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Source: The American Midland Naturalist, 176(1):81-94.
Published By: University of Notre Dame
DOI: http://dx.doi.org/10.1674/0003-0031-176.1.81
URL: http://www.bioone.org/doi/full/10.1674/0003-0031-176.1.81

Am. Midl. Nat. (2016) 176:81–94

Golden-cheeked Warbler Behavior in Relation to Vegetation Characteristics across their Breeding Range

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ABSTRACT.—We examined golden-cheeked warbler (*Setophaga chrysoparia*; hereafter warbler) behavior by age, sex, and habitat characteristics across their breeding range in central Texas (1995–1997). This federally endangered songbird foraged more on oak (*Quercus* spp.) substrates early in the breeding season and more on Ashe juniper (*Juniperus ashei*) late in the breeding season. We observed no overall difference in tree species use by warbler sex and age; however, we detected female and juvenile warblers in the low and middle canopy more often for all behaviors than males. Also, female warblers rested less and foraged twice as much as male warblers, who instead vocalized more than females and juveniles. In the southernmost study location, male warblers foraged more and vocalized less. More specifically, they foraged more on oaks when compared to other tree species, suggesting vegetation may influence warbler behavior in some locations. As the breeding season progressed, warblers increased their use of lower tree height classes for foraging and nonforaging behaviors. Site-specific vegetation management practices incorporating structural and compositional heterogeneity may better address the habitat needs of both warbler sex and age groups.

INTRODUCTION

Understanding species-habitat relationships is fundamental to the conservation of a species (Morrison *et al.*, 2006). Svärdson (1949) and Hilden (1965) conceptualized a two-stage process whereby animals first select broadly from different environments, then base settlement decisions on fine-scale habitat characteristics. After settlement, natural (*e.g.*, vegetation, weather) and anthropogenic (*e.g.*, urbanization, agricultural development)

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factors within habitat influence resource availability and, therefore, drive individual survival and reproductive success (Block and Brennan, 1993). Spatial and temporal variation in these factors among habitats can create local adaptations, even if dispersal and gene flow connect species across their breeding range (Kawecki and Ebert, 2004). Elucidating fine-scale wildlife-habitat relationships can provide land managers with precise requirements of a species at different locations.

For migratory songbirds survival and productivity are constrained by time and energy required to find food (Martin, 1987; Hutto, 1990). Therefore, assessing foraging behavior and habitat use among vegetation types may serve as an indicator of resource availability and resulting habitat quality (Rotenberry and Wiens, 1980; Lovette and Holmes, 1995; Ghosh *et al.*, 2011). At a finer-scale, differential resource availability across vegetation strata (*e.g.*, Robinson and Holmes, 1982) and plant species (*e.g.*, Keane and Morrison, 1999) may also influence avian foraging behavior, and therefore, contribute to patterns in avian demographics among habitats.

The golden-cheeked warbler (*Setophaga chrysoparia*; hereafter warbler) is an insectivorous songbird that nests exclusively in mature oak-juniper (*Quercus-Juniperus*) woodlands in central Texas (Fig. 1; Ladd and Gass, 1999). Habitat loss and fragmentation within the limited breeding range of the species were the primary reasons for listing the warbler as endangered (USFWS, 1990). The warbler uses Ashe juniper (*J. ashei*) as a nesting and foraging substrate, and Pulich (1976) noted the presence of this tree species is the only habitat specific requirement for the warbler. However, warblers also use various hardwood species for foraging and nesting, and studies suggest tree species composition, which varies across the geographic extent of the warbler's breeding range (Diamond, 1997; Ladd and Gass, 1999; Campbell, 2003; Long, 2014), may influence warbler breeding success at local scales (Wahl *et al.*, 1990; Beardmore, 1994; Marshall *et al.*, 2013).

In the northeastern portion of the warbler's breeding range, productivity was higher in woodland stands co-dominated by Texas oak (*Q. texana*) when compared to woodland stands dominated by post oak (*Q. stellata*) (Marshall *et al.*, 2013). Marshall *et al.* (2013) linked this disparity in warbler productivity to differences in arthropod abundance across tree species. Marshall *et al.* (2013) also found warblers foraged primarily on oaks during the early portion of the breeding season and switched their foraging efforts to Ashe juniper as the breeding season progressed. In addition, there appears to be sex-specific stratification in vegetation used by warblers for foraging. For example, male warblers in Travis County foraged primarily on oaks, whereas female warblers foraged primarily on Ashe juniper, and juveniles used both foraging substrates (Beardmore, 1994). These studies have provided a foundation for knowledge of warbler behavior at specific sites within their breeding range. However, we still lack information regarding sex- and age-specific warbler habitat use across their range.

