COMPLETING THE ANNUAL CYCLE: INVESTIGATING THE NON-BREEDING

ECOLOGY OF TWO NEOTROPICAL MIGRANTS

A Dissertation

by

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ABSTRACT

A large majority of migratory bird research has focused on activities on the breeding grounds, but migratory birds spend most of the year engaged in non-breeding activities. To complete some of the knowledge of each bird's annual cycle, I conducted research on the non-breeding ecology of two federally endangered neotropical migrant songbirds, Golden-cheeked Warbler (*Setophaga chrysoparia*) and Black-capped Vireo (*Vireo atricapilla*), that breed in the Texas hill country.

After breeding but before migration, researchers have observed Golden-cheeked Warblers using vegetation different from their breeding vegetation of oak-juniper woodland. To determine vegetation associations during the post-breeding period of 2010-2012, I conducted surveys at 34 locations composed of breeding vegetation in the low stony hill or redlands ecosites and the immediately adjacent non-breeding vegetation made of oak woodland, oak savannah, or riparian strips. Warblers used breeding vegetation more commonly than non-breeding vegetation. Among detections in breeding vegetation, I found warblers most commonly in the low stony hill ecosite which is considered to be the highest quality ecosite type based on breeding success. When I found warblers in non-breeding vegetation, they were most often in riparian strips and oak woodlands adjacent to the low stony hill ecosite. Neither canopy cover nor territory density had a significant relationship on detection rate during the post-breeding period. When I found warbler groups, they were most commonly composed of family groups or lone males that were foraging. These results indicate that, while Golden-cheeked Warblers do use vegetation other than breeding vegetation during the

post-breeding period, high quality breeding vegetation remains the most important vegetation type to these birds during this period of their annual cycle.

To determine the migratory connectivity, the degree to which breeding population structure is maintained on the wintering grounds, of Black-capped Vireos I collected feathers from 158 vireos across their breeding range in Texas and Oklahoma from 2010-2012. I analyzed stable hydrogen isotope composition in vireo feathers to establish a breeding range map to which others could compare feathers collected from birds on the wintering grounds. I found that, unlike most migratory bird species, Black-capped Vireo feather isotope ratios patterns do not match rainfall isotope ratio patterns. This species' feathers also do not follow patterns of groundwater hydrogen isotope ratios. Due to extreme variability of feather hydrogen isotope ratio, I was unable to use a stable isotope analysis to establish a functional breeding ground isotope map for use by other researchers. Other techniques are necessary to determine this important aspect of Black-capped Vireo's annual cycle.

DEDICATION

To My Family and Loved Ones

Rachel
You are the best chordate to whom I could possibly be pair-bonded

Steward, Helen, and Carlton
You are the best genetics experiments I have ever conducted

Mom, Dad, Greg, Brian, Eric, and Jarrod
Your genetic contribution, support, patience, and pestering made me who I am

ACKNOWLEDGMENTS

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CHAPTER I

INTRODUCTION

Conservation efforts for migratory songbirds have historically focused on the

breeding grounds. While breeding success and the ecological circumstances surrounding

that success are clearly important, the breeding season often encompasses much less than

one half of the annual cycle. A clear picture of the evolution, ecology, and conservation

of migratory songbirds requires an understanding of the entire annual cycle (Myers et al.

1987, Faaborg et al. 2010). Complete study of the annual cycle includes the study of

survival, foraging success, and other interactions during the post-breeding period after a

bird ceases breeding behavior but has not migrated to wintering grounds. Additionally,

ecological interactions on the wintering ground affect success on the breeding ground

(Fretwell 1972). Studies have shown this is true of migratory birds that experience

carryover effects between the wintering and breeding grounds of neotropical migrants

(Robbins et al. 1989; Marra et al. 1998; Gill et al. 2001; Norris et al. 2004a,b; Saino et

al. 2004, Harrison et al. 2011, Alves et al. 2013). I have two main objectives for my

study. I first looked at the vegetation associations and behavior of Golden-cheeked

Warbler (*Setophaga chrysoparia*), a federally endangered songbird that breeds in the

Texas hill country, during the post-breeding period. Next, I used a stable isotope

analysis approach to determine the migratory connectivity of Black-capped Vireo (*Vireo

atricapilla*), a federally endangered songbird that breeds in northern Mexico, the Texas

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hill country, and southeast Oklahoma. Migratory connectivity relates population

structure on the breeding ground to population structure on the wintering ground and

helps to inform conservation biologists on priorities for conservation in both

geographical locations a migrant occupies during the annual cycle. Both objectives

target questions for which we currently have no answers regarding the conservation

status of each species and can aid in the recovery of each species.

Post-Breeding Habitat Use of Golden-Cheeked Warbler

The post-breeding period, or time between fledging and the onset of migration, is

the portion of the avian annual cycle about which we know the least (Pärt 1990; Morton

1991; Baker 1993). Because of this lack of knowledge, researchers are unsure about the

importance of the post-breeding period in the ecology and conservation of migratory

birds (Vega Rivera et al. 1998a). Some known information about survival during the

post-breeding period indicates that this time is critical for many migratory species.

Studies have shown that the period of heaviest juvenile and adult mortality is during the

post-breeding period (Dhondt 1979; Krementz et al., 1989; Sullivan 1989; Anders et al.

1997; Thomson, Baillie, and Peach 1999; Sillett and Holmes 2002). This period of

increased risk of mortality may last several months for single-brood species that fledge

early in the breeding season (Faaborg et al. 1996; Anders et al. 1998). This prolonged

amount of time increases risk of mortality due to predation for juveniles which are

inexperienced foragers (Pagen et al. 2000) and adults of species that undergo complete

pre-basic molt and, consequently, need more food to meet energetic demands (Ralph et

al. 1993; Murphy 1996; Pyle 1997; Pagen et al. 2000; Stoleson 2013). This post-

breeding and post-fledging period can be an overlooked period of the annual cycle during which management of a species is critical.

Habitat associations are an intensely studied aspect of wildlife research (Manly et al. 2002; Morrison 2001, Morrison et al. 2006) because information about habitat relationships is important to conservation and management (Barry and Elith 2006). One poorly understood aspect of habitat associations is post-breeding habitat use of adults and fledglings. This poor understanding exists because fledglings and adults are difficult to follow as they move away from the nest site (Nolan 1978; Haas 1995) during the post-breeding period. Some have suggested that after leaving the nest, fledglings begin a slow migration (Hann 1937, Bent 1953, Pulich 1976), whereas others have observed fledglings staying in the vicinity of the nest site but moving into habitats other than the breeding habitat (Nolan 1978; Rappole and Ballard 1987; Bocetti 1993). Some researchers have started to examine habitat associations in the post-breeding period between fledging and migration (Rappole and Ballard 1987; Anders et al. 1998; Vega Rivera et al. 1999; Pagen et al. 2000; Lang et al. 2002; Vormwald et al. 2011).

Studies have shown that several species of passerines leave their typical breeding habitat and occupy alternate habitat during the post-breeding period. Radio-telemetry studies of juvenile and adult Wood Thrush (*Hylocichla mustelina*) revealed that both move out of mature forest breeding habitat into early- and mid-successional forests after breeding and fledging (Anders et al. 1998; Vega Rivera et al. 1998a, 1998b). Pagen et al. (2000) found that adults and juveniles of several upland forest breeding-species are significantly more abundant in early-successional habitats during the post-fledging

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period. Other studies have shown that mature forest species move into early-successional habitats after fledging and nesting are complete (Marshall et al. 2003; Vitz and Rodewald 2006). Akresh et al. (2009) found that Ovenbird (*Seiurus aurocapilla*) juveniles and adults that hatched or bred in upland forests moved to riparian forest habitats in the post-fledging period. Vormwald et al. (2011) found that Willow Flycatchers (*Empidonax traillii*) and Dusky Flycatchers (*E. oberholseri*), which breed in the meadows of central Sierra Nevada, California, often remain in those meadows during the post-fledging period but also move away from natal meadows into upland forests. During this period dispersal into different vegetation and behaviors within each habitat could be critical to fledgling and adult survival. A better understanding of post-breeding dispersal is necessary to understand the ecology and subsequent management of many species.

Habitat quality, measured through some aspect of fitness (i.e. reproductive output) (Morrison 2001, Morrison and Hall 2002), can be studied in many ways. Presence or absence in non-breeding vegetation has inappropriately been used as a way to measure the quality of that vegetation to a species. While presence-absence data can help estimate density and abundance and define distribution (Brotons et al. 2004) it does not have a clear relationship to habitat quality. Habitat selection models predict that high-quality habitats should be occupied more consistently and for longer periods when compared to lower quality habitats (Johnson 2007) but others provide both hypothetical and empirical examples where high density populations achieved low reproductive success (van Horne 1983; Vickery et al. 1992). Many other aspects of the habitat can be

indicators of quality to a species. Other researchers have used structural components, such as song perch availability, as an index of quality (Lack and Venables 1939, Sheldon 1967, Verner et al. 1986). Predation risk can affect the use of high quality habitat (Creel et al. 2005, Fortin et al. 2005, Mao et al. 2005) because individuals learn to avoid areas with elevated risk (Kauffman et al. 2007) or experience reduced foraging efficiency because of increased need for vigilance (Fortin et al. 2004). The presence of a variety of plant species, which influences arthropod abundance, can also be an important factor in determining the quality of habitat because it can lead to increased foraging efficiency (Holmes and Robinson 1981, Robinson and Holmes 1984, Wiens 1985).

All of the previously mentioned habitat characteristics have been used to study habitat quality. However, behavior, one metric I will use to assess use of a vegetation type, can indicate habitat quality and the reasons why a bird has chosen to use a patch of vegetation. Foraging strategy models predict that animals in resource-rich habitat will spend less time foraging and more time engaged in other activities than those in poor environments (McNamara and Houston 1987; Werner and Anholt 1993; Anholt and Werner 1998; Brown 1999; Olsson and Holmgren 1999) because search effort in high-quality habitat is reduced (Blake and Hoppes 1986). Foraging behavior can be analogous to estimates of prey availability (Hutto 1990, Lovette and Holmes 1995) and suggest habitat quality. Recent studies have found a positive relationship between avian attack rate (i.e. number or proportion of prey capture attempts) and prey density (Delestrade 1999; Shepherd and Boates 1999). Lyons (2005) found that attack rates were higher in high-quality habitat (defined based on prior knowledge of differential

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reproductive output) but movement rates were similar in high and low quality habitat. An understanding of the behavior of a species in a habitat can help researchers determine quality and if habitat is used as a travel corridor, foraging area, or otherwise. If a bird moves through an area and does not feed, the area is likely less important than an area where foraging is observed.

Behavior can determine how non-breeding habitat is used during the post-breeding season but it does not allow us to determine why birds move away from breeding habitat and into non-breeding habitat in the post-breeding season. Researchers have suggested that, as the breeding season draws to a close, food availability may be higher in non-breeding habitats than in breeding habitat (Rappole and Ballard 1987; Anders et al. 1998, Pagen et al. 2000; Vitz and Rodewald 2007) and may draw post-breeding birds out of breeding vegetation and toward other vegetation types. Because insect productivity is tied with vegetative diversity (Webb 1989; Tye 1992), comparing areas with described varying vegetative compositions and, subsequently, varying arthropod abundance would allow us to determine if food availability within the breeding habitat patch is related to insectivore movement into non-breeding habitat. Competition over available food resources could also drive movement into non-breeding vegetation. Many theoretical (Wu et al. 1993, Scheuring and Janosi 1996, Veit and Lewis 1996, Foppen et al. 2000) and a few empirical (reviewed in Travis and French 2000 and Lambin et al. 2001) studies have shown density-dependent dispersal in several taxa. However, studies on vertebrate taxa are rare and methods and interpretation of results are ambiguous (Matthysen 2005). Based on demographic models and limited

empirical results, it is generally accepted that in areas of higher territory density, competition may force some individuals to seek foraging opportunities outside of normal breeding vegetation. Many factors, only some of which I investigated, can contribute to movement during the post-breeding season.

I investigated the use of post-breeding habitat by the federally-endangered Golden-cheeked Warbler. Large amounts of research into breeding habitat use and modeling of this species has been conducted to aid in its management and recovery (Ladd and Gass 1999; Groce et al. 2010). Some information from research in breeding habitat will guide my research in non-breeding habitat. For example, Marshall et al. (2013) assessed the impacts of tree species composition on reproductive output in two ecological sites (ecosites) in which Golden-cheeked Warblers commonly occur on Ft. Hood military instillation in central Texas. They found that warbler territories located within the low stony hill ecosite fledged young at a higher rate than territories in the redland ecosite. Marshall et al. determined that the difference in fledging success rate was likely due to difference in oak species; oak species in low stony hill ecosites are predominantly Texas oak (*Quercus buckleyi*) while in redlands ecosites, post oaks (*Q. stellata*) are the most common oak species. This result demonstrates that the low stony hill ecosite is of a higher quality than the redland ecosite when measured using the metric of reproductive output. I designed the present study to include and examination of the effects of habitat quality on post-breeding movement.   Because lower habitat quality (redland ecosite) offers fewer resources to its inhabitants, movement out of this ecosite late in the season is expected.

Little is known about habitat associations of the Golden-cheeked Warbler during the post-breeding period. Research need 1.22 of the Golden-cheeked Warbler recovery plan (USFWS 1992) states that knowledge of warbler movements during the post-breeding period "...is particularly important in relation to habitat types and quality and will be applied to further defining the habitat requirements of the species." All statements of Golden-cheeked Warbler habitat associations during the post breeding period are anectodal and do not reflect results of an empirical study. Researchers have reported seeing Golden-cheeked Warblers outside of breeding habitat after the breeding season. Keddy-Hector (1993) reported aggregations of up to 30 juvenile warblers in an upland oak savanna, and Ladd and Gass (1999) reported that juveniles may forage with mixed-species flocks in habitat that is more open than nesting habitat. Although observations of warblers in more open habitat are often made, no quantifiable research has been done to determine the importance of these habitats to the ecology of Golden-cheeked Warblers and if the current definition of protected habitat should be expanded to include

Migratory Connectivity of Black-Capped Vireo

Research and conservation efforts concerning migratory birds have traditionally focused on the breeding grounds because of the clear importance of breeding success. However, migratory birds spend a large part of the year away from be breeding grounds and are, therefore, exposed to many other ecological conditions absent on the breeding grounds. Fretwell (1972) argued that populations of species living in seasonal environments are subject to the interactions among those seasons. Studies have shown

this is true of migratory birds that experience carryover effects between the wintering and breeding grounds of neotropical migrants (Robbins et al. 1989; Marra et al. 1998; Gill et al. 2001; Norris et al. 2004a,b; Saino et al. 2004, Harrison et al. 2011, Alves et al. 2013). And, recent studies have shown that a bird's ecology on the wintering grounds can have substantial effects on fecundity and recruitment on the breeding grounds (Faaborg et al. 2010; reviewed by Webster and Marra 2005).

Migratory connectivity is the degree to which individuals or populations are geographically arranged among two or more periods of the annual cycle (Webster et al. 2002, Marra et al. 2006). Various degrees of connectivity lead to different conservation strategies (Webster et al. 2002, Webster and Marra 2005, Marra et al. 2006). If individuals and, by extension, populations maintain their associations from the breeding ground to the wintering ground (*i.e.* the same individuals associate with each other on both the breeding and wintering grounds), thus indicating strong connectivity, they may need unique management techniques because they can be thought of as separate populations. However, if individual associations and population structure on the breeding ground do not exist on the wintering ground (weak connectivity), management of populations as independent units may be less important (Marra et al. 2006).

Many methods have been employed to study the connectivity of migratory bird ecology. Morphological variation among populations of breeding birds has been used to assign birds on the wintering grounds to a breeding location (Ramos and Warner 1980; Ramos 1983; Bell 1997). In the absence of morphological variation, information about migratory connectivity can be obtained through individual mark-recapture techniques.

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This method is useful for large birds that can carry visible tags or game birds that are routinely collected through hunting. However, returns from this mark-recapture technique are often low and offer limited information about connectivity (Clark, et al. 2000; Stolt 2000). Genetic approaches have also been used to define migratory connectivity. Wenink and Baker (1996) and Haig et al. (1997) used mtDNA and randomly amplified DNA polymorphism, respectively, in shorebirds to define breeding populations. Each then used these genetically distinct population signatures to assign birds on the wintering grounds to populations on the breeding grounds. Along with each of these approaches, stable-isotope analysis (SIA) has been demonstrated as an option for studying migratory connectivity (Chamberlain et al. 1997, Rubenstein et al. 2002).

Isotopes of a given element possess the same number of protons but have differing numbers of neutrons, and, therefore, a different atomic mass (Reece et al. 2014). Stable isotopes are isotopes of a given element that do not radioactively decay and are, therefore, stable. In nature, stable isotopes of any element vary spatially relative to a variety of meteorological, climatic, and geographic processes such as rainfall amounts, latitude, altitude, seasonal temperature, and distance away from the marine coast (Tieszen and Boutton 1988, Bowen 2010) resulting in large, continent-wide patterns of stable isotope ratios. For example, hydrogen exists in two isotopes, ^{1}H (one proton and no neutrons in the nucleus) and ^{2}H ,also known as deuterium, (one proton and one neutron in the nucleus). Because deuterium is twice as heavy as ^{1}H, it behaves differently when exposed to the environmental processes above. These processes vary

along a spatial continuum and result in predictable hydrogen isotope ratios on a continental scale.

In recent years, researchers have found that the stable isotope ratios in tissues of organisms living in a given geographic location reflect the stable isotope ratios of that geographic location. The hydrogen ratio of a location is primarily dictated by the water in that location and the processes associated with that water (*e.g.* precipitation, evaporation, evapotranspiration, runoff). As plants in that location make use of the water, their biomass incorporates stable isotopes in similar ratios to the original water source. Likewise, any animals in the food web will have tissues with isotope ratios similar to the plants and water sources for those plants. For example, Lott and Smith (2006) collected contour feathers from 12 species of raptors across North America and analyzed them for Hydrogen isotope ratios. Using interpolation methods, the authors generated a North American map of raptor feather Hydrogen isotopes values and compared it with a model of predicted isotope ratios based on precipitation. They found that the feather isotope map and the precipitation map corresponded across most of North America.

Advances in the application of stable-isotope analysis (SIA) have proven useful in discerning the ecology of migratory birds throughout their annual cycle (Hobson 2005). Chamberlain et al. (1997) and Hobson and Wassenaar (1997) independently demonstrated that stable hydrogen isotope ratios (δD) found in the feathers of nearctic-neotropical migrants correlated with rainfall δD collected during the growing season (Boulet and Norris 2006). Birds make ideal study subjects for SIA because feathers are

metabolically inert and, therefore, retain the isotope ratios of locations in which they were grown. Through analysis of stable isotope ratios in feathers and comparison to existing, continent-wide gradients of isotope ratios created from precipitation, one can determine where the sampled feathers were grown. Using this method, researchers can link locations on the breeding grounds where feathers were grown to locations on the wintering grounds where feathers were collected and analyzed.

Numerous studies have taken the stable isotope approach to describe migratory connectivity. The American Redstart (*Setophaga ruticilla*) has been studied using δD and stable carbon isotope ratios (δ^{13}C) and was found to exhibit strong connectivity (Marra et al. 1998; Norris et al. 2005; Norris et al. 2006). Rubenstein et al. (2002) used δD and δ^{13}C and found that Black-throated Blue Warblers (*Setophaga caerulescens*) wintering on western Caribbean islands were strongly connected to populations breeding in the northern portions of this warblers' North American breeding range and those wintering on eastern Caribbean islands were strongly connected to populations breeding in southern portions of the breeding range. Flyways and connectivity of the Yellow Warbler (*Setophaga petechia*) have been revealed using δD (Boulet et al. 2006). Clegg et al. (2003) showed that Wilson's Warbler (*Cardellina pusilla*) demonstrates a leapfrog (Salomonsen 1955) pattern of migration and shows moderate migratory connectivity. The migratory connectivities of the following species are better understood because of the application of SIA: King Eider (*Somateria spectabilis*) (Mehl et al. 2004), Sharp-shinned Hawk (*Accipiter striatus*) (Smith et al. 2003), Red Knot (*Calidris canutus*) (Atkinson et al. 2005), Willow Warbler (*Phylloscopus trochilus*) (Chamberlain

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et al. 2000), Swainson's Thrush (*Catharus ustulatus*) (Wassenaar and Hobson 2001;

Kelly et al. 2005), Black-throated Blue Warbler (*Setophaga caerulescens*) (Chamberlain

et al. 1997, Rubenstein et al. 2002), Common Yellowthroat (*Geothlypis trichas*) (Kelly

2006), White-throated Sparrow (*Zonotrichia albicollis*) (Mazzerolle et al. 2005).

Application of stable isotope markers has primarily been used on long-distance

migrants occupying large breeding and wintering ranges (Webster et al. 2002) with few

exceptions (i.e. Mazzerolle et al. 2005, Mehl et al. 2004, Smith et al. 2003). Studies of

migratory connectivity at these coarse scales allow researchers to understand migratory

populations on a continent-wide scale. However, the biological implications of

connectivity studies are expected to become increasingly stronger as spatial scale

becomes more fine (Hjernquist et al. 2009). At these fine spatial scales, philopatry

becomes more important in limiting gene flow and indicates a need for unique

management of each population. Species that exist only on small spatial scales are

subject to the implications of migratory connectivity.

