q. fusiformis*), pecan (*Carya illinoinensis*), post oak, Texas redbud (*Cercis canadensis* var. *texensis*), shin oak (*Q. sinuata* var. *breviloba*), Texas ash (*F. albicans*), and Texas oak.

At Fort Hood, we surveyed 16 study sites in 2010 and 12 different sites in 2012 (17–79 ha), and at Big Springs RC, we surveyed 6 study sites (12–24 ha) in 2011. We selected study sites within each study area that contained oak-juniper woodlands and at least one Golden-cheeked Warbler territory monitored during the breeding season. All study sites also included oak woodland ($n = 12$ sites), oak savanna ($n = 14$ sites), or riparian vegetation ($n = 8$ sites) adjacent to oak-juniper woodlands (Fig. 1). Hereafter, we refer to the oak-juniper woodland components of our study sites as breeding plots and the adjacent vegetation types as nonbreeding plots (Fig. 1). We considered nonbreeding plots sparsely vegetated with oaks as oak woodland or oak savanna (Fig. 1), depending on the degree of canopy cover according to a supervised classification of 1-m resolution NAIP orthoimagery (i.e., greater or less than 50% cover, respectively; NAIP 2010) and on-the-ground surveys. Riparian plots included strip-type forests near water that were clearly differentiated from patches of oak-juniper woodlands (Fig. 1). All 3 vegetation types were common near oak-juniper woodlands at Fort Hood, but oak woodland and riparian vegetation meeting our study site requirements were limited at Big Springs RC. As such, all 6 study sites at Big Springs RC included oak-juniper woodlands with adjacent oak savannas.

We further stratified our Fort Hood study sites according to the predominant ecological site (hereafter ecosite) within breeding plots, as this feature can be used as a proxy for tree species composition in this region (Marshall et al. 2013). Breeding plots in half of our Fort Hood study sites were characterized as Low Stony Hill (LSH), predominated by Texas oak, and half were characterized as Redlands, predominated by post oak (NRCS 2009). Because potential Redlands study sites were limited, we used the number of available Redlands study sites ($n = 14$) to determine the number of LSH study sites, then selected LSH study sites closest to Redlands sites to minimize differences in precipitation, human disturbance, and other factors that might vary at greater distances. This resulted in 4 oak woodland, 4 oak savanna, and 6 riparian nonbreeding plots adjacent to LSH breeding plots, and 8 oak woodland, 4 oak savanna, and 2 riparian nonbreeding plots adjacent to Redlands breeding plots. Tree species composition did not vary across ecosites within breeding plots at Big Springs RC and resembled that found at our LSH study sites at Fort Hood (NRCS 2009). As such, for analysis purposes, we considered all breeding plots at Big Springs RC to be LSH sites.

Bird Surveys

According to Ladd and Gass (1999), peak breeding for Golden-cheeked Warblers occurs from April to June. We began surveys each year on or after 23 May, which could have biased detection toward oak-juniper woodlands compared to other vegetation types if warblers were still on nests at the start of our sampling period. However, records from a random selection of nests monitored at Fort Hood during the years of our survey suggested that ≥90% of nesting activity during these years was completed before our earliest survey date each year (J. Macey, Fort Hood Military Reservation, unpublished data). We continued surveys until late July or early August, depending on year.

We surveyed all breeding and nonbreeding plots within study sites 5 times each, except for one breeding plot in 2010, in which limited access allowed only 4 visits. We alternated visits between breeding and nonbreeding plots at each study site to limit detection bias based on time of season. We conducted surveys from sunrise and for up to 7 h after sunrise. During surveys, we walked slowly and made sure to reach within 100 m of all portions of the survey area (i.e., plot). We considered each detection of one or more Golden-cheeked Warblers to represent a discrete detection event, and we considered the first individual detected during each event to be the focal bird.

We visually characterized group composition of each detection event as adults only, juveniles only, or family groups (i.e., adults and dependent juveniles observed together). We also recorded the age classes of all individuals detected as adults or juveniles but did not break age down further, as it is difficult to age adult Golden-cheeked Warblers reliably by sight as second-year or after-second-year individuals (Pruett 2014). We determined the sex of each adult warbler according to plumage (Pyle 1997). We followed focal individuals for as long as we could ($\bar{x} = 5$ min, SD 6) and recorded the species of each woody substrate used. We recorded a new substrate each time a focal bird moved between woody species or moved ≥20 m within the same species. We only conducted surveys under fair weather conditions (e.g., light wind, no precipitation), and we maintained a distance of ≥20 m from Golden-cheeked Warblers to avoid influencing their behaviors.