The Golden-cheeked Warbler Recovery Plan indicates the need for a definitive study of the habitat requirements and habitat selection patterns of warblers that measures vegetation structure and form as well as warbler foraging behavior (Keddy-Hector, 1992). Our objectives were to quantify: (1) warbler behavior by time of season (*i.e.*, early vs. late), sex, age, and spatial location; and (2) habitat characteristics associated with warbler foraging and non-foraging behaviors. Given results of previous site-specific studies (Beardmore, 1994; Marshall *et al.*, 2013), we expected to find warblers foraging more on hardwoods (*e.g.*, oaks) early in the breeding season and Ashe juniper later in the season at all sites included in our study. We also expected to find a difference in the proportion of tree species used by warbler sex and age classes across the breeding range with males

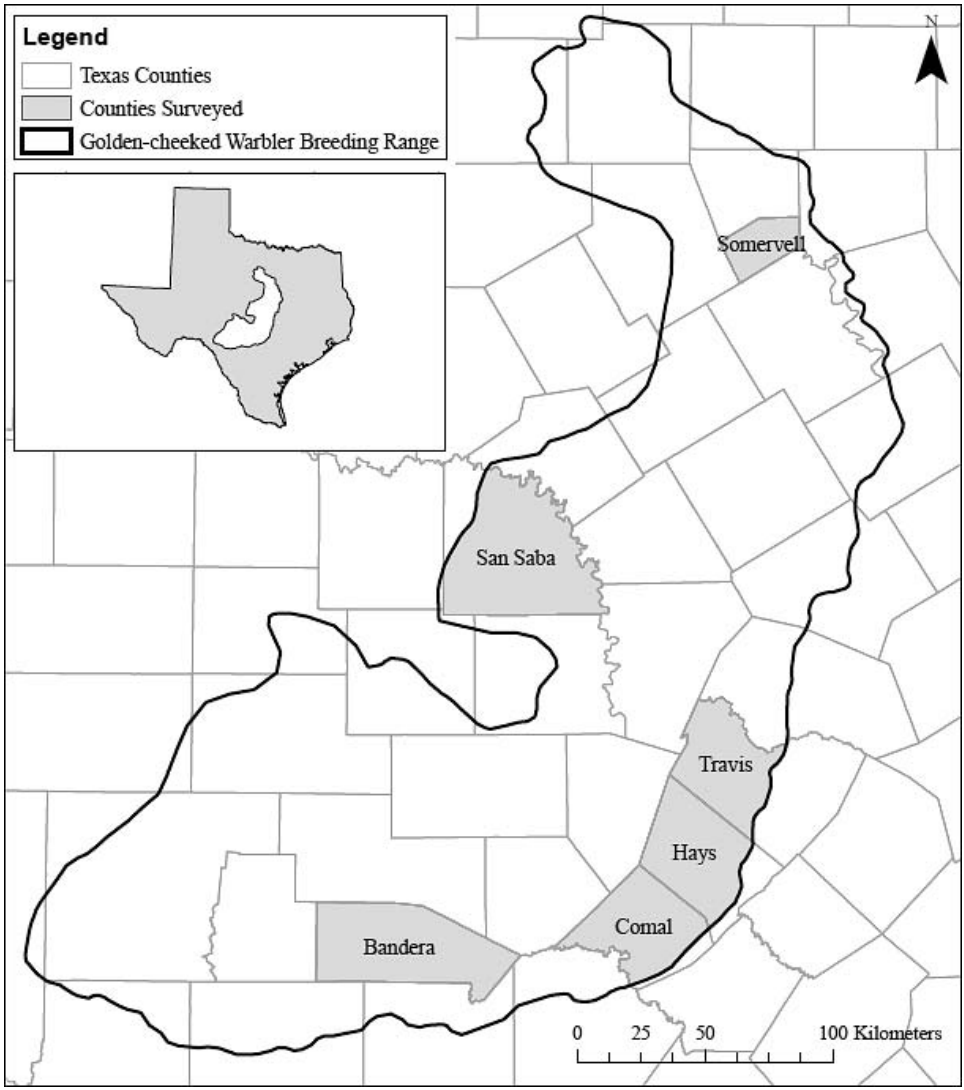

FIG. 1.—Map of counties surveyed for golden-cheeked warblers (*Setophaga chyrsoparia*) within their breeding range (outlined in black) in central Texas, 1995–1997

foraging more on oak species and females and juveniles foraging more on Ashe juniper (Beardmore, 1994). Finally, we expected warblers would spend more time in the upper canopy (Pulich, 1976; Sexton, 1987; Beardmore, 1994), but that warblers would forage more in the lower and middle tree height classes as the breeding season progressed (Beardmore, 1994). Information gained from our study could help land managers predict warbler responses to habitat alteration and help guide conservation strategies for this species.

