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Source: The Condor, 115(4):882-892. 2013.
Published By: Cooper Ornithological Society
URL: http://www.bioone.org/doi/full/10.1525/cond.2013.130013

The Condor 115(4):882–892

TREE SPECIES COMPOSITION AND FOOD AVAILABILITY AFFECT PRODUCTIVITY OF AN ENDANGERED SPECIES: THE GOLDEN-CHEEKED WARBLER

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Abstract. Vegetation characteristics affect avian reproductive success for a variety of reasons, including predators, nesting sites, song perches, and food availability. We investigated the relationship between habitat composition and prey availability and the effect these variables have on reproductive success in the Golden-cheeked Warbler (*Setophaga chrysoparia*). Our objectives were to determine differences in pairing and fledging success of Golden-cheeked Warbler territories in two distinctive vegetation types and to explore the relationship between reproductive success and tree species composition, arthropod density, and foraging effort. We sampled in 2009 and 2010 at Fort Hood, north-central Texas, within 347 territories of two vegetation types: post oak (*Quercus stellata*) habitat and Texas oak (*Q. buckleyi*) habitat. Pairing and fledging success of territories was significantly higher in Texas oak habitat. The birds' rate of movement was considerably higher in post oak habitat, indicating a difference in prey-encounter rate. Golden-cheeked Warblers clearly switched substrates on which they foraged from oaks in April to juniper in May. Arthropod sampling revealed a correlation between preferred foraging substrates and arthropod density. Our study of foraging indicates that the interplay between tree species and the arthropod communities they support is a crucial element driving the Golden-cheeked Warbler's reproductive success.

Key words: foraging, food availability, movement rate, ecological site, Golden-cheeked Warbler, Setophaga chrysoparia.

La Composición de Especies de Árboles y la Disponibilidad de Alimentos Afectan la Productividad de una Especie en Peligro: *Setophaga chrysoparia*

Resumen. Las características de la vegetación afectan el éxito reproductivo de las aves por una variedad de razones, incluyendo depredadores, sitios de nidificación, perchas para canto y disponibilidad de alimentos. Investigamos la relación entre la composición del hábitat y la disponibilidad de presas y el efecto que estas variables tienen sobre el éxito reproductivo de *Setophaga chrysoparia*. Nuestros objetivos fueron determinar diferencias en el éxito de emparejamiento y de emplumamiento de los territorios de *S. chrysoparia* en dos tipos distintivos de vegetación y explorar la relación entre el éxito reproductivo y la composición de especies de árboles, la densidad de artrópodos y el esfuerzo de forrajeo. Muestreamos en 2009 y 2010 en Fort Hood, norte centro de Texas, dentro de 347 territorios de dos tipos de vegetación: hábitat de *Quercus stellata* y hábitat de *Q. buckleyi*. El éxito de emparejamiento y de emplumamiento de los territorios fue significativamente más alto en el hábitat de *Q. buckleyi*. La tasa de movimiento de las aves fue considerablemente más alta en el hábitat de *Q. stellata*, indicando una diferencia en la tasa de encuentro de presas. *S. chrysoparia* claramente cambió de substrato de forrajeo desde los robles en abril a los enebros en mayo. El muestreo de artrópodos reveló una correlación entre los substratos de forrajeo preferidos y la densidad de artrópodos. Nuestro estudio de forrajeo indica que la interacción entre las especies de árboles y las comunidades de artrópodos que soportan es un elemento crucial que conduce el éxito reproductivo de *S. chrysoparia*.

INTRODUCTION

Researchers have reported regional population declines and local extirpations of neotropical migrant birds (Sauer and Droege 1992, Keller and Yahner 2006). Many studies have focused on fragmentation and patch size (Wilcove et al. 1986, Robinson and Wilcove 1994, Burke and Nol 1998) and changes in woody cover (Grubb et al. 1997, Trzcinsky 1999) as reasons for these declines. These are important issues at broad scales, but there has been less focus on the importance of tree species composition in relation to avian productivity at more local scales. Vegetation composition has implications for selection of habitat, including nest sites, foraging areas, roosting sites, and song perches (Sedgwick and Knopf 1992). Some warblers, such as the Black-throated Blue Warbler (*Setophaga caerulescens*) and Townsend's Warbler (*S. townsendi*), appear to use a hierarchical decision process, selecting a patch first on the basis of nesting habitat and second on the basis of foraging habitat within a patch (Steele 1993, Matsuoka et al. 1997).

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The Condor, Vol. 115, Number 4, pages 882–892. ISSN 0010-5422, electronic ISSN 1938-5129. © 2013 by The Cooper Ornithological Society. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, http://www.ucpressjournals.com/reprintInfo.asp. DOI: 10.1525/cond.2013.130013

Food availability affects birds' foraging behavior and consequently their reproductive success. Models of foraging strategies (McNamara and Houston 1987, Werner and Anholt 1993, Olsson and Holmgren 1999) predict that animals in food-rich environments should spend less time foraging than those in poor environments. Given expected trade-offs between foraging and other activities, spatial variation in prey abundance is likely to influence not only birds' abundance and distribution among habitats, but also their reproductive success within a habitat (Lyons 2005). Therefore, assessment of differences in food supply between habitats may yield insights into habitat quality (Lyons 2005), where quality is defined as the relative difference in reproductive success between locations (Morrison and Hall 2002). Areas where insects are abundant may serve as profitable foraging areas by reducing search effort (Blake and Hoppes 1986). For instance, territory size has been related to habitat productivity (Kuitunen and Helle 1988). Specifically, there appears to be an inverse relationship between territory size and resource availability, and birds have been shown to adjust territory size on the basis of resource availability (Smith and Shugart 1987).

Listed as endangered by the U.S. Fish and Wildlife Service, the Golden-cheeked Warbler (*S. chrysoparia*) depends on Ashe juniper (*Juniperus ashei*) for nesting material and mature juniper–oak (*Quercus* spp.) woodlands for breeding habitat (Pulich 1976, Ladd and Gass 1999, DeBoer and Diamond 2006, Magness et al. 2006). The areas in which it occurs vary in tree species composition, and previous research on other avian insectivores suggests that the structural diversity of vegetation is positively correlated with insect productivity (Webb 1989, Tye 1992).

