

EFFECTS OF TREE SPECIES COMPOSITION AND FORAGING EFFORT ON THE
PRODUCTIVITY OF GOLDEN-CHEEKED WARBLERS

A Thesis

by

MIKE E. MARSHALL

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of
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May 2011

Major Subject: Wildlife And Fisheries Sciences

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cheeked Warblers

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Approved by:

Chair of Committee,	Michael Morrison
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Major Subject: Wildlife Ecology

ABSTRACT

Effects of Tree Species Composition and Foraging Effort on the Productivity of Golden-Cheeked Warblers. (May 2011)

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Chair of Advisory Committee: Dr. Michael L. Morrison

The concept of habitat quality is fundamental to the study of ecology. Ecologists have long recognized the importance of vegetation structure and composition in the assessment of wildlife habitat. Vegetative characteristics affect productivity in birds for a variety of reasons (e.g., predator assemblages, nesting sites, song perches, food availability). This research investigated the relationship between habitat quality and prey availability and the effect these parameters have on reproductive success in golden-cheeked warblers (*Dendroica chrysoparia*). The objectives were to: 1) Determine any differences in pairing and fledging success of warbler territories within two ecosites exhibiting two distinctive tree species composition, 2) Explore the relationship between tree species composition, arthropod density, and foraging effort, and the effect these parameters have on reproductive success in golden-cheeked warblers, and 3) Investigate the connection between preferred foraging substrates and changes in arthropod abundance within golden-cheeked warbler territories throughout the breeding season. Individual warbler territories were mapped out and searched for fledglings, foraging behavior observed, and arthropods collected, to determine productivity, foraging effort,

and food availability. These methods were conducted over two seasons in juniper-oak woodlands on Fort Hood, north-central Texas within 347 territories of two vegetative types: those marked by the predominance of post oak (*Quercus stellata*) and those marked by the predominance of Texas oak (*Quercus buckleyi*).

Pairing and fledging success of territories differed substantially between the two vegetative types. Movement rates differed considerably between the two vegetative types, indicating a difference in prey encounter rate. Foraging data indicated a clear switch in preferred foraging substrates from oak species early in the breeding season, to Ashe juniper (*Juniperus ashei*) in mid-May. Arthropod sampling revealed a correlation between preferred foraging substrates and arthropod density. Results suggested that Texas oak was an important foraging substrate for golden-cheeked warblers, and territories that lack this tree species generally did not succeed in fledging young. This study can be used to indicate areas that should be targeted for conservation by local, state, and federal government because they provide high quality habitat based on warbler productivity.

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INTRODUCTION

Literature Review and Problem Statement

Until recently, research in avian ecology has focused on relating presence or absence of species to vegetative characteristics. Presence-absence data are useful for mapping species distribution and estimating density and abundance (Brotons et al., 2004), but it does not tell us if the species is productive in the areas where they are present. It is clear that presence-absence data is not sufficient, so we have been investigating productivity of songbirds, and we know habitat characteristics affect productivity (Van Horne 1983, Donovan et al., 1995).

Studies on the vegetative component of habitat selection have focused on issues of 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). These are important issues, but there has not been enough focus on the importance of tree species composition in relation to avian productivity within remaining habitat fragments. Vegetative composition has implications for a variety of factors. When selecting a territory, a bird will choose a location that provides requisite conditions for survival and breeding, including nest sites, foraging areas, roosting sites, and song perches (Sedgwick and Knopf 1992). Some warblers, such as the black-throated blue warbler (*Dendroica caerulescens*) and the Townsend's warbler (*D. townsendi*), appear to use a hierarchical decision process, with selection for a patch based first on nesting habitat and secondarily on foraging habitat within a patch (Steele 1993, Matsuoka et al.,

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1997). Some evidence (Coldren 1998) supports this hierarchical decision process by golden-cheeked warblers (*D. chrysoparia*).

Food availability affects bird foraging behavior and consequently their reproductive success, as well as their ability to feed young. Models of foraging strategies (McNamara and Houston 1987, Werner and Anholt 1993, Anholt and Werner 1998, Brown 1999, Olsson and Holmgren 1999) predict that animals in food rich environments should spend less time foraging than those in poor environments. Given expected tradeoffs between foraging and other activities, spatial variation in prey abundance is likely to influence not only bird abundance and distribution among habitats, but also reproductive success within habitats (Lyons 2005). Therefore, assessment of differences in food supply between habitats may reveal insights about habitat quality (Lyons 2005).

Availability of food for woodland birds is a function of (1) the types and abundances of prey present, which vary among tree species, (2) the foliage structure and characteristics of the trees, which influence prey detectability and accessibility, and (3) the morphological and behavioral abilities of each bird species to perceive and capture prey (Holmes and Schultz 1988). Food availability therefore cannot be assessed by simply measuring prey abundance alone. Because each tree species provides a differing set of foraging opportunities for birds, the mix of tree species at a site, coupled with the arthropod resources they support, will influence reproductive success for a given bird species.

The golden-cheeked warbler is a federally endangered songbird that depends on Ashe Juniper (*Juniperus ashei*) for nesting material and closed-canopy juniper-oak woodlands for breeding habitat (Pulich 1976, Ladd and Gass 1999, DeBoer and Diamond 2006, Magness et al. 2006). Females can build their nests in junipers or a variety of hardwoods (U.S. Fish and Wildlife 1992), thus nest sites are probably not limiting. Availability of water does not seem to be a problem for golden-cheeked warblers because they will leave their territories and travel long distances for water (Pulich 1976), and distance to water does not influence warbler reproductive success (Arnold et al. 1996). Based on limited data available, the number of roost sites is probably not limited (Coldren 1998). If food is limited, then natural selection should favor birds with better foraging opportunities (Kelly 1993).

The abundance of resources, primarily food, can dramatically affect population numbers (Newton 1993). In temperate forests, food appears to be the most important factor in reproductive success, and its availability frequently limits reproductive output (Holmes et al. 1986). Golden-cheeked warblers occur in areas with varying tree species compositions, and previous research on other avian insectivores has suggested that vegetative structural diversity tends to correlate with insect productivity (Webb 1989, Tye 1992). Theoretically, when migratory birds such as the golden-cheeked warbler arrive upon the breeding grounds, they must quickly assess food supply. Direct assessment of a complex food supply for an insectivore may be difficult if not impossible (Tye 1992), so they 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 who returns from migration in early-mid March, probably before the availability of food is apparent, making a direct assessment of arthropods improbable at best.

Areas with high insect abundances may serve as profitable foraging areas by reducing the search effort (Blake and Hoppes 1986). For instance, territory size is related to habitat productivity (Kuitunen and Helle 1988) and birds have been shown to be able to adjust territory size based on resource availability (Smith and Shugart 1987). Because territory size for golden-cheeked warblers appears inversely related to reproductive success (Coldren 1998), habitat productivity may be related to reproductive success. If so, the relationship may be such that reproductive success is based on food availability and foraging opportunities. Thus, it is plausible that golden-cheeked warblers may select territories within a patch based on foraging opportunities.

Golden-cheeked warblers occupy patches of juniper-oak woodland that contain a variety of plant associations, and these associations broadly relate to ecosite and soil features. Two ecosites in which golden-cheeked warblers commonly occur are the redlands ecosite and the low stony hill ecosite. The redlands ecosite is marked by the predominance of post oak (*Quercus stellata*), whereas the low stony hill ecosite is marked by the predominance of Texas oak (*Quercus buckleyi*). Because the plant communities differ markedly between these two ecosites, the arthropod communities should differ markedly as well (Holmes and Schultz 1988). We know food availability

affects bird foraging behavior (Lyons 2005), so differences in arthropod communities between ecosites should result in differences in foraging behavior between ecosites, and variation in foraging behavior can lead to variation in reproductive success.

Objectives and Research Hypotheses

Objective 1- I will determine any differences in pairing and fledging success of warbler territories within two ecosites exhibiting two distinctive tree species composition.

Research hypothesis 1- I hypothesize territories within the low stony hill ecosite will have higher pairing success, fledging success, and will produce more fledglings per successful territory compared to territories established in the redlands ecosite.

Objective 2- I will explore the relationship between tree species composition, arthropod density, and foraging effort.

Research hypothesis 2- I hypothesize Texas oak will be an important foraging substrate for golden-cheeked warblers during the breeding season. I hypothesize territories in the low stony hill ecosite will have a much higher percentage of Texas oak and a higher density of arthropods, and that this higher percentage of Texas oak and density of arthropods will lead to a lower movement rate and reduced foraging effort.

Objective 3- I will investigate the connection between preferred foraging substrates and changes in arthropod abundance within golden-cheeked warbler territories throughout the breeding season.

Research hypothesis 3- I hypothesize golden-cheeked warblers will change their preferred foraging substrates during the breeding season, and that these changes will be linked to changes in arthropod abundance.

Results of my study could be critical to private land managers and many managing agencies including Texas Parks and Wildlife and US Fish and Wildlife. Recovery of a species requires that there is a high probability of persistence of a viable population for the foreseeable future, meaning that not only factors leading to presence or absence of a species are important, but factors leading to high levels of productivity are critical for long term management of endangered species. If there are major differences in reproductive success between ecosites, 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/or enhancement of golden-cheeked warbler habitat could benefit from further clarification of what constitutes optimal and sub-optimal habitat.

STUDY AREA

I worked on Fort Hood, an 88,500 ha active U.S. Army installation in central Texas occupying both Coryell and Bell counties, which contains the largest golden-cheeked warbler breeding population under a single management agency (Dearborn and Sanchez 2001). Fort Hood occupies land within the Cross Timbers and Southern Tallgrass Prairie ecoregion, near the junction with the Edwards Plateau ecoregion. Sixty-five percent of the land area is described as perennial grassland and 31% as woodland (Unpublished data U.S. Army LCTA program; Loechl et al.. 2008). Dominant tree species include Ashe juniper, Texas oak, live oak (*Quercus fusiformis*), post oak (*Q.*

stellata), Texas ash (*Fraxinus texensis*), blackjack oak (*Q. marilandica*), shin oak (*Q. sinuata*), cedar elm (*Ulmus crassifolia*), hackberry (*Celtis laevigata*), pecan (*Carya illinoensis*), and redbud (*Cercis canadensis*) (Kostecke 2008).

Climate at Fort Hood is characterized by warm summers and mild winters. For Killeen, the city directly adjacent to Fort Hood, annual precipitation averages 78 cm and average temperature is 19.4° C. Precipitation is concentrated in spring and fall; wettest months are May and September, and driest months are July and December (Weatherbase.com 2010). During my study, temperatures were above average for the months of May, June, and July in 2009 and 2010 (Figure 1), and precipitation patterns deviated from the average and varied between 2009 and 2010 (Figure 2). Specifically, in 2009, precipitation was high during March, April, and May, but most of the precipitation occurred during a few rain events (Wunderground.com). In 2010, precipitation was high for March, April, June, and July, and the precipitation was spread out over several rain events (Wunderground.com). These inter-annual differences in temperature and precipitation patterns could be important in that they could be playing a significant role in driving inter-annual differences in arthropod and foraging patterns, which in turn could be driving inter-annual differences in avian productivity.