METHODS

STUDY AREA

We surveyed warbler behavior in six counties (Somervell, San Saba, Travis, Hays, Comal, and Bandera) in central Texas, U.S.A. (Fig. 1) during the breeding seasons of 1995–1997. Study sites included both public and private properties, which we selected because they encompassed known warbler habitat across the breeding range. The locations for the public properties are as follows: San Saba: 31.045122, –98.476335, Somervell: 32.253166, –97.809572, Bandera: 29.823727, –99.577441, Comal: 29.868216, –98.489477. Sites were composed of mature oak-juniper woodland embedded within urban or agricultural matrices. Mean annual temperature across the warbler's breeding range is 18.5–20°C, and mean annual precipitation is 55–85 cm (NOAA, 2014). However, conditions become warmer and drier along a geographic gradient from north to south (NOAA, 2014), and plant species across the range vary with climate (Griffith *et al.*, 2004). Similarly, vegetation characteristics, such as canopy cover and canopy height, also vary across the range (Campomizzi *et al.*, 2012, Klassen *et al.*, 2012, Long *et al.,* 2016).

BEHAVIORAL SURVEYS

We conducted surveys of warbler behavior across the breeding range from 1995–1997. In 1995, we conducted behavioral surveys at sites located in Travis and Hays counties at least once per week from mid-March to mid-June, which encompassed most of the warbler's breeding season (Ladd and Gass, 1999). During the 1996 and 1997 warbler breeding seasons, we conducted behavioral surveys once per week at sites in all six counties (Fig. 1). We conducted behavioral observations from ~0630–1500 h using an instantaneous, focal animal technique, recording warbler behavior every 15 s (Altmann, 1974; Martin and Bateson, 1993). When a team of two observers detected a warbler at a site, they recorded the warbler's sex and age, the date, and the time of day. One observer then followed the focal individual and dictated observations every 15 s (hereafter observation) on the beep of a continuously running stopwatch to a second technician who recorded the data. We defined a "bout" as all observations of one bird recorded consecutively (Wiens *et al.*, 1970).

We followed each focal individual for <70 min. If we could not see the warbler at the 15 s signal to record a behavioral observation, but it was clear the bird was still present, we recorded "out of sight" for the behavior. Once we could no longer detect the bird, we recorded the end time for the bout and continued to search the site for other individuals. We could potentially encounter individual birds repeatedly on the same day, particularly at sites with low warbler abundance. As such, we separated behavioral surveys with the same (or potentially same) individual by at least 30 min. We gave priority to collecting behavioral observations from juveniles and females, because we encountered them less frequently than adult males.

During each observation, we recorded the focal bird's behavior (described below), species of tree occupied, and micro-location (*i.e.*, twigs, branch, trunk, or ground). We also estimated the height from the ground to the bird and tree height to the nearest 1 m using a height pole, with technicians trained to estimate height at the start of each breeding season. We grouped warbler behaviors into the following categories: (1) foraging (*i.e.*, eating, hopping, adult feeding fledgling, fledgling being fed, begging); (2) locomotion (*i.e.*, flying); (3) pair bonding (*i.e.*, chasing, wing/tail flashing, gathering nesting material, copulation); (4) resting (*i.e.*, perching, preening); and (5) vocalizing (*i.e.*, singing, chipping). Warblers

often hop short distances while foraging for food (Robinson and Holmes, 1982); therefore, we recorded short hops (<1 m) as 'foraging' and designated longer movements (≥1 m) as 'locomotion.' To avoid bias towards behaviors that are more detectable (*e.g.,* singing), we removed all observations that occurred in the first minute of each bout.

VEGETATION SURVEYS

To describe vegetation occupied by warblers, we mapped adult warbler locations across each site and marked the tree where we initially encountered each warbler. We returned to marked locations later in the breeding season, before trees exhibited phenological changes, and measured total vegetation volume (TVV) following Mills *et al.* (1991). To measure TVV, we established perpendicular transects by placing two 20 m ropes on the ground that intersected at right angles at the marked trees, with direction of transects randomly determined. We then erected a 6 m retractable pole (13 mm in diameter) at 2 m increments along each perpendicular transect (n = 20 sampling points per transect) and counted the number of vegetation intercepts ("hits") with the pole for each decimeter column, noting the plant species for each "hit." For each transect, we recorded and summed the total number of hits and number of hits per species recorded at each point. We divided this number by 200 to obtain an average of the 20 points (*i.e.*, mean TVV per transect; m^3/m^2). If we followed a warbler over an area larger than one transect within the same encounter, we marked multiple locations and created multiple transects. In these instances, we averaged measurements from the multiple transects associated with the same bird to give one transect value for that bout. TVV estimates for a transect could exceed 1 m^3/m^2, because hits in all meter layers of the canopy were combined.