Theoretically, when migratory birds such as the Golden-cheeked Warbler arrive on their breeding grounds, they must assess current and future food supply quickly. for An insectivore likely finds direct assessment of a complex food supply difficult (Tye 1992), so it might assess a potential territory by features correlated with food supply such as vegetation structure, foliage density, or tree species composition (Smith and Shugart 1987, Tye 1992). This would be especially important for a species such as the Golden-cheeked Warbler that returns from migration in early to mid-March when regrowth of the leaves of many deciduous plants is only beginning and cold temperatures are still prevalent, making a direct assessment of arthropods improbable. The size of Golden-cheeked Warbler territories appears inversely related to reproductive success (Coldren 1998), suggesting reproductive success is based on food availability and opportunities for foraging. Thus it is plausible that Golden-cheeked Warblers may select territories on the basis of their potential.

Golden-cheeked Warblers occupy patches of juniper–oak woodland consisting of a variety of plant associations broadly defined by ecological features of the site and soil. An ecological site is defined as a kind of land with a specific potential natural community and specific physical characteristics, differing from other kinds of land in its ability to produce vegetation and to respond to management (Society for Range Management 1989). At a local scale, it can be assumed that climate is more or less uniform, so variation in growing conditions is related mainly to differences in physical factors such as soil texture, soil moisture, and topography (Society for Range Management 1989). Two ecological sites in which Golden-cheeked Warblers occur commonly are redlands and low stony hill, which differ markedly in their plant communities. The main difference between these ecological sites lies in the deciduous component: the low stony hill is dominated by Texas oak, whereas the redlands are dominated by post oak. Thus we refer to low stony hill as Texas oak habitat and redlands as post oak habitat. During a concurrent study (M. Marshall, unpubl. data) we found a disparity between these two vegetation types in the warbler's reproductive success, which was greater at Texas oak sites than at post oak sites. Because these plant communities differ markedly, their arthropod communities should differ markedly as well (Holmes and Schultz 1988). Food availability affects birds' foraging behavior (Lyons 2005), so differences in arthropod communities should result in differences in foraging behavior, and variation in foraging behavior can lead to variation in reproductive success.

Our objectives were to quantify differences in vegetation, determine differences in the warbler's pairing and fledging success, assess differences in the density and composition of arthropod communities, and compare the warbler's rates of foraging and movement between territories within Texas oak habitat and post oak habitat. We predicted that in Texas oak habitat pairing success, fledging success, and production of fledglings per successful territory should be greater than in post oak habitat, and that this difference should be tied to differences in food availability based on tree species composition. If there are major differences in reproductive success between vegetation types, and this difference is linked to food availability, our ability to make informed management decisions will increase substantially. Specifically, practices aimed at conservation, restoration, and enhancement of Golden-cheeked Warbler habitat could benefit from further clarification of what promotes high-quality habitat.

METHODS

STUDY SITES

Our study areas were located on Fort Hood, an 88 500-ha installation of the U.S. Army in central Texas within both Coryell and Bell counties. Fort Hood straddles the Cross Timbers and Southern Tallgrass Prairie ecoregions, near their junction with the Edwards Plateau ecoregion. Sixty-five percent of the land area is described as perennial grassland, and 31% as woodland (U.S. Army Land Condition Trend Analysis program, unpubl. data; Loechl et al. 2008).

Dominant tree species within Golden-cheeked Warbler habitat are Ashe juniper, Texas oak, post oak, and live oak (*Q. fusiformis*).

Our sampling unit was the territory. In 2009, we sampled within nine broad study areas, ranging in size from 103 to 410 ha, totaling 2179 ha. In 2010, we sampled one additional 275-ha area. We sampled patches within these study areas that contained both post oak and Texas oak habitats. These patches have been previously occupied by Golden-cheeked Warblers (M. Marshall, unpubl. data) and met criteria thought to be important for Golden-cheeked Warbler productivity: patches >30 ha (Butcher et al. 2010), canopy closure >50% (Campbell 2003), and stems of mature juniper stems ≥13 cm in diameter at breast height (dbh) (Campbell 2003). Using these criteria allowed us to assume that any biologically significant change in avian productivity reflected tree species composition and not small patch size, inadequate canopy cover, or lack of nesting materials. The vegetation (in terms of tree species composition by habitat type) in these areas was patchy, making use of discrete study sites inappropriate, so we sampled territories across the 10 broad study areas. Once we obtained the location of a Golden-cheeked Warbler (see below), we subsampled by randomly selecting territories in both habitat types within each broad study area. By spreading our sampling units across 10 large disconnected areas, we ensured replication sufficient to minimize the bias associated with site-specific confounding variables (e.g., different predator assemblages, landscape contexts, management regimes) that might be affecting warbler productivity. Complete stratified or random selection of study areas was not possible because of constraints imposed by military activities.

TERRITORY MAPPING AND PRODUCTIVITY

We used transect surveys within each of the 10 broad study areas to select Golden-cheeked Warblers for territory mapping and monitoring. Transect length varied from 400 m to 1.7 km, depending on the study area. We spaced transects systematically at least 75 m apart to cover the entire study area then defined points along the transects at 50-m intervals. At each point along a given transect, surveyors spent 2 min recording all singing male Golden-cheeked Warblers. We recorded the location of a male with a hand-held GPS device and estimated the direction and distance of neighboring Golden-cheeked Warblers. We restricted this distance to 150 m from a transect because the density of birds was high and we wanted to increase our spatial coverage rather than sample more birds in any particular study area. We mapped each Golden-cheeked Warbler territory detected in the study sites by taking GPS points in each territory once a week throughout the breeding season (March–June), which gave us ≥10 total visits for each territory. We recorded ≥15 points per male for all territories analyzed.

We recorded behavior in each territory by a modified version of the Vickery index (Vickery et al. 1992) to represent reproductive success in the territory, specifically males' pairing success and fledging success. The Vickery index is a method of estimating reproductive success that avoids potential biases associated with nest data collected nonrandomly, and it does not disrupt nesting, which is critically important in studies of rare or endangered species (Vickery et al. 1992). Each territory is ranked (1–5) on the basis of a specific reproductive behavior (1 = territorial male present ≥4 weeks; 2 = pair present; 3 = carrying of nest material observed; 4 = carrying of food by adult observed; 5 = fledgling sighted). Christoferson and Morrison (2001) and Rivers et al. (2003) tested the effectiveness of this index and were able to predict the correct level of reproductive activity 61–79% of the time.