The Black-capped Vireo (*Vireo atricapilla*), an endangered songbird, is an

example of a short distance migrant that also occupies both a small breeding and a small

wintering range (Grzybowski 1995). The connectivity of this species is unknown and

could be critical to its proper management. Black-capped Vireo is a candidate for

studies of migratory connectivity because recent studies have found that it exhibits

breeding populations that are genetically distinguishable. Fazio III et al. (2004) and Barr

et al. (2008) both found significant interpopulation divergence of breeding populations

of Black-capped Vireos which allows researchers to identify an individual to a

population based on genetic markers. Although recent genetic research shows that populations of each species are diagnosably distinct, it is unclear whether SIA will be useful in determining migratory connectivity in the species because it breeds and winters on such fine spatial scales. Black-capped Vireo breeding range extends from western Oklahoma through central Texas and into Coahuila, Mexico (Grzybowski 1995). This breeding range is much smaller than the continent-wide ranges of previously mentioned passerines studied using SIA. Maps created from rainfall isotope ratios, the typical method of studying connectivity using SIA, lack the precision necessary to aid in understanding the vireo's migratory connectivity. A fine-scale isotope map is necessary to draw any useful conclusions from the study. To increase the accuracy of SIA, a map of isotope ratios created using feathers of known origin from the study species can be used. This increases the precision of the results needed to accurately infer migratory connectivity (K. Hobson, personal communication).

Using stable hydrogen isotope ratios gleaned from feathers cut from Black-capped Vireos across the breeding range in Texas and Oklahoma, I will develop a set of maps to be used in future migratory connectivity studies with this species. These maps will serve as a baseline against which future researchers can compare isotope ratios of vireo feathers collected on the wintering grounds. Ratios of winter-collected feathers can then be matched to the map's ratios to determine the most likely location where the feathers were grown during the previous breeding season. Through this comparison of ratios, one could determine the migratory connectivity of the Black-capped Vireo.

CHAPTER II

POST-BREEDING HABITAT USE OF GOLDEN-CHEEKED WARBLER

The post-breeding period, or time between fledging and the onset of migration, is the portion of the avian annual cycle about which we know the least (Pärt 1990; Morton 1991; Baker 1993). Because of this lack of knowledge, researchers are unsure about the importance of the post-breeding period in the ecology and conservation of migratory birds (Vega Rivera et al. 1998a). Some known information about survival during the post-breeding period indicates that this time is critical for many migratory species. Studies have shown that the period of heaviest juvenile and adult mortality is during the post-breeding period (Dhondt 1979; Krementz et al., 1989; Sullivan 1989; Anders et al. 1997; Thomson, Baillie, and Peach 1999; Sillett and Holmes 2002). This period of increased risk of mortality may last several months for single-brood species that fledge early in the breeding season (Faaborg et al. 1996; Anders et al. 1998). This prolonged amount of time increases risk of mortality due to predation for juveniles which are inexperienced foragers (Pagen et al. 2000) and adults of species that undergo complete pre-basic molt and, consequently, need more food to meet energetic demands (Ralph et al. 1993; Murphy 1996; Pyle 1997; Pagen et al. 2000; Stoleson 2013). This post-breeding and post-fledging period can be an overlooked period of the annual cycle during which management of a species is critical.

Habitat associations are an intensely studied aspect of wildlife research (Manly et al. 2002; Morrison et al. 2001, 2006) because information about habitat relationships is

important to conservation and management (Barry and Elith 2006). One poorly understood aspect of habitat associations is post-breeding habitat use by adults and fledglings. This poor understanding exists because fledglings and adults are difficult to follow as they move away from the nest site (Nolan 1978; Haas 1995) during the post-breeding period. Some have suggested that after leaving the nest, fledglings begin a slow migration (Hann 1937, Bent 1953, Pulich 1976), whereas others have observed fledglings staying in the vicinity of the nest site but moving into habitats other than the breeding habitat (Nolan 1978; Rappole and Ballard 1987; Bocetti 1993). Some researchers have started to examine habitat associations in the post-breeding period between fledging and migration (Rappole and Ballard 1987; Anders et al. 1998; Vega Rivera et al. 1999; Pagen et al. 2000; Lang et al. 2002; Vormwald et al. 2011).

Studies have shown that several species of passerines leave their typical breeding habitat and occupy alternate habitat during the post-breeding period. Radio-telemetry studies of juvenile and adult Wood Thrush (*Hylocichla mustelina*) revealed that both move out of mature forest breeding habitat into early- and mid-successional forests after breeding and fledging (Anders et al. 1998; Vega Rivera et al. 1998a, 1998b). Pagen et al. (2000) found that adults and juveniles of several upland forest breeding-species are significantly more abundant in early-successional habitats during the post-fledging period. Other studies have shown that mature forest species move into early-successional habitats after fledging and nesting are complete (Marshall et al. 2003; Vitz and Rodewald 2006). Akresh et al. (2009) found that Ovenbird (*Seiurus aurocapilla*) juveniles and adults that hatched or bred in upland forests moved to riparian forest

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Flycatchers (*Empidonax traillii*) and Dusky Flycatchers (*E. oberholseri*), which breed in

the meadows of central Sierra Nevada, California, often remain in those meadows during

the post-fledging period but also move away from natal meadows into upland forests.

During this period dispersal into different vegetation and behaviors within each habitat

could be critical to fledgling and adult survival. A better understanding of post-breeding

dispersal is necessary to understand the ecology and subsequent management of many

species.

Habitat quality, measured through some aspect of fitness (i.e. reproductive

output) (Morrison 2001, Morrison and Hall 2002), can be studied in many ways.

Presence or absence in non-breeding vegetation has inappropriately been used as a way

to measure the quality of that vegetation to a species. While presence-absence data can

help estimate density and abundance and define distribution (Brotons et al. 2004) it does

not have a clear relationship to habitat quality. Habitat selection models predict that

areas with all of the appropriate resources to have high reproductive output should be

occupied more consistently and for longer periods when compared to areas with fewer

resources (Johnson 2007) but others provide both hypothetical and empirical examples

where high density populations achieved low reproductive success (van Horne 1983;

Vickery et al. 1992). Many other aspects of the habitat can be indicators of quality to a

species. Other researchers have used structural components, such as song perch

availability, as an indicator of potential quality (Lack and Venables 1939, Sheldon 1967,

Verner et al. 1986). Predation risk can affect the use of habitat that would otherwise

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create high reproductive output (Creel et al. 2005, Fortin et al. 2005, Mao et al. 2005) because individuals learn to avoid areas with elevated risk (Kauffman et al. 2007) or experience reduced foraging efficiency because of increased need for vigilance (Fortin et al. 2004). The presence of a variety of plant species, which influences arthropod abundance, can also be an important factor in determining the quality of habitat because it can lead to increased foraging efficiency (Holmes and Robinson 1981, Robinson and Holmes 1984, Wiens 1985).

All of the previously mentioned habitat characteristics have been used to study habitat quality. However, behavior, one metric I will use to assess use of a vegetation type, can indicate the reasons why a bird has chosen to use a patch of vegetation. Foraging strategy models predict that animals in resource-rich habitat will spend less time foraging and more time engaged in other activities than those in poor environments (McNamara and Houston 1987; Werner and Anholt 1993; Anholt and Werner 1998; Brown 1999; Olsson and Holmgren 1999) because search effort in high-quality habitat is reduced (Blake and Hoppes 1986). Foraging behavior can be analogous to estimates of prey availability (Hutto 1990, Lovette and Holmes 1995) and suggest habitat quality. Recent studies have found a positive relationships between avian attack rate (i.e. number or proportion of prey capture attempts) and prey density (Delestrade 1999; Shepherd and Boates 1999). Lyons (2005) found that attack rates were higher in high-quality habitat (defined based on prior knowledge of differential reproductive output) but movement rates were similar in high and low quality habitat. An understanding of the behavior of a species in a habitat can help researchers determine quality and if habitat is used as a

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Behavior can determine how non-breeding habitat is used during the post-

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breeding birds out of breeding vegetation and toward other vegetation types. Because

insect productivity is tied with vegetative diversity (Webb 1989; Tye 1992), comparing

areas with described varying vegetative compositions and, subsequently, varying

arthropod abundance would allow us to determine if food availability within the

breeding habitat patch is related to insectivore movement into non-breeding habitat.

Competition over available food resources could also drive movement into non-breeding

vegetation. Many theoretical (Wu et al. 1993, Scheuring and Janosi 1996, Veit and

Lewis 1996, Foppen et al. 2000) and a few empirical (reviewed in Travis and French

2000 and Lambin et al. 2001) studies have shown density-dependent dispersal in several

taxa. However, studies on vertebrate taxa are rare and methods and interpretation of

results are ambiguous (Matthysen 2005). Based on demographic models and limited

empirical results, it is generally accepted that in areas of higher territory density,

competition may force some individuals to seek foraging opportunities outside of normal

breeding vegetation. Many factors, only some of which I investigated, can contribute to movement during the post-breeding season.

I investigated the use of post-breeding habitat by the federally-endangered Golden-cheeked Warbler (*Setophaga chrysoparia*). Large amounts of research into breeding habitat use and modeling of this species has been conducted to aid in its management and recovery (Ladd and Gass 1999; Groce et al. 2010). Some information from research in breeding habitat will guide my research in non-breeding habitat. For example, Marshall et al. (2013) assessed the impacts of tree species composition on reproductive output in two ecological sites (ecosites) in which Golden-cheeked Warblers commonly occur on Ft. Hood military instillation in central Texas. They found that warbler territories located within the low stony hill ecosite fledged young at a higher rate than territories in the redland ecosite. Marshall et al. determined that the difference in fledging success rate was likely due to difference in oak species; oak species in low stony hill ecosites are predominantly Texas oak (*Quercus buckleyi*) while in redlands ecosites, post oaks (*Q. stellata*) are the most common oak species. This result demonstrates that the low stony hill ecosite is of a higher quality than the redland ecosite when measured using the metric of reproductive output. I designed the present study to include an examination of the effects of habitat quality on post-breeding movement. Because lower habitat quality (redland ecosite) offers fewer resources to its inhabitants, movement out of this ecosite late in the season is expected.

Little is known about habitat associations of the Golden-cheeked Warbler during the post-breeding period. Research need 1.22 of the Golden-cheeked Warbler recovery

plan (USFWS 1992) states that knowledge of warbler movements during the post-breeding period "...is particularly important in relation to habitat types and quality and will be applied to further defining the habitat requirements of the species." All statements of Golden-cheeked Warbler habitat associations during the post breeding period are anectodal and do not reflect results of an empirical study. Researchers have reported seeing Golden-cheeked Warblers outside of breeding habitat after the breeding season. Keddy-Hector (1993) reported aggregations of up to 30 juvenile warblers in an upland oak savanna, and Ladd and Gass (1999) reported that juveniles may forage with mixed-species flocks in habitat that is more open than nesting habitat. Although observations of warblers in more open habitat are often made, no quantifiable research has been done to determine the importance of these habitats to the ecology of Golden-cheeked Warblers.

In addition to describing vegetation associations during the post-breeding period, I also wanted to describe movements based on warbler sex and age and which tree species are used commonly during this period. Dispersal during the post-breeding period has commonly focused on fledgling movements because fledgling survival is critical to population viability. In the present study, I want to quantify movements of both family groups (i.e. warbler groups with at least one adult and one fledgling) and individual adults to see if most movement into non-breeding vegetation primarily involves fledglings in family groups or just adults. Several studies have found prolonged parent-juvenile associations into the post-breeding period and suggest that the association may result from adults shifting juvenile philopatry in subsequent breeding

seasons (Drent 1984; Knopf and Rupert 1996; Mauser et al. 1994; Salinas-Melgoza and Renton 2007; Matthyson et al. 2010). A shift in philopatry would prompt juveniles to select breeding territories outside of their natal territory and reduce competition between adults and juveniles for mates and other resources.

Adult movement without fledglings can also help us understand the warbler's ecology during the post-breeding period. Adult sex-biased dispersal is generally attributed to a species' mating system (Dobson 1982; Moore and Ali 1984). Dispersal in polygynous species should be male-biased as younger, inexperienced, or unsuccessful breeding males would seek areas unoccupied by a dominant male in search of opportunities for greater fitness. Monogamous species should show approximately equal dispersal between sexes (Greenwood 1980) because males and females share nearly equal dispersal costs and benefits. However, most monogamous bird species show female-biased dispersal (Greenwood 1980). Based on these observations, Greenwood suggested that a system where males partition resources (i.e. acquire and defend a territory) prior to females selecting a mate should result in increased female dispersal. Females in this resource defense system would have a lesser investment in resources and more to gain in seeking a different breeding territory in subsequent years (i.e. better resources, inbreeding avoidance) than males of the same species (Greenwood 1980). Golden-cheeked Warblers are considered monogamous (Ehrlich et al. 1988) and males generally arrive before females to establish and defend territories. I would expect Golden-cheeked Warbler post-breeding dispersal to be female-biased.

The most common Golden-cheeked Warbler foraging substrates have been studied during the breeding season but nothing is known of which tree species they use during the post-breeding season. Marshall et al. (2013) found that during the breeding season, warblers foraged on oak species in April but switched to juniper in May. The authors also found a correlation between preferred foraging substrate and arthropod density suggesting that this switch probably results from a change in food availability on oaks and junipers. In the post-breeding period, I would expect to see use of juniper rather than oaks or other deciduous species as a foraging substrate in vegetation previously used for breeding. I will also examine which species are used most often in vegetation not used for breeding. These data will help me determine which non-breeding vegetation and tree species are most important to Golden-cheeked Warblers during the post-breeding period.

Objectives and Hypotheses

Objective 1: Determine which vegetative and demographic characteristics affect warbler presence during the post-breeding period:

> H1: Canopy cover will have a significant positive relationship with warbler presence in breeding and non-breeding vegetation.

> H2: When study areas are classified using dominant vegetation type, there will be no difference in detection among vegetation types.

> H3: There will be no difference in detection rate between non-breeding vegetation when the adjacent breeding habitat is part of the redland ecosite rather than the low stony hill ecosite.

> H4: There will be no difference between detection rates in breeding sublocations in the low stony hill and redlands ecosites.

> H5: Density of the adjacent breeding vegetation will have a significant positive relationship with presence in non-breeding vegetation.

Biological Significance: Based on the pilot study (see below for methods and results), one non-breeding vegetation type was used almost three times more often than any other categories. Other studies (Pagen et al. 2000, Akresh et al. 2009) captured many forest breeding species at rates over twice as high in non-breeding habitat than in breeding habitat. In the interest of being conservative, I considered presence that is twice as high in one category as the others to be biologically significant.

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Objective 2: Determine if age and sex affect the use of non-breeding habitat in the post-breeding period:

> H1: Among all warbler groups found, there will be no difference between the detection rate of family groups and individual adult warblers in non-breeding vegetation

> H2: There will be no difference between adult male and adult female detection rate in non-breeding vegetation.

Biological Significance: In the 2009 pilot season (see below for methods and results), 8 of 13 detections were family groups of warblers consisting of at least one adult and one juvenile warbler. I will consider a presence of family groups that is 50% greater than the presence of individuals to mean that family groups use non-breeding habitat more often than individuals. Additionally, 9 males and 4 females were detected in 2009. Pagen et al. (2000) also found that the males of many forest breeding species moved to non-breeding habitat at rates from twice to five times as high as females. Based on these rates, I will consider a male presence twice as high as that of females to mean that males use non-breeding habitat more often than females.

Objective 3: Determine the behavior of warblers in each vegetation type:

> H1: There will be no difference between frequency of observed foraging behavior (foraging or feeding nestlings) in breeding vegetation than in non-breeding vegetation.

> H2: There will be no difference between frequency of observed foraging behavior in low stony hill and redland ecosites.

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H3: There will be no difference between frequency of flights (both long and

short) in non-breeding vegetation and in breeding vegetation.

H4: There will be no difference in frequency of flights between redland ecosites

and low stony hill ecosites.

Biological Significance: I will consider any behavior rate to be higher in breeding or

non-breeding vegetation if the rate is 25% higher in one than the other. I will consider

behavior rates to be higher in the redland ecosite or the low stony hill ecosite if the rate

is 25% higher in one than the other.

Objective 4: Determine the substrate that is used most frequently in the post-breeding

period:

H1: There will be no difference between the use of deciduous substrates and

Ashe juniper in non-breeding vegetation.

H2: There will be no difference between use and availability of Ashe juniper and

other tree species as foraging substrates in breeding vegetation.

Biological Significance: In 2009, 80 of 110 recorded substrates were a live oak or

deciduous species. I considered warbler use of live oak or deciduous tree species to be

biologically significant if the proportion of these substrates is twice as high as the

proportion of juniper substrates. Conversely, in breeding vegetation, I will consider

warbler use of Ashe juniper that is twice as high as deciduous species to be biologically

significant.

Study Area

My study area covered approximately 1,850 hectares in Bell, Bosque, Coryell, Real, and Travis counties, Texas. In 2009 as part of a pilot study, I conducted surveys on 21 study sites (259 ha) on private properties in Bell, Coryell, and Bosque counties surrounding Ft. Hood Military Reservation and 9 study sites (128 ha) on private property in Travis County. In 2010, I surveyed 16 sites (822 ha) on Ft. Hood Military Reservation in Bell County. In 2011, I surveyed 6 sites (120 ha) on Big Springs Ranch, a 2,800-ha private property in Real County where most juniper-oak woodland has been left unaltered. In 2012, I surveyed 12 sites (521 ha) on Ft. Hood Military Reservation in Bell and Coryell counties. During each season, I selected all redlands sites available that clearly fit into both the breeding and non-breeding criteria (see methods below). Because there were limited redlands sites that met all required criteria, I used the number of redlands sites available to select low stony hill sites. Of the low stony hill sites available, I selected those nearest redlands sites to minimize differences in precipitation, human disturbance, and vegetative characteristics that could vary with greater distance from one location to another.

Each of the selected study sites is in either the Cross Timbers (sites in Bell, Coryell and Bosque counties) or Edwards Plateau (Real and Travis counties) ecoregions and contains populations of breeding Golden-cheeked Warblers. The sites in Bell, Bosque, and Coryell counties were located in one of two ecosites known to be suitable habitat for breeding warblers. While oak juniper woodlands are present in both ecosites, the oak component is predominately Texas oak in low stony hill ecosites and

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predominately post oak in redlands ecosites. All sites in Real and Travis counties are in low stony hill ecosites. Other plant species common to all sites included ashe juniper (*Juniperus ashei*), live oak (*Quercus virginiana*), cedar elm (*Ulmus crassifolia*), ash spp. (*Fraxinus* spp.), hackberry (*Celtis* spp.), and pecan (*Carya illinoinensis*).

The climate on Ft. Hood in Bell and Coryell counties is characterized by mild winters and warm summers. Average annual temperature in Killeen, the closest city to the 2010 and 2012 study sites on Ft. Hood is 18.9 ^{0}C (66.0 ^{0}C) and the average annual precipitation is 84cm (33.1") (Weatherbase.com 2014).   The average monthly temperatures in May-August in 2010 and 2012 were higher than 30 year averages and the monthly rainfall totals were lower than normal except for July 2010 (Fig. 2.1) (NCDC.NOAA.gov 2014).

The climate in Camp Wood, the closest city to the 2011 sites on the Big Springs Ranch in Real County is characterized by mild winters and warm summers as well. Average annual temperature in Camp Wood is 19 ^{0}C (66.2 ^{0}C) and the average annual precipitation is 69.9cm (27.5") (Weatherbase.com 2014). Average monthly temperatures in May-August in 2011 were higher than 30 year averages and monthly rainfall totals were lower than normal (Fig. 2.2) (NCDC.NOAA.gov 2014).