Analyses

We used a general additive model (GAM) with a Poisson distribution to compare detection frequencies (i.e., detection events/visit) in breeding and nonbreeding plots. Similarly, we used GAMs to test for interactions of plot type and group composition, age, and sex that could indicate differences in habitat use by different warbler classes. We included day of year as a smoothed term in all models to account for decreased counts over time as birds began migration. We also included an offset term to account for variation in survey effort across visits. For each visit, we calculated effort as the number of hectares per plot divided by the survey time, then multiplied by 60 to get a rate of survey in hectares per hour

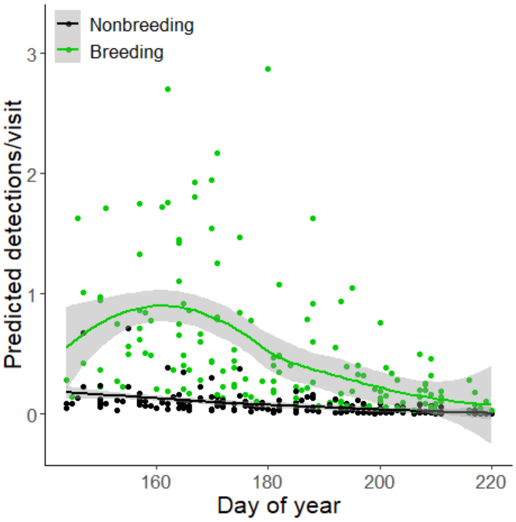


Fig. 2. Predicted number of Golden-cheeked Warbler (*Setophaga chrysoparia*) detection events per visit in breeding and nonbreeding habitat given day of year and mean survey rate during the postbreeding season (late May–August).

(ha/h). We considered the survey time equal to the total visit time minus any time spent following focal individuals. Lastly, we included plot identification number (Location ID) as a random effect to account for within-site correlations due to repeated visits to each plot. For age- and sex-class models, we referred to the number of individuals observed during detection events. We fit all models to the data and calculated the mean predicted detection frequencies.

We also used GAMs to test whether percent canopy cover, breeding season territory density, or the ecosite of breeding plots influenced detection event frequency. Canopy cover varied considerably among the different vegetation types in nonbreeding plots, so we conducted separate analyses for each plot type (i.e., breeding, nonbreeding). We applied a smooth function to the canopy cover term in both models, based on exploratory analyses indicating model improvement over the linear form. We quantified territory density within each breeding plot by dividing the number of territories observed during each breeding season (monitored from March to April, unpublished data, ML Morrison, Texas A&M University, 2010–2012) by the number of hectares. We then examined the relationships between territory density and detection event frequency in both breeding plots and in adjacent nonbreeding plots. We similarly tested for differences in detection in both breeding and nonbreeding plots according to the ecosite of the breeding plot. We used a 2-sample *t* test to compare territory densities in LSH and Redlands breeding plots.

We calculated the percentage of detection events in which Golden-cheeked Warblers used different tree species, regardless of how long or how often they used each tree species during each event. We then used exact goodness-of-fit tests to compare the consistency of use of the most common tree species among age and sex classes, plot types, and ecosites. We calculated Cramer's *V* as a measure of effect size for all comparisons. We conducted all analyses using the open-source statistical program R (R Core Team, Vienna, Austria). Herein we present means with standard deviations (SDs) and ranges.

RESULTS

Across years, we observed 98 detection events (i.e., ≥1 Golden-cheeked Warbler), with 85 (87%) occurring in breeding plots and 13 (13%) occurring in nonbreeding plots. Given mean survey effort (i.e., 24.5 ha/h, SD 13.3), the predicted number of detection events generally declined with day of year (Fig. 2), with a predicted mean that was 84% lower in nonbreeding plots (0.08 events/visit, SD 0.10; range 0.01–0.70) than in breeding plots (0.50 events/visit, SD 0.58; range 0.01–3.23) (Table 1). Small sample sizes precluded statistical comparison of detection events by vegetation type within nonbreeding plots (oak woodland $n = 1$ event, oak savanna $n = 4$ events, riparian $n = 8$ events).