We considered a male successfully paired if we detected a female within his territory for ≥4 weeks. We considered a territory reproductively successful if we located ≥1 fledgling within a territory. We calculated territory success as the number of territories with ≥1 fledgling relative to the total number of territories within each habitat type. We counted the number of fledglings found in each territory, which facilitated comparison of the mean number of fledglings found in both vegetation types and also further helped us assign reproductive success to specific territories we had delineated. Because this was a short-term study, we could not expend the effort necessary to color-band a large proportion of the breeding pairs. Therefore, we took care to ensure that we properly linked the outcome of breeding with a specific territory by visiting each territory repeatedly near the estimated time of fledging. If we could not determine the breeding status of a territory, we dropped that territory from the data set. In both 2009 and 2010, we dropped fewer than 5% of territories from the dataset because we were unable to link specific fledglings with a specific territory. Additionally, because we were comparing two vegetation types of similar structure (both mature oak–juniper woodland), we were confident in assuming that that detection of fledglings or females, and thus any error in identifying the outcome of reproduction in a territory, was similar in both types.

TREE SPECIES COMPOSITION

Using ArcGIS (ESRI 2005), we established territory boundaries by constructing minimum convex polygons around the collection of points (range 15−62 per territory) constituting a Golden-cheeked Warbler territory. To assess the vegetation composition of each territory, we established a systematic grid of points (range 11−182 per territory) spaced 20 m within the territory with the Hawth's tools extension in ArcGIS (ESRI 2005). At each point within a territory, we noted if any woody cover was directly overhead. On the basis of a previous study of arthropod sampling in Golden-cheeked Warbler habitat, we considered the canopy to be any vegetation ≥2 m above ground (Butcher et al. 2010). If woody cover at a point was ≥2 m in height, we estimated canopy cover visually to the nearest 10%, identified the species of trees, and estimated vegetation height to the nearest 0.5 m by looking straight up through a tubular densitometer.

To estimate canopy cover within a territory, we averaged the estimates of canopy cover at each sampling point. To estimate tree species composition within a territory, we calculated percent abundance of the six dominant tree species at our study sites (Texas oak, live oak, post oak, shin oak, Texas ash, and Ashe juniper) as the proportion of each species with respect to the total number of tree species in a territory.

FORAGING SURVEYS

We estimated the warblers' foraging effort and movement rate and identified their foraging substrates throughout the breeding season. We observed foraging in a randomly selected subsample of territories (4–15 territories per study area) in each vegetation type in mid-April when all the males and females had arrived and settled and another in mid-May when the first nest of the season had been attempted in a majority of territories and many pairs had fledged young. Because there were three times more territories in the Texas oak habitat than in the post oak habitat, we sampled all territories within the post oak habitat. We determined the number of territories within Texas oak habitat to sample within each study area by dividing the number of Golden-cheeked Warblers in Texas oak habitat in the study area by the total number of Golden-cheeked Warblers across all study areas and multiplied this proportion by the total number of territories sampled in the post oak habitat to ensure equal sample sizes.

We entered previously mapped territories and observed the behavior of the first Golden-cheeked Warbler encountered. We recorded foraging only between 07:00 and 12:00. Once we detected a warbler, we watched it for 5 sec without taking data to minimize bias to the most conspicuous activities (Noon and Block 1990, Keane and Morrison 1999). We observed the bird for 3–6 min, recording observations continuously with a hand-held tape recorder. During this time we recorded the bird's sex, activity (e.g., perching, feeding, singing, short flight, long flight, preening), and foraging substrate. We estimated the bird's rate of movement during the observation by defining each flight as short (<2 m) or long (≥2 m). We chose the 2-m cutoff because flights of >2 m tended to be flights between trees, whereas flights of <2 m tended to be contained within a tree (pers. obs.).

ARTHROPOD SAMPLING

We sampled arthropods by clipping branches in the same territories in which we recorded foraging. We sampled three times during the breeding season, the first two within 2 days of foraging surveys between 07:00 and 12:00, with the intention of linking foraging behavior to food availability. We added a third sampling period in mid-June because we were interested in how the arthropod community changed during this time. We did not observe foraging in June because individuals and family groups moved beyond territory boundaries estimated earlier in the season.

We sampled trees for arthropods in the area generally delineated by an individual bird during the associated foraging survey. We established a systematic grid of points spaced by 10 m within each of these areas and randomly selected four points to sample for arthropods. At these four locations, we walked at a random bearing and sampled the first juniper or oak tree encountered by placing a trash bag over the branch and cutting it off at its base. We sampled two Ashe juniper trees and two oak trees within each territory. In 2009 we limited our oak sampling to the two focal species, post oak and Texas oak. In 2010, we sampled the first oak species we encountered along the random bearing, which resulted in live oak and shin oak being represented in the overall sampling. We clipped four branches per tree, for a total of 16 branches clipped per territory per sampling period. On the basis of a previous study (Butcher et al. 2010) of arthropod assemblages in Golden-cheeked Warbler territories, we clipped branches approximately 2 m from the ground.

We stored clipped branches in a freezer for at least 1 week, then placed them in a plant drier for another week. After drying, we separated arthropods from branches and leaves and weighed the arthropods to the nearest 0.0001 gram and the leaves to the nearest 0.01 gram. We estimated arthropod density as the total weight of arthropods/total weight of the branch. In 2009, we compared total arthropod density in the two vegetation types. In 2010, we identified arthropods to order, which allowed us to make fine-scale comparisons in biomass between the 2 vegetation types, observe changes in arthropod assemblages through time and by tree species, and to link these changes to preferred foraging substrates.