Differences in weather patterns between the Ft. Hood and Big Springs Ranch sites, particularly in 30 year monthly rainfall averages and actual rainfall totals could lead to differences in plant phenology, arthropod abundance and phenology, and as a result, warbler foraging behavior.
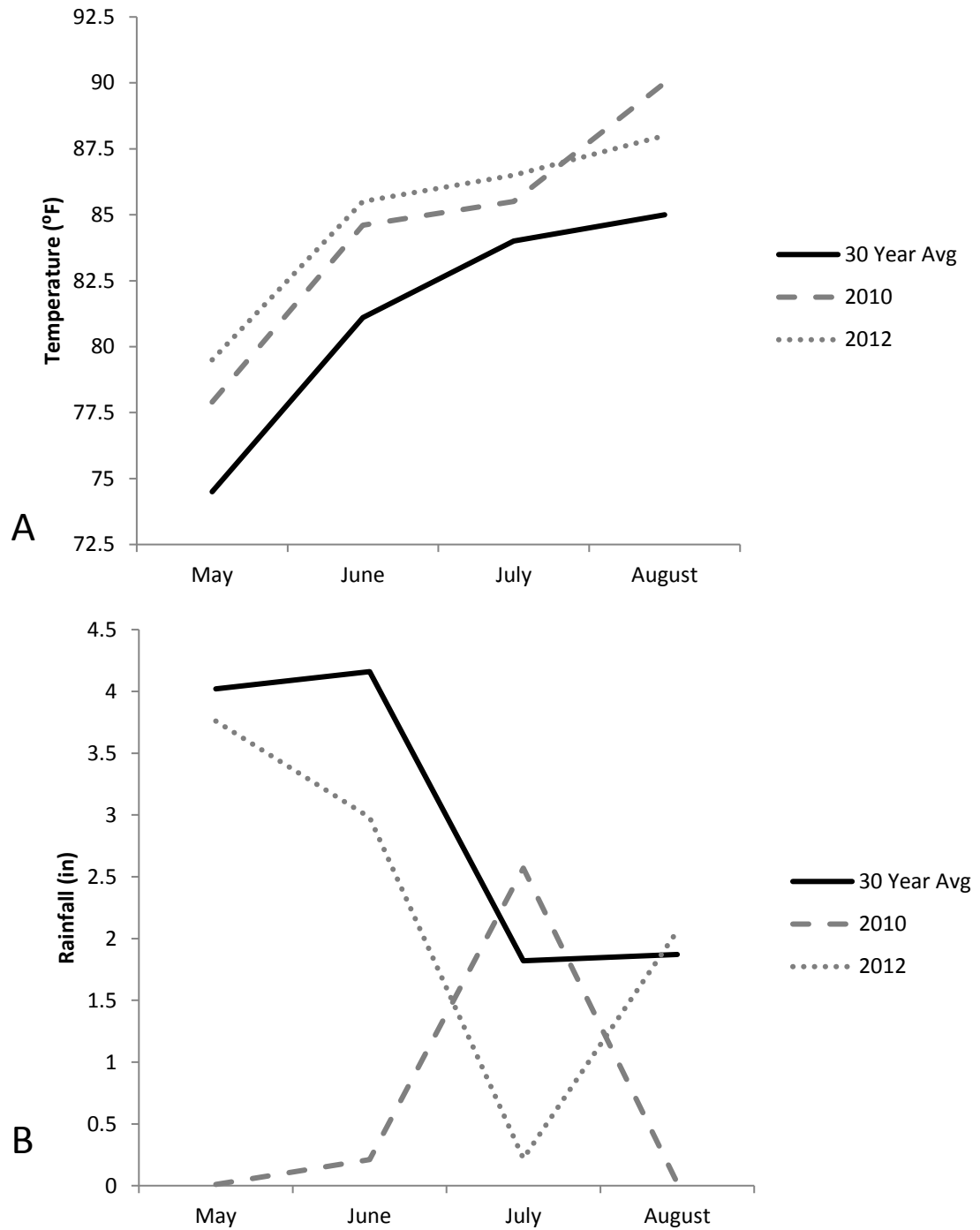
Figure 2.1. Mean monthly temperature and 30 year monthly average temperature (**A**) and total monthly rainfall and 30 year monthly average rainfall (**B**) in the Ft. Hood area during 2010 and 2012.
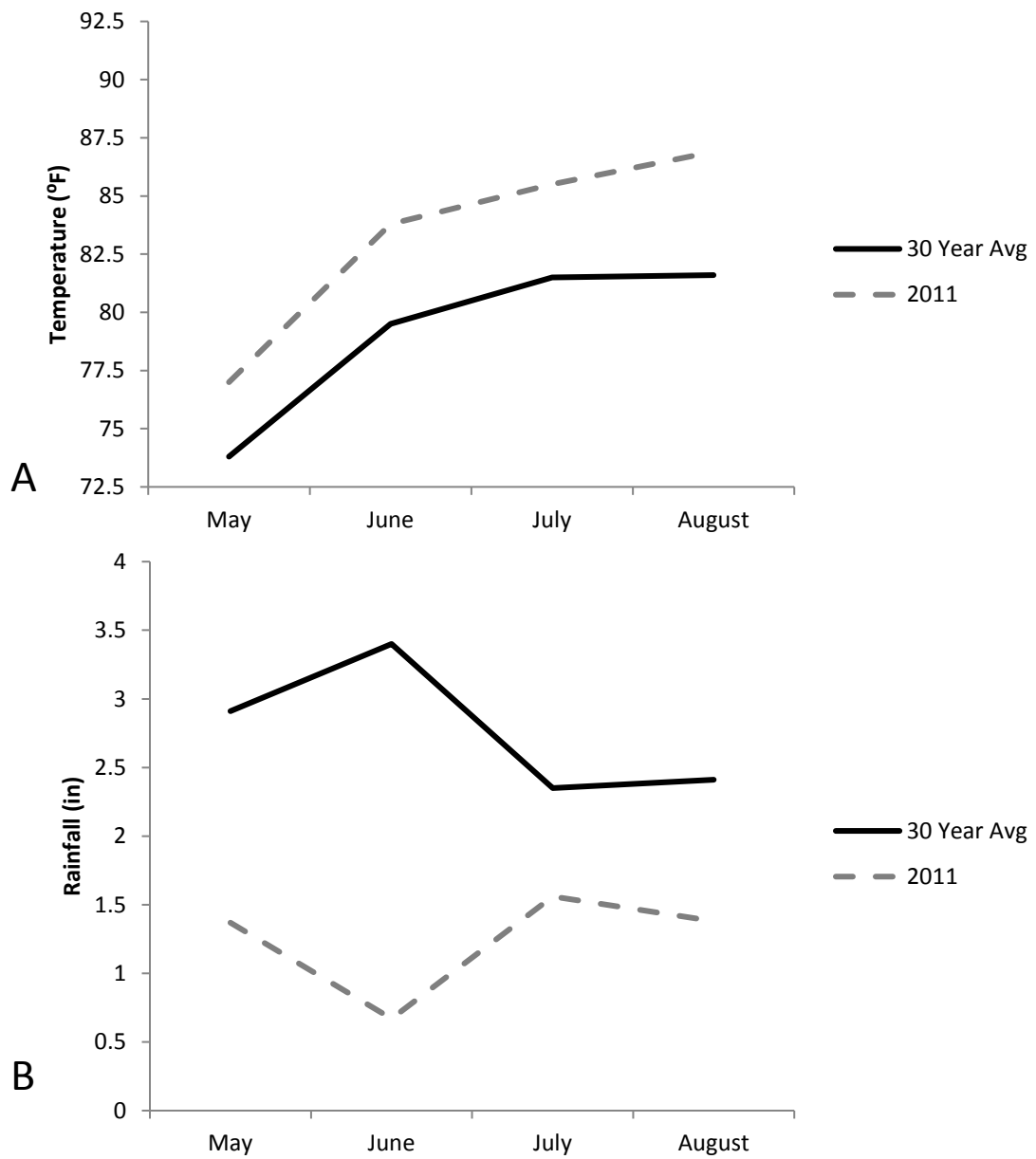
Figure 2.2. Mean monthly temperature and 30 year monthly average temperature (**A**) and total monthly rainfall and 30 year monthly average rainfall (**B**) in the Big Springs Ranch/ Real County area during 2011.

Methods

Study Design

In 2009 I conducted a pilot study to determine what methods were appropriate for my post-breeding surveys. My objective was to survey many sites with varying vegetative characteristics to identify which vegetative sites were being used by warblers during the post-breeding period. I selected riparian, oak savannah, oak woodland, and low canopy (< 30% canopy cover) juniper monoculture sites that were adjacent to breeding vegetation known to contain breeding warblers in that year or previous years. From May to August, I surveyed 30 sites with various habitat characteristics on private properties in Bell, Coryell, Bosque, and Travis Counties in the Texas Hill Country. I visited each site either six or seven times and spent approximately one hour at each site unless I found warblers before the hour had elapsed. Upon completion of this field season, I dropped the low canopy juniper monoculture sites as those sites were rarely available adjacent to breeding habitat.

In 2010 and 2012, my research was focused in and around Ft. Hood so I could include ecosite type (low stony hill and redland) in my study design. Soil type, the main driver of ecosite classification, is variable on Ft. Hood. Consequently, warbler breeding habitat on Ft. Hood is located in both ecosites and effects of ecosite on the bird's ecology can be studied. In other portions of the warbler's breeding range, soil types are less variable so almost all breeding vegetation is in the low stony hill ecosite. My primary objective while working on Ft. Hood was to determine the effects of ecosite type on warbler movement into non-breeding habitat during the post-breeding season. I

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additionally wanted to determine how non-breeding vegetation type, canopy cover, and density affect use of non-breeding vegetation during the post-breeding season. In these years, I selected (see below for site selection criteria) an approximately equal number of breeding sublocations in each ecosite that were immediately adjacent to one of three non-breeding vegetation types (riparian, oak woodland, and oak savannah).

In 2011, I conducted surveys in Real County in an effort to determine warbler movements during the post-breeding period in other portions of the bird's breeding range. However, most of the Golden-cheeked Warbler's breeding range south of Ft. Hood Military Reservation is found exclusively in the low stony hill ecosite (personal observation) and the landscape becomes much less varied in vegetative composition. Most vegetation adjacent to oak-juniper woodland is oak woodland. Therefore, to reflect the available ecosite and non-breeding vegetation in much of the warbler's range, all breeding sites selected for study were in the low stony hill ecosite and were adjacent to the oak woodland vegetation type.

Site Selection Process

Because my research relied on the known presence of breeding warblers in the vegetation I surveyed, I used study sites that were already being surveyed by other projects during the breeding season. In 2010-2012, I used the following criteria to select study sites for my post-breeding project from each of the study sites surveyed during the breeding season:

1. The breeding vegetation in the site must contain at least one Golden-cheeked Warbler territory during the breeding season in which my post-breeding surveys occurred.

2. The site must contain both a breeding sublocation containing oak-juniper woodland and a non-breeding sublocation assignable to one of the following vegetation categories (oak savannah, oak woodland, or riparian woodland).

3. The breeding sublocation at each site must be assignable to either the low stony hill or redland ecosite based on soil and vegetative characteristics.

In 2009, I had fewer criteria for site selection. I only surveyed non-breeding vegetation adjacent to patches of breeding habitat. My criteria for site selection were:

1. The non-breeding location must be assignable as one of the following vegetation types: riparian woodland, oak woodland, oak savannah, and juniper monoculture with <30% canopy cover.

2. The non-breeding location must have an immediately adjacent patch of oak-juniper woodland known to contain breeding warblers during the same year.

Field Measurements

Site surveys: Each site was divided into one breeding sublocation and one non-breeding sublocation (Fig. 2.3). One site visit involved a survey of either the breeding or non-breeding sublocation followed immediately by a survey of the other sublocation at the site. Each sublocation was visited 5 times unless access was restricted during any part of the study period. Sites were surveyed 5 times to increase detection probability.

This was necessary because detection probability decreases as the breeding season

progresses (Collier et al. 2010) and is very low during the post-breeding season.

I began surveys at sunrise and continued until seven hours after sunrise. I

recorded start and end time of each survey for use in later analyses. To ensure that

Figure 2.3. A site broken into two sub-locations. Sublocations were surveyed

independently but each was surveyed during the same visit.

detectability was as high as possible, surveys were only conducted under fair weather

conditions (e.g. light wind, no precipitation). I walked slowly over each study site at a

speed of ~ 1 km/hr (Er et al. 2003) making sure to reach within 100 m of all portions of the site as this is the distance a warbler chip can be hear on a normal day (personal observation). While walking, I listened for and looked for Golden-cheeked Warblers. Each time one or more warblers were detected, I considered the event one detection. For each detection, I recorded time of day, age, sex, observed behaviors, and substrate for each warbler at the detection. In instances where identifications of individuals were unconfirmed, I conducted a short playback of a Golden-cheeked Warbler song and call to draw the individual into visual contact to confirm identification. To avoid unnecessary disturbance, I conducted playbacks only as needed at a volume no louder than 60 dB and a duration no longer than 5 seconds. While observing birds, I maintained a distance of 20 meters or more to avoid influencing the bird's behavior.

Behavioral observations: When I detected a warbler or warblers, I observed for five seconds without recording any behavior to eliminate bias toward the most conspicuous behaviors (Noon and Block 1990, Keane and Morrison 1999). I then recorded all behaviors (Table 2.1) observed on a handheld audio recorder for the next one to eight minutes. Each time the bird moved from one substrate to another or moved >20m, a new location was taken using a handheld GPS unit (Garmin, Ltd., Olathe, KS) and the behaviors at that location were recorded.

Behaviors were recorded as discrete events. The number of events for each behavior was totaled for each observation and divided by the duration of the observation (in seconds). I discarded any observations that totaled fewer than 60 seconds.

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Behavior:	Description:
Intraspecific interaction	Warbler flying within 5< m of another golden-cheek
Interspecific interaction	Warblers flying within 5< m of a different species
Vocalizing	Singing or calling
Vocalization change	Singing to calling, A song to B song, etc.
Courtship interaction	Male-female interaction, displays, copulation, etc.
Long flight	Duration longer than 2 seconds
Short flight	Duration less than 2 seconds
Scanning	Looking around
Foraging	Gleaning, hover gleaning, etc.
Grooming	Preening
Food carry to nest	Carrying food to a nest
Food carry to fledglings	Carrying food to fledglings
Other	Bird not engaged in any other behaviors

Table 2.1. Behaviors recorded during behavioral surveys of Golden-cheeked Warblers during the post-breeding period (Bell, Coryell, Bosque, and Real counties, Texas).

Calculated Information

To calculate canopy cover, I used the spatial analyst tool in ArcGis 10.1 (Environmental System Research Institute, Redlands, CA) to perform a supervised classification of the canopy cover in each selected site. I reclassified 1-m resolution National Agricultural Imagery Program (NAIP) orthoimagery of each study site into two classes (canopy and not canopy). I then calculated canopy cover using the number of pixels classified as canopy and the total number of pixels in each location.

To calculate territory density, I used ArcGis 10.1 to select minimum convex polygons (generated during breeding project analyses, unpublished data Texas A&M) that were inside of or within 50m of the borders for each breeding sublocation. I then divided the number of territories selected by the above criteria by the hectares of the corresponding breeding sublocation.

Analyses

For all statistical analyses, I used R (R-core members, et al., 2013). If an analysis did not require detections to be separated into age, sex, and group composition (i.e. individual, or family) detection rates, I calculated mean detection rate using detections of all birds at each sublocation. Any detection including one or more unknown Golden-cheeked Warbler (i.e. a warbler was seen but could not be identified to age or sex) was still included in the overall detection rate analyses but was excluded from analyses in which detection composition, sex, and age were analyzed using mean detection rate.

In looking at detection rates for various analyses, I first examined mean detection rate across years to determine if it was appropriate to pool rates across all years. I used a one-way ANOVA (Ott and Longnecker 2001: 853-859) to determine if breeding sub-location detection rates were different among years. I also used a one-way ANOVA (Ott and Longnecker 2001: 853-859) to examine if non-breeding sub-locations were different among years. If either ANOVA was statistically significant, I conducted a Tukey's HSD comparison of means to determine which years were different to aid in decisions on how I should handle analyses across years.

Objective 1: Determine which vegetation types are most frequently used during the post-breeding period

Analysis*:* I summarized the number of sublocations surveyed and the detections in each breeding sublocation based on ecosite and in each non-breeding sublocation based on vegetation type and ecosite of the adjacent breeding sublocation. I conducted a chi-squared goodness of fit test (Ott and Longnecker 2008: 515-518) to determine if the proportion of detections in each sublocation type (breeding ecosite and non-breeding vegetation type) was different from the expected proportion of detections based on the proportion of each sublocation type.

To compare presence with regard to sublocation type, canopy cover, vegetation type, ecosite, and density, I calculated the detection rate of each visit by dividing the number of birds detected during each visit by the duration of each visit (in 30 minute intervals). I then calculated the mean detection rate for each breeding and non-breeding sublocation.

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Because the number of detections in breeding and non-breeding sublocations was so different, I used a *t*-test (Ott and Longnecker 2001:211-228) to compare detection rates between the two sublocation types. For this and all following *t*-tests, I first tested for a significant difference in variances between the two compared means (Ott and Longnecker 2001: 275-276). If there was no difference, I used a standard *t*-test assuming equal variances. If the variances were significantly different, I used a Welch-Satterwaite *t*-test (Ott and Longnecker 2001: 275-276) which assumes unequal variances.

After examining a graph of detection rate plotted against percent canopy cover for linearity, I used linear regression (Ott and Longnecker 2001:540-548) to determine the relationship between percent canopy cover and detection rate in breeding and non-breeding sublocations. To compare detection rates among the non-breeding vegetation types, I used a one-way ANOVA (Ott and Longnecker 2001: 853-859) to determine if the mean detection rates for each vegetation type were the same. To determine if the ecosite of breeding vegetation affects movement into adjacent non-breeding vegetation, I used a two sample *t*-test (Ott and Longnecker 2001:211-228) to compare detection rates in non-breeding vegetation. Likewise, I used the Welch-Satterwaite two sample *t*-test (Ott and Longnecker 2001:275-278) to compare detection rates of breeding vegetation within each ecosite. I investigated the relationship between breeding site density and detection rate by regressing (Ott and Longnecker 2001:540-548) density (number of territories/ha in each breeding study site) with detection rate in the adjacent non-

breeding site to determine if higher density breeding sites cause greater movement into non-breeding vegetation.

Objective 2: Determine if group composition, sex, and age affect the use of non-breeding habitat in the post-breeding period

Analysis: For mean detection rates associated with group composition, I identified all detections that contained one adult (of either sex) and at least one fledgling (i.e. a family group) and those containing only adults (i.e. a lone male, female, or both sexes without fledglings).

For mean detection rates associated with sex, I identified all detections that contained either a male or a female adult warbler regardless of the composition of the entire group. Detections containing at least one adult of either sex were used to calculate mean detection rate for males and females.

 I calculated detection rates by dividing the number of detections of each type (family group or adult only) by the duration of the survey (in 30 minute intervals). To determine the effects of age, sex, and the presence of family groups (defined as an adult with at least one fledgling), I calculated the detection rate for family groups and individual adult warblers in non-breeding vegetation. I compared these rates using a two sample *t*-test (Ott and Longnecker 2001:211-228) to determine if non-breeding detections more frequently consist of family groups than just individual adults. To determine if males use non-breeding vegetation more often than females, I calculated the detection rate for each sex in non-breeding vegetation and compared them using a two sample *t*-test (Ott and Longnecker 2001:211-228) as well. Similarly, detection rates of

adults (i.e. after hatch year birds) and fledglings were compared using the two sample *t*-test (Ott and Longnecker 2001:211-228) to determine if movement into non-breeding vegetation was more common in adults or juveniles.

Objective 3: Determine the behavior of warblers in each vegetation type

Analysis: I calculated the frequency for each recorded behavior by dividing the total number of observations for each behavior in a detection by the number of seconds that detection lasted. I then calculated a mean detection frequency for all detections occurring in each breeding and non-breeding vegetation type based on ecosite. These means are summarized in a table comparing each behavior's frequency among each of the four vegetation types in which a behavioral observation was conducted (low stony hill breeding, redland breeding, riparian, and oak woodland). Because foraging frequencies and search effort were of particular interest, I further investigated the effects of breeding and non-breeding sublocations on frequency of foraging, long flights, and short flights by comparing mean frequency of each behavior in each sublocation with a *t*-test (Ott and Longnecker 2001:211-228). Using another *t*-test (Ott and Longnecker 2001:211-228), I compared the frequency of foraging, long flights, and short flights between the low stony hill and redland ecosites in breeding sublocations to determine if ecosite has an effect on these behaviors.

Objective 4: Determine the foraging substrate that is used most frequently in the post-breeding period

Analysis: I presented the number and proportion of all substrates composed of each of the most common tree species in a table to compare proportion of use of each

substrate in each vegetation type. I then examined the proportion of substrates composed of juniper and deciduous species in each breeding ecosite to determine which species are used most frequently in the post-breeding period. For the most common species found in each breeding ecosite (ashe juniper, Texas oak, and post-oak), I conducted a chi-squared goodness of fit test (Ott and Longnecker 2008: 515-518) to determine if warblers used each of those substrates differently from what was available in each ecosite. I obtained expected frequencies from vegetation data collected by Marshall (2011) who used study sites that were divided by ecosite (Low Stony Hill and Redland) and were similar in location and vegetation composition to those I used in my project.

Pilot Study Results

I found no warblers in riparian vegetation. I found warblers in 0-25%, 26-50%, and 51-75% canopy cover patches on 19.2%, 6.6%, and 7.1% of all visits made to these categories, respectively. These data indicated that areas of low canopy cover, most often represented by the oak savannah vegetation type, are used more heavily than other available non-breeding vegetation. I most commonly observed adults feeding fledglings in vegetation with 0-25% canopy cover which demonstrates that this vegetation type was used more by family groups than the other canopy cover categories. Other observed behaviors included adults and fledglings foraging separately, vocalizations (calls and rarely songs), and scanning, intraspecific interactions (Table 2.2). I collected 110 foraging substrate points during this pilot study. Foraging substrates used most often were live oak (35.5%), Ashe juniper (24.5%), Texas pecan (10%), hackberry (6.4%), Texas oak (5.5%), and cedar elm (4.5%). Use of Ashe juniper indicates that this species is still important to the warbler in the post-breeding season but they also spend a large amount of time in deciduous tree species. Observed distances away from the edge of a patch of breeding habitat ranged from 15m-200m. The mean distance was 69.5m (SD=51.4, N=13) from edge which shows that, when in non-breeding habitat, warblers did not just use the edge of the non-breeding habitat but went a large distance into the non-breeding habitat.

These results from a preliminary season helped to guide my research for subsequent seasons. Most of my hypotheses were developed from this preliminary study and other studies on post-breeding habitat use. For example, use of habitat was skewed

to the lower canopy cover and oak savannah vegetation type in the pilot study. Although

I did not classify sites with respect to dominant vegetation type, sites with a heavier

component of deciduous species most often produced detections throughout the season

and deciduous species were used as foraging substrates throughout the season.

Additionally, most of the detections in 2009 involved males or family groups in non-

breeding habitat. Keddy-Hector (1993) and Ladd and Gass (1999) also found juveniles

or groups of warblers in upland oak savannah habitat that was more open than breeding

habitat. Adult males have been found to disperse farther and use post-breeding habitat

more frequently than females (Pagen et al. 2000, Lang et al. 2002). While these

preliminary results were used to guide my formal study design, I did not include these

data in the analyses as the methods and overall design were dramatically different from

the study conducted from 2010-2012.

	0-25% canopy	26-50% canopy	51-75% canopy
N	69	31	10
Foraging	47.8%	64.5%	30%
Feeding Fledglings	26.1%	--	10%
Vocalizing[a]	20.3%	19.4%	40%
Short Flight	1.4%	--	--
Long Flight	1.4%	6.5%	20%
Other	2.9%	9.7%	--

[a] Vocalizing includes both vocalizations and vocalization changes

Table 2.2. Behaviors observed during pilot study surveying Golden-cheeked Warbler use

of non-breeding vegetation (Bell, Coryell, and Bosque counties). Percentages represent

each behavior's proportion of all behaviors observed in each canopy cover category.