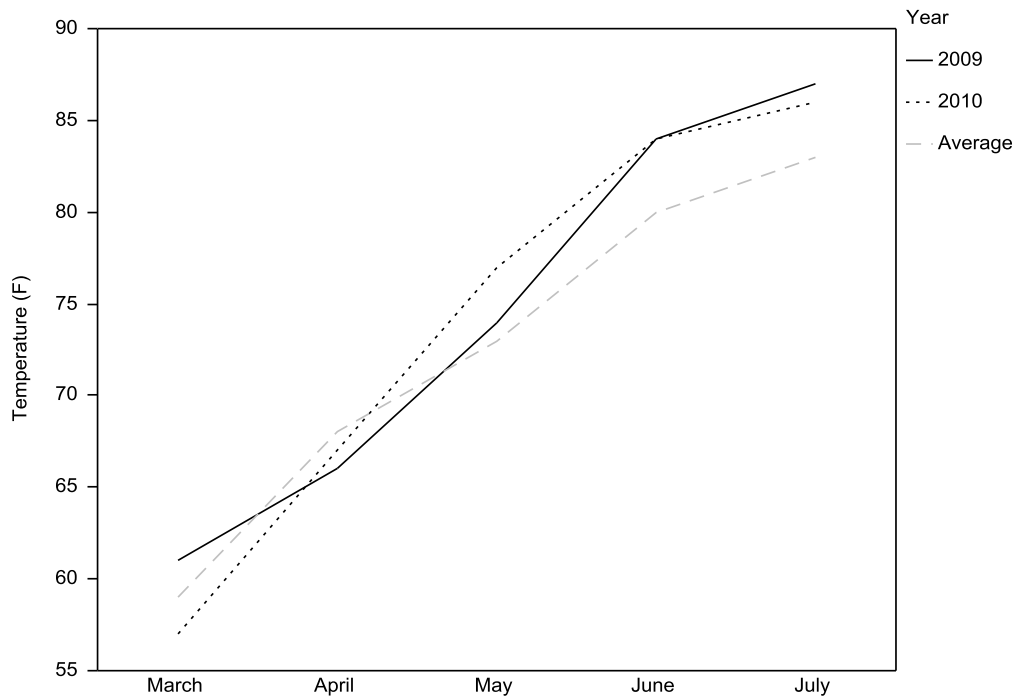


Figure 1. Mean monthly and mean annual temperature during the golden-cheeked warbler breeding season for the Killeen/Fort Hood area in central Texas during 2009 and 2010.

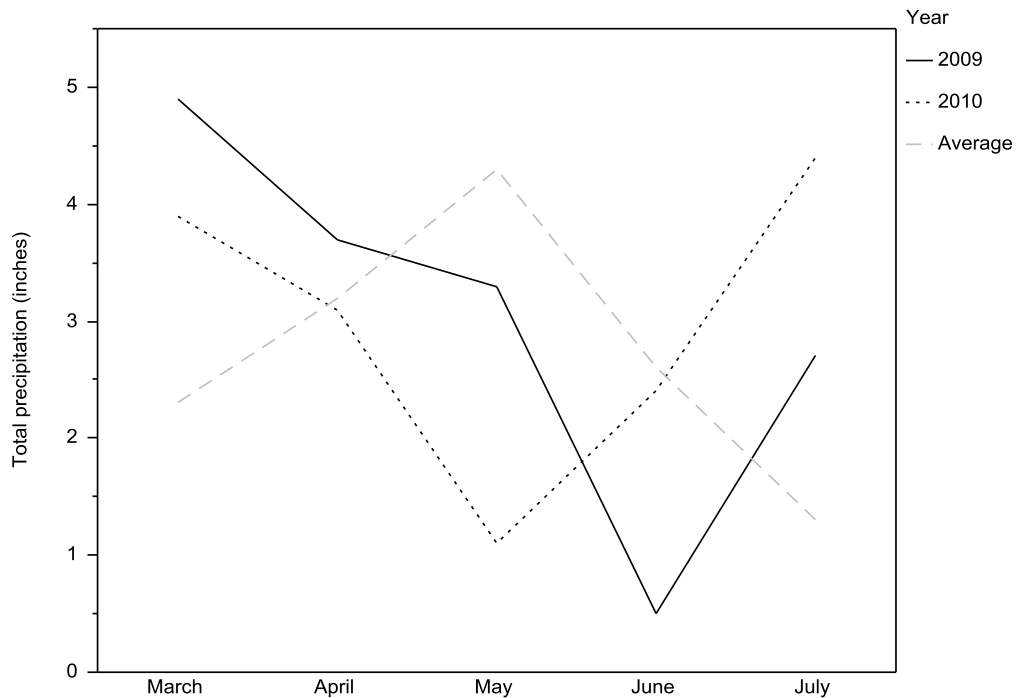


Figure 2. Total precipitation during the golden-cheeked warbler breeding season for the Killeen/Fort Hood area in central Texas during 2009 and 2010, with the annual average.

My study sites were located on the eastern portion of the base (Figure 3), and were contained within areas demarked as training area 11 (area of approximately 528 ha), land group 2 (area of approximately 2750 ha), land group 3A (area of approximately 940 ha), and land group 3B (area of approximately 2740 ha). I chose these specific sites because the Army had granted Texas A&M University access to work in these areas for another unrelated study. I sampled patches within these study sites that contained both redlands and low stony hill ecosites, thus offering areas characterized by presence of post oak or Texas oak respectively. Nonprobability sampling is appropriate in my study

(Gilbert 1987, Morrison et al.. 2008: 142) because I am interested in comparing two vegetation types within areas known to be representative of habitat for golden-cheeked warblers (Campbell 2003, Butcher 2010). These patches have been previously occupied by golden-cheeked warblers (unpublished data Texas A&M 2008) and meet criteria thought to be important for golden-cheeked warbler productivity: patch size of >30 ha (Butcher et al.. 2010), canopy closure >50% (Campbell 2003), and presence of at least 15 mature juniper stems with a diameter at breast height of at least 13 centimeters (Campbell 2003). Using these criteria allowed me to be certain that any biologically significant change in avian productivity was indicative of tree species composition and not small patch size, inadequate canopy cover, or lack of nesting materials. Individual warbler territories were my sampling units. The vegetation (in terms of tree species composition by ecosite) in these areas was patchy making use of discrete study sites inappropriate, so I sampled territories across the 4 broad areas indicated in Figure 3. Once I obtained the location of individual golden-cheeked warblers, I sub-sampled by randomly selecting individual territories in both ecosites within each broad study area. By spreading my sampling units across 4 large disconnected areas, sufficient replication was ensured so as 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.

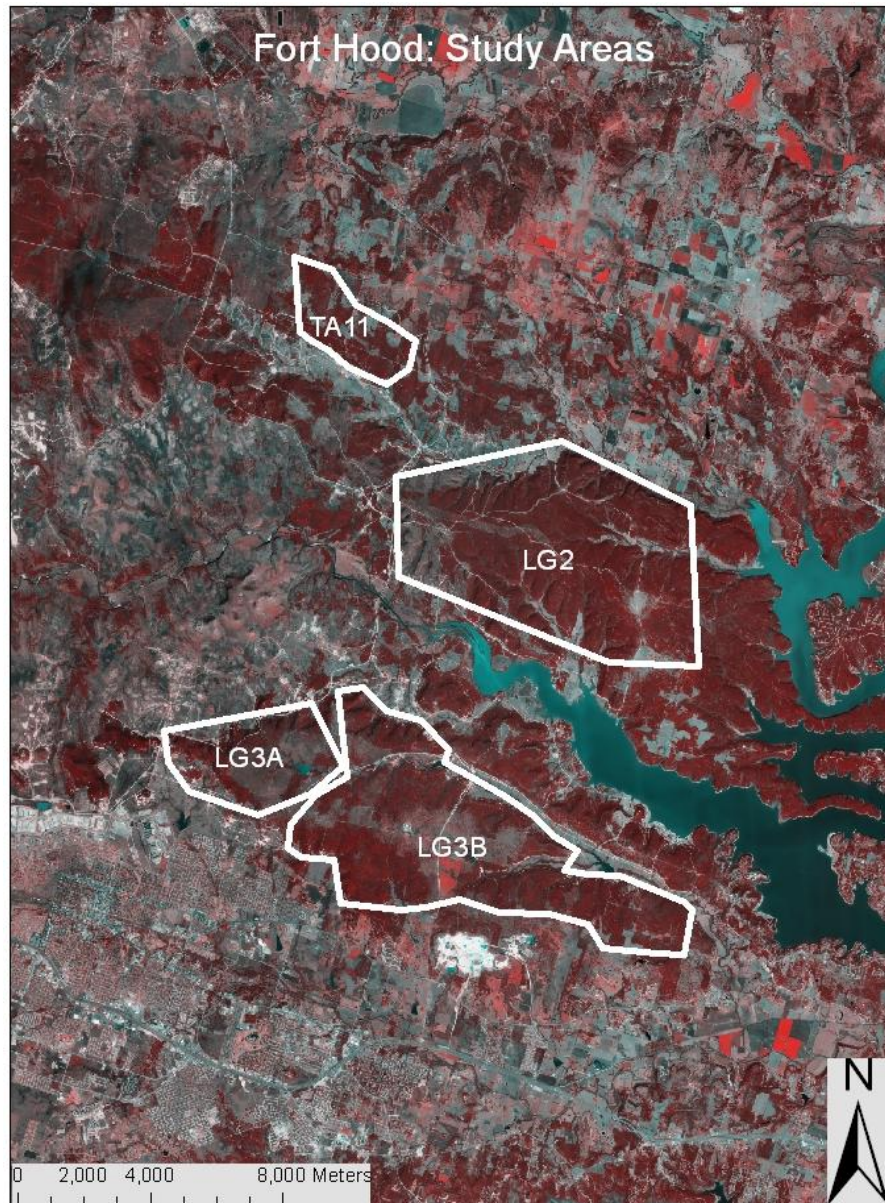


Figure3. East Fort Hood: white polygons refer to 2009-2010 study area.

METHODS

Territory Mapping and the Vickery Index

I used preliminary transect surveys to detect and locate golden-cheeked warblers present at all study sites. Transect distances varied between 400 m to 1.7 km, depending on patch size. I systematically placed transects spaced at least 75 meters apart to cover the entire study site. I placed points along transects at a 50 meter spacing. At each point along a given transect, surveyors spent several minutes recording all singing male golden-cheeked warblers. I recorded the location of a male with a Global Positioning System (GPS) handheld device, as well as the direction and distance of any neighboring golden-cheeked warblers. I then mapped each golden-cheeked warbler territory detected in the study sites.

I used territory mapping to approximate the spatial location of territories of each focal male or pair by taking sequential GPS locations of focal birds to determine the areas they used and encompassed. I defined territories by the presence of a singing, territorial male for at least 4 weeks. I took territory points for each male or pair on each visit to a study site. I gathered a minimum of 15 points for each territory for the season to adequately identify the territory. Once the male or female was located, I recorded a point. I recorded another point once the bird moved at least 20 meters from the location it was last observed. I continued to record bird location points each time the bird moved ≥ 20 m until at least 3 points had been recorded. I visited territories once every 7–10 days starting in early March, when golden-cheeked warblers arrived from their wintering

grounds. These measurements provided a complete, or near complete, census of golden-cheeked warbler abundance in the study sites.

I conducted behavioral surveys in each territory to determine territory reproductive success. I used a modified version of the Vickery index (Vickery et al., 1992) to assess productivity in golden-cheeked warblers in my study. The Vickery index is a method of estimating reproductive success that avoids potential biases associated with nonrandomly collected nest data, and it does not disrupt nests, which is critically important when studying rare or endangered species (Vickery et al., 1992). Reproduction indices are often used in lieu of direct measurements of reproductive success for rare or elusive species. While these estimates may be biased, they are often the most accurate measurements that can be obtained.

I visited territories every 7–10 days in most cases (issues of access limited certain visit times for certain territories). For a period of no more than 60 minutes, surveyors systematically searched each territory for pairs and for any signs of nesting behaviors (e.g. alarm calls, nest material carries, food carries). If breeding or nesting behavior was observed within the 60 minute period, I recorded the behavior, marked a GPS waypoint for the observed behavior, and moved on to the next territory. I recorded observations in GIS with a unique territory ID for the focal bird, the date of the observation, the observer, any breeding behaviors observed, and the associated Vickery rank (Table 1).