Group Composition, Sex, and Age

In breeding plots, there were 46 adult-only events, 2 juvenile-only events, 34 family group events, and 3 events of unknown group composition. In nonbreeding plots, there were 4 adult-only events, 4 juvenile-only events, and 5 family group events. Given equal survey effort, there was no difference in the predicted mean numbers of adult-only and family group events per visit in breeding (0.24 events/visit, SD 0.27; range 0–1.62) or nonbreeding (0.03 events/visit, SD 0.03;

TABLE 1. General additive model (GAM) results examining the effects of plot type on the numbers of Golden-cheeked Warbler (*Setophaga chrysoparia*) detection events and individual observations during the postbreeding period (from late May to August) in central Texas, overall and according to group composition, age, and sex.

	Total detection events	Adults vs. family groups	Adults vs. juveniles	Males vs. females
Intercept[a]	−6.01 (0.42)	−7.23 (0.57)	−7.68 (0.94)	−8.75 (1.05)
Breeding[a]	1.52 (0.52)	2.13 (0.63)	2.41 (1.21)	2.67 (1.10)
Breeding P value	0.00	0.00	0.05	0.01
Covariate[b]		0.22 (0.67)	0.47 (0.40)	2.20 (1.05)
Covariate P value[b]		0.74	0.24	0.04
Interaction[b]		−0.53 (0.71)	−0.86 (0.43)	−0.90 (1.08)
Interaction P value[b]		0.46	0.05	0.40
Day of year[c]	2.78 (37.23)	4.47 (38.07)	7.46 (99.85)	6.72 (49.1)
Location ID[c]	40.11 (96.54)	33.10 (72.73)	53.15 (139.12)	35.79 (78.80)
Adjusted pseudo R^2	0.55	0.29	0.50	0.46
Deviance explained	62.8%	49.5%	66.4%	58.4%

[a] Model estimates (standard error); nonbreeding = 0, breeding = 1.

[b] Covariates included group composition (adult = 0, family group = 1), age (adult = 0, juvenile = 1), or sex (female = 0, male = 1); interactions include covariate * sublocation type.

[c] Estimated degrees of freedom (chi-square statistic); significant at $P \leq 0.01$; Location ID = random effect, significant at $P \leq 0.05$ in all models.

TABLE 2. Predicted mean number of Golden-cheeked Warbler (*Setophaga chrysoparia*) observations per visit ± standard deviation (range in parentheses) by sex and age in breeding and nonbreeding plots given mean survey effort during the postbreeding period (from late May to August) in central Texas.

Class	Breeding	Nonbreeding
Adult	0.55 ± 0.92 (0.00–5.17)	0.06 ± 0.15 (0.00–0.98)
Juvenile	0.37 ± 0.62 (0.00–3.50)	0.09 ± 0.24 (0.00–1.57)
Male	0.43 ± 0.52 (0.00–2.84)	0.05 ± 0.07 (0.00–0.68)
Female	0.12 ± 0.14 (0.00–0.78)	0.01 ± 0.01 (0.00–0.08)

range 0–0.03) plots (Table 1). The mean number of juveniles per family group or per juvenile-only detection event was 1.7 (SD 0.8; range 1–3). There were too few juvenile-only events for statistical comparisons.

During detection events, we recorded 93 observations of adults in breeding plots and 10 in nonbreeding plots, and we recorded 63 observations of juveniles in breeding plots and 16 in nonbreeding plots. The number of adults and juveniles observed per visit was similar (Table 1), but the interaction of age class and plot type was significant (Table 1), suggesting differences in habitat use by adults and juveniles. The predicted mean number of juveniles per visit was 50% higher than the predicted mean number of adults in nonbreeding plots and 33% lower than that of adults in breeding plots (Table 2).

Of detection events with adult Golden-cheeked Warblers, we recorded 73 observations of males in breeding plots and 9 observations in nonbreeding plots, and we recorded 20 observations of females in breeding plots and 1 observation in nonbreeding plots. Overall, we recorded males significantly more often than females, but the interaction of sex and plot type was not significant, suggesting that males and females used breeding and nonbreeding plots similarly (Table 1). The predicted mean number of females per visit in nonbreeding plots was 80% lower than that for males, and the predicted mean in breeding plots was 72% lower (Table 2).