Main Study Results

Summary of Detections

I visited 16 sites in 2010, 6 sites in 2011, and 12 sites in 2012. The number and type of each sublocation are summarized in Table 2.3. In 2010, 2011, and 2012, I made 42, 28, and 28 detections, respectively for a total of 98 detections. Most detections (86.7%, N=85) occurred in breeding vegetation. Of the 85 detections within breeding vegetation, 72 occurred in breeding vegetation within the low stony hill ecosite. I made 13 detections in non-breeding vegetation. Non-breeding detections occurred most frequently when the adjacent breeding vegetation was within the low stony hill ecosite (76.9%, $N = 10$). Non-breeding detections were most common in riparian vegetation ($N = 9$) and oak woodland vegetation ($N = 4$). One detection occurred in an oak savannah. All detections are summarized in Table 2.4.

Vegetation Types

The proportion of detections in each vegetation type were significantly different from expected values ($\chi^2 = 97.13$, $df = 7$, $P = 2.2e\text{-}16$; Fig. 2.4). Specifically, detections in breeding vegetation in low stony hill ecosites represented a higher proportion (73.5%) than expected (29.4%) and the proportion of detections in all other vegetation types was lower than expected.

The detection rates for breeding and non-breeding sublocations were significantly different ($t = 2.943$, $df = 57.386$, $P = 0.005$; Fig. 2.5). The mean detection rate in breeding sublocations ($\bar{x} = 0.391$, $SD = 0.449$) was 3.7 times greater than the mean detection rate in non-breeding sublocations ($\bar{x} = 0.119$, $SD = 0.298$).

Detection rates in non-breeding sublocations did not differ among years ($F = 2.617$, $df = 2,31$, $P = 0.089$) and the number of detections in these sublocations was small so all years were pooled for non-breeding analyses. Detection rates in breeding sublocations did differ among years ($F = 5.331$, $df = 2,31$, $P = 0.010$). Post hoc comparisons using the Tukey HSD test indicated that mean detection rate in 2010 ($\bar{x} = 0.190$, $SD = 0.186$) was significantly different from the mean detection rate in 2011 ($\bar{x} = 0.801$, $SD = 0.284$). However, the mean detection rate in 2012 ($\bar{x} = 0.454$, $SD = 0.605$) was not different from the 2010 and 2011 mean detection rates. Because detection rates in 2010 and 2012 were generated in the same portion of the study area (i.e. the Ft. Hood area) and were not statistically different, I analyzed detection rates from those years together. I analyzed detection rates from 2011 (Real County) alone.

*Canopy***:** The relationship between detection rate and percent canopy cover was linear for both breeding (in all years) and non-breeding sublocations. I found no statistical relationship between canopy cover and mean detection rate in non-breeding sublocations ($r^2 = 0.004$, $df = 32$, $P = 0.739$). Mean detection rates in breeding sublocations in 2010 and 2012 also showed no relationship to canopy cover ($r^2 = 0.01$, $df = 26$, $P = 0.613$). Mean detection rates in 2011 breeding sublocations also had no relationship with canopy cover ($r^2 = 0.0002$, $df = 4$, $P = 0.982$).

	Low Stony Hill Ecosite				Redland Ecosite				
Year	Breeding	Oak Woodland	Oak Savannah	Riparian Woodland	Breeding	Oak Woodland	Oak Savannah	Riparian	Totals
2010	8	3	2	3	8	5	2	1	32
2011	6	6	--	--	--	--	--	--	12
2012	6	2	1	3	6	2	3	1	24
Total	20	11	3	6	14	7	5	2	68

Table 2.3. Summary of surveys conducted to determine vegetation type used most often by Golden-cheeked Warbler during the post-breeding period. I conducted surveys in Coryell and Bell counties (2010 and 2012) and Real County (2011).

Year	Low Stony Hill Ecosite				Redland Ecosite				Totals
	Breeding	Oak Woodland	Oak Savannah	Riparian Woodland	Breeding	Oak Woodland	Oak Savannah	Riparian Woodland	
2010	25	1	0	4	10	1	0	1	42
2011	26	2	0	0	0	0	0	0	28
2012	21	0	0	3	3	0	1	0	28
Total	72	3	0	7	13	1	1	1	98

Table 2.4. Summary of Golden-cheeked Warbler detections during the post-breeding period in Coryell and Bell

counties (2010 and 2012) and Real County (2011). Columns represent different vegetation types surveyed.
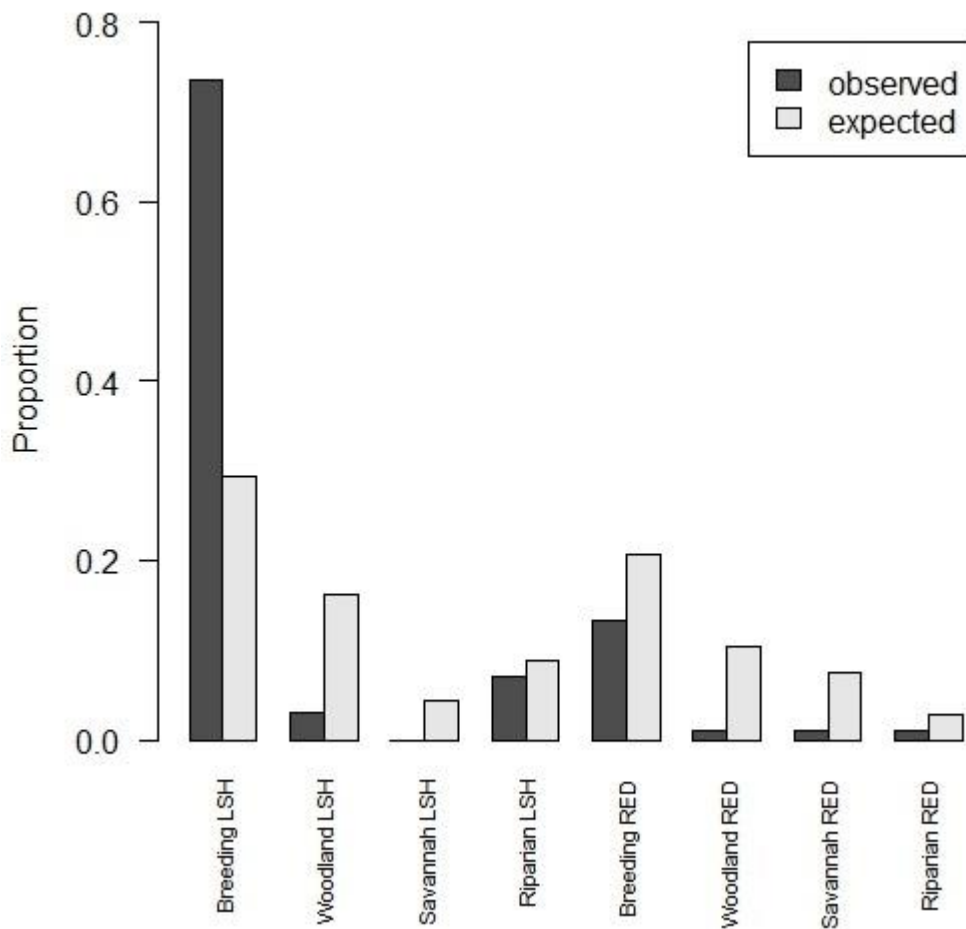
Figure 2.4. Observed vs. expected frequency of detections in each sublocation type surveyed. Sublocations are divided into those in or adjacent to low stony hill (LSH) and redland (RED) ecosites. Observed levels represent proportion of detections in a given sublocation/total detections. Expected levels represent proportion of each sublocation type/total number of sublocations.
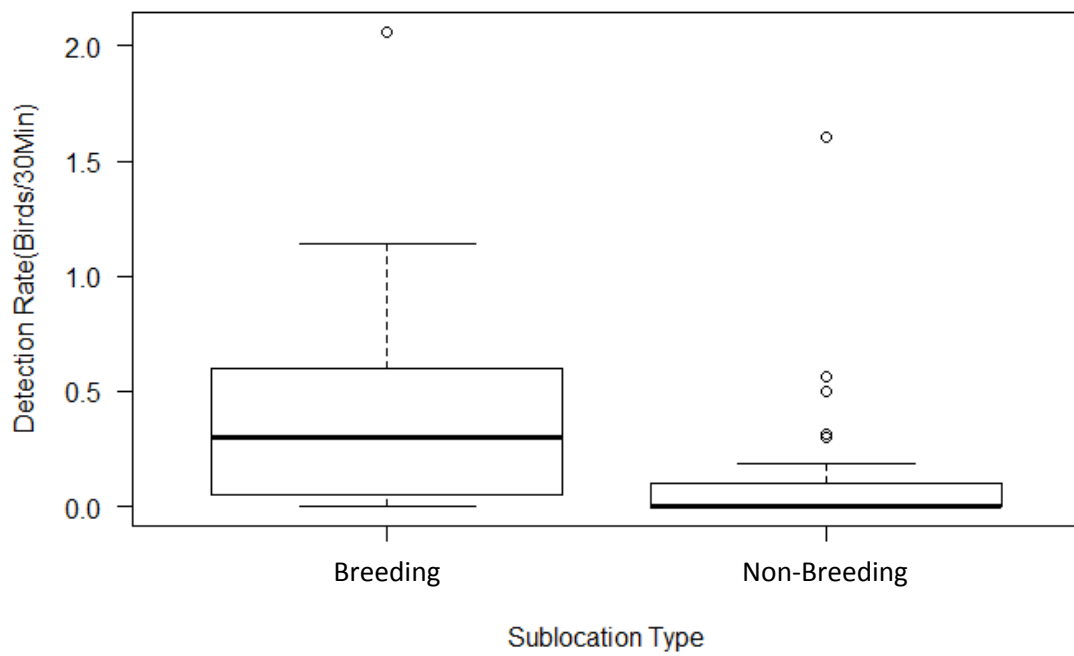
Figure 2.5. Mean detection rates in breeding and non-breeding sublocations.

Vegetation Types (non-breeding sublocations): Mean detection rates in non-breeding vegetation types were not significantly different ($F = 0.605$, $df = 2,31$, $P = 0.553$). While not statistically significant, detection rates in the oak woodland and riparian vegetation types ($\bar{x} = 0.154$, SD = 0.394; $\bar{x} = 0.143$, SD = 0.159) were almost 10 times higher than the detection rates in oak savannah vegetation types ($\bar{x} = 0.017$, SD = 0.047).

Effects of Ecosite on Mean Detection rate: The mean detection rate non-breeding vegetation adjacent to low stony hill and redland ecosites were not significantly different ($t = 1.573$, $df = 21.938$, $P = 0.130$). While not significant, mean detection rate in non-breeding sublocations adjacent to low stony hill ecosites was 4.5 times higher ($\bar{x} = 0.176$, SD = 0.376) than detection rates of non-breeding sublocations adjacent to redland ecosites ($\bar{x} = 0.038$, SD = 0.089), a difference that is likely to be biologically significant.

The mean detection rates between low stony hill and redland breeding sites were significantly different ($t = 2.370$, $df = 15.686$, $P = 0.031$). The mean detection rate of breeding sublocations in low stony hill ecosites ($\bar{x} = 0.482$, SD = 0.537) was significantly higher than those of the redland ecosites ($\bar{x} = 0.125$, SD = 0.173; Figure 2.6).

Density: To determine the effect of territory density in breeding sublocations on mean detection rates in non-breeding sublocations, I regressed territory density (# territories in breeding sublocation/hectares) with mean detection rate for all non-

breeding sublocations. Territory density did not have a significant relationship with mean detection rate in non-breeding sublocations (r^2 = 0.02403, df = 32, P = 0.3814).

Effects of Group Composition, Sex, and Age

Group Composition: The mean detection rate of family groups was not significantly different from the mean detection rate of lone adults (t = 0.940, df = 45.179, P = 0.352). While not statistically significant, family group detection rate ($\bar{x}$ =0.026, SD = 0.07827) was over twice the lone adult detection rate ($\bar{x}$ =0.012, SD = 0.034).

Sex: The mean detection rate of males and females in non-breeding sublocations were significantly different (t = 2.159, df = 43.016, P = 0.036; Fig. 2.7). Male detection rate ($\bar{x}$ =0.038, SD = 0.082) was significantly higher than female detection rate in non-breeding vegetation ($\bar{x}$ =0.0056, SD = 0.032).

Age: The variances of fledgling and adult mean detection rates were unequal (fledglings: σ^2 = 0.048, adult σ^2 = 0.009; F = 5.144, df = 33, 33, P = 8.884e-06). The mean detection rate of fledglings was not significantly different from the mean detection rate of adults (t = 0.778, df = 45.364, P = 0.441). The fledgling detection rate ($\bar{x}$ =0.076, SD = 0.220) was 70% higher than the adult detection rate ($\bar{x}$ =0.043, SD = 0.097).
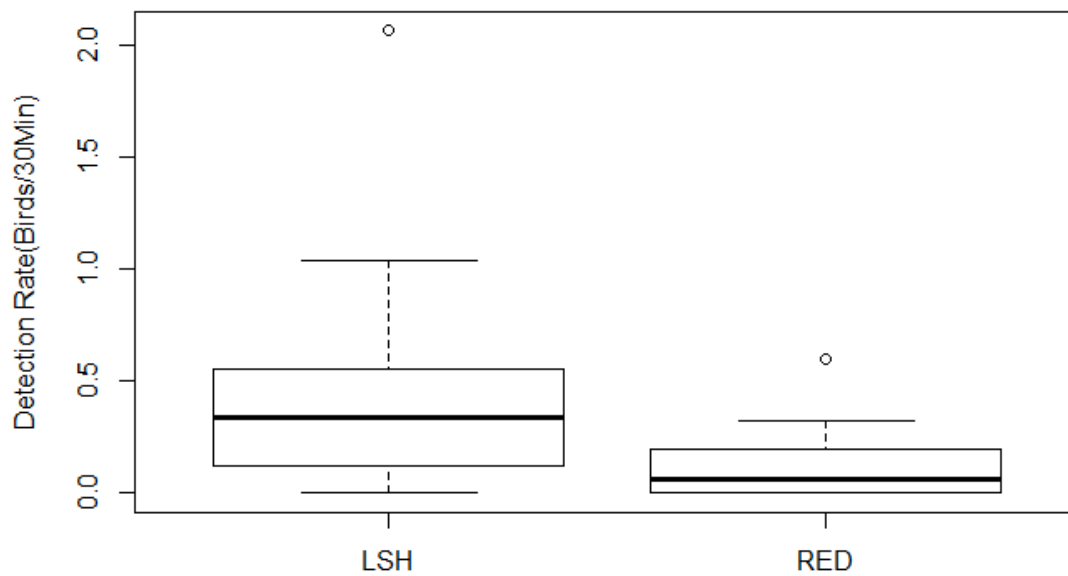
Figure 2.6. Mean detection rates in breeding sublocations within the low stony hill

(LSH) or redland (RED) ecosites. Detection rates are from the 2010 and 2012 datasets.
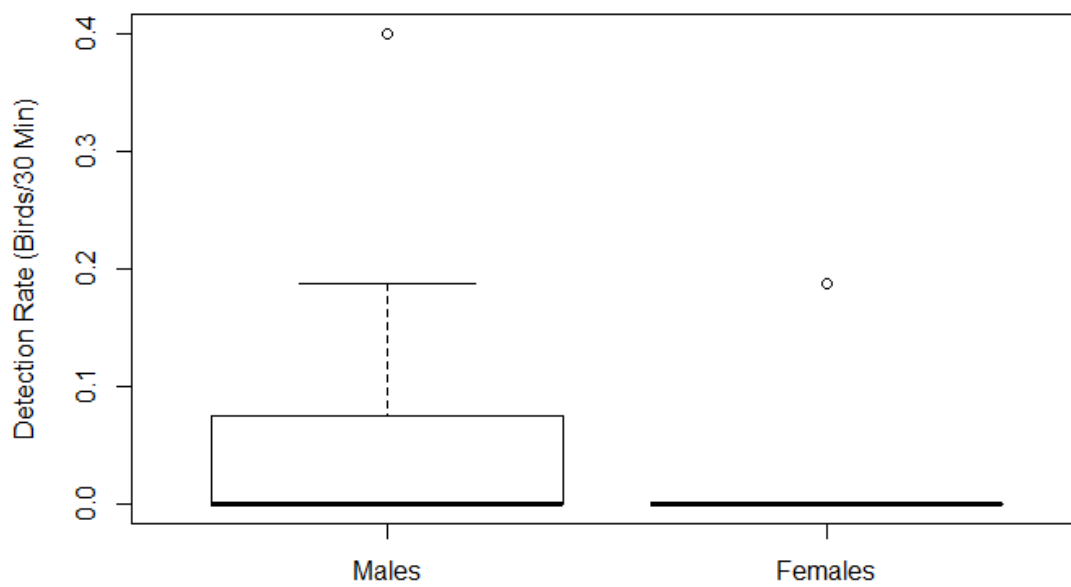
Figure 2.7. Mean detection rate of male and female Golden-cheeked Warblers in non-breeding sublocations in Bell, Coryell, and Real counties, Texas.

Effects of Vegetation Type and Ecosite on Behavior

I conducted 26 observations in 2010, 22 observations in 2011, and 22 observations in 2012. Because most detections occurred in breeding vegetation within the low stony hill ecosite, most behavioral observations (77.1%, $N = 54$) also occurred in low stony hill breeding vegetation (Table 2.5).

I reported behavior rates for each sublocation in which behavioral observations occurred (i.e. low stony hill breeding, redland breeding, riparian, and oak woodland) (Table 2.6). I pooled rates for behaviors in riparian and oak woodland observations adjacent to each ecosite because separation would result in too few observations for analysis. Additionally, rates reported in the following sections pertaining to breeding and non-breeding sublocations are different from rates reported in table 2.6 because breeding and non-breeding values for analyses pool both breeding ecosites and both non-breeding sublocations into one rate.

Foraging rates were not significantly different between breeding and non-breeding sublocations ($t = 0.676$, $df = 57$, $P = 0.502$) but the foraging rate in breeding sublocations ($\bar{x} = 0.031$, SD $= 0.031$) was 38% higher than the foraging rate in non-breeding sublocations ($\bar{x} = 0.023$, SD $= 0.022$).

Long flight rates were not significantly different between breeding and non-breeding sublocations ($t = 0.573$, $df = 52$, $P = 0.569$). Long flight frequencies were 28% higher in breeding sublocations than in non-breeding sublocations which suggests that the difference may be biologically significant (breeding: $\bar{x} = 0.012$, SD $= 0.012$; non-breeding: $\bar{x} = 0.009$, SD $= 0.008$).

Year	Breeding (LSH)	Breeding (RED)	Riparian Woodland	Oak Woodland	Totals
2010	15	6	3	2	26
2011	20	--	--	2	22
2012	19	2	1	--	22
Totals	54	8	4	4	70

Table 2.5. Number of Golden-cheeked Warbler behavioral observations during the post-breeding period in each vegetation type surveyed in Coryell, Bell and Real counties, Texas.

Behavior	Breeding (LSH)		Breeding (RED)		Riparian Woodland		Oak Woodland	
	N	Mean±SD	N	Mean±SD	N	Mean±SD	N	Mean±SD
Foraging	43	0.032±0.033	8	0.028±0.016	4	0.025±0.033	4	0.022±0.004
Long Flight	39	0.011±0.010	8	0.017±0.017	4	0.010±0.011	3	0.008±0.004
Short Flight	47	0.059±0.078	8	0.063±0.086	4	0.022±0.015	4	0.024±0.019
Vocalization	50	0.042±0.037	7	0.071±0.075	3	0.050±0.027	4	0.023±0.022
Vocalization Change	6	0.010±0.005	1	0.044	--	--	--	--
Scanning	24	0.013±0.008	7	0.012±0.006	3	0.021±0.016	2	0.007±0.002
Intraspecific Interaction	11	0.005±0.004	4	0.009±0.008	--	--	1	0.006
Interspecific Interaction	3	0.002±0.0004	--	--	--	--	--	--
Grooming	9	0.011±0.011	1	0.036	--	--	--	--
Other Behaviors	1	0.003	1	0.008	--	--	1	0.008

Table 2.6. Golden-cheeked Warbler behavior rates during the post-breeding period in each vegetation type recorded during behavioral observations in Coryell, Bell, and Real counties, Texas.

Short flight rates were significantly higher in breeding vegetation compared to non-breeding vegetation ($t = 3.085$, $df = 54.7$, $P = 0.003$; breeding: $\bar{x} = 0.060$, SD = 0.078; non-breeding: $\bar{x} = 0.023$, SD = 0.016).

Foraging rates were not significantly different between breeding sublocations in the two ecosites ($t = 0.479$, $df = 20.594$, $P = 0.637$). Foraging rates in the two ecosites were very similar (LSH: $\bar{x} = 0.032$, SD = 0.033; RED: $\bar{x} = 0.028$, SD = 0.016).

Long flight rates were not significantly different between breeding sublocations in the two ecosites ($t = -1.394$, $df = 45$, $P = 0.170$). Despite not being significantly different, long flight rates in the low stony hill ecosite was 58% higher than that of the redland ecosite (LSH: $\bar{x} = 0.011$, SD = 0.011; RED: $\bar{x} = 0.017$, SD = 0.016).

Short flight rates were not significantly different between breeding sublocations in the two ecosites ($t = -0.134$, $df = 53$, $P = 0.894$). Short flight rates in the two ecosites were very similar (LSH: $\bar{x} = 0.059$, SD = 0.078; RED: $\bar{x} = 0.063$, SD = 0.087).