STATISTICAL ANALYSES

Because we recorded unequal bout lengths, we randomly sub-sampled ≤4 observations per bout for our analyses. At each study site, we calculated the relative proportions of behavior by sex and age class. We also calculated relative proportions of tree species within occupied habitat, and the relative proportion of tree species used by warblers for foraging per age and sex class and time of season. Because vegetation height varied across the warbler's range, and we wanted to make our results comparable to previous studies (Pulich, 1976; Beardmore, 1994) of tree height use, we calculated the observed height of each bird as a proportion of tree height by dividing tree height by height of bird. We then divided the proportions into three categories: low (lower third), mid (middle third), and high (top third) and calculated the relative proportion of warbler behavioral observations per tree height class by sex, age, and time of season at each site. Finally, we calculated the relative proportion of warbler behavioral observations per primary tree species by sex, age, and time of season at each site. We classified time of season into three categories *(i.e.,* early, middle, and late) by dividing site visit dates into thirds (16 March–11 April; 12 April–14 May; 15 May–17 June). In order to make the differences in behavior and tree use across the season more distinct, we only present data collected in early and late time periods in our analyses. We performed Chi-square analyses to determine if there were important differences in behavior, height class, or tree species between sex, age, or time of season (Agresti, 2007). We analyzed all data using R software for statistical computing and graphics (R Core Development Team, 2013).

TABLE 1.—Summary of sampled golden-cheeked warbler (*Setophaga chrysoparia*) behavioral observations by behavior category, sex, age, and time of season for six sites surveyed across the warbler's breeding range in central Texas, 1995–1997

	Sex and age						Time of season					
	Male		Female		Juvenile		Early		Late		Total	
Behavior[a,b]	#	%	#	%	#	%	#	%	#	%	#	%
Foraging	**537**	**19**	**223**	**42**	65	24	383	25	192	27	825	23
Pair bonding	**6**	**0**	**10**	**2**	N/A	N/A	8	1	1	0	18	<1
Vocalizing	**483**	**17**	**14**	**3**	16	6	208	13	82	12	513	14
Movement	**115**	**4**	**37**	**7**	12	4	76	5	41	6	164	5
Resting	**1634**	**59**	**252**	**47**	176	65	872	56	384	55	2062	58
Total	2775		536		269		1547		700		3582	

[a] "#" indicates number of observations and "%" indicates the relative proportion of observations per behavior category

[b] Bold numbers indicate statistical significance by sex, age, or time of season

RESULTS

From 1995–1997, we recorded 30,652 instantaneous behavioral observations in 1495 bouts across the six sites (Table 1). The mean number of observations per bout was 26 ± 33 (6.5 min ± 8.3 min). We recorded more observations of males (74%) than females (14%) or juveniles (12%). We observed most juveniles while they were still dependent on adults for food. We conducted most surveys in March, April, and May with more observations during the early breeding season (44%) than late (20%). Across sites, we recorded ≤1% of warbler observations on the ground or on tree trunks, 27–40% of warbler observations on branches, and 60–73% of warbler observations on twigs extending from branches. Of the 30,652 observations, 24,628 belonged to bouts >1 min. After we randomly sub-sampled ≤4 observations from bouts >1 min and excluded observations categorized as "out of sight," we retained 3582 observations (Table 1).

Though we recorded more observations of males than females and more observations during the early breeding season when compared to the late breeding season, the proportions of male and female behavioral observations used for analyses were similar within each time period. Of the total analyzed observations, 46% of male and 47% of female observations occurred during the early breeding season, and 17% of male and 10% of female observations occurred during the late breeding season. We recorded more observations, by sex and age, in Travis than at other sites while we recorded the least observations, proportionally, in Somervell (Table 2). We conducted more observations during the early breeding season at all sites; however, observations were more evenly distributed across sites during the late breeding season (Table 2).

We observed resting and foraging more than all other behavioral categories ($X^2 = 206.3$, $df = 4$, $P < 0.01$). Females foraged twice as often as males or juveniles, and males vocalized ~3–5 times more than females or juveniles (Table 1). Males also spent more time resting than females (Table 1). Female warblers rested less and moved around and foraged more at Somervell (our northernmost site) than at other sites (Fig. 2); however, the sample size of female warblers was much lower in Somervell ($n = 7$) than at other sites ($n > 50$). Male warblers at Bandera (our southernmost site) foraged ~10% more than at other sites (Fig. 2). Warbler behavior did not vary with time of season ($X^2 = 5.2$, $df = 4$, $P = 0.27$; Table 1).