Canopy Cover, Territory Density, and Ecosite

Canopy cover in breeding plots ranged from 64% to 99% ($\bar{x}$ = 88%, SD 9%). In nonbreeding plots, canopy cover ranged from 13% to 89% ($\bar{x}$ = 56%, SD 25%), with means of 69% (SD 10%; range 55% to 84%) in oak woodlands, 29% (SD 10%; range 13% to 49%) in oak savannas, and 82% (SD 4%; range 78% to 89%) in riparian areas. We found no relationship between canopy cover and frequency of detection events in breeding or nonbreeding plots (Table 3).

Similarly, the frequency of detection events in both breeding plots and adjacent nonbreeding plots was unrelated to breeding season territory density ($\bar{x}$ = 0.18 territories/ha, SD 0.12; range 0.06–0.56; Table 3). However, though density of breeding season territory was similar across ecosites ($t_{31.99} = 0.79$, $P = 0.43$), there were 82% fewer postbreeding detection events in Redlands breeding plots ($n = 13$) than in LSH breeding plots ($n = 87$). Given mean survey effort, the mean predicted number of detection events per visit in breeding plots was 74% lower in Redlands ($\bar{x} = 0.19$ events/visit, SD 0.19; range 0.01–1.27) compared to LSH sites ($\bar{x} = 0.73$ events/visit, SD 0.61; range 0.03–2.86). There was no difference in predicted detection event frequency in nonbreeding plots as a function of the ecosites of adjacent breeding plots (Table 3).

Tree Species Use

We followed focal individuals (i.e., those first detected) during 96% ($n = 94$) of detection events. Seventy-one percent ($n = 67$) of focal individuals were male, 9% ($n = 8$) were female, and 20% ($n = 19$) were hatch-year birds. Focal individuals used Ashe juniper at least once during 77% of detection events. Other common species used by Golden-cheeked Warblers included live oak (27%), Texas oak (26%), Texas ash (11%), and shin oak (10%). Use of Ashe juniper was similar among age and sex classes ($P = 0.54$, $V = 0.08$), in breeding and nonbreeding plots ($P = 0.61$, $V = 0.08$), and across ecosites within breeding plots ($P = 0.31$, $V = 0.14$).

DISCUSSION

Golden-cheeked Warblers primarily used oak-juniper woodlands (i.e., breeding habitat) throughout the postbreeding period, but they also used oak woodlands, oak savannas, and riparian vegetation (i.e., nonbreeding habitat) to a lesser extent. We detected adults alone and those in family groups in equal proportions in breeding and nonbreeding habitat. We also detected males and females in equal proportions in both habitat types, but juveniles used nonbreeding habitat more than adults did. We found no evidence that canopy cover, breeding season territory density, or the ecosite of breeding habitat influenced use of adjacent nonbreeding habitat during the postbreeding period. Similarly, we found no evidence that canopy cover or territory density influenced postbreeding habitat use within breeding habitat. However, despite similar breeding territory densities, we detected Golden-cheeked Warblers significantly less often in oak-juniper woodlands in

Table 3. General additive model (GAM) results examining the relationships of canopy cover, territory density, and ecosite (i.e., covariates) to the number of Golden-cheeked Warbler (*Setophaga chrysoparia*) detection events by plot type during the postbreeding period (from late May to August) in central Texas.

	Canopy cover		Territory density		Ecosite	
	Breeding	Nonbreeding	Breeding	Nonbreeding	Breeding	Nonbreeding
Intercept[a]	−4.46 (0.31)	−36.26 (67.72)	−4.54 (0.60)	−21.64 (24.39)	−3.92 (0.29)	−21.99 (27.55)
Covariate[b]	1.57 (0.29)	8.86 (5.00)	0.34 (2.72)	2.08 (2.30)	−1.26 (0.50)	−0.38 (1.75)
Covariate P value	0.71	0.82	0.90	0.37	0.01	0.83
Day of year[c]	2.09 (33.26)	7.87 (8.78)	2.09 (31.93)	7.64 (6.96)	2.11 (30.35)	7.69 (7.50)
Location ID[c]	23.93 (62.09)	6.99 (15.19)	24.95 (67.62)	18.49 (29.99)	20.52 (49.34)	19.83 (33.06)
Adjusted pseudo R^2	0.46	0.63	0.47	0.52	0.46	0.56
Deviance explained	60.8%	81.8%	61.2%	78.2%	58.8%	79.5%

[a] Model estimates (standard error).