STATISTICAL ANALYSIS

For analysis, we combined all data on tree species and canopy cover from 2009 and 2010 because we could assume that canopy vegetation within an ecosite did not change during our study and because there were no catastrophes such as fire, disease, or defoliation. We did, however, analyze all data on foraging, arthropods, and avian productivity for 2009 and 2010 separately because precipitation and temperature patterns in the two years were very different from each other and from the average (Fig. 1). We used a mixed-model analysis of variance (ANOVA) to compare the number of territories with pairs and successful reproduction by study site (random effects) and habitat type (fixed effects). We used a t-test to compare the mean number of fledglings per successful territory in the two habitat types (Zar 1999:663). Throughout we use the territory as the basis for reporting reproductive outcome because it was our sampling unit.

We tested for a relationship between fledging success (yes/no) and canopy cover with logistic regression (Zar 1996:317–330). We used a t-test to compare mean tree species composition by habitat type. We used logistic regression to test for a relationship between fledging success (yes/no)

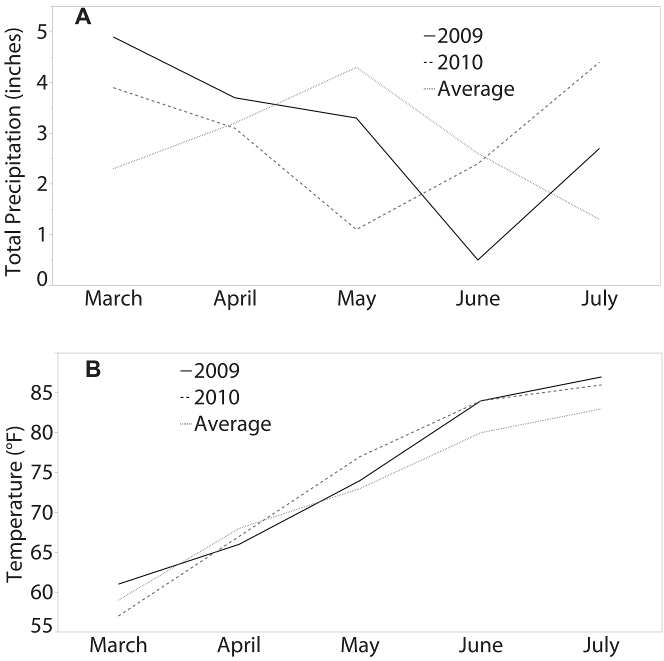

FIGURE. 1. Weather during the Golden-cheeked Warbler's breeding season in the Killeen/Fort Hood area of central Texas. (A) Monthly precipitation in 2009 and 2010 and annual average from 1950 to 2011. (B) Mean monthly temperature in 2009 and 2010 and mean annual temperature from 1950 to 2011.

and percentage of Texas oak within a territory with fledging success as a dependent binary variable and percent Texas oak within a territory as the independent variable.

We calculated a Golden-cheeked Warbler's rates of foraging and movement in its territory by dividing the time spent engaged in foraging and flight by the total time observed. We used mixed-model ANOVAs to compare mean rates of foraging (number of foraging bouts/total time observed), singing (number of singing bouts/total time observed), and movement (number of short and long flights/time) by study site (random effects) and habitat type (fixed effects). To quantify a switch in foraging substrates across the season, we compared the total number of times a warbler was observed foraging on juniper or oak for April and May separately. We used a factorial ANOVA to evaluate use versus availability for foraging behavior by vegetation type for four focal tree species (juniper, live oak, post oak, and Texas oak), by sampling period and year (Zar 2010:265–269). We investigated the link between foraging and movement rates and Texas oak composition within a territory by running a general linear model with the 2010 data that removed sources of variation in the following order: percent Texas oak, sampling period, and percent Texas oak × sampling period (Zar 2010:265–269).

We calculated an average density of arthropods within a territory by taking an average for all trees sampled within that territory during a particular sampling period. We used a mixed-model ANOVA to compare total arthropod density by study site (random effects) and habitat type (fixed effects). For the 2010 data, we used *t*-tests to compare density of all arthropod orders by vegetation type. We used a factorial ANOVA (Zar 2010:265–269) to compare densities of particular arthropod orders in each tree species by sampling period. For all multiple comparisons we used Tukey's range test to find means that were significantly different from each other (Zar 1999:177–214). Values reported under Results are means ± SE. We set $\alpha = 0.05$ and ran all analyses in JMP statistical software (SAS Institute 2007).

RESULTS

TERRITORY MAPPING AND PRODUCTIVITY

In 2009, we monitored 154 Golden-cheeked Warbler territories, 115 in Texas oak habitat, 39 in post oak habitat. We did not see a significant difference in the proportion of territories with pairs among study sites ($\chi^2_8 = 15.19$, $P = 0.06$) or between the two habitat types ($\chi^2_1 = 3.09$, $P = 0.08$). In the proportion of territories that fledged young, there was no significant difference among study sites ($\chi^2_8 = 7.95$, $P = 0.44$) but there was beteen the habitats ($\chi^2 = 6.98$, $P = 0.01$): fledging success was significantly higher in Texas oak habitat (Fig. 2). In 2010, we monitored 194 Golden-cheeked Warbler territories, 128 in Texas oak habitat, 66 in post oak habitat. Again, we saw no significant difference in the proportion of territories with pairs among study sites ($\chi^2_9 = 7.48$, $P = 0.59$) or between the two habitats ($\chi^2_1 = 1.71$, $P = 0.19$). And again there was no significant difference among study sites in the proportion of territories that fledged young ($\chi^2_9 = 4.38$, $P = 0.89$) but there was between the habitat types ($\chi^2_1 = 4.65$, $P = 0.03$): fledging success was again significantly higher in Texas oak habitat (Fig. 2).

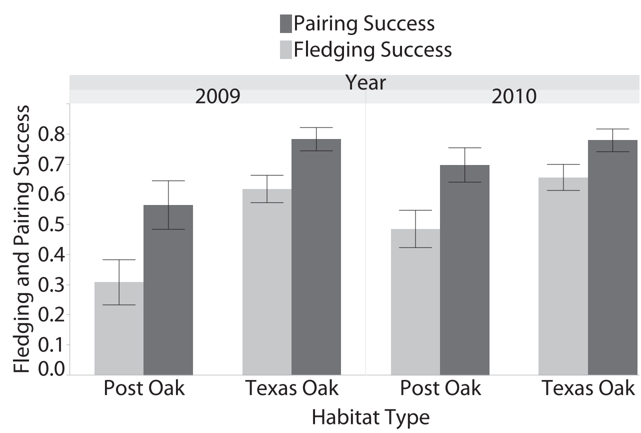

FIGURE 2. Rates of success at pairing and fledging for Golden-cheeked Warbler territories within Texas oak and post oak habitats on Fort Hood, Texas, in 2009 and 2010.