Effects of Vegetation Type and Ecosite on Tree Species Use

In breeding vegetation, I recorded 316 individual substrates that warblers were using during the behavioral observations. While in breeding vegetation, warblers used Ashe juniper 59.5% of the time. Other tree species commonly used in breeding vegetation included live oak (14.5%), Texas oak (13.0%), Texas ashe (3.8%), shin oak (4.1%), and post oak (2.2%). Species used at least once included cedar elm, elbowbush, and Lacey oak. Additionally, snags (standing dead trees) of unknown species were used occasionally (1.3%). In non-breeding vegetation, 32.4% of all observations (n=37) occurred in ashe juniper. Deciduous tree species were used twice as often as Ashe

juniper in non-breeding vegetation. I also commonly found warblers in Texas oak

(13.5%), cedar elm (13.5%), live oak (8.1%), and pecan (8.1%). Warblers used ash spp.,

black cherry, Carolina buckthorn, gum bumelia, green ash, little walnut, redbud, and

snags at least once during the post-breeding period (Table 2.7).

In low stony hill breeding vegetation, 63.5% of all substrates used (n=255) were

Ashe juniper compared to 42.6% in redland breeding vegetation (n=61). In redlands

breeding vegetation, live oak (19.7%), post oak (6.6%), Texas oak (16.4%), and shin oak

(8.2%) were used more commonly than they were in low stony hill breeding vegetation

(13.3%, 1.2%, 12.2%, and 3.1%, respectively).

I found no statistical difference between observed and expected use of ashe

juniper, Texas oak, and post oak in the low stony hill breeding sublocations (χ^2= 0.0157,

df = 3, P = 0.9995). Likewise, I found no statistical difference between observed and

expected use of the same tree species in the redlands breeding sublocations (χ^2= 0.2405,

df = 3, P = 0.9708).

	Ashe Juniper	Live Oak	Texas Oak	Post Oak	Shin Oak	Texas Ash	Ash spp.	Black Cherry	Carolina Buckthorn	Cedar Elm	Elbowbush	Gum Bumelia	Green Ash	Lacey Oak	Little Walnut	Pecan	Redbud	Snag	Total:
Breeding Sublocations																			
LSH Ecosite	162	34	31	3	8	11	0	0	0	0	1	0	0	2	0	0	0	3	255
	.635	.133	.122	.012	.031	.043	--	--	--	--	.004	--	--	.008	--	--	--	.012	
RED Ecosite	26	12	10	4	5	1	1	0	0	1	0	0	0	0	0	0	0	1	61
	.426	.197	.164	.066	.082	.016	.016	--	--	.016	--	--	--	--	--	--	--	.016	
															Breeding Sublocation Total:				316
Non-Breeding Sublocations																			
Oak Savannah	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	1.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	
Oak Woodland	4	3	1	0	0	0	2	1	0	0	0	1	1	0	0	0	1	1	15
	.267	.2	.067	--	--	--	.133	.067	--	--	--	.067	.067	--	--	--	.067	.067	
Riparian Woodland	7	0	4	0	0	0	0	0	1	5	0	0	0	0	1	3	0	0	21
	.333	--	.190	--	--	--	--	--	.048	.238	--	--	--	--	.048	.143	--	--	
															Non-breeding Sublocation Total:				37

Table 2.7. Substrates used by warblers during behavioral observations in low stony hill (LSH) ecosite, redland (RED) ecosite, and non-breeding vegetation types. Whole numbers represent the number of times a warbler used substrate in a given breeding ecosite of non-breeding vegetation type. Decimals represent the proportion of observations occurring in a given tree species for each row of observations.

Discussion

During the post-breeding period of the Golden-cheeked Warbler's annual cycle, it makes use of the same vegetation in which it breeds, oak-juniper woodlands, as well as other vegetation (i.e. oak woodland, oak savannah, and riparian woodland) not used during the breeding season. While all of these vegetation types were used, I found that warblers used the same vegetation they use for breeding much more commonly than vegetation not used for breeding in the post-breeding period. When found in non-breeding vegetation, warblers were detected at rates almost 10 times higher in oak woodlands and riparian woodlands than in oak savannahs. I failed to reject the hypothesis that one non-breeding vegetation type would have detection rates twice as high as the other non-breeding vegetation types. During the post-breeding period, warblers clearly use juniper-oak woodland vegetation (the same vegetation type in which they breed) more commonly than any other vegetation type, but when they do use other vegetation types, use some vegetation types more often than others. Many different aspects of these vegetation types could explain the warbler's vegetative associations during this part of the annual cycle.

Canopy cover, a metric frequently used to define high quality breeding habitat for Golden-cheeked Warblers (Campbell 2003) did not have a significant positive relationship with detection rates in breeding or non-breeding vegetation during the post-breeding period. Other studies have also shown that other vegetative characteristics (i.e. tree species composition) affect Golden-cheeked Warbler breeding success more than canopy cover (Marshall et al. 2013). I also rejected the hypothesis that territory density

of the adjacent breeding sublocation would have a significant positive relationship with detection rate in non-breeding sublocations. Neither greater territory density during the breeding season nor the increased number of birds in high breeding density areas after the breeding season led to greater emigration out of breeding vegetation toward adjacent non-breeding vegetation. Other studies have shown that birds and mammals do commonly exhibit density-dependent dispersal (almost half of all studies reviewed) and it is most often positive density-dependence (Matthysen 2005). However, of the half found not to experience density-dependent dispersal, most studies focused on local dispersal (i.e. study was in a confined area). Because my study focused on local dispersal, lack of density-dependent effects is consistent with previous studies.

Other research has shown that structural diversity of vegetation positively correlates with insect production (Webb 1989, Tye 1992, Holmes and Schultz 1988). Marshall et al. (2013) found that differences in vegetative composition between the low stony hill ecosite and the redland ecosite resulted in differential breeding success for the Golden-cheeked Warbler. They also found that arthropod density in breeding vegetation positively correlated with preferred foraging substrates during the breeding season. Marshall et al. (2013) found that the most likely reason for differential breeding success between the two ecosites was greater prey availability in the low stony hill ecosite because of the vegetative composition of that ecosite. The association between vegetative composition and arthropod availability likely continues into the post-breeding period. While doing behavioral observations in breeding vegetation, I found that Ashe juniper is the most commonly used substrate in both low stony hill and redland breeding

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sublocations but I rejected my hypothesis that Ashe juniper use would be twice that of deciduous tree species. Marshall et al. (2013) found that Golden-cheeked Warblers forage in Ashe junipers at a higher rate than it is available late in the breeding season and arthropod densities on Ashe juniper increase late in the breeding season. I expected to find similarly biased use of certain species during the post-breeding period in the breeding sublocations but, instead, found that warbler use of ashe juniper, Texas oak, and post oak is not significantly different from the availability of these species. The importance of Ashe juniper as a foraging substrate continues into the post-breeding period and is likely a driving factor for heavy juniper-oak woodland use in the post-breeding season. However, based on similarities between use and availability of ashe juniper and the two oak species, it appears that golden-cheeked warblers may be foraging at random in breeding vegetation.

Some warblers move into non-breeding vegetation that has a greater diversity in vegetative composition and structure when compared with non-breeding vegetation not commonly used (personal observation). In non-breeding vegetation, I failed to reject my hypothesis that warblers would use deciduous trees twice as often as Ashe juniper. During the post-breeding period, warblers heavily use deciduous tree species as foraging substrates in non-breeding vegetation likely because the increased vegetative diversity of these vegetation types contributes to greater insect productivity in non-breeding vegetation.

The effect of ecosite in breeding sublocations demonstrates that Golden-cheeked Warblers stay in the high quality habitat during the post-breeding period. I failed to

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reject the hypothesis that, in breeding vegetation, warblers would be found in the low stony hill ecosite more than in the redland ecosite. Marshall et al. (2013) found that warblers placing their territories in Texas oak habitat (i.e. low stony hill ecosites) had higher fledging success. Higher post-breeding detection rates in low stony hill breeding sublocations indicates that this ecosite is also of a higher quality in the post-breeding period. I rejected the hypothesis that, in non-breeding vegetation, I would find warblers in vegetation adjacent to redlands breeding sublocations twice as often as vegetation adjacent to low stony hill breeding sublocations. On the contrary, I detected warblers in non-breeding sublocations adjacent to the low stony hill ecosite at rates 4.5 times greater than those adjacent to redlands ecosites. I expected the opposite relationship between non-breeding sublocations regarding adjacent breeding ecosite because the redland ecosite is known to be of a lower quality during the breeding season. The lower quality breeding sublocations should have forced competing warblers out of resource-depleted breeding vegetation to the adjacent non-breeding vegetation that had not been exploited during the breeding season. However, because this movement did not occur but the detection rate in redland ecosite breeding sublocations was lower than that of the low stony hill ecosite, I am unsure where the warblers breeding in redland ecosites went. Did they move from the low-quality redland ecosite into the higher quality low stony hill ecosite or did they leave the immediate area and begin their fall migration earlier than other warblers breeding in higher quality habitat? Future studies should focus on banded warbler populations to answer some of these questions about post-breeding vegetation use.

In addition to which vegetation types were used during the post-breeding period, I wanted to address which warblers (i.e. family groups, males, females, or juveniles) use these vegetation types and if behavior is different among the vegetation types. Though not statistically significant, I failed to reject the hypothesis that Golden-cheeked Warbler family groups emigrated into non-breeding vegetation at a rate 50% greater than the rate of individual adults. I found family groups at a rate over twice that of individual adults. Movement of family groups may be associated to parent-directed dispersal of juveniles away from the breeding grounds. Several studies have documented long-term associations between parents and offspring prior to migration (Drent 1984; Knopf and Rupert 1996; Mauser et al. 1994; Salinas-Melgoza and Renton 2007; Matthyson 2010) and suggest that parent-guided dispersal may influence dispersal direction and philopatry in subsequent breeding seasons. A shift in philopatry from the natal site to a post-breeding site may reduce male competition for mates and other resources in subsequent years by encouraging second-year males to select territories outside of their natal territory.

I found that males move into non-breeding vegetation at a significantly higher rate than females. I failed to reject the hypothesis that males would move into non-breeding vegetation twice as often as females. Sex-biased dispersal is commonly recorded in many vertebrates and is typically attributed to the species' mating system (Dobson 1982; Moore and Ali 1984). Polygamous species generally have a male-biased dispersal rate as young and less competitive males leave areas occupied by a dominant male in search of opportunities for greater fitness. Monogamous species should show

approximately equal dispersal between sexes (Greenwood 1980) because dispersal costs and benefits are equal, or nearly so, between sexes. However, Greenwood (1980) noted that a majority of bird species, 90 % of which are monogamous (Lack 1968), show female-biased dispersal. He suggests that a system where males partition resources (i.e. acquire and defend a territory) prior to females selecting a mate should result in increased female dispersal. Golden-cheeked Warblers are considered monogamous (Ehrlich et al. 1988) so I would expect dispersal to be female-biased. Logically, dispersal in this species should be female-biased.

Several factors could lead to a discrepancy in expectations and my research findings. First, males may be leaving natal territories at higher rates than females to prospect for suitable future breeding locations. Farrell et al. (2012) found that conspecific cues (i.e. conspecific songs and fledgling calls) played during the late breeding and post-breeding period increased Golden-cheeked Warbler territory density threefold in treatment versus control plots the year following the treatment. These data indicate that some warblers prospect during the post-breeding period to gain social information on the quality of potential future breeding locations. This prospecting behavior could lead to movement out of breeding vegetation into adjacent non-breeding vegetation in search of social cues. Second, male warblers are more conspicuous than female warblers during the post-breeding period. While males sing less during the post-breeding season than the breeding season (personal observation), I was occasionally alerted to the presence of singing warblers that I otherwise might have failed to detect. Additionally, male calls were louder and more frequent than female calls during the

post-breeding season. This increase in detectability may have caused male detection rate to be higher during the post-breeding period in non-breeding vegetation. Last, Golden-cheeked Warblers are known to split broods during the post-breeding period (Gass 1996). Because many female warblers are responsible for feeding fledglings, their ability to disperse from the breeding vegetation may be limited by fledgling movement. However, responsibility for fledglings may also limit male dispersal as some males are equally responsible for offspring. The difference between my findings and expectations of dispersal are likely due to some combination of the above factors.

I failed to reject the hypothesis that the foraging rate would be 25% higher in breeding than non-breeding vegetation. However, I rejected the hypotheses that long flight and short flight rates would be 25% higher in non-breeding than breeding vegetation. Foraging and long flight frequency were not significantly different between breeding and non-breeding sublocations but rates in breeding sublocations were 33% and 28% higher than frequencies in non-breeding sublocations, respectively. Additionally, short flight frequencies were significantly higher in breeding than non-breeding sublocations. Movement rates are expected to increase when a bird is foraging in an area with fewer food resources (Hutto 1990). While detection rates were much higher in breeding than non-breeding sublocations, behavioral data seems to indicate that breeding vegetation is of a poorer quality than non-breeding vegetation during the post-breeding period. The increased foraging rate in breeding vegetation suggests that more food was available in this vegetation type so the movement and foraging rate differences are also in conflict with each other about the quality of the breeding vegetation. Within breeding

vegetation, I rejected the hypothesis that foraging rates would be 25% higher in low stony hill than in redlands ecosites. I also rejected the hypotheses that short flight rate would be 25% higher in the redlands than low stony hill ecosite and that long flight rate would be 25% higher in the redlands ecosite than the low stony hill ecosite. Long flight rate was actually significantly different between low stony hill and redland ecosites but the relationship was opposite of what I expected. Birds spent more time making flights longer than 2 seconds in low stony hill ecosites than in redland ecosites. This is, again, a counterintuitive result. I expected behavior in the ecosite in which most detections occurred to be consistent with behavior in high quality habitat. However, increased search effort in low stony hill ecosite seems to indicate that warblers foraging there are working harder to find food than those in redland ecosites.

Much of the discussion above mentions trends in the data involved in this study but does not reflect statistically significant findings using traditional null hypotheses. Though my findings often reveal large differences between two or more means, percentages, or other metrics, my sample sizes were commonly insufficient to make any certain claims about Golden-cheeked Warbler's vegetation associations, behavior, and substrate use during the post-breeding period. To reinforce this study's findings and alleviate some of the problem of sample size insufficiency, more work needs to be done to confirm that some of the trends I discussed above are, in fact, biologically and statistically important findings that can help us manage this species' habitat requirements more appropriately throughout the annual cycle.

Conclusions and Management Implications

Research need 1.22 of the Golden-cheeked Warbler recovery plan (USFWS 1992) states that knowledge of warbler movements during the post-breeding period "...is particularly important in relation to habitat types and quality and will be applied to further defining the habitat requirements of the species." Previous studies have helped define high quality breeding habitat (Campbell 2003, Marshall et al. 2013) but this is the first study to examine vegetation associations in the post-breeding period and infer habitat quality from those associations. Number of detections and detection rate indicate that juniper-oak woodland, the vegetation used for breeding, is the vegetation type Golden-cheeked Warblers use most heavily during the post-breeding period. Specifically, warblers use juniper-oak woodland in the low stony hill ecosite at the highest rate of any vegetation type surveyed. These results help to extend current habitat requirements beyond the breeding season into the post-breeding period. Current guidelines for determining high quality breeding habitat focus on canopy cover (Campbell 2003) but other studies have found that using canopy cover alone, while necessary, is insufficient to predict reproductive output. Marshall et al. (2013) suggests that instead of using canopy cover alone, we should include tree species composition in conjunction with percent canopy cover as predictors of habitat quality. My results also indicate that ecosite, which varies in tree species composition, is a good predictor of presence-absence in the post-breeding period and can be used as a guideline for defined habitat requirements in the post-breeding period.

While in post-breeding vegetation, Ashe juniper is the most commonly used foraging substrate in all vegetation types surveyed. Currently, juniper's role in this species' annual cycle is related only to stripping bark being used as nesting material (Campbell 2003). However, this study indicates that juniper is important to the species as a foraging substrate after the breeding season. This conclusion is consistent with other studies finding that Ashe juniper is not only important as a source of nesting material but also as a foraging substrate during the breeding season (Marshall et al. 2013). Current management guidelines suggest that removal of immature (i.e. <5 inch dbh) junipers that are <15 feet in height will not harm the warbler's reproductive success. However, removal of these trees is likely to alter the warbler's foraging success and, therefore, reproductive success by changing tree species composition. To make informed decisions about management of habitat for the recovery of this species, managers will need to consider tree species composition, particularly abundance of Ashe juniper and Texas oak, as predictors of high quality habitat in the future.

Increased family group and juvenile warbler movement into non-breeding vegetation compared to breeding vegetation indicates that non-breeding vegetation may represent a particularly important resource to hatch year Golden-cheeked Warblers during the post-breeding period. Vitz and Rodewald (2011) found that in ovenbirds and worm-eating warblers (*Helmintheros vermivorum*), fledgling survival was positively related to body condition and density of vegetation during the post-fledging period. When juvenile Golden-cheeked Warblers moved out of breeding vegetation, they typically moved into areas with higher vegetative density than other non-breeding

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vegetation. Fledgling affinity for density during the post-fledging period is typically

attributed to concealment from predators (King et al. 2006, Vitz and Rodewald 2011)

and may be an influencing factor in fledgling warbler movement from some breeding

sublocations but not others. Future research should focus on factors (i.e. arthropod and

predator abundance) that could influence habitat choices during the post-breeding period

to gain a more complete understanding of Golden-cheeked Warbler vegetative

associations during the post-breeding period.

CHAPTER III[*]

MIGRATORY CONNECTIVITY OF BLACK-CAPPED VIREO

Conservation efforts for migratory songbirds have historically focused on the breeding grounds. While these efforts are important, a clear picture of the evolution, ecology, and conservation of migratory songbirds requires an understanding of the entire annual cycle (Myers et al. 1987, Faaborg et al. 2010). Complete study of the annual cycle includes the study of survival, foraging success, and other interactions on the wintering ground and how those events affect success on the breeding ground. Fretwell (1972) argued that populations of species living in seasonal environments are subject to the interactions among those seasons. Studies have shown this is true of migratory birds that experience carryover effects between the wintering and breeding grounds of neotropical migrants (Robbins et al. 1989; Marra et al. 1998; Gill et al. 2001; Norris et al. 2004a,b; Saino et al. 2004, Harrison et al. 2011, Alves et al. 2013). And, recent studies have shown that a bird's ecology on the wintering grounds can have substantial effects on fecundity and recruitment on the breeding grounds (Faaborg et al. 2010; reviewed by Webster and Marra 2005).

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[*] Part of the data presented in this chapter is reprinted with permission from "GIS-based model of stable hydrogen isotope ratios in North America growing-season precipitation for use in animal movement studies" by Meehan, T. D., J. T. Giermakowski, and P. M. Cryan, Isotopes in Environmental and Health Studies, 40:4, 291-300. Copyright (2004) by http://www.tandfonline.com

Part of the data presented in this chapter is reprinted with permission from "A geographic-information-system approach to estimating the origin of migratory raptors in North America using stable hydrogen isotope ratios in feathers" by Lott, C. A. and J. P. Smith, The Auk, 123:822-835. Copyright (2006) by The Auk.

Migratory connectivity is the degree to which individuals or populations are geographically arranged among two or more periods of the annual cycle (Webster et al. 2002, Marra et al. 2006). Various degrees of connectivity lead to different conservation strategies (Webster et al. 2002, Webster and Marra 2005, Marra et al. 2006). If individuals and, by extension, populations maintain their associations from the breeding ground to the wintering ground (*i.e.* the same individuals associate with each other on both the breeding and wintering grounds), thus indicating strong connectivity, they may need unique management techniques because they can be thought of as separate populations. However, if individual associations and population structure on the breeding ground do not exist on the wintering ground (weak connectivity), management of populations as independent units may be less important (Marra et al. 2006).

Many methods have been employed to study the connectivity of migratory bird ecology. Morphological variation among populations of breeding birds has been used to assign birds on the wintering grounds to a breeding location (Ramos and Warner 1980; Ramos 1983; Bell 1997). In the absence of morphological variation, information about migratory connectivity can be obtained through individual mark-recapture techniques. This method is useful for large birds that can carry visible tags or game birds that are routinely collected through hunting. However, returns from this mark-recapture technique are often low and offer limited information about connectivity (Clark, et al. 2000; Stolt et al. 2000). Genetic approaches have also been used to define migratory connectivity. Wenink and Baker (1996) and Haig et al. (1997) used mtDNA and randomly amplified DNA polymorphism, respectively, in shorebirds to define breeding

populations. Each then used these genetically distinct population signatures to assign birds on the wintering grounds to populations on the breeding grounds. Along with each of these approaches, stable-isotope analysis (SIA) has been demonstrated as an option for studying migratory connectivity (Chamberlain et al. 1997, Rubenstein et al. 2002).

Isotopes of a given element possess the same number of protons but have differing numbers of neutrons, and, therefore, a different atomic mass (Reece et al. 2014). Stable isotopes are isotopes of a given element that do not radioactively decay and are, therefore, stable. In nature, stable isotopes of any element vary spatially relative to a variety of meteorological, climatic, and geographic processes such as rainfall amounts, latitude, altitude, seasonal temperature, and distance away from the marine coast (Tieszen and Boutton 1988, Bowen 2010) resulting in large, continent-wide patterns of stable isotope ratios. For example, hydrogen exists in two isotopes, ^{1}H (one proton and no neutrons in the nucleus) and ^{2}H, also known as deuterium, (one proton and one neutron in the nucleus). Because deuterium is twice as heavy as ^{1}H, it behaves differently when exposed to the environmental processes above. These processes vary along a spatial continuum and result in predictable hydrogen isotope ratios on a continental scale (Fig. 3.1)

In recent years, researchers have found that the stable isotope ratios in tissues of organisms living in a given geographic location reflect the stable isotope ratios of that geographic location. The hydrogen ratio of a location is primarily dictated by the water in that location and the processes associated with that water (*e.g.* precipitation, evaporation, evapotranspiration, runoff). As plants in that location make use of the

water, their biomass incorporates stable isotopes in similar ratios to the original water source. Likewise, any animals in the food web will have tissues with isotope ratios similar to the plants and water sources for those plants. For example, Lott and Smith (2006) collected contour feathers from 12 species of raptors across North America and analyzed them for Hydrogen isotope ratios. Using interpolation methods, the authors generated a North American map of raptor feather Hydrogen isotopes values (Fig. 3.2) and compared it with a model of predicted isotope ratios based on precipitation. They found that the feather isotope map and the precipitation map corresponded across most of North America (Fig. 3.3).