Table 1. Modified Vickery ranks. A territory with a rank of 5 or higher is considered reproductively successful, whereas a rank of 2 or higher is considered successfully paired.

Numerical Rank	Associated Behavior
1	Territorial Male (male present >4weeks)
2	Pair (female and male present)
3	Material carry (to presumed nest)
4	Food carry (to presumed nestlings)
5	Fledgling (sighted by observer)
6	Double brooding (2 nd set of fledglings sighted)

If a female was located within a male's territory, I considered that male successfully paired. I considered a pair reproductively successful if at least one fledgling was located within a territory. I calculated territory success as the number of territories with a least one fledgling relative to the total number of territories, thus territory success is a function of both pairing and fledging success. I counted the number of fledglings found in each territory which facilitated comparison of the mean number of fledglings found in various tree species compositions. I compared pairing

success, territory success, and fledgling numbers within successful territories, between territories in both of the ecosites of interest (see analyses below).

Tree Species Composition

I established territory boundaries by constructing minimum convex polygons around the collection of points constituting an individual golden-cheeked warbler territory using Arc GIS (ESRI 2008). I delineated territories based on data collected during territory mapping described above. To assess vegetative composition of each territory, I established a systematic grid of points at 20 m spacing within golden-cheeked warbler territories across my broad study areas using the Hawth's tools extension in Arc GIS. At each point within a territory, I noted if any woody cover was present. If the woody cover was taller than 2 m, I made visual canopy cover estimates as well as canopy species identification and height. I looked straight up through a tubular densiometer and estimated the total canopy cover to the nearest 10%. I identified all tree species in the canopy and estimated their height to the nearest half-meter.

To estimate canopy cover within a territory, I combined all point canopy estimates and took the mean. To estimate tree species composition within a territory, I took a count of all tree species present in a territory and divided each individual species by the total present to get a percent abundance for each of 6 individual tree species representing the dominant tree species at my study sites: Texas oak, live oak, post/blackjack oak, shin oak, Texas ash, and Ashe juniper.

Foraging Surveys

I used behavioral foraging surveys to estimate foraging effort and movement rate for golden-cheeked warblers, and to ascertain foraging substrates throughout the breeding season. Using bird behavior as a supplemental measure for food availability is biologically meaningful, in that it helps ensure that the birds perception of food availability is not ignored, scale of measurement questions are automatically resolved, and renewal rates are automatically integrated (Hutto 1990). I conducted a set of foraging observations on a sub-sample of golden-cheeked warbler territories in each ecosite twice during the breeding season; once in mid-April when all the males and females have arrived and settled, and another in mid-May when a majority of territories have finished nesting attempts, and many have fledged young. I entered previously mapped territories and observed the behavior of the first golden-cheeked warbler encountered. Once a warbler was detected, I watched the bird for 5 s without taking data to minimize bias to the most conspicuous activities (Noon and Block 1990, Keane and Morrison 1999). I observed the bird for three to six minutes, taking continuous measurements using a hand held tape recorder. During this time I recorded the sex of the bird, activity (e.g., perching, feeding, singing, short flight, long flight, preening), and foraging substrate. I also estimated movement rate during foraging bouts by delineating any movement as a short flight (movement of < 2 meters) or long flight (movement > 2 meters). I chose the 2 meter cutoff because flights of $>2m$ tended to be flights between trees, whereas flights of $<2m$ tended to be contained within an individual tree. Movement rate might decrease when a bird is in a relatively food-rich area (Hutto 1990).

Area-restricted searching would also predict a slower rate of beeline progression with an increase in prey availability (Hutto 1990).

Arthropod Sampling

Golden-cheeked warblers are generalist feeders who glean prey from the foliage, stems, and petioles of trees (Pulich 1976). This fact, coupled with the need for an estimate of relative abundance of arthropods, indicate branch clipping is the best method for this study. Advantages of branch clipping are that it is relatively inexpensive, it targets foliage-dwelling arthropods readily accessible by gleaning birds, and it captures many arthropods missed by other techniques such as sweep netting and pole pruning (Cooper and Whitmore 1990).

I selected a random sub-sample of territories within low stony hill and redlands ecosites that were dispersed throughout the 4 broad study areas. I sampled 3 times throughout the breeding season. The first two sampling periods occurred within two days of foraging surveys, with the intention of linking foraging behavior to food availability. I took the first sample in early-mid April once territories were established, the second in early-mid May when a majority of territories have finished nesting attempts, and the third in early-mid June, towards the end of the season when most territories should have fledged young.

I sampled trees for arthropods in the area generally delimited by an individual bird during a foraging survey. I established a systematic grid of points at 10 m spacing within these generally delimited areas, and randomly selected 4 points to sample for arthropods. At these four locations, I walked at a random bearing and sampled the first

juniper or oak tree I encountered. I sampled 2 Ashe juniper trees and 2 oak trees within each territory. In 2009 I limited my sampling of oaks to 2 focal species: post oak and Texas oak. In 2010, I sampled the first oak species I encountered along the random bearing, which resulted in live oak and shin oak being represented in the overall sampling. I took four branch clippings from individual trees, for a total of 16 branch clippings per territory per sampling period. Newnam (2008) found that prey available for golden-cheeked warblers did not differ at various tree canopy levels. I took branch clippings from branches found approximately two meters from the ground based on a previous study (Butcher 2010) on arthropod assemblages in golden-cheeked warbler territories.

At an individual tree, I quickly placed a bag over the branch and held it shut. I then clipped the branch, tied it closed, and marked the bag. I placed the bag in a freezer for at least 5 days. I separated the main branch from the loose leaves and placed it in a press to be dried in a herbarium for a minimum of 7 days. I placed the loose leaves and the remainder of the litter into a small paper bag and dried it at 60° C for a minimum of 5 days. I separated arthropods from branches and leaves and weighed them to the nearest 0.0001 gram, whereas leaves were weighed to the nearest 0.01 gram. I expressed arthropod density as the total weight of arthropods/total weight of the branch. Arthropod density is a relative measure of food availability for my study (Keane and Morrison 1999). In 2009, I compared total arthropod density between the two ecosites. In 2010, I identified arthropods to order, which allowed me to make fine scale comparisons in biomass between the two ecosites. This also allowed me to observe changes in

arthropod assemblages through time and across various tree species, and to link these changes to preferred foraging substrates.

Analyses

I used Pearson's chi-square test to compare the number of successfully paired territories and number of reproductively successful territories between the two ecosites. I used a *t*-test to compare the mean number of fledglings within successful territories between the two ecosites. My sample size was >30 territories in each ecosite, making this statistical test appropriate (Zar 1999: 663).

I used a *t*-test to compare tree species composition and canopy characteristics between ecosites. I tested for a relationship between fledging success (yes/no) and percentage of Texas oak within a territory by running logistic regression with fledging success as a dependent binary variable, and percent Texas oak within a territory, year, and the interaction of year and percent Texas oak as independent variables.

I calculated foraging and movement rates for golden-cheeked warblers in their respective territory by taking the ratio of time spent engaged in foraging behavior and flights divided by the total time observed. I used *t*-tests to compare mean foraging effort (number of foraging bouts/time) and mean movement rate (number of short and long flights/time) between territories in low stony hill and redlands sites. To quantify a switch in foraging substrates I compared the total number of foraging attempts on juniper versus oak for April and May separately. I used ANOVAs to evaluate use versus availability for foraging behavior between ecosites for specific tree species, by sampling period and year.

I 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. I used a series of two-tailed unpaired t-tests to compare average arthropod density for 1) all trees sampled 2) junipers only and 3) oaks only, between territories in the two ecosites of interest, for all three sampling periods. For the 2010 data, I was able to compare density for specific arthropod orders between ecosites. I used t-tests to compare density of all arthropod orders between ecosites. I used a factorial ANOVA to compare densities of particular arthropod orders between different tree species by sampling period. I conducted all statistical analyses using the SAS statistical software JMP (JMP 2007).

RESULTS

Territory Mapping and the Vickery Index

I monitored 154 golden-cheeked warbler territories in 2009. One-hundred and fifteen (115) territories were established in the low stony hill site, and 39 were established in the redlands site. Pairing success differed significantly between ecosites ($\chi^2 = 7.010$, $df = 1$, $P < 0.05$), with 90 of 115 territories containing pairs in the low stony hill site (78% pairing success, $n = 115$) and 22 of 39 territories containing pairs in the redlands site (56% pairing success, $n = 39$) (Figure 4). Fledging success differed significantly between ecosites ($\chi^2 = 11.242$, $df = 1$, $P < 0.05$) (Figure 4). Seventy-one territories successfully fledged at least one young in the low stony hill site (62% success, $n = 115$), whereas 12 territories successfully fledged at least one young in the redlands site (31% success, $n = 39$).

I monitored 194 golden-cheeked warbler territories in 2010. One-hundred and twenty eight (128) of these territories were established in the low stony hill site, and 66 were established in the redlands site. Pairing success did not differ significantly between ecosites ($\chi^2 = 1.073$, $df = 1$, $P = 0.3003$; Figure 4). The low stony hill site had 76% pairing success and the redlands site had 70% pairing success. Fledging success differed significantly between ecosites ($\chi^2 = 3.920$, $df = 1$, $P < 0.05$; Figure 4). The low stony hill site had 64% fledging success, whereas the redlands site had 48% fledging success. Interestingly, pairing and fledging success were higher in the redlands ecosite in 2010 compared to 2009.

In 2009, the low stony hill ecosite produced an average of 1.9 fledglings/successful territory and the redlands ecosite produced an average of 2.0 fledglings/successful territory (Figure 5). In 2010, both the low stony hill and redlands sites produced an average of 2.1 fledglings/successful territory (Figure 5). Although there was a significant difference in fledging success of territories between the two ecosites in both years, there was not a significant difference in the average number of young fledged from successful territories in each ecosite for 2009 ($t = 0.2238$, $df = 1$, $P = 0.73$) or 2010 ($t = 0.0570$, $df = 1$, $P = 0.81$).