Territories in Texas oak habitat produced an average of 1.9 ± 0.1 and 2.1 ± 0.1 fledglings per successful territory, and territories in post oak habitat produced an average of 2.0 ± 0.2 and 2.1 ± 0.1 fledglings per successful territory, in 2009 and 2010, respectively; these differences were not significant for 2009 ($t_1 = 0.22$, $P = 0.73$) or 2010 ($t_1 = 0.06$, $P = 0.81$).

TREE SPECIES COMPOSITION

We did not find a significant difference in canopy cover among study sites ($F_{9,144} = 0.43$, $P = 0.92$) or between habitat types ($F_{9,144} = 0.94$, $P = 0.33$). Regardless of habitat type, canopy cover was not a useful predictor of whether a territory successfully fledged young ($\chi^2_1 = 0.87$, $P = 0.73$).

Territories in Texas oak habitat had significantly more Texas oak ($t_1 = 3.41$, $P < 0.01$) and juniper ($t_1 = 3.47$, $P < 0.01$) than did those in post oak habitat, while the post oak habitat had significantly more post oak ($t_1 = 6.00$, $P < 0.01$) and live oak ($t_1 = 2.37$, $P = 0.02$) than did Texas oak habitat (Table 1). Because of the apparent importance of Texas oak as a foraging substrate (see Foraging Surveys below), we tested for a link between fledging success and Texas oak composition within a territory. Although the average proportion of Texas oak was higher within territories that successfully fledged young (unsuccessful = 8%; successful = 10%), the proportion of Texas oak in a territory was not a good predictor of whether a territory fledged young ($\chi^2 = 0.98$, $P = 0.54$).

FORAGING SURVEYS

In 2009, we did not find any significant differences among study sites in the four behaviors (Table 2), and the only significant differences in foraging behavior between the habitat types were in the mean rate of long flights in May ($F_{1,43} = 5.31$, $P = 0.03$) and the mean rate of singing in April ($F_{1,43} = 5.17$, $P = 0.03$). In post oak habitat, warblers were engaged in long flights in May 10% more often, on average, than were those in Texas oak habitat. In April, male warblers in post oak habitat sang only 2% more than males in Texas oak habitat, likely making this statistically significant result biologically uninformative. In 2010, we found no significant differences in foraging behavior between study sites (Table 2), but there was a significant difference between habitat types in the May foraging rate ($F_{1,89} = 5.43$, $P = 0.02$). Warblers in territories established in Texas oak habitat foraged, on average, 22% more frequently in May than did warblers in post oak habitat.

Golden-cheeked Warblers' use of foraging substrates changed through the breeding season in 2009 and 2010. The birds did not forage on juniper ($F_{4, 267} = 11.05$, $P < 0.05$), live oak ($F_{4, 267} = 6.30$, $P < 0.05$), Texas oak ($F_{4,267} = 2.95$, $P < 0.05$), or post oak ($F_{4,267} = 4.65$, $P < 0.05$) in proportion to their availability (Fig. 3). In April of 2009, those in Texas oak habitat foraged in juniper 40% less than expected from its availability, and use of Texas oak was 130% greater than expected. In May of 2009, warblers in Texas oak habitat switched to juniper as the main foraging substrate, using it 40% more than expected from its availability. In April of 2009, Golden-cheeked Warblers in post oak habitat foraged in juniper 70% less than expected from its availability, in live oak 120% more than expected, and in Texas oak 130% more than expected. In May of 2009, warblers in post oak habitat also switched to juniper as their main foraging substrate,

TABLE 1. Average percent composition of four common tree species within Golden-cheeked Warbler territories on Fort Hood, Texas, by vegetation type. Values are mean s± SE. Sample size (*n*) ia the number of territories analyzed for each vegetation type.

Tree	Texas oak habitat ($n = 79$)	Post oak habitat ($n = 76$)
Juniper	60 ± 1.89	51 ± 1.70
Texas oak	12 ± 1.30	6 ± 0.97
Post oak	3 ± 0.91	15 ± 1.85
Live oak	9 ± 1.18	13 ± 1.02

TABLE 2. Activity budget for Golden-cheeked Warblers in Texas oak and post oak habitats on Fort Hood, Texas, 2009 and 2010. Values represent the proportion of each activity with respect to the total observation time and are means ± SE. Proportions do not sum to 1 because loafing/scanning and preening were not included in activities.

	Texas oak	Post oak	Test statistic	*P*
2009				
n	34	18		
Short flight, April	0.051 ± .008	0.051 ± .012	$F_{1,43} = 0.07$	0.79
Short flight, May	0.053 ± .008	0.068 ± .011	$F_{1,43} = 1.99$	0.17
Long flight, April	0.015 ± .002	0.018 ± .003	$F_{1,43} = 0.46$	0.50
Long flight, May	0.016 ± .002	0.026 ± .003	$F_{1,43} = 5.31$	0.03
Singing, April	0.066 ± .005	0.084 ± .007	$F_{1,43} = 5.17$	0.03
Singing, May	0.065 ± .006	0.060 ± .009	$F_{1,43} = 0.13$	0.72
Foraging, April	0.029 ± .004	0.034 ± .006	$F_{1,43} = 0.67$	0.42
Foraging, May	0.039 ± .008	0.036 ± .011	$F_{1,43} = 0.39$	0.53
2010				
n	51	53		
Short flight, April	0.068 ± .009	0.064 ± .009	$F_{1,93} = 0.01$	0.92
Short flight, May	0.136 ± .014	0.113 ± .014	$F_{1,93} = 0.50$	0.48
Long flight. April	0.022 ± .003	0.021 ± .003	$F_{1,93} = 0.02$	0.90
Long flight, May	0.026 ± .004	0.024 ± .004	$F_{1,93} = 2.97$	0.09
Singing, April	0.088 ± .008	0.087 ± .007	$F_{1,93} = 0.02$	0.89
Singing, May	0.070 ± .006	0.069 ± .005	$F_{1,93} = 0.18$	0.67
Foraging, April	0.009 ± .003	0.013 ± .003	$F_{1,93} = 1.58$	0.21
Foraging, May	0.034 ± .006	0.012 ± .006	$F_{1,93} = 5.43$	0.02