Advances in the application of stable-isotope analysis (SIA) have proven useful in discerning the ecology of migratory birds throughout their annual cycle (Hobson 2005). Chamberlain et al. (1997) and Hobson and Wassenaar (1997) independently demonstrated that stable hydrogen isotope ratios (δD) found in the feathers of nearctic-neotropical migrants correlated with rainfall δD collected during the growing season (Boulet and Norris 2006). Birds make ideal study subjects for SIA because feathers are metabolically inert and, therefore, retain the isotope ratios of locations in which they were grown. Through analysis of stable isotope ratios in feathers and comparison to existing, continent-wide gradients of isotope ratios created from precipitation, one can determine where the sampled feathers were grown. Using this method, researchers can link locations on the breeding grounds where feathers were grown to locations on the wintering grounds where feathers were collected and analyzed.

Numerous studies have taken the stable isotope approach to describe migratory connectivity. The American Redstart (*Setophaga ruticilla*) has been studied using δD and stable carbon isotope ratios ($\delta^{13}C$) and was found to exhibit strong connectivity (Marra et al. 1998; Norris et al. 2005; Norris et al. 2006a). Rubenstein et al. (2002) used δD and $\delta^{13}C$ and found that Black-throated Blue Warblers (*Setophaga caerulescens*) wintering on western Caribbean islands were strongly connected to populations breeding in the northern portions of this warblers' North American breeding range and those
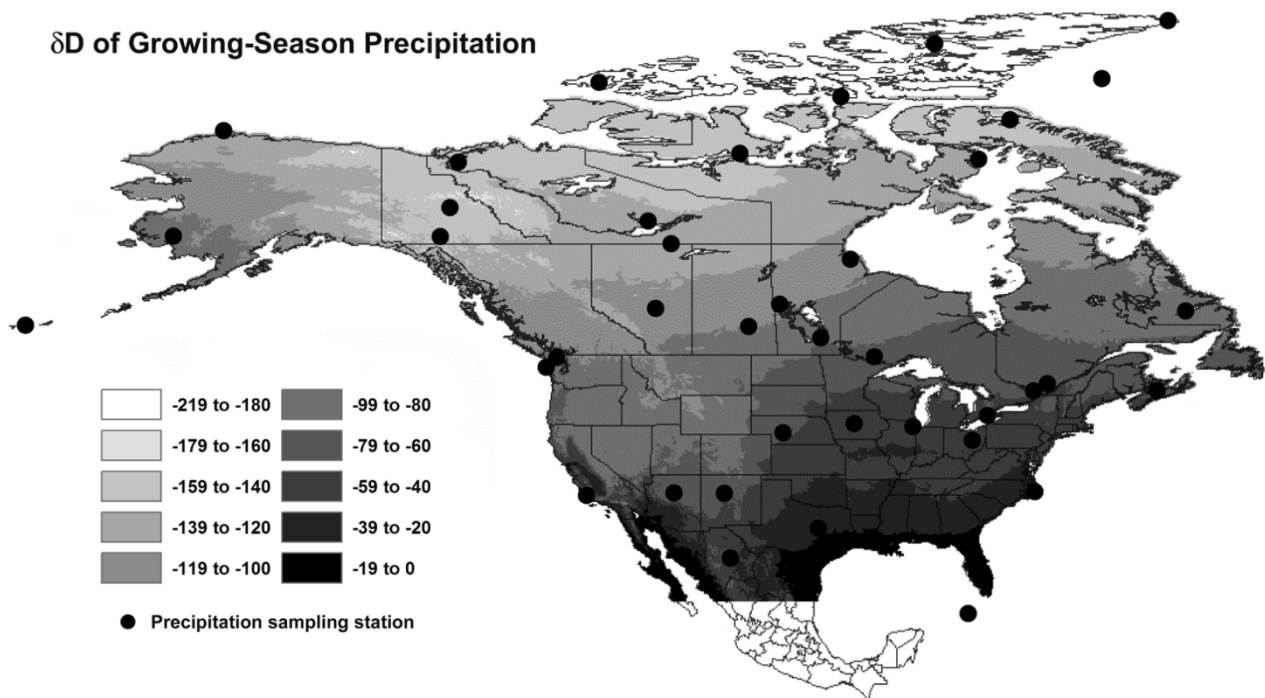
Figure 3.1. Continent-wide map of δD values (expressed as parts per thousand or ‰) predicted from growing-season precipitation (Figure reprinted with permission from Meehan et al. 2004, Copyright 2004 by http://www.tandfonline.com).
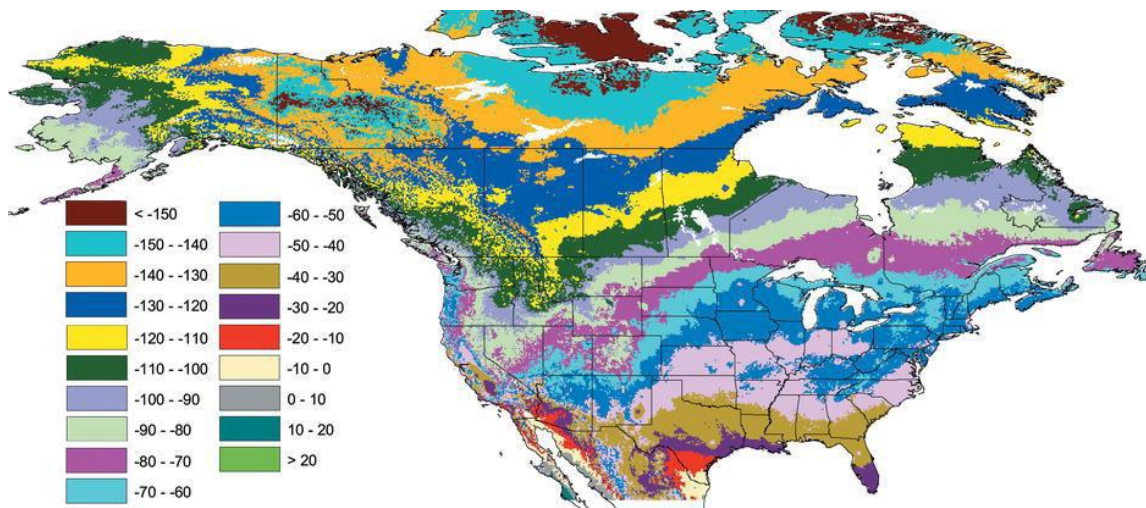
Figure 3.2 Continent-wide map of δD values (expressed as parts per thousand or ‰)

predicted from North American raptor feathers (Figure reprinted with permission from

Lott and Smith 2006, Copyright 2006 by The Auk).
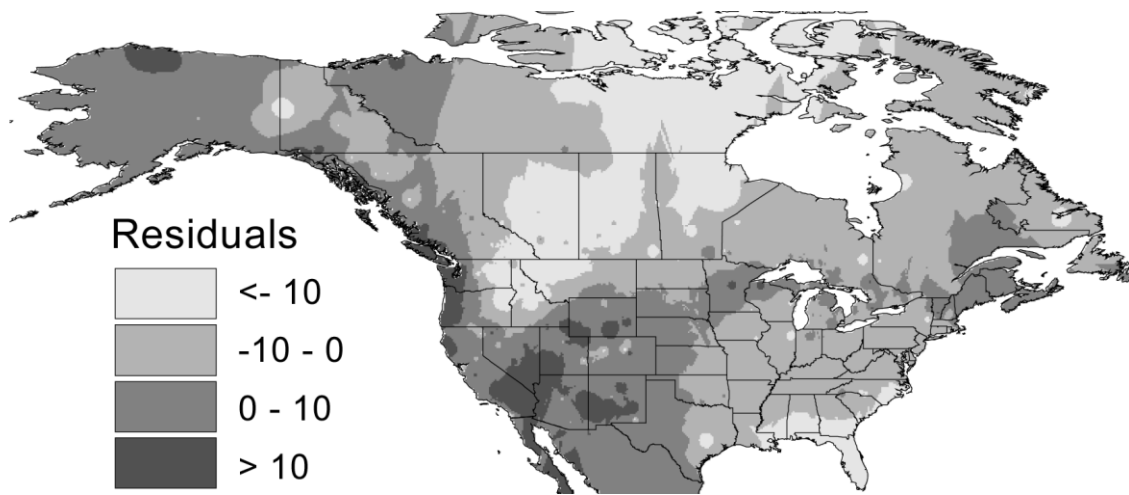
Figure 3.3 Continent-wide map depicting residual of feather δD-precipitation δD across North America. Positive values indicate that feather δD were higher than expected. Negative values indicate feather δD were lower than expected (Figure reprinted with permission from Lott and Smith 2006, Copyright 2006 by The Auk).

wintering on eastern Caribbean islands were strongly connected to populations breeding in southern portions of the breeding range. Flyways and connectivity of the Yellow Warbler (*Setophaga petechia*) have been revealed using δD (Boulet et al. 2006). Clegg et al. (2003) showed that Wilson's Warbler (*Cardellina pusilla*) demonstrates a leapfrog (Salomonsen 1955) pattern of migration and shows moderate migratory connectivity. The migratory connectivities of the following species are better understood because of the application of SIA: King Eider (*Somateria spectabilis*) (Mehl et al. 2004), Sharp-shinned Hawk (*Accipiter striatus*) (Smith et al. 2003), Red Knot (*Calidris canutus*) (Atkinson et al. 2005), Willow Warbler (*Phylloscopus trochilus*) (Chamberlain et al. 2000), Swainson's Thrush (*Catharus ustulatus*) (Wassenaar and Hobson 2001; Kelly et al. 2005), Black-throated Blue Warbler (*Setophaga caerulescens*) (Chamberlain et al. 1997, Rubenstein et al. 2002), Common Yellowthroat (*Geothlypis trichas*) (Kelly 2006), White-throated Sparrow (*Zonotrichia albicollis*) (Mazzerolle et al. 2005).

Application of stable isotope markers has primarily been used on long-distance migrants occupying large breeding and wintering ranges (Webster et al. 2002) with few exceptions (i.e. Mazzerolle et al. 2005, Mehl et al. 2004, Smith et al. 2003). Studies of migratory connectivity at these coarse scales allow researchers to understand migratory populations on a continent-wide scale. However, the biological implications of connectivity studies are expected to become increasingly stronger as spatial scale becomes more fine (Hjernquist et al. 2009). At these fine spatial scales, philopatry becomes more important in limiting gene flow and indicates a need for unique

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management of each population. Species that exist only on small spatial scales are subject to the implications of migratory connectivity.

The Black-capped Vireo (*Vireo atricapilla*), an endangered songbird, is an example of a short distance migrant that also occupies both a small breeding and a small wintering range (Grzybowski 1995). The connectivity of this species is unknown and could be critical to its proper management. Black-capped Vireo is a candidate for studies of migratory connectivity because recent studies have found that it exhibits breeding populations that are genetically distinguishable. Fazio III et al. (2004) and Barr et al. (2008) both found significant interpopulation divergence of breeding populations of Black-capped Vireos which allows researchers to identify an individual to a population based on genetic markers. Although recent genetic research shows that populations of each species are diagnosably distinct, it is unclear whether SIA will be useful in determining migratory connectivity in the species because it breeds and winters on such fine spatial scales. Black-capped Vireo breeding range extends from western Oklahoma through central Texas and into Coahuila, Mexico (Grzybowski 1995). This breeding range is much smaller than the continent-wide ranges of previously mentioned passerines studied using SIA. Maps created from rainfall isotope ratios, the typical method of studying connectivity using SIA, lack the precision necessary to aid in understanding the vireo's migratory connectivity. A fine-scale isotope map is necessary to draw any useful conclusions from the study. To increase the accuracy of SIA, a map of isotope ratios created using feathers of known origin from the study species can be

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used. This increases the precision of the results needed to accurately infer migratory connectivity (K. Hobson, personal communication).

Hydrogen isotope ratios vary from year to year based on atmospheric precipitation and temperatures (Bowen and West 2008) and can lead to interannual variation on fine scales. Powell (2013) found that δD values in Black-capped Vireo feathers collected from the breeding grounds were significantly depleted relative to expected δD precipitation values. In addition to numerous other possibilities he gave, Powell suggested one reason for the discrepancy between feather δD and precipitation δD values was that groundwater may be the main source of δD in this species across most of its breeding range.

Groundwater in a given area has been found to have a different δD than precipitation in that same area. For instance, Musgrove and Banner (1993) found that spring water originating from aquifers beneath the Missouri-Oklahoma border had greatly depleted δD values (-108‰) relative to expected growing season precipitation values of -45‰--35‰. Musgrove and Banner found that the aquifer under the spring in question was mixing with depleted (more negative) water from high elevation sources in Colorado causing an artificially depleted δD signature. Additionally, Oetting et al. (1996) found that stable isotope ratios of strontium, oxygen and hydrogen, as well as dissolved solids of magnesium, sodium, chlorine, sulfate, and bicarbonate values in the Edwards aquifer, which underlies much of the Black-capped Vireo's breeding range in Texas, experience extensive mixing with saline "badwaters" underlying the aquifer, brines in the nearby hydrostratigraphy, and freshwater that has interacted heavily with

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surrounding rock to alter isotopic and dissolved solids content. For these reasons, it is possible that the unexpected feather δD values in Powell (2013) were due to groundwater δD sources mixing with other water sources and creating a very different isotope signature for the bird's breeding ground than precipitation predicts.

Using stable hydrogen isotope ratios gleaned from feathers cut from Black-capped Vireos across the breeding range in Texas and Oklahoma, I developed a set of maps to be used in future migratory connectivity studies with this species. These maps will serve as a baseline against which future researchers can compare isotope ratios of vireo feathers collected on the wintering grounds. Ratios of winter-collected feathers can then be matched to the map's ratios to determine the most likely location where the feathers were grown during the previous breeding season. Through this comparison of ratios, one could determine the migratory connectivity of the Black-capped Vireo.

Objectives and Hypotheses

Objective 1: Create an isotope map for Black-capped Vireo using feathers collected across its breeding range in Texas and Oklahoma:

> H1: Isotope ratios in feathers collected across the bird's breeding range will be sufficiently different from one region to the next to allow me to distinguish among different regions of the breeding range.

> H2: The species-specific isotope map will be similar to isotope maps based on rainfall isotope ratios found in Meehan et al. 2004.

Biological Significance: The predominant purpose of this objective is to determine if breeding populations across the vireo's breeding range can be separated and consistently distinguished from each other. Because the main goal of building a feather-based isotope map is to distinguish among breeding population, statistically significant differences of isotope ratios among breeding populations is the only way to ensure that a particular feather of unknown growth origin can reliably be assigned to one breeding population or another. There is no meaningful biological significance that can substitute for statistically significant separation of isotope ratios from one breeding region to the next.

Objective 2: Create an isotope map of ground water collected from areas in and around locations where feathers were collected:

> H1: Ground water maps of the Texas breeding range will vary with regard to geographic location.

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H2: Ground water maps will trend similarly to the maps created using stable

hydrogen isotopes from collected feathers.

Biological Significance: Similarly to the first objective, this objective relies on

statistically significant differences in mean isotope ratios from one breeding population's

groundwater supply to the next. There is no biologically significant substitute for this

statistical significance. Regarding comparison of feather-based isotope maps and

groundwater-based isotope maps, I will compare maps generated from feather analyses

with those generated from groundwater. Similar patterns on each map would indicate

that the feather δD and groundwater δD are closely related and groundwater is a likely

source for δD in Black-capped Vireo feathers.

Study Area and Methods

From 2010-2012, I selected sites at which our research group was already working to conduct feather collection. Because the Black-capped Vireo recovery plan (USFWS 1991) dictates that recovery of this species must include viable populations in Oklahoma, four of six regions in Texas, and Mexico, I chose sites located within as many of the recovery regions in Texas and Oklahoma as I could. I collected feathers from nine locations at which our research group was working during the vireo's breeding season (Fig. 3.4). These study sites Ft. Hood military reservation in Coryell and Bell counties, Kerr Wildlife Management Area and private properties in Kerr County, Balcones Canyonlands National Wildlife Refuge in Travis, Williamson, and Burnet counties, private properties in Taylor County, Devil's River State Natural Area in Val Verde County, private properties in Real County, Kickapoo Cavern State Park and surrounding private properties in Edwards and Kinney counties, Mason Mountain Wildlife Management Area in Mason County, and Ft. Sill Military Reservation in Comanche County, Oklahoma. In Texas, I collected feathers at two sites in recovery region two: Ft. Hood military reservation (FH) and Balcones Canyonlands National Wildlife Refuge (BCNWR). I collected feathers at four sites in recovery region three: Kerr Wildlife Management Area (KWMA), Kickapoo Cavern State Park and private properties in Edwards and Kinney counties(KICK), private properties in Real County (H83), and Mason Mountain Wildlife Management Area (MMWMA). I collected feathers from one site in recovery region four: private property in Taylor County (TAY).

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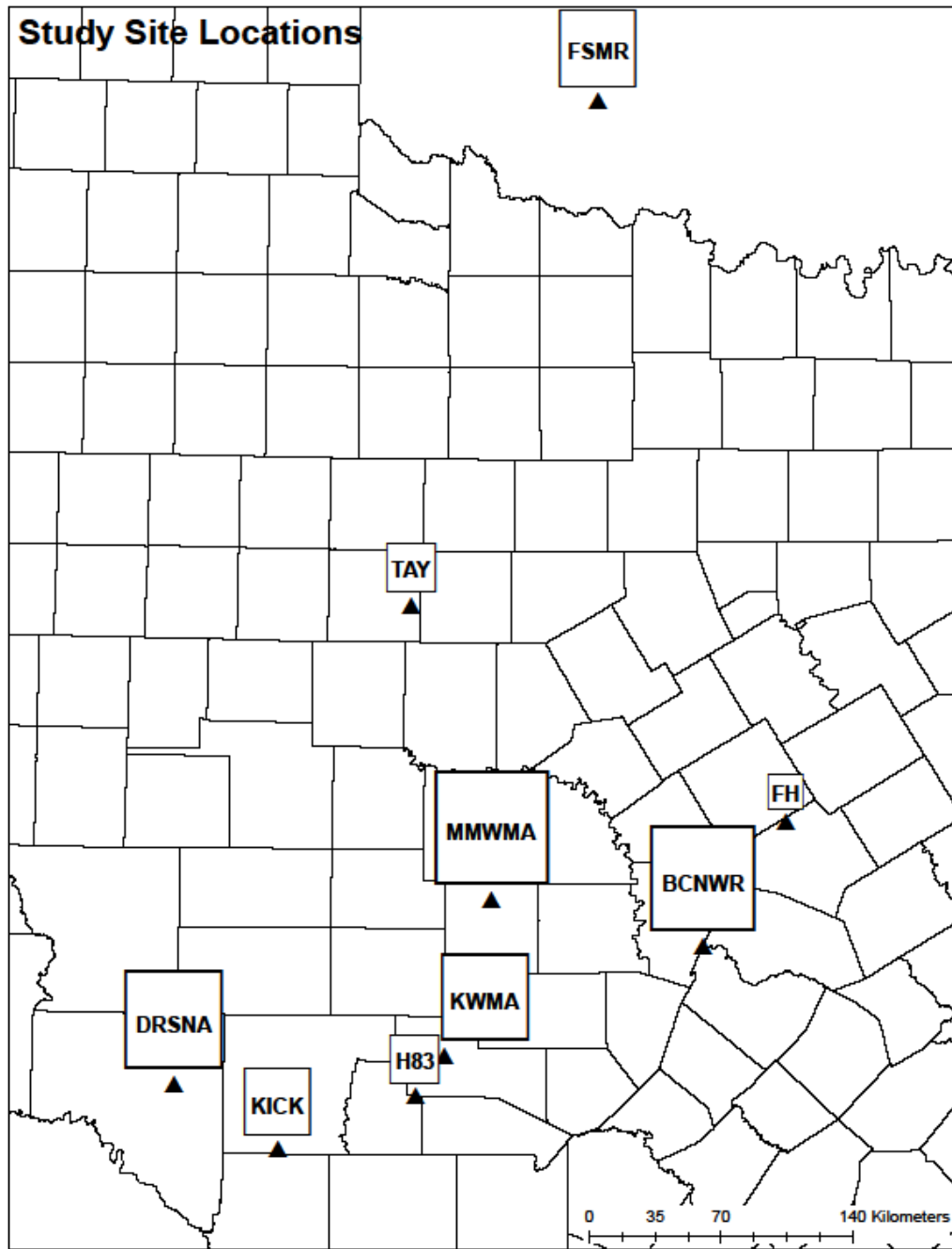
Figure 3.4 Feather collection sites from 2010 to 2012. Each site at which feathers were collected is also a site at which other research objectives were being studied.

I collected feathers from one site in recovery region five: Devil's River State Natural Area (DRSNA). In addition to all Texas collecting sites, I also collected feathers from Ft. Sill Military Reservation (FSMR) in Oklahoma. All locations are known to have breeding populations of Black-capped Vireo.