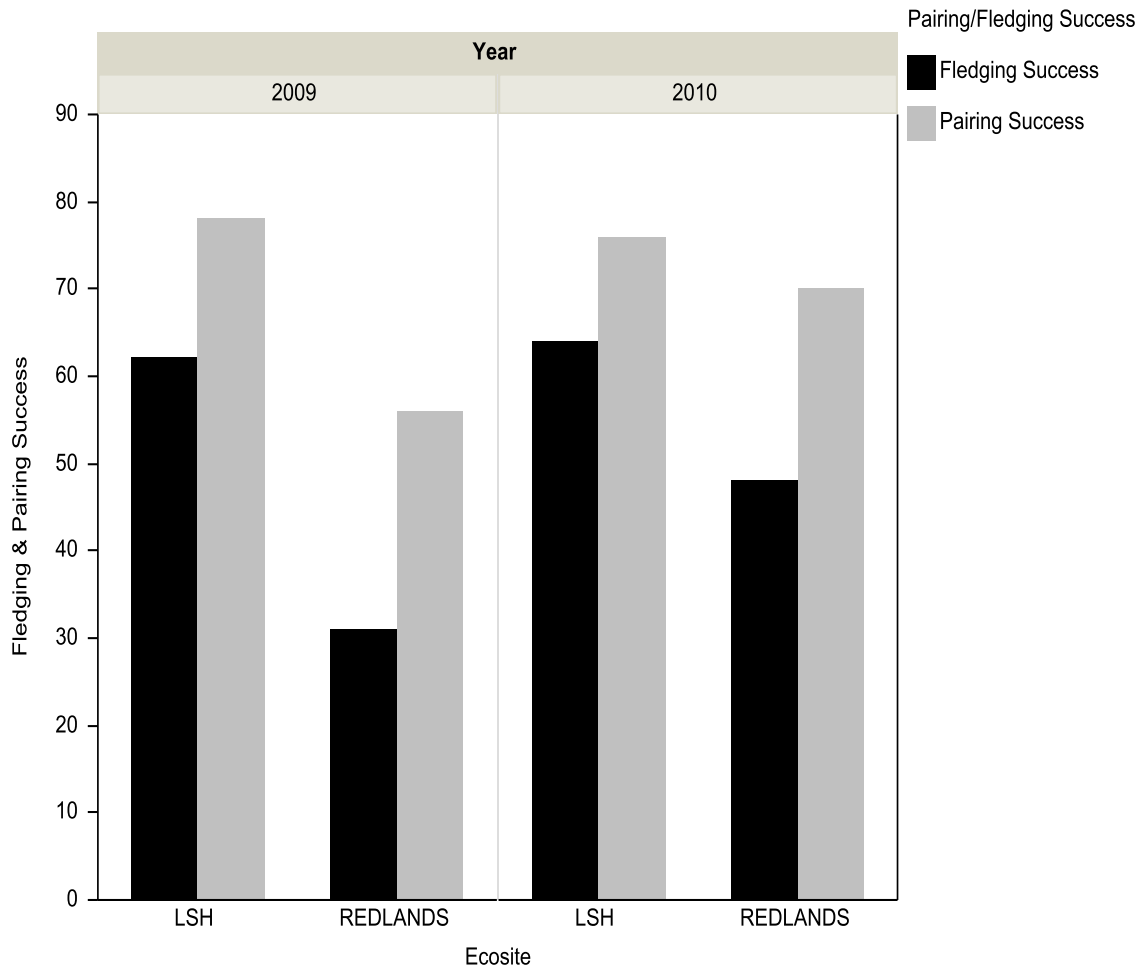


Figure 4. Pairing and fledging success for golden-cheeked warbler territories within low stony hill (LSH) and redlands (REDLANDS) ecosites in 2009 and 2010.

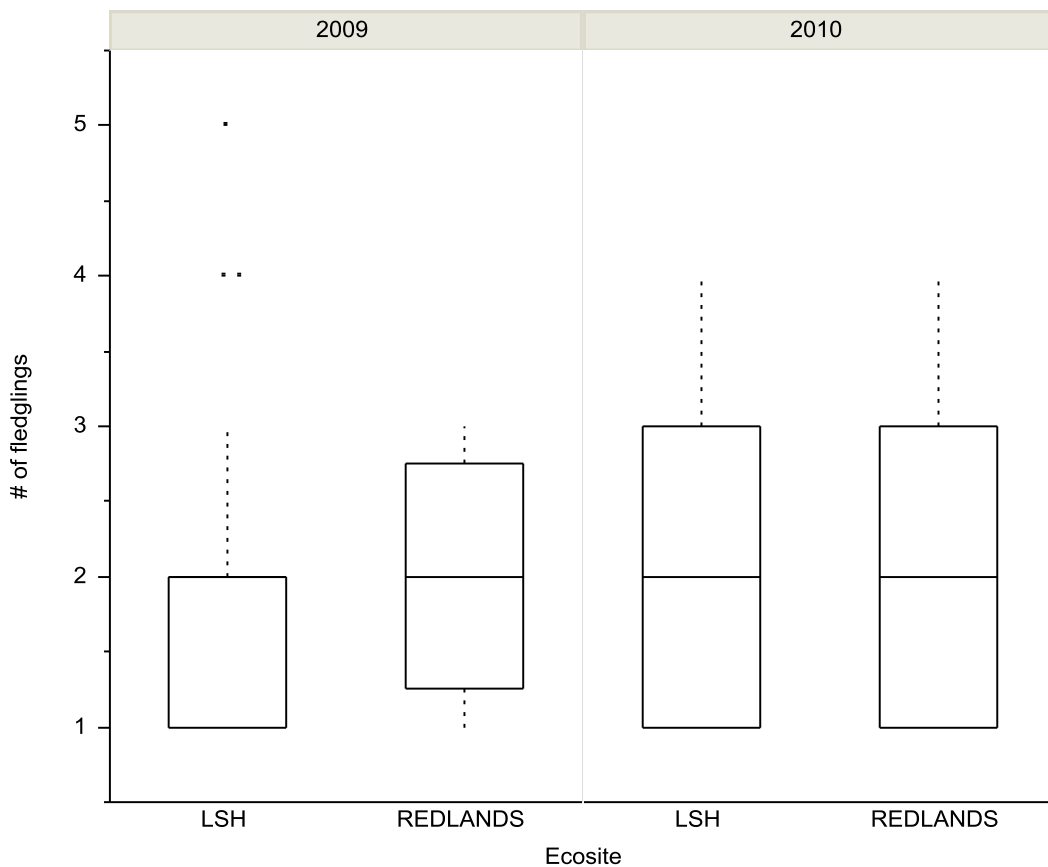


Figure 5. Average number of warbler fledglings per successful territory within low stony hill (LSH) and redlands (REDLANDS) ecosites for both 2009 and 2010.

Tree Species Composition

In 2009, there was no significant difference in canopy cover between the two ecosites ($t = 0.7417$, $df = 1$, $P = 0.39$), although the low stony hill ecosite did have a slightly higher mean canopy cover (LSH = 51%; Redlands = 49%). Regardless of ecosite, canopy cover was not a useful predictor of whether a territory successfully fledged young ($\chi^2 = 1.1923$, $df = 1$, $P = 0.2749$). In 2010, there was a statistically significant difference in

canopy cover between ecosites ($t = 6.9761$, $df = 1$, $P < 0.05$), however the magnitude of difference was only 6% (LSH = 53%; Redlands = 59%), likely making this biologically uninformative. Plus, canopy cover was again not a useful predictor of whether a territory successfully fledged young ($\chi^2 = 0.1416$, $df = 1$, $P = 0.7067$).

When comparing tree species composition for territories by ecosite, there are a few notable differences (Tables 2 and 3). Territories in the low stony hill ecosite had 5–10% more Texas oak and juniper on average, while the redlands site had 10–20% more post/blackjack oak on average. There are clear inter-annual differences in tree species composition within territories between the two ecosites, which is mainly seen in the percentage of Texas oak. In 2009 there was a significantly higher percentage of Texas oak within low stony hill territories ($t = 6.2449$, $df = 1$, $P < 0.05$), whereas in 2010, this difference was not as drastic ($t = 2.0762$, $df = 1$, $P = 0.1528$).

Because of this substantial between-year difference in Texas oak composition, I tested for a link between fledging success and percentage of Texas oak within a territory with the 2009 and 2010 vegetation data. Although the average proportion of Texas oak was higher within territories that successfully fledged young in 2009 (Unsuccessful = 11%; Successful = 12%) and 2010 (Unsuccessful = 6%; Successful = 9%), proportion of Texas oak was not a good predictor of whether a territory fledged young ($\chi^2 = 1.6479$, $df = 1$, $P = 0.1992$).

Table 2. Average tree species composition within GCWA territories by ecosite (2009).

	<i>Low Stony Hill</i>	<i>Redlands</i>	<i>t Ratio</i>	<i>P-value</i>
% Texas Oak	15% ± 1.9	5% ± 2.3	11.085	0.0016
% Post/Blackjack Oak	3% ± 2.6	24% ± 3.1	26.541	0.0001
% Ash	6% ± 1.1	5% ± 1.2	0.2687	0.6064
% Live Oak	11% ± 1.8	12% ± 2.2	0.3321	0.5669
% Shin Oak	6% ± 1.3	3% ± 1.5	3.2610	0.0766
% Juniper	55% ± 2.5	47% ± 2.9	4.7044	0.0346

Table 3. Average tree species composition within GCWA territories by ecosite (2010).

	<i>Low Stony Hill</i>	<i>Redlands</i>	<i>t Ratio</i>	<i>P-value</i>
% Texas Oak	10% ± 1.4	6% ± 2.7	2.0762	0.1528
% Post/Blackjack Oak	2% ± 1.5	11% ± 1.4	17.730	0.0001
% Ash	5% ± 4.8	7% ± 6.9	2.5678	0.1123
% Live Oak	8% ± 1.4	13% ± 1.3	6.9578	0.0097
% Shin Oak	7% ± 1.2	4% ± 1.2	1.5147	0.2214
% Juniper	64% ± 2.4	54% ± 2.2	10.386	0.0017

Foraging Surveys

In 2009 I sampled a total of 52 territories, 34 territories in the low stony hill ecosite and 18 in the redlands ecosite, for foraging and activity budget information (Table 4). The

only statistically significant differences between ecosites were found in the mean rate of long flights for the late sampling period ($t = 6.2369$, $df = 1$, $P < 0.05$) and the mean singing rate for the early sampling period ($t = 5.3252$, $df = 1$, $P < 0.05$). Warblers in redlands sites were engaged in long flights in May 10% more often, on average, than warblers in low stony hill sites. Male warblers in redlands sites only sang 2% more than males in low stony hill sites in April, likely making this statistically significant result biologically uninformative.

In 2010 I sampled 104 territories, 51 territories in the low stony hill ecosite and 53 in the redlands ecosite, for foraging and activity budget information (Table 4). There was a notable difference between ecosites in the May foraging rate ($t = 3.7956$, $df = 1$, $P = 0.0542$). Warblers in territories established in low stony hill sites foraged, on average, 22% more frequently in May than warblers in redlands sites.

Table 4. Activity budget for low stony hill (LSH) and redlands (REDLANDS) ecosites.

Values represent the proportion of individual activities to the total observation time.

Proportions do not sum to 1 because loafing/scanning was not included in activities.

	2009		2010	
	<u>LSH</u>	<u>REDLANDS</u>	<u>LSH</u>	<u>REDLANDS</u>
Short flight (early)	0.051 ± .008	0.051 ± .012	0.068 ± .009	0.064 ± .009
Short flight (late)	0.053 ± .008	0.068 ± .011	0.136 ± .014	0.113 ± .014
Long flight (early)	0.015 ± .002	0.018 ± .003	0.022 ± .003	0.021 ± .003
Long flight (late)	0.016 ± .002	0.026 ± .003	0.026 ± .004	0.024 ± .004
Preen (early)	0.017 ± .006	0.002 ± .009	0.008 ± .005	0.020 ± .005
Preen (late)	0.019 ± .005	0.014 ± .007	0.007 ± .003	0.012 ± .003
Singing (early)	0.066 ± .005	0.084 ± .007	0.088 ± .008	0.087 ± .007
Singing (late)	0.065 ± .006	0.060 ± .009	0.070 ± .006	0.069 ± .005
Foraging (early)	0.029 ± .004	0.034 ± .006	0.009 ± .003	0.013 ± .003
Foraging (late)	0.039 ± .008	0.036 ± .011	0.034 ± .006	0.012 ± .006

Golden-cheeked warblers use of foraging substrates changed through the breeding season in 2009 (Figure 6) and 2010 (Figure 7). In general, golden-cheeked warblers foraged more on oak species in April, and more on juniper in May, although in April 2010, within the low stony hill site, warblers foraged on juniper and oak spp. at a similar proportion. When comparing ecosites, it is interesting to note that juniper is being used to a greater extent in April, within the low stony hill, for both years.