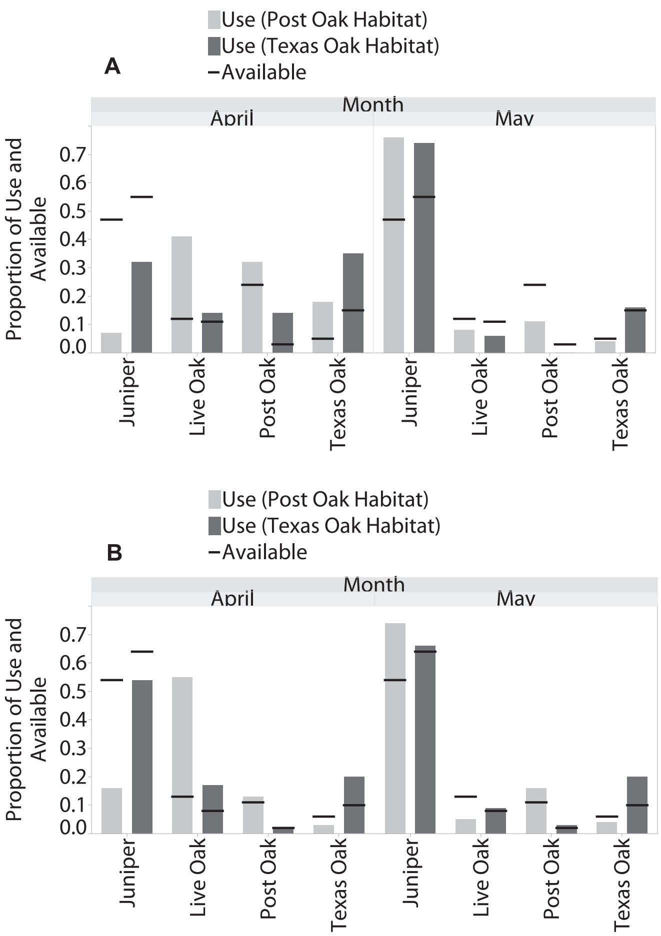

FIGURE. 3. Use vs. availability for four substrates on which Golden-cheeked Warblers forage commonly at Fort Hood, Texas, in Texas oak and post oak habitats in (A) 2009 and (B) 2010. Use represents the proportion of observations of foraging by tree species. Available represents the percentage of that tree species within a territory.

using it 58% more than expected from its availability, and using post oak 54% less than expected.

In April of 2010, Golden-cheeked Warblers in Texas oak habitat foraged in juniper 16% less than expected from its availability, and use of Texas oak increased 100% above the proportion expected from availability. In May of 2010, warblers in Texas oak habitat switched to juniper as their main foraging substrate, using it in proportion to its availability. In April of 2010, Golden-cheeked Warblers in post oak habitat foraged in juniper 70% less than expected, and use of live oak increased 320% above what was expected from that species' availability. In May of 2010, warblers in post oak habitat again switched to juniper as their main foraging substrate, using it 37% more than expected.

We investigated the link between proportion of Texas oak within a territory and rates of foraging and movement. The proportion of Texas oak within a territory by sampling period was not a good predictor of number of long flights ($R^2_{adj} = 0.01$, $P = 0.45$). The associations of foraging rate ($R^2_{adj} = 0.07$, $P < 0.01$) and number of short flights ($R^2_{adj} = 0.14$, $P < 0.01$) were statistically significant but had low explanatory power. For number of short flights, sampling period accounted for much of the variation between groups. Specifically, in May, the proportion of Texas oak within a territory was significantly related to the number of short flights ($R^2_{adj} = 0.07$, $P = 0.03$). In April, Golden-cheeked Warblers foraging in territories with a high proportion of Texas oak engaged in more short flights than did those foraging in territories with a low percentage of Texas oak.

ARTHROPOD SAMPLING

In 2009 we sampled arthropods on three focal tree species within 12 territories in Texas oak habitat and 10 territories in post oak habitat (Table 3). The total density of arthropods did not differ significantly by study site ($F_{3, 976} = 1.46$, $P = 0.23$) or habitat ($F_{3, 976} = 1.93$, $P = 0.16$). In 2010, we sampled arthropods in 20 territories in Texas oak habitat and 20 in post oak habitat (Table 3). Again, the total density of arthropods did not differ significantly by study site ($F_{9, 1903} = 0.79$, $P = 0.63$) or habitat ($F_{1, 1903} = 0.40$, $P = 0.53$). In both vegetation types, the density of arthropods in juniper was low at the beginning of the season, then increased through the next two sampling periods. The density of arthropods on oak species started out high, relative to juniper, then became more variable during the later sampling periods.

There were no significant differences between the two habitats in density of arthropods when analyzed by order (Table 4), although the densities of Coleoptera ($F_{5, 1903} = 4.16$, $P < 0.01$), Homoptera ($F_{5, 1903} = 3.48$, $P < 0.01$), and Lepidoptera ($F_{5, 1903} = 2.69$, $P = 0.02$) differend significantly on different tree species (Fig. 4). Samples of live oak, shin oak, and Texas oak all had a similar proportion of arthropod orders. A majority of the arthropods found on Texas oak were Lepidoptera, whereas post oak had many fewer Lepidoptera and many more Coleoptera and Homoptera (Fig. 4).

The density of arthropod orders ($n = 13$) changed through the breeding season on different tree species ($F_{13, 1903} = 2.12$, $P = 0.01$; Fig. 5). In April, when warblers were foraging mainly on oaks, live oak had a significantly higher density of arthropods ($F_{5, 633} = 2.66$, $P = 0.01$), especially of the order Lepidoptera ($F_{5, 633} = 2.69$, $P = 0.01$). In Texas oak habitat, warblers foraged at a high rate on Texas oak during April but used live oak in proportion to its availability (Fig. 3). In post oak habitat, warblers did not forage at a high rate on post oak but instead used live oak at a rate much higher than expected from its availability (Fig. 3).