By collecting samples from birds in a subset of the recovery regions in Texas and Oklahoma, I was able to sample across a broad range of ecological situations. Additionally, sampling from each of these locations will likely provide the geographic separation in samples required to get differentiation in stable-isotope analyses.

Field Measures

Target mist-netting and banding: During the breeding seasons in 2010-2012, I target netted adult birds in each study location listed above using playbacks and 6-m mist-nets. Upon identification of defended territories, I set up mist nets and broadcast speakers to attract territorial males and females toward the nets. I constantly monitored each net and played conspecific songs and calls at natural frequency and volume levels. If caught, I extracted birds as quickly and safely as possible as stored them in cloth bird bags while finalizing banding and feather collection preparations. Each adult bird was banded with a red, annodized USGS band and a unique color band combination.

Feather collection for SIA: While adult birds were banded, I cut two crown feathers and one inner rectrix (r4) for stable-isotope analysis. In Black-capped Vireos, crown feathers and inner rectrices are grown on the breeding grounds (Pyle 1997, Butler et al. 2008) and can, therefore, be used to create a map of the isotope concentrations

across the bird's breeding range. I stored all collected feathers in envelopes at room temperature for future analyses.

At each feather collection site, I was permitted to actively collect rectrix and capital tract feathers from 10 individuals. I was additionally allowed to collect any feathers that passively fell out during the process of banding birds. I attempted to collect feathers from the permitted amount of individuals at each collection site because sample sizes for other stable isotope analyses indicate that more feathers are always preferable to fewer feathers. While most stable isotope studies attempt to match feather isotope signatures to an existent growing season isotope map, I attempted to generate a new map using isotopes from feathers. This method requires as many feathers as possible to increase accuracy of species-specific feather isotope map generation. For this reason, I collected as many feathers as I could from as many locations as I could to increase my likelihood of success in this study.

Regional Water Samples: In 2011, I collected ground water samples at each study site to which I had access. At each study site, I identified ground water sources in or very near the study site that were protected from evaporative fractionation of isotopes. To reduce the likelihood that I collected ground water sustaining fractionation, any source of ground water (i.e. windmills or electric pumps), I allowed the water source to run for one minute to flush water exposed to the atmosphere prior to collection. I attempted to collect three sources for groundwater at each study location but was not able to do so at each study site. For each source, I collected two samples for separate

analyses. I collected and stored water samples in water-tight containers wrapped in plastic to prevent evaporative fractionation during storage and transport for analysis.

Laboratory Measures

Isotope Ratio Determinations: Because hydrogen isotope ratios are most likely to be useful for discrimination among different regions of the breeding range, I only analyzed the collected feathers for this element's isotopic ratios. All analyses were conducted at the Colorado Plateau Stable Isotope Laboratory (CPSIL) at Northern Arizona University in Flagstaff, Arizona. Prior to analysis, feathers were washed in a solvent to remove all surface debris and lipids. They were then dried in an oven at 100 ˚C to remove all water. Segments of the feather were cut from the distal end, pulverized using a mortar and pestle, and wrapped in a silver capsule and weighed. Samples from each rectrix included enough feather vane to fall within the optimal weight range for Hydrogen isotope analyses (0.33-0.37 mg). However, many feathers from the capital tract were not large enough to fall within this weight range. For these samples, the entire feather was pulverized, weighed, and encapsulated. All samples were then analyzed via high-temperature pyrolysis using Finnigan Delta continuous flow isotope mass spectrometers that had been calibrated for specific isotopes.

Isotope ratios are conventionally expressed in delta notation ($\delta=(($isotope ratio$_{sample}$/isotope ratio$_{standard})-1)\text{X}1,000)$ (Werner and Brand 2001, Coplen 2011). This delta notation standardizes the expression of isotope ratios by comparing the isotope ratio of a given sample to that of an international standard. The accepted standard for most hydrogen isotopes is Vienna Standard Mean Ocean Water (vSMOW) which has a

hydrogen isotopic ratio of 0.00015575 (Colorado Plateau of Stable Isotopes Laboratory

2015). If a given sample's hydrogen isotope ratio is larger than the standard's ratio, the

delta value is positive for that sample and the sample is said to be enriched. Conversely,

if a given sample has a ratio lower than the standard's ratio, that sample's delta value

will be negative and is said to be depleted.

Analyses

For all statistical analyses, I used R (R-core members, et al., 2013). Because

some capital tract feathers were too small to produce reliable isotope ratio results,

sample sizes are different between the analysis of rectrices and capital tract feathers. To

determine if I could analyze rectrix and capital tract feathers together, I conducted a

Pearson correlation analysis (Sokal and Rohlf 1987 271-280). If correlation was low

between capital tract feathers and rectrices, I conducted all subsequent analyses

separately.

Objective 1: Create an isotope map for Black-capped Vireo using feathers

collected across its breeding range in Texas and Oklahoma

Analysis: I summarized the feathers collected at each study site and in each

recovery region. I conducted a one-way ANOVA (Ott and Longnecker 2001: 853-859)

to determine if isotope ratios from each study site were sufficiently different to allow

assignment of feathers of unknown origin to a particular site. Additionally, I conducted a

second one-way ANOVA (Ott and Longnecker 2001: 853-859) to determine if isotope

ratios among the recovery regions were significantly different. Because I collected

feathers from both the bird's tail (rectrices) and the capital tract, I conducted separate

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analyses for each feather tract to determine if either rectrices or capital tract feather isotope ratios more closely matched expected ratios in precipitation isotope ratio maps. If I found any analyses detected a significant difference among feather stable isotope ratios, I used a Tukey's HSD post-hoc comparison (Urdan 2010: 110-111) test to determine which study sites or recovery regions were significantly different. I also compared study sites based on physical location by dividing sites into categories based on proximity to each other. Because average rainfall totals can heavily affect stable isotope ratios in feathers, I also grouped study sites based on 30 year average rainfall totals and conducted a t-test. Additionally, I used linear regression (Ott and Longnecker 2001:540-548) to determine if there is a relationship between δD and latitude or longitude. To generate feather-based isotope maps of the Texas and Oklahoma breeding range, I used ArcMap™ (ESRI® 2005, Redlands, California, USA) and a simple interpolation technique (example in Figs. 3.2, 3.3, and 3.4). Interpolation techniques are used to predict the value of regions between or around locations at which a sample has been taken. Interpolation techniques assume that the values of samples are spatially related to each other and the surrounding area at which no samples were taken. Through this assumption, these techniques are able to generate a continuous surface of values throughout a given area without having samples representing each portion of that area.

Objective 2: Create an isotope map of ground water collected from areas in and around locations where feathers were collected

Analysis: I summarized the groundwater collection results for each site and recovery region. I conducted a one-way ANOVA(Ott and Longnecker 2001: 853-859)

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to determine if hydrogen isotope ratios in ground water collected from the Texas

breeding sites was significantly different. I also divided the breeding sites into their

respective recovery regions and conducted another one-way ANOVA (Ott and

Longnecker 2001: 853-859) to determine if ground water hydrogen isotope ratios were

significantly different across recovery regions. If I found any analyses detected a

significant difference among stable isotope ratios in ground water samples, I used a

Tukey HSD post-hoc comparison to determine which study sites or recovery regions

were significantly different. Additionally, if I found that isotope ratios were different

among the collection sites, I regressed (Ott and Longnecker 2001:540-548) δD with

latitude to determine if the groundwater differs along a latitudinal gradient. To generate

ground water-based isotope maps of the Texas breeding range, I used ArcMap™

(ESRI® 2005, Redlands, California, USA) and a simple interpolation technique.

Results

Summary of Feathers and Water Collected

From 2010-2012, I collected feathers from 158 Black-capped Vireos across nine different study locations. In 2010, I collected feathers from 19 individuals; 9 individuals from Balcones Canyonlands National Wildlife Refuge, 4 from Devil's River State Natural Area, and 6 from Kerr Wildlife Management Area (Table 3.1a). In 2011, I collected feathers from 69 individuals; 10 from Balcones Canyonlands National Wildlife Refuge, 12 from Ft. Hood Military Reserve, 10 from private property in Real County, 10 from Kerr Wildlife Management Area, 11 from Kickapoo Cavern State Park and private properties in Edwards and Kinney counties, 12 from Mason Mountain Wildlife Management Area, and 4 from private property in Taylor County (Table 3.1b). In 2012, I collected feathers from 52 individuals; 16 from Balcones Canyonlands National Wildlife Refuge, 3 from Ft. Hood Military Reserve, 7 from private property in Real County, 10 from Kickapoo Cavern State Park and private property in Edwards and Kinney counties, 11 from Mason Mountain Wildlife Management Area, 2 from private property in Taylor County, and 3 from Ft. Sill Military Reserve in Comanche County, Oklahoma. In addition to the 3 feathers collected in Oklahoma, J. Grzybowski provided me with feathers collected from 18 Black-capped Vireos in Comanche County, Oklahoma in 2002 to increase my sample size of feathers representing the breeding range in Oklahoma (Table 3.1c).

Correlation between stable isotope ratios in rectrices and capital tract feathers was low (ρ=0.2736, df=109) and suggests that, though there is a positive correlation

a) 2010 Locations	Recovery Region	Collected	Rectrices Analyzed	Capital Tract Analyzed
Balcones	2	9	9	––
Devil's River	5	4	4	––
Kerr	3	6	6	––

b) 2011 Locations	Recovery Region	Collected	Rectrices Analyzed	Capital Tract Analyzed
Balcones	2	10	10	8
Ft. Hood	2	12	12	11
Real County	3	10	10	8
Kerr	3	10	10	6
Kickapoo	3	11	11	8
Mason	3	12	12	10
Taylor County	4	4	4	4

c) 2012 Locations	Recovery Region	Collected	Rectrices Analyzed	Capital Tract Analyzed
Balcones	2	16	16	12
Ft. Hood	2	3	3	3
Real County	3	7	7	4
Kickapoo	3	10	10	7
Mason	3	11	11	9
Taylor County	4	2	2	2
Oklahoma	N/A	3(18)	21	19

Table 3.1 Feather collection sites and the number of rectrices and capital tract feathers analyzed from each site in **a)** 2010, **b)** 2011, and **c)** 2012. Numbers in parentheses are those collected from J. Grzybowski in 2002 to be analyzed as part of my study.

between feathers from these two tracts, the relationship is insufficient to indicate that these data should be analyzed together. I analyzed all stable isotope ratios of feathers from the two tracts separately.

In 2011, I collected groundwater from groundwater samples from 7 study sites across three recovery regions in the Texas breeding range. In recovery region 3, I collected three samples from Kickapoo Cavern State Park, three samples from Kerr Wildlife Management Area, three samples from private properties in Real County, and two samples from Mason Mountain Wildlife Management Area. In recovery region 2, I collected three samples from Balcones Canyonlands National Wildlife Refuge, and three samples from Ft. Hood Military Reserve. In recovery region 4, I collected one sample from private property in Taylor County.

Isotope Analysis of Black-capped Vireo Feathers

Isotope ratios of rectrices from the different study sites were not significantly different (F=1.525, $df = 8$, 149, P=0.153). Though not statistically significant, the Devil's River State Natural Area study site did have more enriched deuterium isotope concentrations than other study sites (Fig. 3.5). Isotope ratios of rectrices divided by Texas recovery regions and Oklahoma were not significantly different (F=2.226, $df = 1$, 156, P=0.138). While not significantly different, there was a general trend that deuterium isotope concentrations become increasingly enriched from the northernmost region sampled (Oklahoma) to the southernmost region sampled (Recovery Region 5; Fig. 3.6). However, the regression of rectrices by latitude (r^2= 0.0092, $F = 1.009$, $df =$
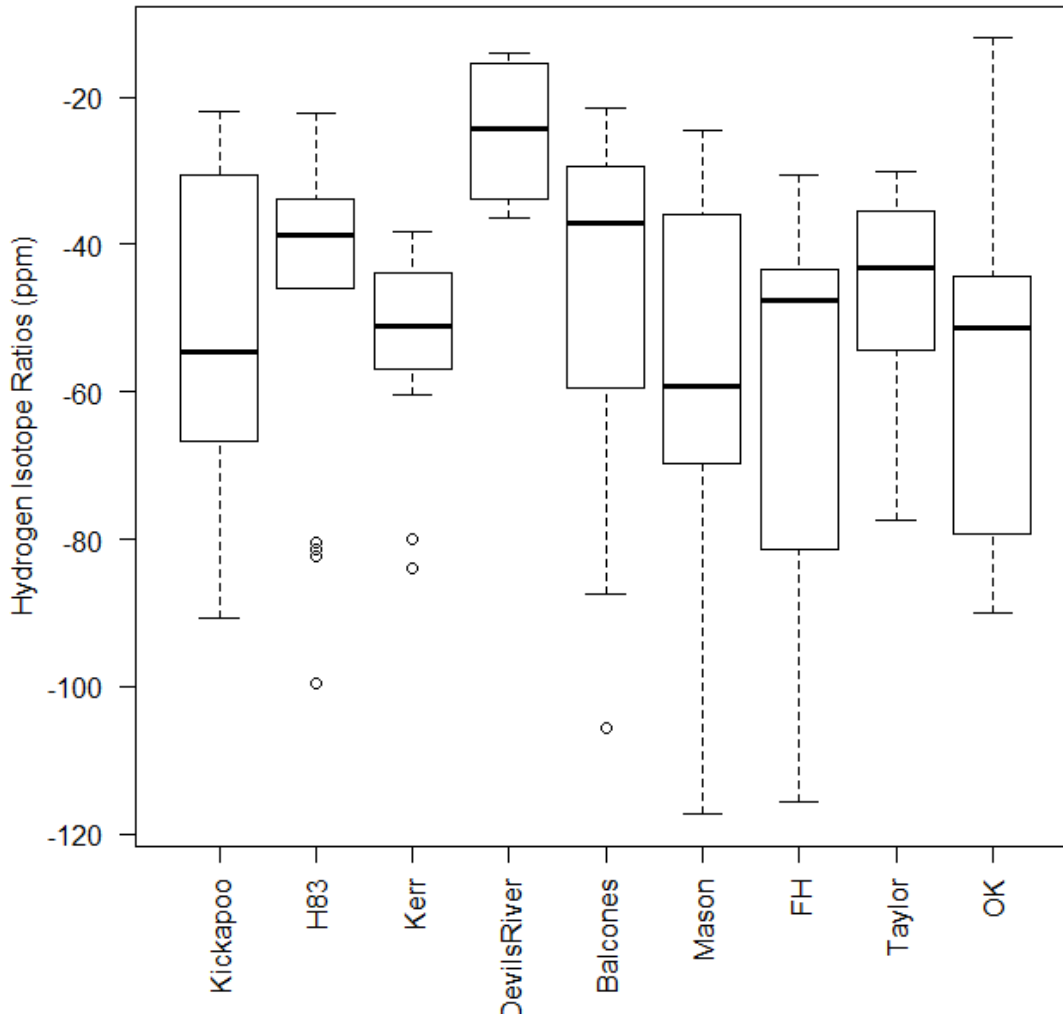
Figure 3.5 Mean δD values of rectrices divided among all collection sites. Sites, from left to right, are ordered from the southernmost site to the northernmost site.
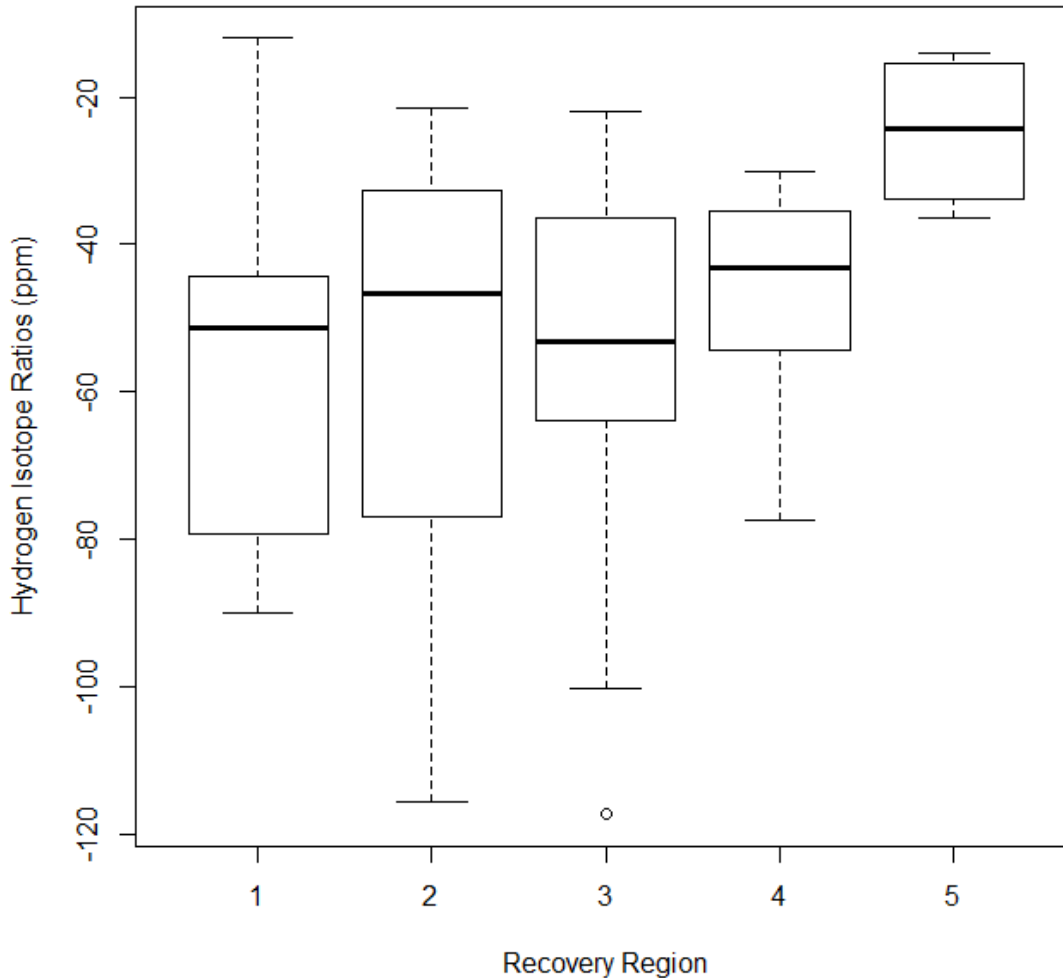
Figure 3.6 Mean δD values of rectrices divided among recovery regions. Recovery
region numbers reflect the assigned numbers in the Black-capped Vireo recovery plan
(USFWS 1992) except recovery region 1. For this fig., recovery region 1 represents the
breeding range in Oklahoma. Study sites in each recovery region are: 1 - Fort Sill
Military Reservation; 2 – Balcones Canyonlands NWR and Ft. Hood Military Reserve; 3
– Kerr WMA, Mason Mountain WMA, Kickapoo Cavern SP, and private properties in
Real County; 4 – private property in Taylor County; 5 – Devil's River SNA.

109, $P = 0.3174$) and longitude ($r^2 = 0.0183$, $F = 2.033$, $df = 109$, $P = 0.1568$) were not significant.

Isotope ratios of capital tract feathers taken from different study sites were not significantly different at $\alpha = 0.05$ ($F = 2.0$, $df = 7, 103$, $P = 0.0621$). Because it was significant at $\alpha = 0.1$, this result is suggestive of a difference among sites. For example Mason Mountain Wildlife Management Area, appears to have a more depleted deuterium concentration than the majority of study sites (Fig. 3.7). Isotope ratios of capital tract feathers divided by Texas recovery regions and Oklahoma were also not significant ($F = 0.435$, $df = 1, 109$, $P = 0.511$; Fig. 3.8). Additionally, the regression of capital tract feathers by latitude ($r^2 = 0.0086$, $F = 0.9483$, $df = 109$, $P = 0.3323$) and longitude ($r^2 = 0.0216$, $F = 2.406$, $df = 109$, $P = 0.1237$) were not significant.

Because stable isotope ratios are so heavily determined by rainfall in most systems, I also looked at annual rainfall totals as a possible driver of feather stable isotope ratios among my feather collection sites. I divided each site into a high and low category of rainfall based on rainfall totals from the months during which black-capped vireo molt most commonly occurs. In rectrices, stable isotope ratios in feathers from high rainfall collection sites were significantly different from those from low rainfall sites ($t = -2.4149$, $df = 109$, $P = 0.0174$). In capital tract feathers, feather stable isotope ratios were significantly different at $\alpha = 0.1$ in high and low rainfall collection sites ($t = -1.6927$, $df = 109$, $P = 0.0934$).

Isotope Analysis of Ground Water Collected

Isotope ratios in ground water collected from each study site were significantly different (F=11.55, df = 6, 29, P=1.37e-6; Fig. 3.9). The Tukey's HSD post-hoc comparison determined that the ground water deuterium isotope ratio at Ft. Hood Military Reservation was significantly different from all other sites except that of Mason Mountain Wildlife Management Area. Additionally, the isotope ratios of ground water collected from Mason Mountain WMA and Taylor County private property was significantly different from that of ground water from Kerr WMA.

Isotope ratios in ground water analyzed by recovery region were significantly different (F=14.33, df = 1, 34, P=0.000595; Fig. 3.10). A Tukey's HSD post-hoc comparison determined that recovery region 2 isotope ratios are significantly different from both regions 3 and 4. Regions 3 and 4 are not significantly different from each other at α=0.05 but are significantly different at α=0.1.

Because I found statistically significant differences among the water collection sites, I also regressed δD with latitude to determine if water isotope ratios vary along a latitudinal gradient. The regression was not significant (r^2= 0.0225, df = 34, P = 0.3826).

Figure 3.7 Mean δD values of feathers taken from the capital tract divided among all
collection sites.