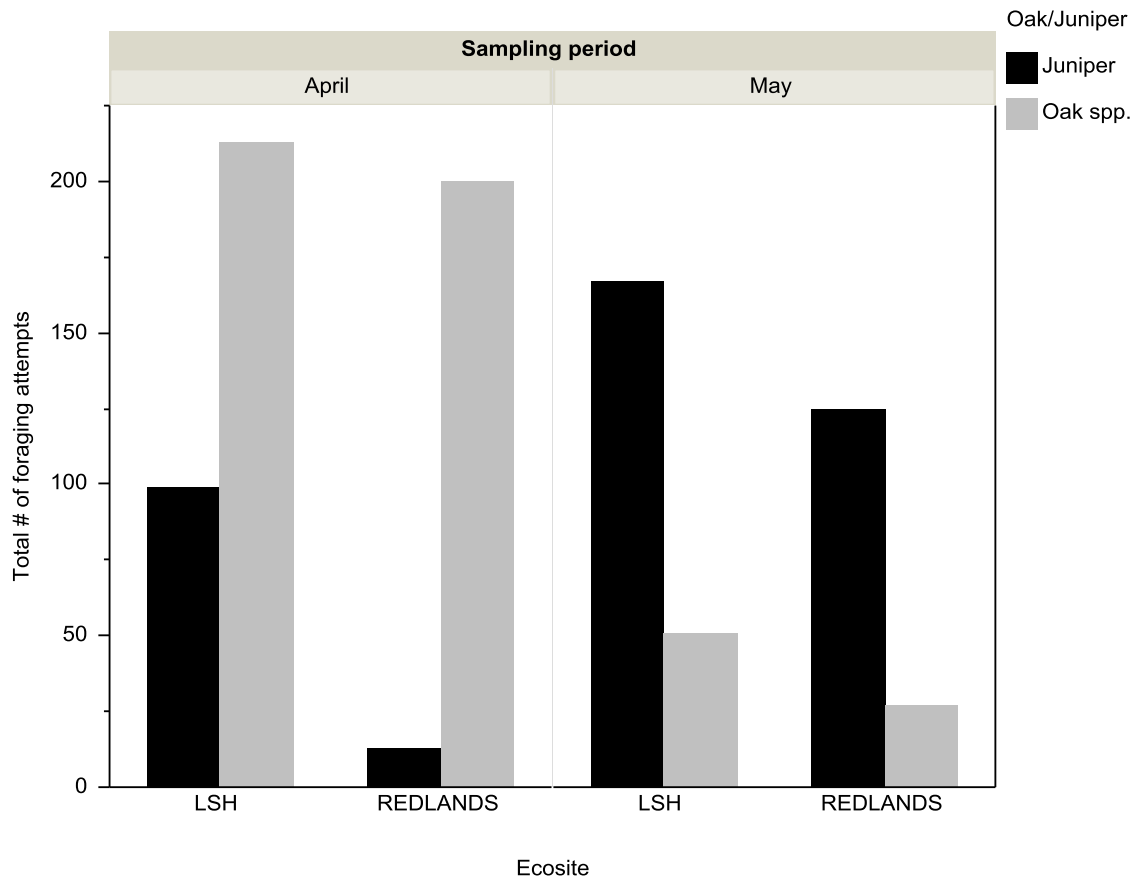


Figure 6. Total number of foraging attempts by golden-cheeked warblers in April and May of 2009 by foraging substrate (juniper vs. oak spp.)

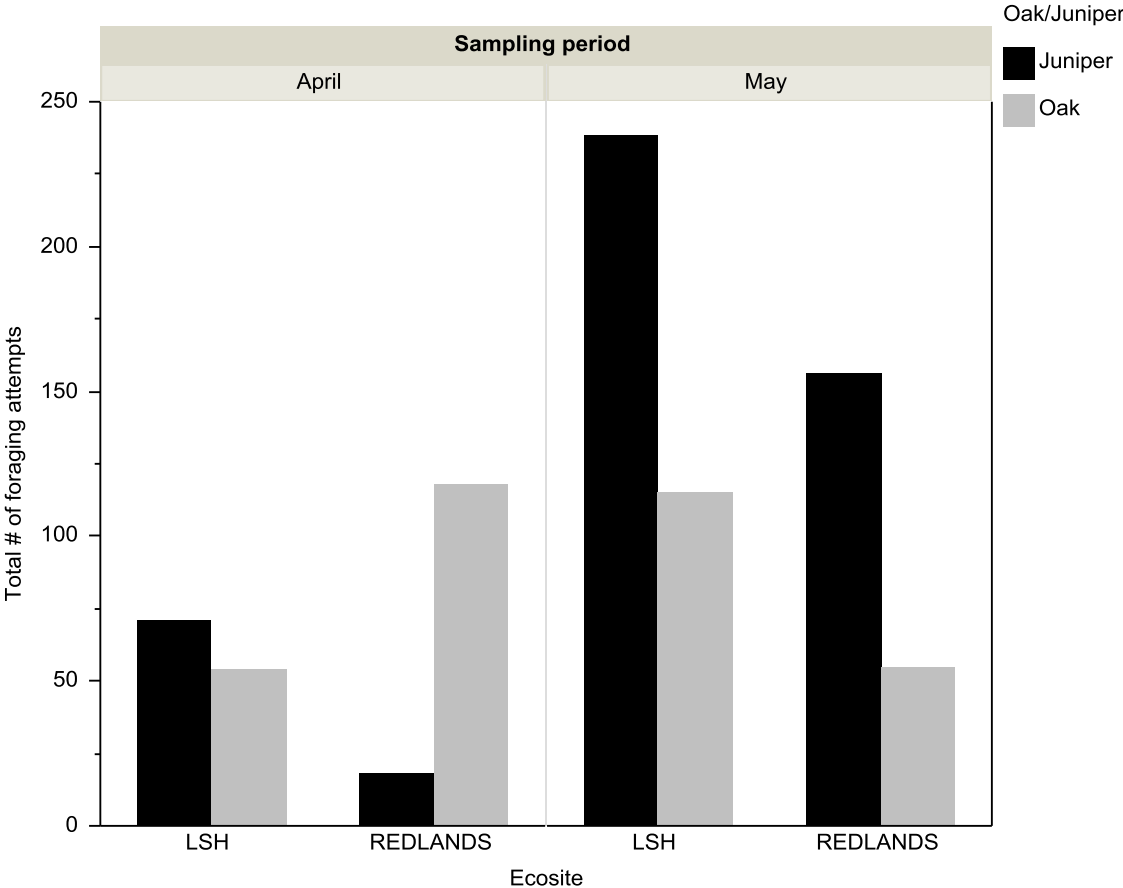


Figure 7. Total number of foraging attempts by golden-cheeked warblers in April and May of 2010 by foraging substrate (juniper vs. oak spp.)

I ran ANOVAs for the four most commonly used foraging substrates (Ashe juniper, live oak, post oak, and Texas oak) to test for differences in use versus available by month, and between ecosites and years (2009 and 2010). Golden-cheeked warblers were not using juniper ($F = 11.0500$, $df = 4, 267$, $P < 0.05$), live oak ($F = 6.3021$, $df = 4, 267$, $P < 0.05$), Texas oak ($F = 2.9542$, $df = 4, 267$, $P < 0.05$), or post oak ($F = 4.6508$, $df = 4, 267$, $P < 0.05$) as foraging substrates proportional to their availability (Figures 8 and 9).

In April of 2009, golden-cheeked warblers in low stony hill sites foraged in juniper 40% less than available, and use for Texas oak was 130% greater than available (Figure 8). In May of 2009, warblers in low stony hill sites switched to juniper as the main foraging substrate, using it 40% more than available. In April of 2009, golden-cheeked warblers in redlands sites foraged in juniper 70% less than available, use of live oak increased 120% above available, and use of Texas oak increased 130% above available. In May of 2009, warblers in redlands sites switched to juniper as the main foraging substrate, where use was 58% above available, but also used post oak 54% less than available.

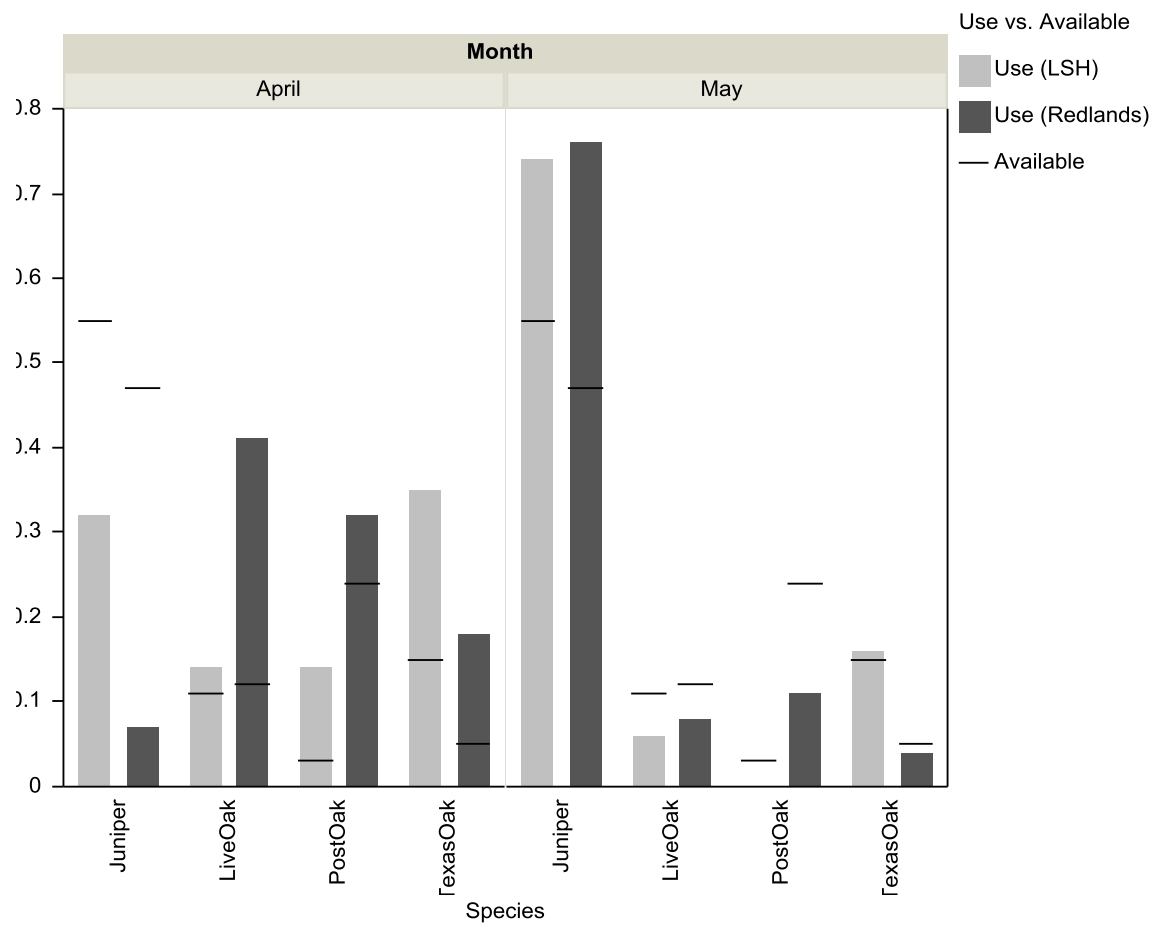


Figure 8. Use vs. availability for 4 common foraging substrates within GCWA territories in the low stony hill (LSH) and redlands ecosites (2009). Use represents the proportion of foraging attempts by tree species. Available represents the percentage of individual tree species within a territory.

In April of 2010, golden-cheeked warblers in low stony hill sites foraged in juniper 16 % less than available, and use of Texas oak increased 100% above what was available (Figure 9). In May of 2010, warblers in low stony hill sites switched to juniper as the main foraging substrate, using it in proportion to its availability. In April of 2010, golden-cheeked warblers in redlands sites foraged in juniper 70% less than available, and use of live oak increased 320% above what was available. In May of 2010, warblers in redlands sites switched to juniper as the main foraging substrate, using it 37% more than available.