TABLE 2.—Number (#) and relative proportion (%) of sampled golden-cheeked warbler (*Setophaga chrysoparia*) behavioral observations per site surveyed across the warbler's breeding range in central Texas, 1995–1997, by sex, age, and time of season

	Sex and age						Time of season					
	Male		Female		Juvenile		Early		Late		Total	
Site	#	%	#	%	#	%	#	%	#	%	#	%
Somervell	352	11	8	1	39	17	106	6	144	19	399	10
San Saba	574	18	108	18	17	7	328	19	146	19	699	18
Travis	932	30	166	27	103	44	611	35	111	14	1201	30
Hays	505	16	144	24	73	31	226	13	171	22	722	18
Comal	329	11	50	8	17	7	147	8	67	9	396	10
Bandera	437	14	132	22	53	23	313	18	135	17	622	16
Total	3129	79	608	15	232	6	1731	44	774	20	3969	

Females used the middle height class twice as often as males for non-foraging behaviors ($X^2 = 67.5$, df = 4, $P < 0.01$), and juveniles foraged in the middle height class twice as often as adult warblers ($X^2 = 20.3$, df = 4, $P < 0.01$; Table 3). At Bandera, warblers used the mid and low height classes more often than at other sites, with females being more than twice as likely to use the mid height class as compared to other sites. Overall, warblers used the high height class more than the other height classes for all behaviors throughout the season ($X^2 = 15.4$, df = 2, $P < 0.01$; Table 3). During the late breeding season, warblers foraged more often in the mid height class than early in the season ($X^2 = 23.9$, df = 2, $P < 0.01$).

We observed male, female, and juvenile warblers using Ashe juniper most often, followed by live oak and Texas oak (Table 4). Juveniles used shin oak slightly more often than adults (Table 4). Overall, warblers used tree species similarly for foraging ($X^2 = 6.6$, df = 6, $P = 0.36$) and non-foraging ($X^2 = 12.2$, df = 6, $P = 0.06$) behaviors. Warblers used Ashe juniper and oak species evenly early in the season but switched to Ashe juniper later in the season ($X^2 = 135.9$, df = 6, $P < 0.01$) and decreased their use of Texas oak later in the breeding season (Table 4). It appears this shift in overall tree species used may be at least partially explained by the warbler's shift in tree species used for foraging across the breeding season ($X^2 = 107.1$, df = 6, $P < 0.01$; Table 4).

Adult warblers foraged in Ashe juniper less than it was available within warbler territories at all sites except Somervell (our northernmost site) (Fig. 3). Warblers foraged on all oak species in proportion to their availability within warbler territories at all sites except at Bandera where they foraged ~10% less in live and Lacey oak than it was available (Fig. 3). Cedar elm was uncommon within warbler territories at most study sites, but both male and female warblers used it for foraging in similar proportions to its availability within territories (Figs. 3 and 4). Male warblers at San Saba used oak species more often than females for foraging, which used more Ashe juniper (Fig. 4). Use of Ashe juniper for foraging generally decreased for both sexes from north to south, but this trend was more consistent for females (Fig. 4).

DISCUSSION

Our results suggest that warblers occupy the highest portions of the canopy, selectively use certain tree species over others within their breeding habitat, and shift habitat use through the breeding season. Our findings are similar to those of others (Sexton, 1987; Beardmore,