We found a few significant increases in arthropods during the May sampling period (Fig. 5). From April to May, the density of Lepidoptera on Texas oak increased ninefold. At this time, warblers in both vegetation types used Texas oak in proportion to its availability but started foraging on juniper

TABLE 3. Density of arthropods in Golden-cheeked Warbler territories on Fort Hood, Texas, by vegetation type in 2009 and 2010. Values refer to the density of arthropods on focal tree species in three periods of sampling. Value in parentheses is the sample size, and refers to the number of branches sampled.

	Texas oak habitat			Post oak habitat		
	April	May	June	April	May	June
2009						
Juniper	0.016 (90)	0.220 (75)	0.350 (77)	0.022 (79)	0.150 (71)	0.400 (81)
Post oak	0.075 (18)	0.370 (7)	0.00 (4)	0.650 (65)	0.780 (68)	0.230 (74)
Texas oak	0.029 (71)	0.240 (66)	0.040 (76)	0.162 (7)	0 (4)	0.004 (4)
2010						
Juniper	0.0120 (153)	0.076 (151)	0.130 (151)	0.017 (169)	0.100 (169)	0.429 (167)
Live oak	0.341 (23)	0.114 (24)	0.297 (24)	2.364 (60)	0.293 (40)	0.118 (48)
Post oak	0.287 (12)	0.00 (8)	0.012 (4)	0.357 (41)	0.349 (71)	0.717 (64)
Shin oak	0.346 (43)	0.269 (57)	0.412 (52)	0.408 (24)	0.044 (19)	0.072 (24)
Texas oak	0.209 (72)	0.686 (63)	0.867 (72)	0.050 (39)	1.517 (33)	0.096 (32)

at a disproportionately high rate. In April, juniper was nearly devoid of arthropods, but by May the numbers of Lepidoptera had increased by factor of 3 and those of Homoptera by a factor of 20. Compared to other tree species, juniper had the highest density of Homoptera in May ($F_{5, 629} = 3.67, P < 0.01$), the same month warblers foraged proportionally more on juniper.

DISCUSSION

As we hypothesized, warblers that occupied territories within Texas oak habitat had substantially higher breeding success than those that occupied territories dominated by post oak, and success was based on success at fledging, not on number of fledglings. Because the proportion of territories that

TABLE 4. Density of arthropod orders within Golden-cheeked Warbler territories on Fort Hood, Texas, by habitat type in 2010. Values are the weight of arthropods/weight of clipped branch in milligrams. Data for all three sampling periods are combined; df = 1 for all tests.

Arthropod order	Texas oak	Post oak	t	P
Acarina	0.00104	0.00009	1.1407	0.2856
Araneida	0.01200	0.03000	0.8597	0.3539
Coleoptera	0.01400	0.02700	1.0849	0.2977
Diptera	0.00099	0.00089	0.0147	0.9035
Hemiptera	0.01500	0.01500	0.0006	0.9799
Homoptera	0.02400	0.05000	1.1780	0.2779
Hymenoptera	0.00105	0.00213	1.3797	0.2403
Isopoda	0.00073	0.00168	0.7013	0.4024
Lepidoptera	0.07200	0.16000	1.1181	0.2905
Mecoptera	0.00009	0.00019	0.2244	0.6358
Neuroptera	0.00014	0.00003	0.6080	0.4356
Orthoptera	0.08300	0.04100	0.8904	0.3455
Phalangida[a]	0	0.00004	0.9017	0.3424
Plecoptera[a]	0	0.00003	1.2250	0.2685
Spirobolida[a]	0	0.00666	4.4036	0.0360
Total	0.24900	0.40300	1.1701	0.2795

[a]No specimens for Texas oak habitat, and density values for post oak habitat are based on a single sample.

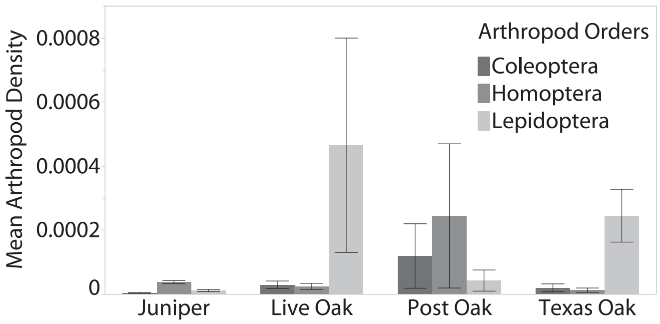

FIGURE 4. Mean density of three arthropod orders whose density differed significantly in six tree species sampled at Fort Hood, Texas, in 2010.

successfully fledged young was higher within Texas oak habitat but there were no statistically significant differences between Texas oak and post oak habitats in the average number of young fledged from successful territories, it seems that survival of nestlings is not the primary factor accounting for the difference in breeding success between the two habitats. Also, there were no significant differences in pairing success between the habitats, suggesting the disparity in breeding success was not due to the males' inability to pair successfully with a female. Because the warblers' rate of movement was higher in post oak habitat and Lepidoptera were more abundant in Texas oak habitat, we attribute the disparity in fledging success to differences in foraging behavior and arthropod abundance.

Alternatively, differences in predator guilds or differences between the habitats in predation rates could be a mechanism driving differences in fledging success. At Austin, Texas, and Fort Hood, Reidy et al. (2008) found that predation was the most frequent cause of nest failure and identified the rat snake *Elaphe obsoleta* as the warbler's primary nest predator. Future studies should compare predator guilds and snake densities in Texas oak and post oak habitat to clarify the mechanisms driving the disparities in reproductive success seen in our study.