Because of the apparent importance of Texas oak as a foraging substrate based on arthropod and use versus availability data, I decided to investigate the link between foraging and movement rates, and Texas oak composition within territories by running a general linear model with the 2010 data that removed sources of variation in the following order: % Texas oak, sampling period, and % Texas oak x sampling period. Proportion of Texas oak within a territory by sampling period was not a good predictor of number of long flights ($r = .01$, $P = 0.4514$), but was a good predictor of foraging rate ($r = .07$, $P < 0.05$) and number of short flights ($r = .14$, $P = 0.05$), although sampling period accounted for much of the variation between groups. Specifically, in May, proportion of Texas oak within a territory was a good predictor for the number of short flights ($r = .07$, $P < 0.05$). Golden-cheeked warblers foraging in territories with a high proportion of Texas oak in April were engaged in more short flights than those that were foraging in territories with a low percentage of Texas oak.

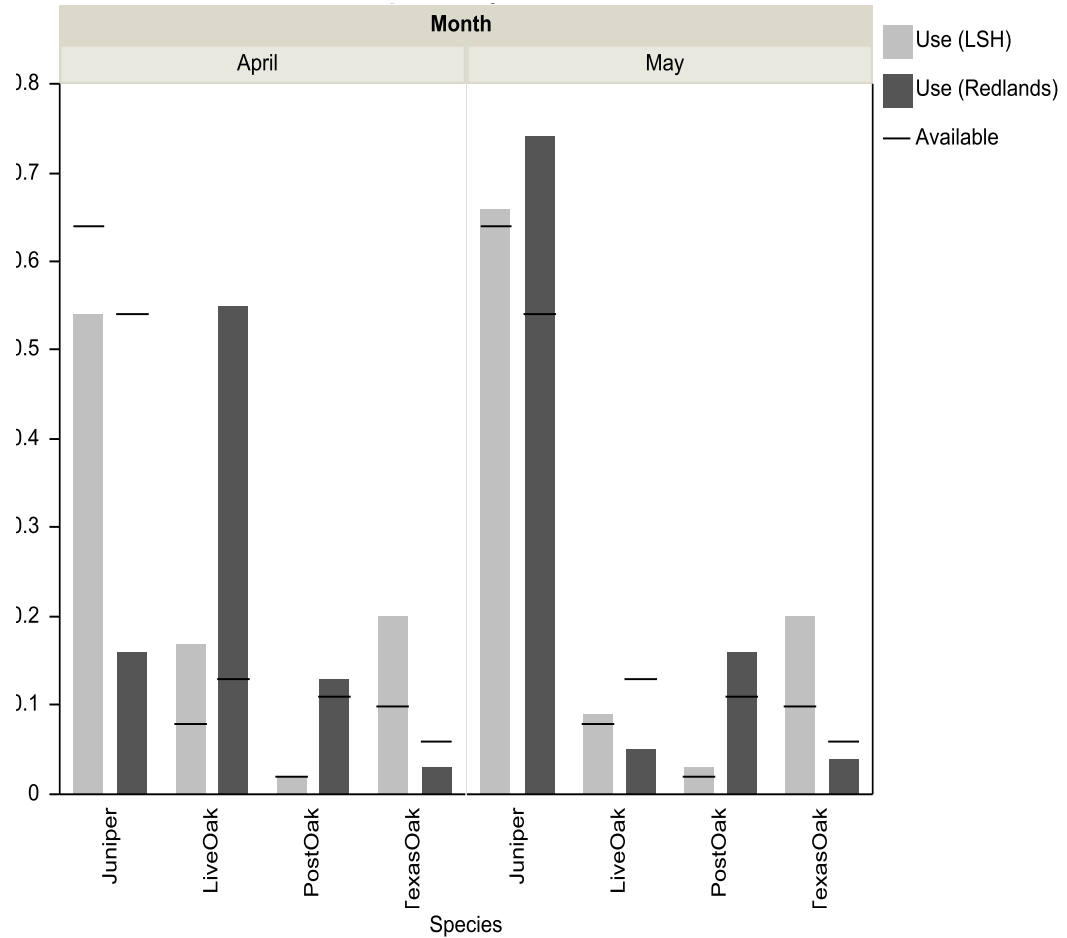


Figure 9. Use vs. availability for 4 common foraging substrates within GCWA territories in the low stony hill (LSH) and redlands ecosystems (2010). Use represents the proportion of foraging attempts by tree species. Available represents the percentage of individual tree species within a territory.

Arthropod Sampling

In 2009 I sampled arthropods in 22 territories, 12 territories in the low stony hill site and 10 in the redlands site. I only sampled 3 focal tree species during the 2009 season: Ashe juniper, post oak, and Texas oak (Table 5). Density of arthropods did not differ significantly between ecosites for all trees sampled ($t = 1.9359$, $df = 1$, $P = 0.1644$). Density of arthropods did not differ significantly between ecosites for juniper ($t = 0.0084$, $df = 1$, $P = 0.9272$) or oak species ($t = 1.9549$, $df = 1$, $P = 0.1627$). Although there were no statistically significant differences in arthropod density between ecosites, a few trends were obvious (Figure 10). In both ecosites, juniper had a low density of arthropods in the beginning of the season, followed by an increase through the next two sampling periods. Density of arthropods on oak species started out high, relative to juniper, and then became more variable throughout the later sampling periods. In general, regardless of ecosite, juniper had a low density of arthropods in April, followed by an eruption in May, whereas density of arthropods on oak was more variable.

Table 5. Density of Arthropods by Ecosite (2009). Values refer to the density of arthropods (weight of arthropods/weight of branch, in milligrams) on 3 focal tree species, for 3 sampling periods in 2009. Sample size (n) refers to the number of branches sampled.

	<u>Low Stony Hill</u>			<u>Redlands</u>		
	<i>April</i>	<i>May</i>	<i>June</i>	<i>April</i>	<i>May</i>	<i>June</i>
Juniper	0.016 (n=90)	0.220 (n=75)	0.350 (n=77)	0.022 (n=79)	0.150 (n=71)	0.400 (n=81)
Post Oak	0.075 (n=18)	0.370 (n=7)	0 (n=4)	0.650 (n=65)	0.780 (n=68)	0.230 (n=74)
Texas Oak	0.029 (n=71)	0.240 (n=66)	0.040 (n=76)	0.162 (n=7)	0 (n=4)	0.004 (n=4)

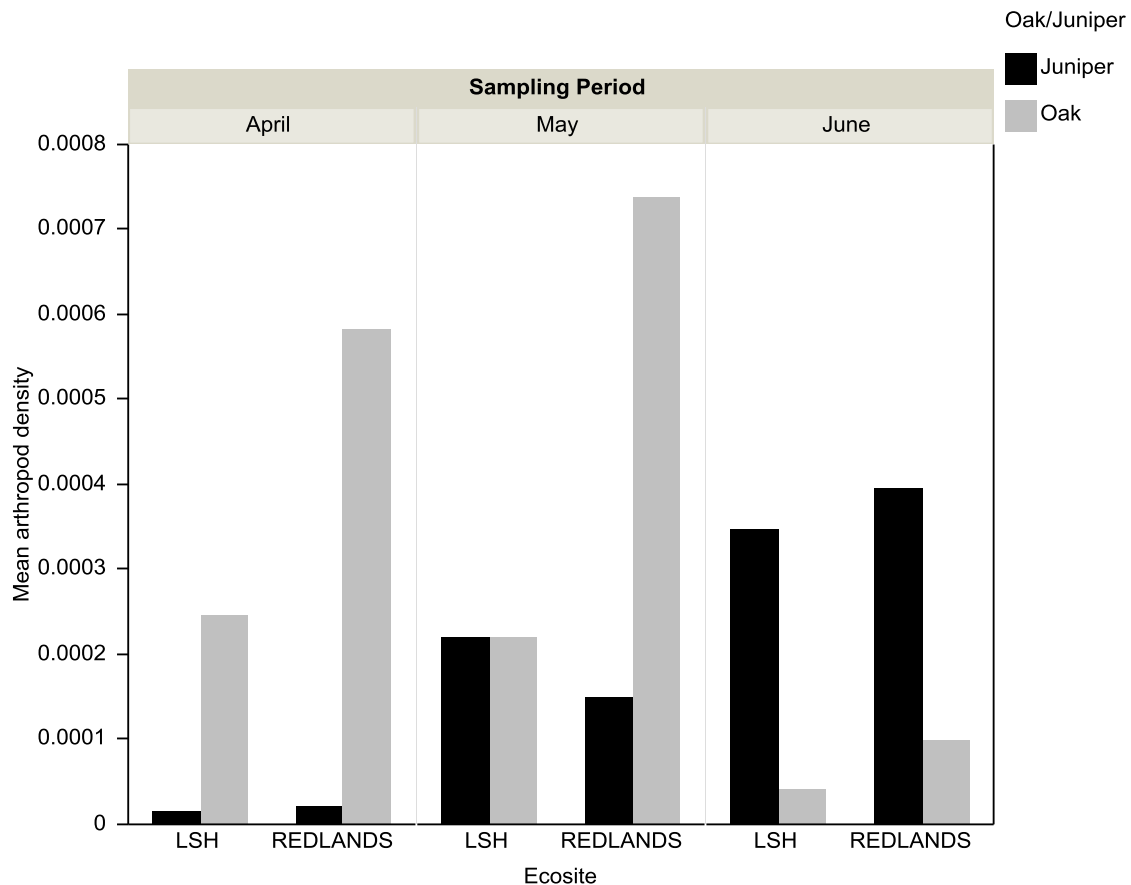


Figure 10. Arthropod density vs. ecosite for oak and juniper through 3 sampling periods in 2009.

I sampled arthropods in 40 territories, 20 in the low stony hill site and 20 in the redlands site in 2010 (Table 6). Density of arthropods did not differ significantly between ecosites for all trees sampled ($t = 1.1701$, $df = 1$, $P = 0.2795$). Density of arthropods did not differ significantly between ecosites for juniper ($t = 3.6184$, $df = 1$, $P = 0.0574$) or oak species ($t = .5248$, $df = 1$, $P = 0.4690$). Although there were no statistically significant differences in arthropod density between ecosites, a few trends

were obvious (Figure 11). In both ecosites, density of arthropods on juniper was low in April and increased during May and June. In both ecosites, density of arthropods was higher on oak species in April compared to juniper, but the pattern in arthropod density on oaks between the two sites was quite different throughout the entire season. In the low stony hill site, arthropod density on oaks increased from April to June. In the redlands site, arthropod density on oaks decreased from April to June.

Table 6. Density of Arthropods by Tree Species by Ecosite (2010). Values refer to the density of arthropods (weight of arthropods/weight of branch, in milligrams) on 3 focal tree species, for 3 sampling periods in 2010. Sample size (n) refers to the number of branches sampled.