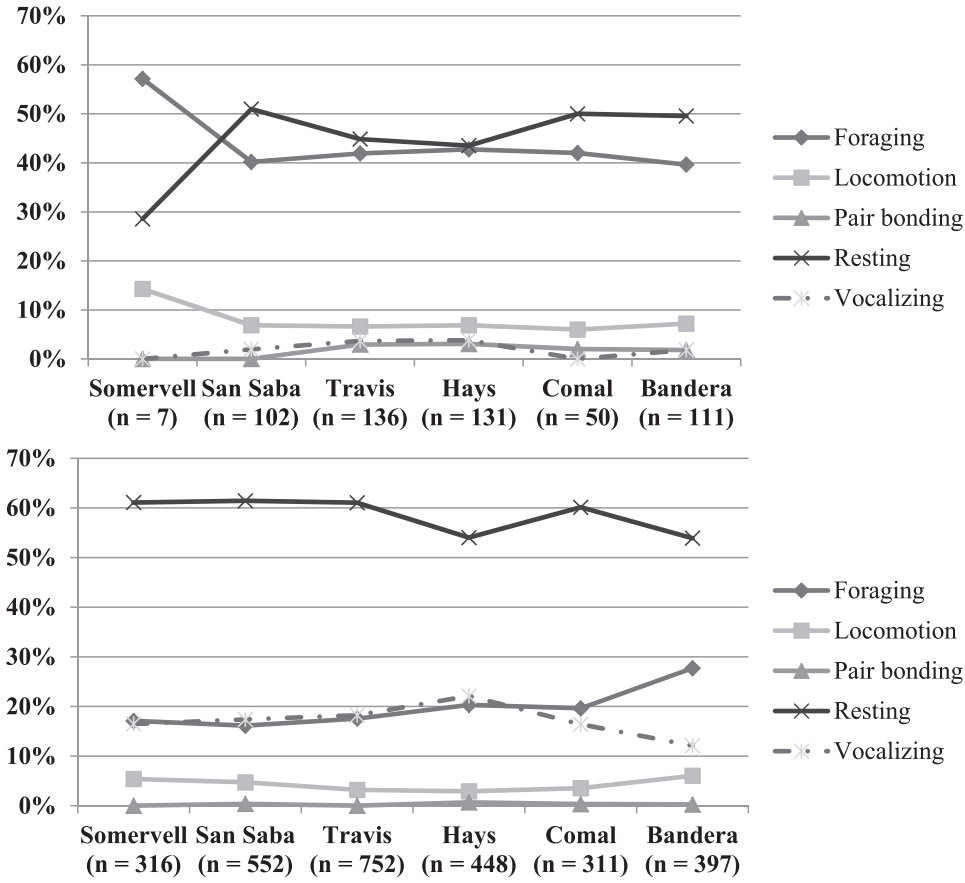

FIG. 2.—Proportion of behavioral observations of female (top) and male (bottom) golden-cheeked warblers (*Setophaga chrysoparia*) at sites located across their breeding range in central Texas. We collected data in Travis and Hays counties in 1995 and from all sites in 1996 and 1997. Sites are presented geographically by county from northeast to southwest

1994; Marshall *et al.*, 2013). However, we also documented notable differences in behavior and habitat use by male and female warblers, adult and juvenile warblers, and warblers occupying different geographic locations.

As predicted, warblers foraged more on oak substrates early in the breeding season and more on Ashe juniper late in the season at all sites. Beardmore (1994) and Marshall *et al.* (2013) also noted increased use of Ashe juniper as a foraging substrate later in the breeding season. As changes in arthropod abundance influenced within-season shifts in the use of plant species by other warbler species (Petit *et al.*, 1990; Keane and Morrison, 1999), we suggest that the seasonal patterns observed here were also likely due to shifts in the availability of Lepidopteran larvae, which constitute a large portion of adult warbler's diets and may be especially important to warbler nestlings (Pulich, 1976; Kroll, 1980; Ladd and Gass, 1999; Quinn, 2000; Marshall *et al.*, 2013). Warblers arrive on the breeding grounds in early to mid-March (Pulich, 1976; Ladd and Gass, 1999; Peak and Thompson, 2014) during a

TABLE 3.— Number (#) and relative proportion (%) of golden-cheeked warbler (*Setophaga chrysoparia*) behavioral observations per tree height class by sex, age, and time of season for six sites surveyed across the warbler's breeding range in central Texas 1995–1997

		Sex and age						Time of season			
		Male		Female		Juvenile		Early		Late	
Behavior	Height zone	#	%	#	%	#	%	#	%	#	%
Non-foraging[a,b]	Low	**18**	**1**	**15**	**6**	**6**	**3**	**16**	**2**	**11**	**2**
	Mid	**148**	**7**	**44**	**16**	**19**	**10**	**70**	**7**	**61**	**12**
	High	**1913**	**92**	**211**	**78**	**173**	**87**	**962**	**92**	**420**	**85**
Foraging[b]	Low	**9**	**2**	**17**	**7**	**2**	**3**	**13**	**3**	**9**	**5**
	Mid	**65**	**12**	**29**	**12**	**14**	**21**	**33**	**8**	**41**	**23**
	High	**478**	**87**	**194**	**81**	**52**	**76**	**347**	**88**	**132**	**73**

[a] Warbler behavioral observations include pair bonding, vocalizations, locomotion, resting, maintenance, and out of sight

[b] Bold numbers indicate statistical significance by sex, age, or time of season

time of new leaf growth for oak species (Frankie *et al.*, 1979). During this period, Lepidopteran larvae density is greater on oak species than on Ashe juniper (Quinn, 2000; Marshall *et al.,* 2013). By May, the density of Lepidopteran larvae on Ashe junipers increases three-fold (Marshall *et al.*, 2013), corresponding to a period when many adult warblers are caring for young (Pulich, 1976; Ladd and Gass, 1999).

TABLE 4.— Number (#) and relative proportion (%) of golden-cheeked warbler (*Setophaga chrysoparia*) behavioral observations per primary tree species by sex, age, and time of season at six sites surveyed across the warbler's breeding range in central Texas, 1995–1997