[b] For canopy cover models, covariate = estimated degrees of freedom (chi-square statistic); for territory density and ecosite models, covariate = model estimates (standard error).

[c] Day of year is significant at $P \leq 0.01$ in all breeding models and nonsignificant in nonbreeding models, with $P = 0.36$ for the canopy cover model, $P = 0.49$ for the territory density model, and $P = 0.45$ for the ecosite model; Location ID = random effect, significant at $P \leq 0.05$ in all models.

Redlands sites compared to Low Stony Hill (LSH) sites.

Our observations are consistent with others (Farrell et al. 2012, Smith-Hicks et al. 2016, Trumbo 2019), who observed Golden-cheeked Warblers in oak-juniper woodlands in summer months. However, unlike Keddy-Hector (1993) and Ladd and Gass (1999), we did not observe large aggregations of juvenile Golden-cheeked Warblers or independent juveniles among mixed-species flocks. In fact, only 6% of all detection events were composed of only juveniles, suggesting that these events were rare, difficult to detect, or occurred at greater distances from breeding habitat than those we surveyed. Nonetheless, we detected independent juveniles twice as often in nonbreeding habitat as in breeding habitat. Adult Golden-cheeked Warblers exhibit high breeding site fidelity (Pulich 1976, Peak and Thomas 2010), with an average dispersal distance of a few hundred meters between years (Jette et al. 1998). In contrast, warblers banded as juveniles are often resighted at much greater distances from their natal areas (Jette et al. 1998). Increased use of nonbreeding habitat by juvenile birds during the postbreeding period may reduce competition with adults, while facilitating movement between patches of breeding habitat and thereby increasing opportunities for prospecting (Greenwood and Harvey 1976, Jackson 1994). Nonbreeding areas with dense shrub cover, like some of our oak woodland and oak savanna plots, may also provide inexperienced, young birds with increased protection from predators (Anders et al. 1998, Vitz and Rodewald 2007).

Management prescriptions for Golden-cheeked Warbler breeding habitat typically focus on percent canopy cover as a measure of habitat quality (Campbell 2003, DeBoer and Diamond 2006), but several studies have demonstrated that canopy cover alone is an insufficient metric for predicting reproductive success (Farrell et al. 2012, Klassen et al. 2012). We found no relationship between canopy cover and the frequency of detecting Golden-cheeked Warblers in typical breeding habitat or adjacent vegetation types during the postbreeding period. Other environmental factors that contribute to postbreeding habitat use may be more indicative of postbreeding habitat quality. For example, Ashe juniper was the most consistently used woody species throughout the postbreeding period. Golden-cheeked Warblers increase their use of Ashe juniper during the breeding season concomitantly with increased larval abundance on this substrate (Quinn 2000, Marshall et al. 2013, Smith-Hicks et al. 2016). Though we did not examine the abundance of Lepidopteran larvae during the postbreeding period, our observations suggest that Ashe juniper continues to be a valuable foraging resource, which may contribute to warbler survival in the months leading up to migration (but see Trumbo 2019).

Marshall et al. (2013) demonstrated that ecosite (as a proxy for tree species composition) can influence Golden-cheeked Warbler productivity, with higher productivity in LSH sites predominated by Texas oak, compared to Redlands sites predominated by post oak. Our finding that Golden-cheeked Warblers were more abundant in LSH sites compared to Redlands sites during the postbreeding period despite equal breeding territory densities suggests that individuals may leave Redlands breeding sites earlier than LSH sites. However, we found no evidence that use of poorer-quality Redlands sites during breeding encouraged postbreeding use of nonbreeding habitat. Conspecific cues, including adult songs and fledgling calls, during the postbreeding period can provide information to prospecting individuals regarding potential habitat quality (e.g., Farrell et al. 2012), and it is possible that individuals that make unsuccessful breeding attempts in Redlands sites may be attracted to LSH sites during the postbreeding period. However, longer-term studies of banded individuals are needed to identify adult dispersal behaviors in this species.

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