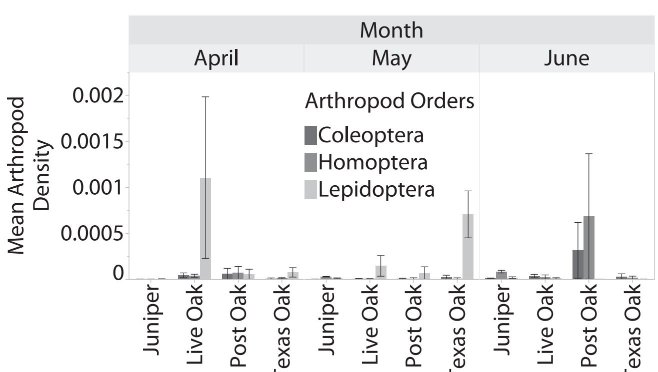

FIGURE 5. Phenology of three arthropod orders collected in Golden-cheeked Warbler territories over three periods of sampling at Fort Hood, Texas, in 2010.

It is likely that early arriving migratory insectivores such as the Golden-cheeked Warbler use tree species composition as a proxy for food availability because direct assessment of food supply is difficult. The availability of prey in the prebreeding season, during which females must accumulate reserves for eggs, is responsible for the breeding success of most insectivorous birds (Keast 1990, Tye 1992). Thus early arrival at the breeding grounds precludes any direct assessment of future food supplies, especially the food needed to provision nestlings (Smith and Shugart 1987, Tye 1992).

Because each tree species offers birds a differing set of opportunities for foraging, the mix of tree species at a site, coupled with the arthropod resources they support, influence reproductive success (Holmes and Schultz 1988). It is clear, however, that overall density of arthropods alone does not seem to be driving productivity of the Golden-cheeked Warbler. Rather, we found that the interplay between tree species and the arthropod communities they support is a crucial element driving the Golden-cheeked Warbler's reproductive success. We found that Texas oak was an important foraging substrate for Golden-cheeked Warblers, and it seemed that the more Texas oak there was in a territory, the less the bird had to move to find food. Texas oak also had a high density of lepidopteran larvae, indicating the Lepidoptera are important as a food source for Golden-cheeked Warblers during the breeding season. Perrins (1991) concluded that female Great Tits (*Parus major*) start breeding as soon as caterpillars are available and thus time their breeding to have their nestlings when caterpillars were most abundant. Pulich (1976) noted the close relation between the Golden-cheeked Warbler's schedule of breeding and the appearance of numerous lepidopteran larvae in deciduous trees such as Texas oak and shin oak. Also, most Golden-cheeked Warblers stop breeding in June, the same time that essentially all lepidopteran larvae have metamorphosed (M. Marshall, pers. obs.).

We found that juniper is a frequent substrate for foraging Golden-cheeked Warblers, especially later in the breeding season. Golden-cheeked Warblers foraged on juniper 20–30% more than expected from its availability in May, and use of juniper increased by as much as 70% from April to May. Thus management guidelines need to be modified for maintenance of juniper within warbler habitat, at least in our study region. The Natural Resources Conservation Service's "no take guidelines" for the Golden-cheeked Warbler, based on Campbell (2003), state that "juniper less than 15 feet tall, which exists under the canopy of mature juniper and hardwoods, may be removed." The restriction against removal of large juniper trees is based on the warbler's need for shredded juniper bark as a nesting material (i.e., only large juniper trees provide strips of bark sufficient for nest construction). We do not have data on the sizes of junipers in which warblers forage, but our study indicates juniper is an important foraging substrate, especially later in the breeding season. We suggest future studies investigate the role of juniper cover and height further as these variables relate to the Golden-cheeked Warbler's reproductive success. There may be a point at which a small change in juniper composition of an area produces large responses in this system, and identification of thresholds can lead to development of specific management practices, such as maintenance of a specific range of juniper composition (Denoel and Ficetola 2007).

Oak wilt is a tree disease caused by *Ceratocystis fagacearum* and is a common disturbance in warbler habitat (Appel and Camili 2010). In terms of numbers of trees, live oak is the species most severely affected by oak wilt, though red oaks such as Texas oak are also highly susceptible to the disease (Appel and Camili 2010). Oaks, particularly Texas oak and live oak, are important substrates for foraging warblers, especially during the early portion of the breeding season. Our study highlights the importance of oak wilt management, particularly in the context of foraging and arthropod availability. Because control of oak wilt can be quite expensive, we suggest land managers controlling for oak wilt direct their efforts at Texas oak habitat, where fledging success indicates high-quality habitat.

The importance of the phenology of vegetation on foraging behavior and food availability is well known (Holmes and Schultz 1988, Perrins 1991, Keane and Morrison 1999), but, to our knowledge, ours is the first study to link these factors to ecological sites. The main advantage of the ecological site as a proxy for vegetation composition is that it can be used easily by resource managers, whereas identification of plants through remote sensing is often difficult. On a broad spatial scale, the ecological site can be used to identify areas for targeted management and conservation goals. At a more local scale, the ecological site can be used to guide property-specific guidelines for tree retention. Additionally, tree species composition can be incorporated into management guidelines related to tree removal and planting (Morrison 2009:63–67).

If the ecological site can indicate areas of potentially high- and/or low-quality habitat, as it did in our study, managers can use this information to target areas for conservation on the basis of readily available GIS layers. In the context of restoration, the ecological site can aid in the selection of reference conditions. When reference conditions for a restoration project are selected, it is critically important that the reference sites in question be of similar ecological setting and have similar site-level structural characteristics (Merkey 2005). Many restoration projects derive these characteristics from regional measures such as the ecoregion and watershed (Merkey 2005), but an important limitation of regional classifications is that the scale may be too large for monitoring of restoration. Smaller, state-level ecosystem classifications can be useful in differentiating plant communities (Albert 1995, Merkey 2005). Our study revealed differences in tree species composition at such a scale (ecological site), and these differences were associated with differences in reproductive success.

ACKNOWLEDGMENTS

We thank the US Army Fort Hood for funding, and the research team at the Texas A&M Institute of Renewable Natural Resources for their guidance and logistical support. Specifically, we thank Brian and Amy Hays for help with housing, funding, access to study sites, and invaluable insight directly applicable to the project. J. Packard, S. Popescu, and two anonymous referees provided helpful review comments on earlier drafts. H. Mathewson and B. Collier provided invaluable assistance with statistical analysis and reviews on earlier drafts. We also thank the many field technicians for all of their hard work.

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