	<u>Low Stony Hill</u>			<u>Redlands</u>		
	<i>April</i>	<i>May</i>	<i>June</i>	<i>April</i>	<i>May</i>	<i>June</i>
Juniper	0.0120 (n=153)	0.076 (n=151)	0.130 (n=151)	0.017 (n=169)	0.100 (n=169)	0.429 (n=167)
Live Oak	0.341 (n=23)	0.114 (n=24)	0.297 (n=24)	2.364 (n=60)	0.293 (n=40)	0.118 (n=48)
Post Oak	0.287 (n=12)	0 (n=8)	0.012 (n=4)	0.357 (n=41)	0.349 (n=71)	0.717 (n=64)
Shin Oak	0.346 (n=43)	0.269 (n=57)	0.412 (n=52)	0.408 (n=24)	0.044 (n=19)	0.072 (n=24)
Texas Oak	0.209 (n=72)	0.686 (n=63)	0.867 (n=72)	0.050 (n=39)	1.517 (n=33)	0.096 (n=32)

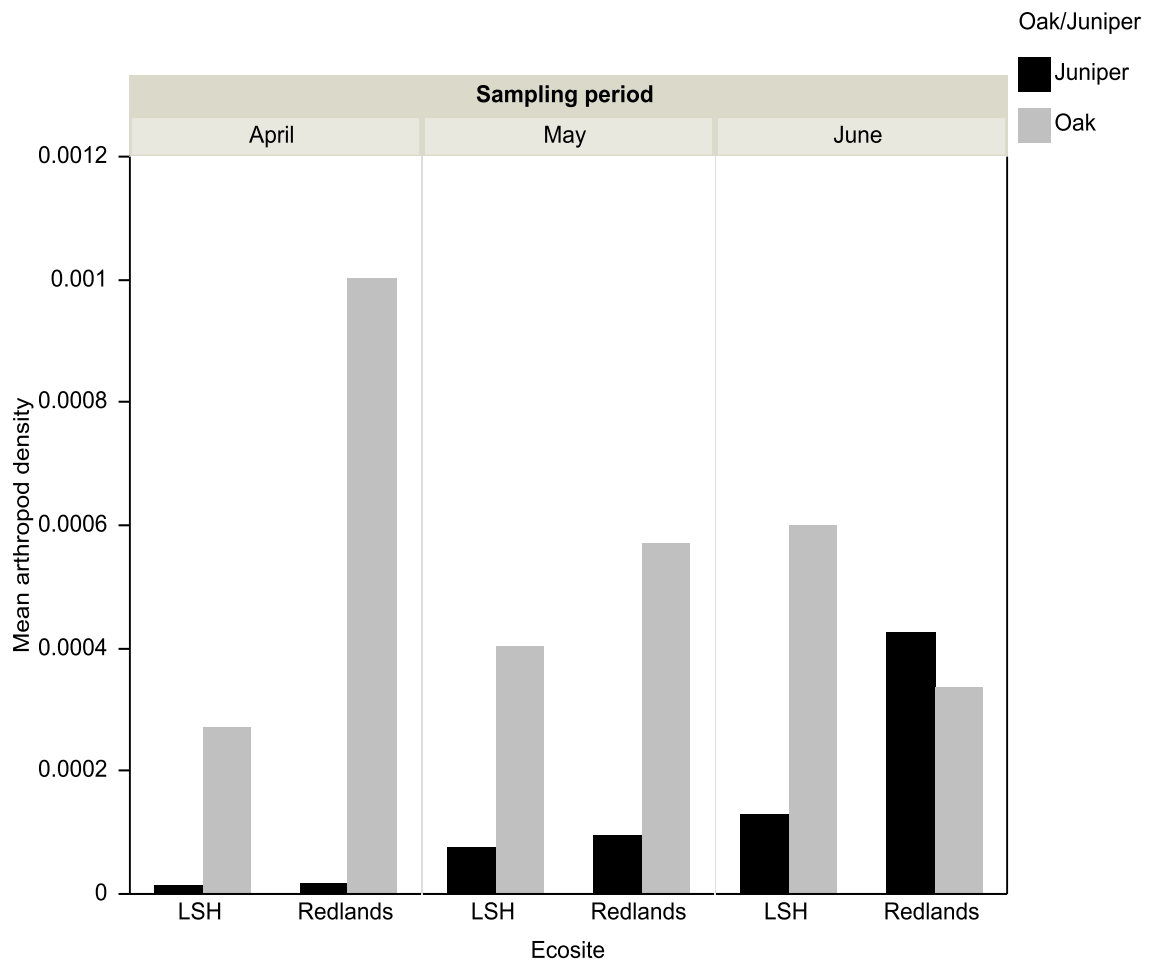


Figure 11. Arthropod density vs. ecosite for oak and juniper through 3 sampling periods in 2010.

I identified all arthropods to order so more specific comparisons could be made between ecosites. A few interesting patterns emerged when looking at density between different arthropod orders. There were no significant differences in density of arthropod orders between ecosites ($t = 1.1701$, $df = 1$, $P = 0.2795$; Table 7). I ran one-way

ANOVAs to see if there were significant differences in density of arthropod orders on the 6 tree species in which I took branch clippings ($n = 1903$). Coleoptera ($F = 4.1630$, $df = 5$, 1903 , $P < 0.05$), Homoptera ($F = 3.4831$, $df = 5$, 1903 , $P < 0.05$), and Lepidoptera ($F = 2.6884$, $df = 5$, 1903 , $P < 0.05$) had significantly different densities on different tree species (Figure 10). Live oak, shin oak, and Texas oak samples all had a similar proportion of arthropod orders. Lepidoptera made up the majority of the arthropod diversity found on these trees. In contrast, post oak and blackjack oak samples had a high proportion of Coleoptera and Homoptera. Lepidoptera made up only a small part of the arthropod diversity on post oak and blackjack oak. It is clear that although the focal oak species in this study (i.e. Texas oak and post/blackjack oak) had similar total arthropod densities, they differed in the proportion of arthropod orders that make up this total density (Figure 12). A majority of the arthropods found on Texas oak belong to Lepidoptera, whereas post oak had much less Lepidoptera and much more Coleoptera and Homoptera.

Table 7. Density of arthropod orders by ecosite (2010). Values refer to density of various arthropod orders (weight of arthropod/weight of branch in milligrams) for territories within low stony hill and redlands sites. All three sampling periods are combined. *For orders Phalangida, Plecoptera, and Spirobolida, there were no specimens for low stony hill sites, and density values for redlands are based off of a single sample.

<i>Arthropod order</i>	<i>Low Stony Hill</i>	<i>Redlands</i>	<i>t-Ratio</i>	<i>df</i>	<i>p-value</i>
Acarina	0.00104	0.00009	1.1407	1	0.2856
Araneida	0.01200	0.03000	0.8597	1	0.3539
Coleoptera	0.01400	0.02700	1.0849	1	0.2977
Diptera	0.00099	0.00089	0.0147	1	0.9035
Hemiptera	0.01500	0.01500	0.0006	1	0.9799
Homoptera	0.02400	0.05000	1.1780	1	0.2779
Hymenoptera	0.00105	0.00213	1.3797	1	0.2403
Isopoda	0.00073	0.00168	0.7013	1	0.4024
Lepidoptera	0.07200	0.16000	1.1181	1	0.2905
Mecoptera	0.00009	0.00019	0.2244	1	0.6358
Neuroptera	0.00014	0.00003	0.6080	1	0.4356
Orthoptera	0.08300	0.04100	0.8904	1	0.3455
Phalangida*	0	0.00004	0.9017	1	0.3424
Plecoptera*	0	0.00003	1.2250	1	0.2685
Spirobolida*	0	0.00666	4.4036	1	0.0360
Total	0.24900	0.40300	1.1701	1	0.2795

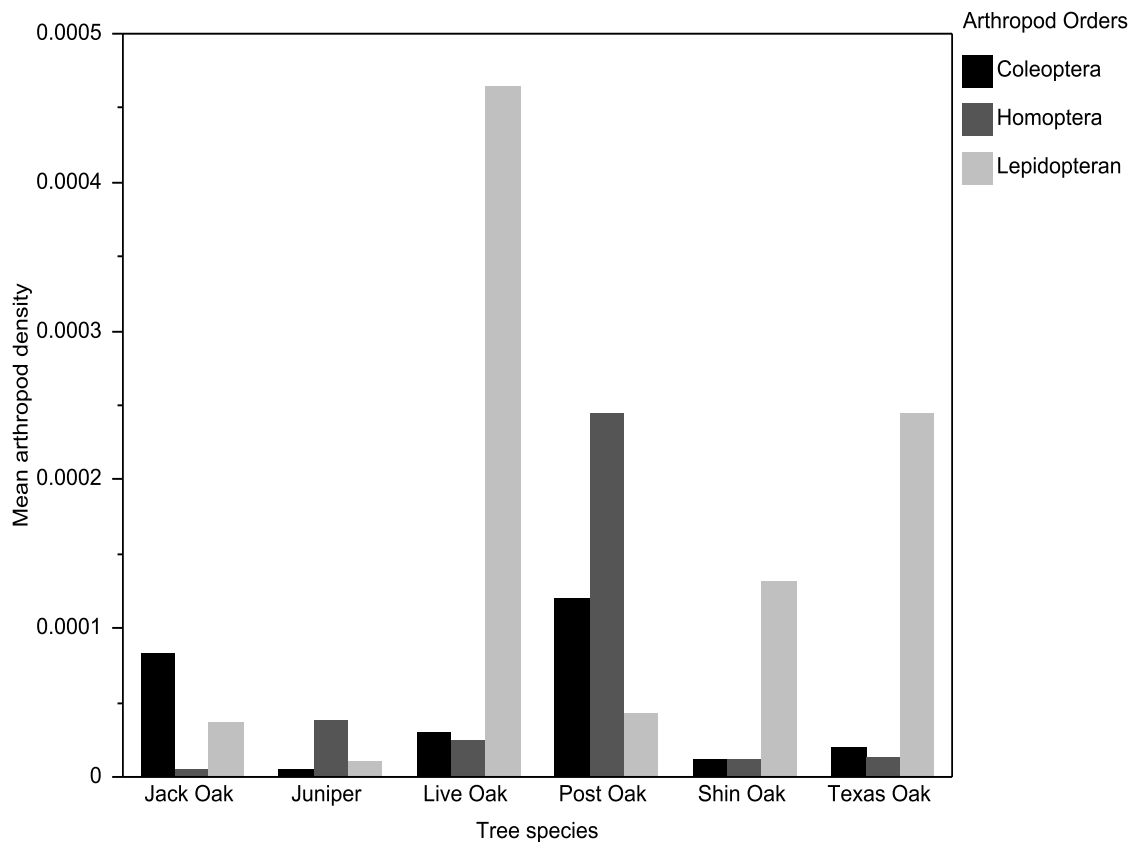


Figure 12. Mean arthropod density for three arthropod orders that differed significantly between 6 tree species sampled at study sites in central Texas within the 2010 study year.

Density of arthropod orders ($n = 13$) changes throughout the breeding season on different tree species (ANOVA, $F = 2.1201$, $df = 13, 1903$, $P < .05$; Figure 12). In April, when warblers are foraging mainly on oak species, live oak has a significantly higher total density of arthropods (ANOVA, $F = 2.66$, $df = 5, 633$, $P < 0.05$), specifically in the order Lepidoptera (ANOVA, $F = 2.69$, $df = 5, 633$, $P < 0.05$). In the low stony hill

ecosite, where Texas oak is more abundant, warblers are foraging preferentially on Texas oak during April but use live oak in proportion to what is available (Figures 8&9). Interestingly, in the redlands ecosite, where post oak is more abundant, warblers are not foraging preferentially on post oak, but instead use live oak at a much higher rate than is available (Figures 8&9).

My results reveal a few arthropod explosions in the May sampling period (Figure 13). There is a nine-fold increase in Lepidopteran density from April to May on Texas oak. At this time, warblers in both ecosites use Texas oak proportional to their availability, but start foraging on juniper at a much higher rate than what is available. This switch in foraging substrate could be explained by the explosion of arthropods seen on juniper between April and May. In April, juniper is nearly devoid of arthropods, but has a three-fold increase in Lepidoptera and a twenty-fold increase in Homoptera. Juniper has the highest density of Homoptera in May (ANOVA, $F = 3.67$, $df = 5, 629$, $P < 0.05$), the same month warblers foraged proportionally more on juniper.