		Sex and age						Time of season			
		Male		Female		Juvenile		Early		Late	
Behavior	Tree species[a]	#	%	#	%	#	%	#	%	#	%
Non-foraging[a,b]	*Juniperus ashei*	704	35	108	41	93	48	**299**	**29**	**225**	**48**
	Quercus buckleyi	392	19	45	17	14	7	**280**	**28**	**47**	**10**
	Q. fusiformis/glaucoides	645	32	65	25	49	26	**302**	**30**	**115**	**25**
	Ulmus crassifolia/americana	143	7	18	7	6	3	**74**	**7**	**31**	**7**
	Q. sinuata	59	3	12	5	16	8	**33**	**3**	**14**	**3**
	Fraxinus texensis	44	2	6	2	0	0	**21**	**2**	**4**	**1**
	Juglans major	26	1	7	3	14	7	**5**	**0**	**33**	**7**
Foraging[b]	*Juniperus ashei*	156	29	82	35	29	45	**95**	**25**	**84**	**49**
	Q. buckleyi	118	22	43	19	5	8	**104**	**28**	**12**	**7**
	Q. fusiformis/glaucoides	172	32	66	29	18	28	**113**	**30**	**34**	**20**
	Ulmus crassifolia/americana	43	8	18	8	1	2	**43**	**11**	**11**	**6**
	Q. sinuata	16	3	8	3	5	8	**15**	**4**	**6**	**3**
	Fraxinus texensis	9	2	2	1	0	0	**6**	**2**	**0**	**0**
	Juglans major	16	3	12	5	6	9	**1**	**0**	**26**	**15**

[a] Warbler behavioral observations include pair bonding, vocalizations, locomotion, resting, maintenance, and out of sight

[b] Bold numbers indicate statistical significance by sex, age, or time of season

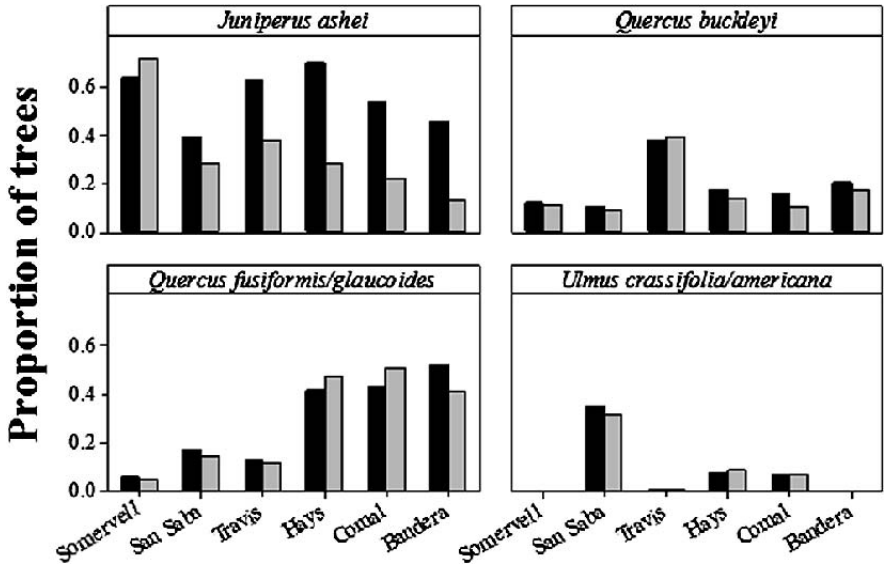

FIG. 3.—Proportion of tree species within occupied habitat (black bars) and proportion of tree species used by golden-cheeked warblers (*Setophaga chrysoparia*) for foraging (gray bars) at six sites surveyed across the warbler's breeding range in central Texas. We collected data from Travis and Hays counties in 1995 and from all sites in 1996 and 1997

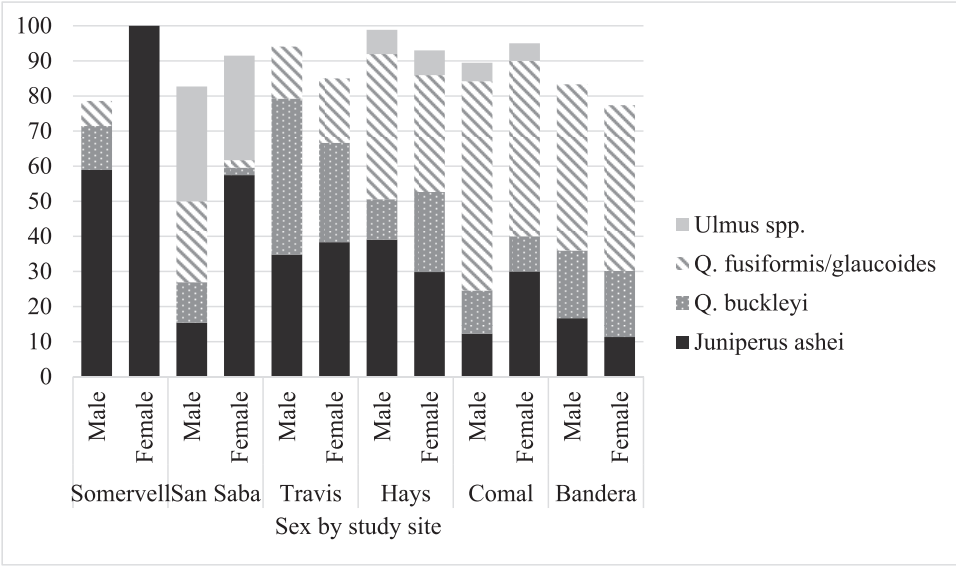

FIG. 4.—Percentage of most used tree species for foraging by male and female golden-cheeked warblers (*Setophaga chrysoparia*) at six sites surveyed across their breeding range in central Texas. We collected data from Travis and Hays counties in 1995 and from all sites in 1996 and 1997