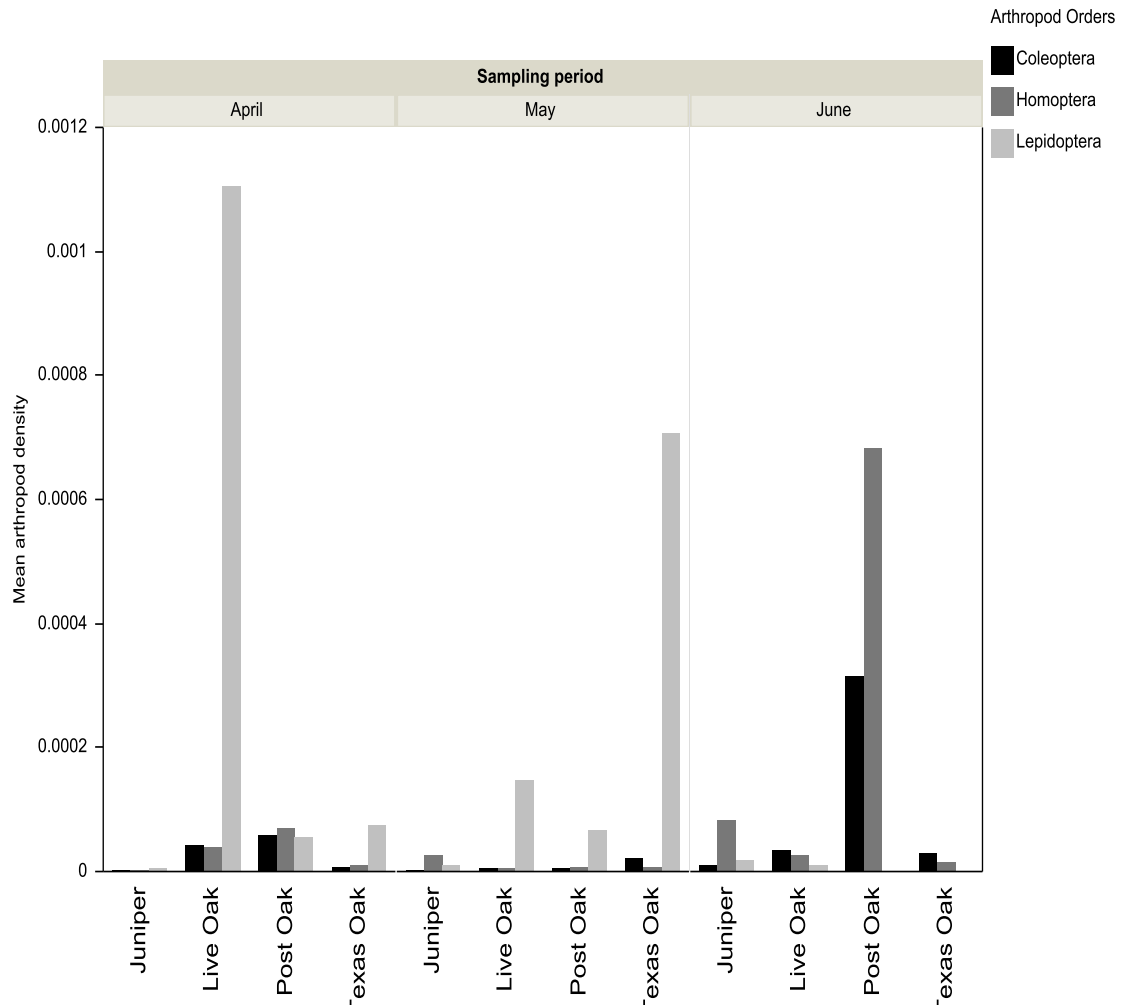


Figure 13. Phenology of three arthropod orders over three sampling periods in 2010.

DISCUSSION

Golden-cheeked warbler pairing and reproductive success were much higher in low stony hill sites compared to redlands sites, and territories in low stony hill sites have significantly more Texas oak available, on average, than territories in the redlands sites. All patches surveyed were of sufficient size (>30 hectares) and had adequate amounts of juniper for nesting. Also, all patches had at least 50% canopy cover, there were no significant differences in canopy cover between ecosites, and canopy cover was not a useful predictor in whether a territory fledged young. All of this information taken in aggregate, makes it likely that tree species composition within these ecosites is acting as a proximate factor affecting reproductive success.

To begin to answer the question of why tree species composition would affect avian productivity, we must unravel how tree species composition may be acting as a proxy for food availability. The abundance of resources, primarily food, provides an important check on population numbers (Newton 1993). In temperate forests, food appears to be the most important factor in reproductive success, and its availability frequently limits reproductive output (Holmes et al. 1986). When migratory birds such as the golden-cheeked warbler arrive upon the breeding grounds, they must quickly assess food supply. Direct assessment of a complex food supply for an insectivore may be difficult if not impossible (Tye 1992), so they 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 who returns from migration

in early-March, probably before the availability of food is apparent. Most of the deciduous trees are still devoid of leaves at this time, and because insect abundance is highly correlated with the phenology of the vegetation, making a direct assessment of arthropods before leaves begin to bud out, would be improbable at best (Tye 1992).

Results of the foraging surveys hint at the importance of food availability in this system. Redlands sites had lower pairing and fledging success in both years, but it was in 2009 that the difference was the greatest. In 2009, golden-cheeked warblers in redlands sites were moving around at a much greater rate during foraging bouts, especially in regards to flights of greater than two meters. Increased movement rate has implications for reproductive success. Food availability affects bird foraging behavior and consequently their reproductive success, as well as their ability to feed young. Movement rate should increase when a bird is in a relatively food-poor area (Hutto 1990), and area-restricted searching would also predict a faster rate of beeline progression with a decrease in prey availability (Hutto 1990). The increase in pairing and fledging success seen in 2010 could be due to a combination of differential precipitation between years driving different patterns in arthropods, and the fact that redlands territories in 2010 had, on average, more Texas oak compared to redlands territories in 2009. Texas oak is an important foraging substrate for golden-cheeked warblers, and it seems as if the more Texas oak there is in a given territory, the less the bird has to move around while foraging, perhaps leaving the bird with more time to be vigilant at the nest. Future studies should expand on this work to attempt to link nest attentiveness with food availability and tree species composition.

It is clear that overall density of arthropods alone does not seem to be driving productivity in this system. It seems logical based on the results of this study that the order Lepidoptera is important for golden-cheeked warblers as a food source during the breeding season. Perrins (1991) concluded that female British Tits start breeding as soon as caterpillars, or some other foods, are available and, as a result, timed their breeding to have their nestlings when caterpillars were most abundant. Pulich (1976) pointed out the close relation between the breeding time of golden-cheeked warblers and the appearance of numerous soft-bodied Lepidopteran larvae in deciduous trees such as Texas oak and shin oak. The existence of this relationship is supported by the observations of Kroll (1980), Sexton (1987), and Beardmore (1994) that golden-cheeked warblers spend disproportionately more time in oaks (compared to the relative abundance of oaks) than in junipers. Beardmore (1994) also determined that golden-cheeked warblers did not show this strong preference for oaks later in the season, but split their foraging time between oaks and junipers. Not only have Lepidoptera been shown to be exceptionally abundant as caterpillars on Texas oak and live oak early in the breeding season, but they have also been shown to be the most abundant material in gut content analyses of golden-cheeked warbler (Pulich 1976, Wharton 1996, Newnam 2008, Texas A&M University, unpublished data). The results of this study have confirmed the importance of Texas oak and live oak as foraging substrates early in the season, and that these oak species also have a high density of Lepidoptera compared to other available tree species during this time (Figure 8). Also, golden-cheeked warbler territories begin to break down in the month of June, the same time that essentially all

Lepidoptera are devoid from trees within the territories (Figure 11). All of these facts taken in tandem underline the importance of this order as prey for golden-cheeked warblers.

The importance of Ashe juniper for nesting material is well noted (Pulich 1976, Ladd and Gass 1999, DeBoer and Diamond 2006, Magness et al. 2006), but its importance as a foraging substrate is relatively unexplored. It is clear that juniper is a critical foraging substrate for golden-cheeked warblers, especially in the month of May. Golden-cheeked warblers are using juniper as a foraging substrate 20-30% more than is available within a territory in May, and use of juniper increase by as much as 70% from April to May. Interestingly, juniper has a much lower density of total arthropods and Lepidoptera in May. Why are they using primarily juniper as a foraging substrate in May? Perhaps Homoptera is an important part of the golden-cheeked warbler's diet during this time. Juniper is the most dominant tree in this system, and juniper has a higher density of Homoptera compared to all other tree species during May. In May, by chance alone, golden-cheeked warblers would likely encounter Homoptera at a high rate, making it a logical prey choice for these birds. Another potential explanation for the high use of juniper during May could be related to prey detectability and avian perception and capture capabilities. Prey availability is not only influenced by the abundance and types of prey but also by the foliage structure and characteristics of the trees, which influence prey detectability and accessibility, and the morphological and behavioral abilities of each bird species to perceive and capture those prey (Holmes and Schultz 1988). Whatever the reason for increased use of juniper may be, it is clear that

juniper is a critical foraging substrate, and informed management should take this fact into account.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Results of my study could be critical to private land managers and many managing agencies including Texas Parks and Wildlife and US Fish and Wildlife Service.

Recovery requires that there is a high probability of persistence of a viable population for the foreseeable future, meaning that not only factors leading to presence or absence of a species are important, but factors leading to high levels of productivity are critical for long term management of endangered species. Results of this study can be used to indicate areas that should be targeted for conservation by local, state, and federal government because they provide high quality habitat based on warbler productivity. Current management guidelines for golden-cheeked warblers are focused on canopy cover playing a large role in determining high quality habitat (Campbell 2003). The

results of my study indicate canopy cover was not a good predictor of whether a territory successfully fledged young, rather the tree species composition was an important factor in determining warbler productivity.

The role of juniper as a foraging substrate has been overlooked, or at the very least, downplayed. Juniper is seen primarily as a source of nesting material, but evidence suggests only a few are needed for this purpose (Campbell 2003). The belief that the primary importance of juniper is for nest material, could lead to the idea that selective removal of small juniper trees will lead to little or no impact on the persistence of the golden-cheeked warbler. However, removal of juniper affects tree species composition of the area, and the relative importance of juniper and oak species for golden-cheeked warbler foraging is not well studied. This study indicates that juniper is a critical foraging substrate for the golden-cheeked warbler. The current management guidelines require 15 mature juniper stems (Campbell 2003), but this was based on the idea that juniper was required for nesting. If juniper is critical for foraging and nest building, perhaps 15 stems would be insufficient to support breeding pairs of golden-cheeked warblers.

Declining oak regeneration is listed as an under-studied secondary factor potentially affecting the long term persistence of golden-cheeked warblers (USFWS 1992). One of the main reasons for habitat loss is clearing of juniper, and to a lesser extent hardwoods, to improve conditions for cattle grazing residential development, and military training amongst others (USFWS 1992, Ladd and Gass 1999, Campbell 2003). These human driven mechanisms of vegetation loss, coupled with the idea that

destruction of oaks via various fungal infections such as oak wilt reduces habitat quality for golden-cheeked warblers (Johnson and Appel 1984; USFWS 1992), underlines the importance of future studies integrating ideas of regeneration. The knowledge that oak composition seems to driving reproductive success in this study, highlights the importance of knowing what an area will look like after thinning of juniper or loss of hardwoods, particularly oak species, has occurred. Will the soil support a diverse community of hard woods? Which soil types support which tree species? Do oaks regenerate at different rates in different areas? Questions such as these will be important questions to address as we look to restore and maintain optimal breeding habitat for these endangered birds.

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