Food availability may also influence variation in behavior and tree species use by geographic location. Males at Bandera were less vocal and spent more time foraging than males at other locations. Birds in areas with low food availability often display increased movement compared to other areas (Hutto, 1990), and warblers at Fort Hood moved more frequently when foraging at sites with lower arthropod density than warblers at sites with greater arthropod density (Marshall *et al.*, 2013). Thus, limited food resources may explain the between-site variability we observed; however, additional research is needed to assess food availability across the warbler's breeding range.

As predicted, males and females use tree species differently across their breeding range. This trend is consistent with Beardmore (1994) who found that females foraged more on Ashe juniper, and males more on live oak. In contrast, however, our results indicate this tendency was not consistent across sites. Overall, we observed warblers using Ashe juniper most often followed by live oak and Texas oak, but warblers at most sites used Ashe juniper considerably less than it was available within their territories. This is somewhat consistent with Sexton (1987) who reported that Ashe juniper was the most abundant tree species in his study area, but warblers only used it for foraging approximately 17% of the time and instead preferred to forage in live oak. Beardmore (1994) also noted greater use of live oak for both foraging and nonforaging behaviors. Our results indicate that warbler use of Ashe juniper varied considerably across their range. Our study encompassed more of the warbler's breeding range than either Sexton (1987) or Beardmore (1994), and variation in tree species composition between our sites may explain the differences we observed in tree species use compared to previous studies.

We predicted that warblers would use the same tree species for foraging at each of our sites relative to the availability of tree species within their territories. Notably, however, warblers used Ashe juniper for foraging much more in proportion to its availability at Somervell than at other locations. Although the availability of Texas oak in occupied habitat at our Somervell site was comparable to other sites, live oak was less abundant than at other locations. The lack of this substrate within occupied habitat, especially early in the season, may explain the greater use of Ashe juniper by warblers at this site.

Male warblers at our sites used tree species more equitably than females throughout the season for all behaviors, perhaps because oaks and junipers both provide adequate singing perches. Several species of female warblers center their activities nearer to the nest, which they incubate alone (Morrison, 1982; Franzreb, 1983; Holmes, 1986). Ashe juniper is the most common nesting substrate for golden-cheeked warblers (Ladd and Gass, 1999; Reidy and Thompson, 2012), so greater use of this substrate by females is not surprising.

Male warblers spend the majority of their time singing from the tops of the trees to be more conspicuous while maintaining and defending territories, especially early in the season (Pulich, 1976; Ladd and Gass, 1999). Similar to cerulean warblers (*Setophaga cerulea*), golden-cheeked warblers at our sites increased their use of lower height classes for foraging later in the season but continued to use the highest class for non-foraging behaviors (Barg *et al.*, 2006; Wood and Perkins, 2012). The shift from higher to lower height may be due to a greater abundance of arthropods or their larvae in the lower canopy later in the season (Holmes and Schultz, 1988; Ticehurst and Yendol, 1989; Quinn, 2000).

CONSERVATION IMPLICATIONS

Current management guidelines focus on the importance of canopy cover and the presence of mature Ashe juniper for high quality warbler habitat (Campbell, 2003). Our research indicates Ashe juniper is an important foraging substrate across the warbler's

breeding range. However, live, Lacey, and Texas oak are also important foraging substrates, especially early in the breeding season. Active management should focus on maintaining or increasing a mix of oak species within warbler habitat and account for the variation across the breeding range. Although warblers used the highest height classes most often, we observed increased use of the lower height classes later in the season when many warblers are caring for young. Research is needed to determine if management practices that alter vegetation in the lower height classes (*e.g.*, understory thinning) impact adult and juvenile survival.

Acknowledgments.—We thank D. Riskind, M. Lockwood and many park superintendents of the Texas Parks and Wildlife Department, C. Abbruzzese of the City of Austin, P. Sunby, S. Paulson, and private landowners for providing access to our sites. B. Archer, M. Bailey, D. Booher, J. Brawner, C. Chisum, K. Couch, G. Oliver, K. Newcomb, A. Sugeno, D. Sugeno, D. Ricks, and D. Thompson provided field assistance; we are grateful for their contributions to this project. We thank D. Booher and P. Lee for help with data management. We also thank Drs. K. A. Arnold, R. D. Slack, W. E. Grant, F. E. Smeins, J. A. Butcher, and B. Collier as well as D. Robinson for their helpful comments on earlier drafts of this manuscript.

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SUBMITTED 5 JUNE 2015 ACCEPTED 8 MARCH 2016