Capital Tract Deuterium Isotope Ratios (Region)
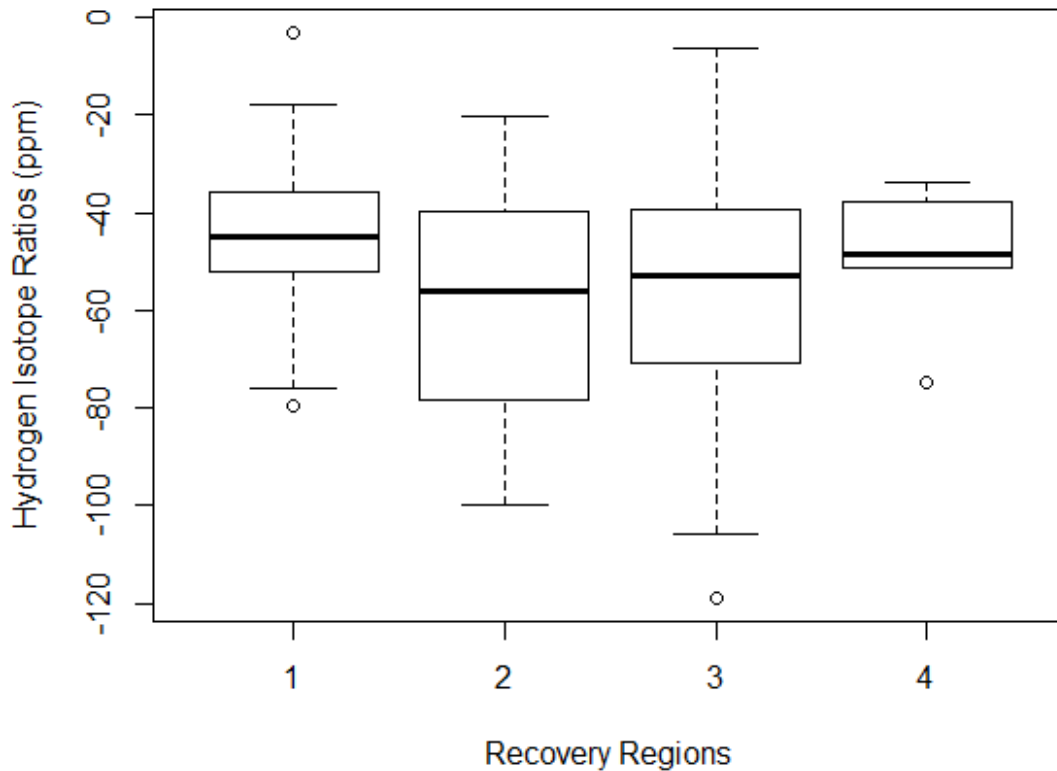
Figure 3.8 Mean δD values of feathers taken from the capital tract divided among recovery regions. Recovery region numbers reflect the assigned numbers in the Black-capped Vireo recovery plan (USFWS 1992) except recovery region 1. For this Figure, recovery region 1 represents the breeding range in Oklahoma. Study sites in each recovery region are: 1 - Fort Sill Military Reservation; 2 – Balcones Canyonlands NWR and Ft. Hood Military Reserve; 3 – Kerr WMA, Mason Mountain WMA, Kickapoo Cavern SP, and private properties in Real County.
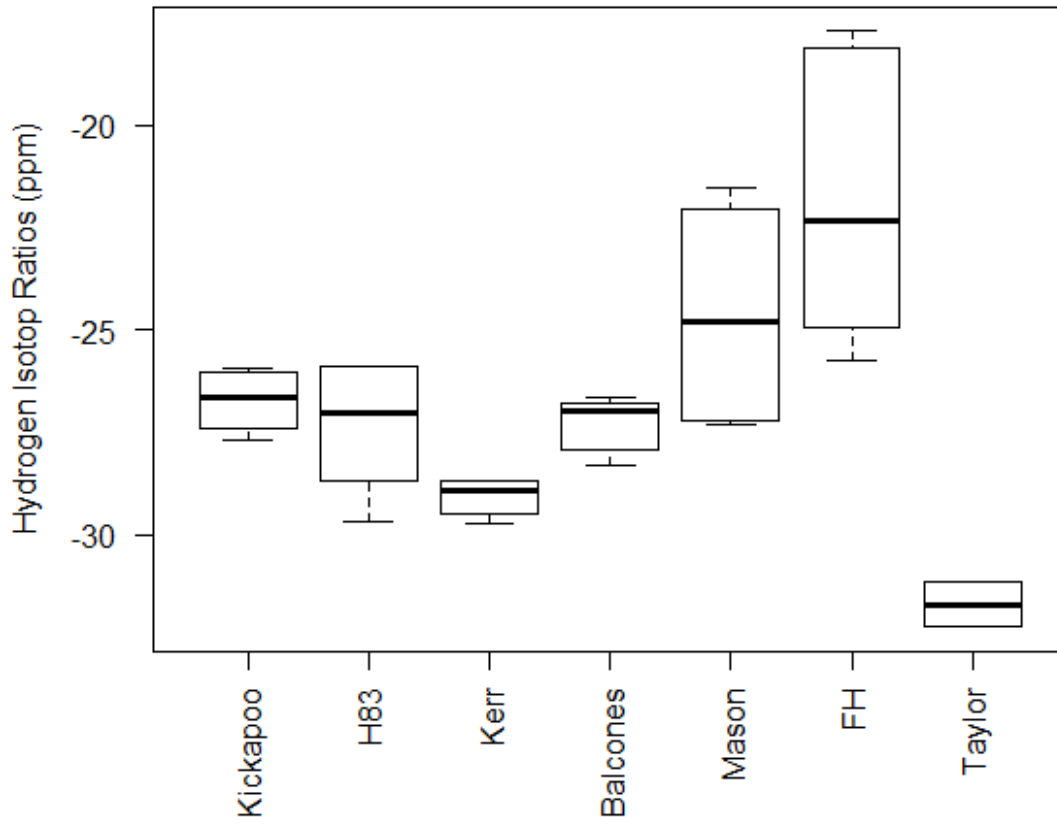
Figure 3.9 Mean δD values of groundwater collected from feather collection sites.

Groundwater Deuterium Isotopes (Recovery Region)
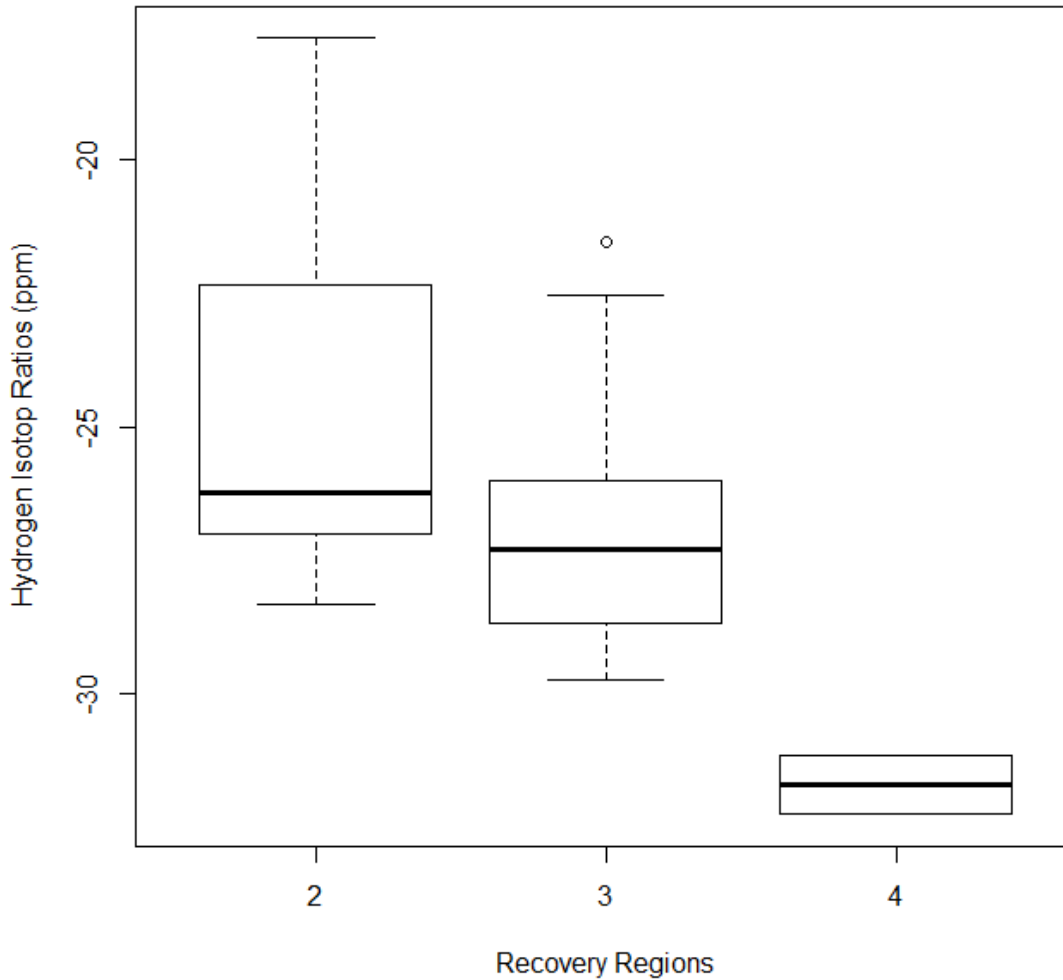
Figure 3.10 Mean δD values of groundwater collected from feather collection sites divided by recovery region. Recovery region numbers reflect the assigned numbers in the Black-capped Vireo recovery plan (USFWS 1991). Study sites in each recovery region are: 2 – Balcones Canyonlands NWR and Ft. Hood Military Reserve; 3 – Kerr WMA, Mason Mountain WMA, Kickapoo Cavern SP, and private properties in Real County; 4 – private property in Taylor County.

Interpolated Maps of Deuterium Isotopes

Using a simple interpolation technique and the deuterium isotope values of feathers and ground water samples, I created three maps of different regions of the Black-capped Vireo breeding region in Texas and Oklahoma. These maps use isotope ratios of collected feather and groundwater samples from known locations to predict ratios of feathers and ground water samples in areas between and surrounding the collection sites. The maps created using rectrices (Fig. 3.11) and capital tract feathers (Fig. 3.12) show no relationship between deuterium isotope ratios and latitude and are substantially different than the continent-wide pattern seen in precipitation δD (Fig.3.1) . The map created using ground water samples shows a greater relationship between deuterium isotope ratios and latitude (Fig. 3.13) but still does not show a clear relationship with precipitation δD.
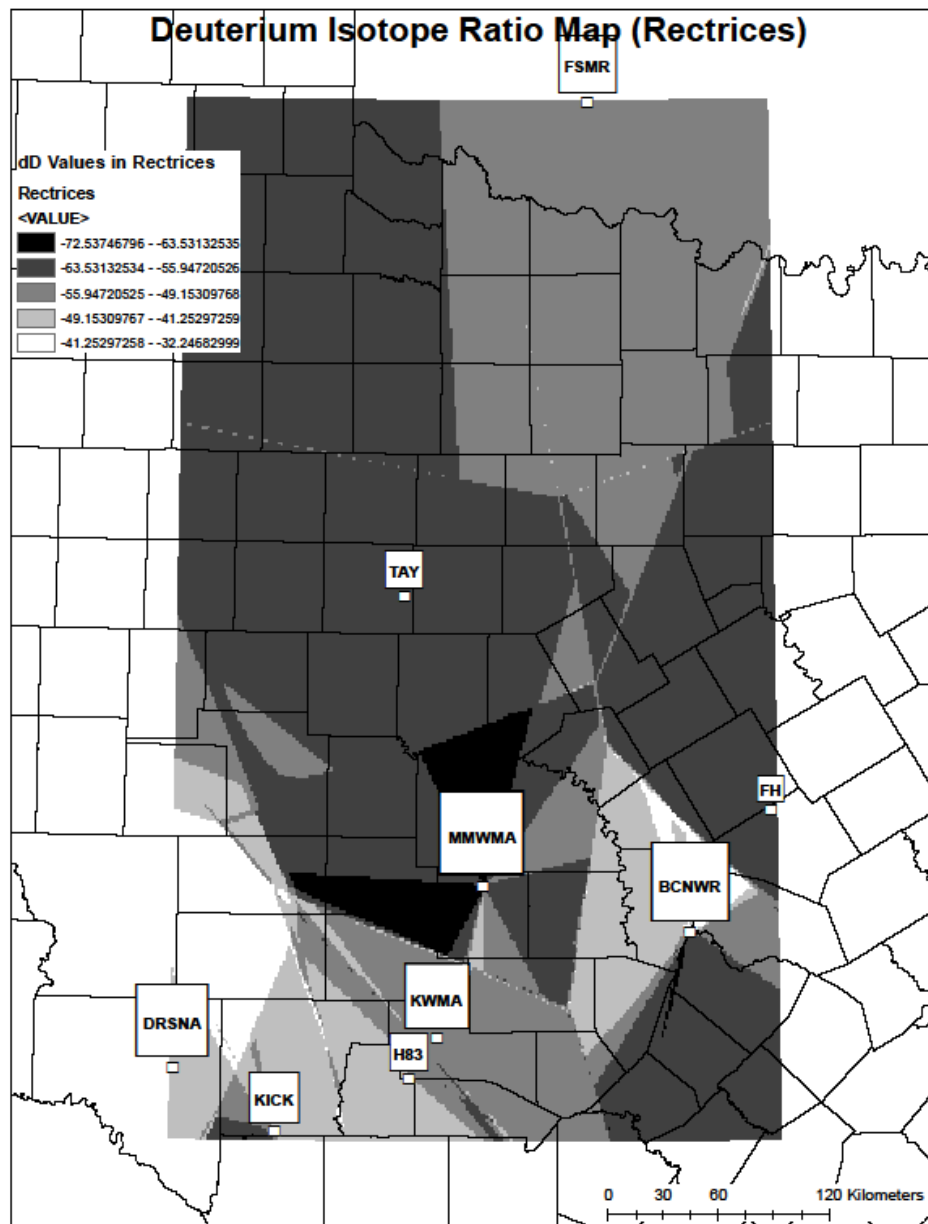
Figure 3.11. Interpolated map predicting values of feather δD (expressed as parts per thousand or ‰) using Black-capped Vireo rectrices of known origin. Shade areas indicate regions for which the interpolation is valid. Labelled boxes indicate sites at which feathers were collected. Background lines indicate Texas counties.
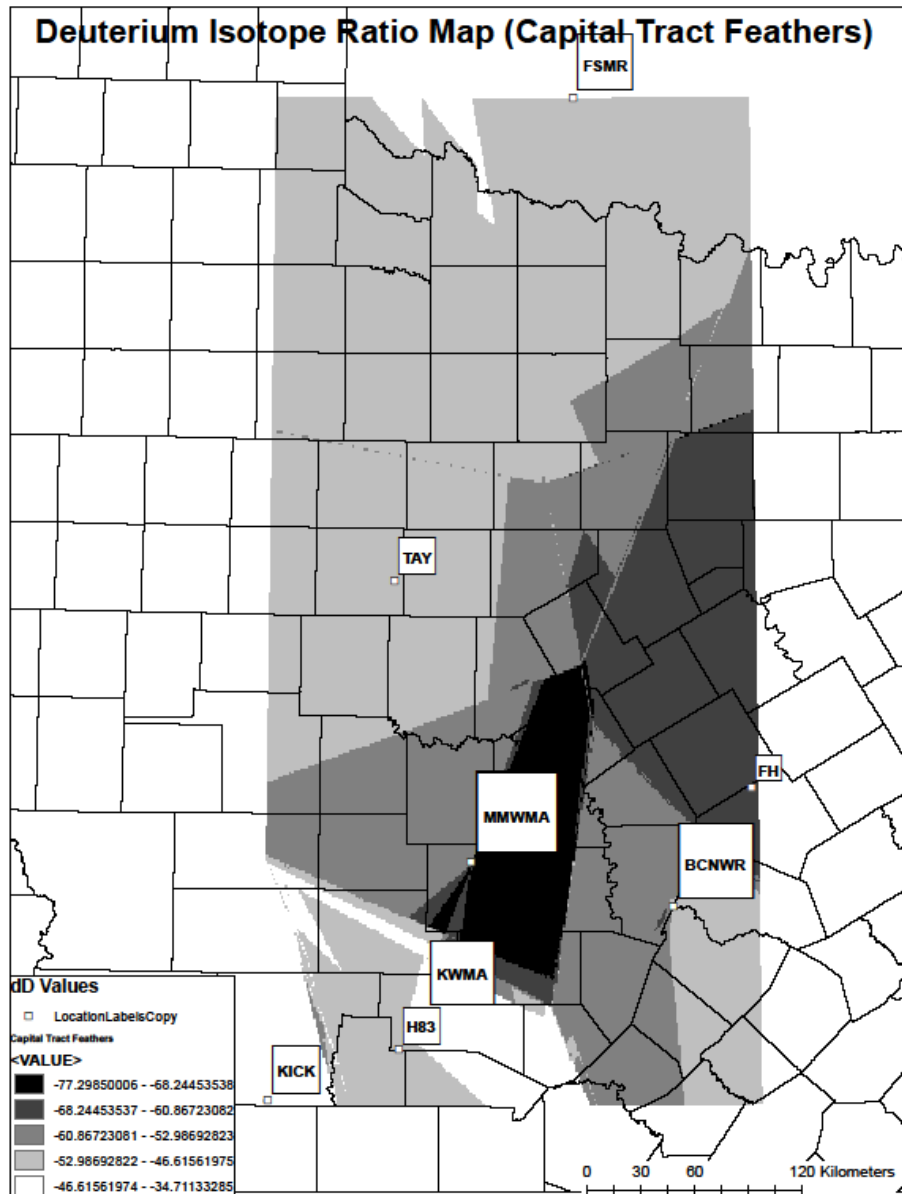
Figure 3.12. Interpolated map predicting values of feather δD (expressed as parts per thousand or ‰) using Black-capped Vireo capital tract feathers of known origin. Shade areas indicate regions for which the interpolation is valid. Labelled boxes indicate sites at which feathers were collected. Background lines indicate Texas counties.

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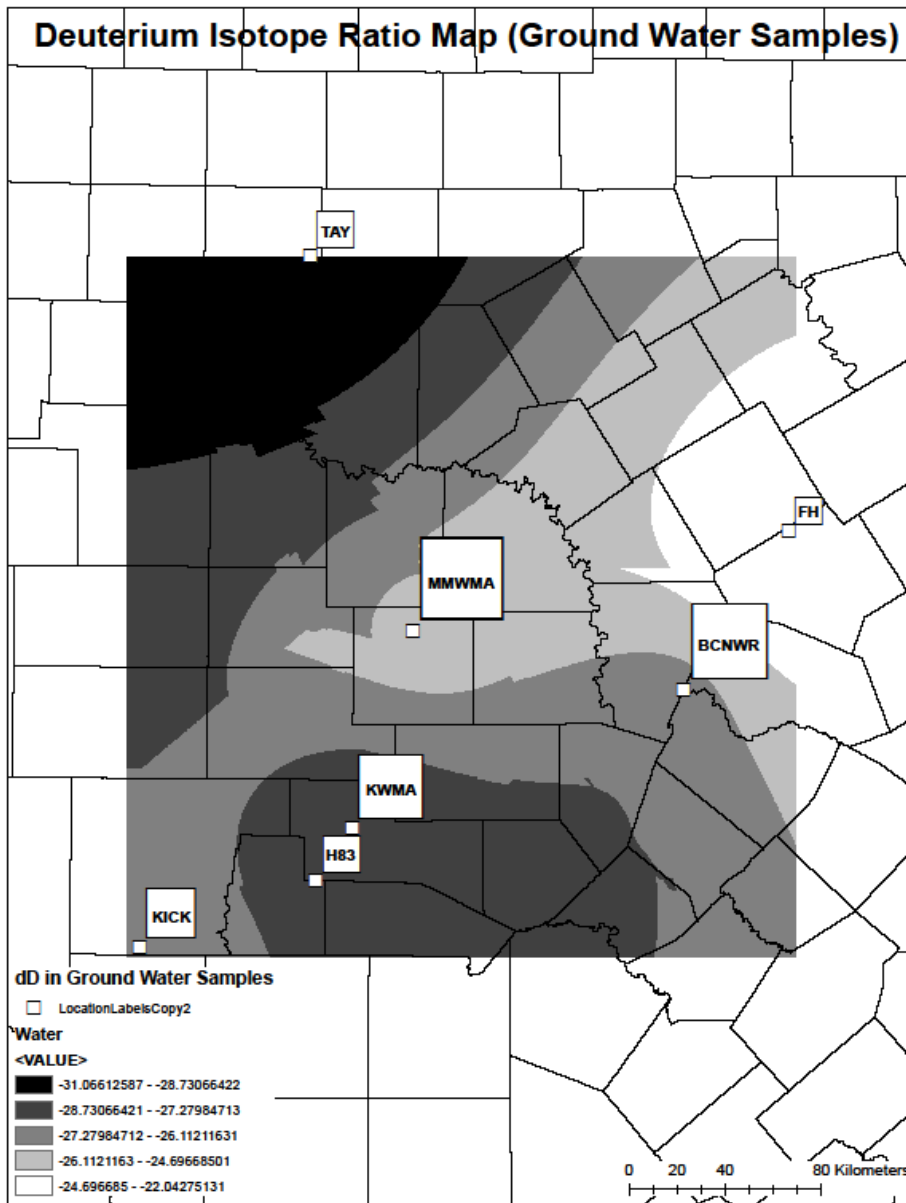
Figure 3.13. Interpolated map predicting values of groundwater δD (expressed as parts per thousand or ‰) using groundwater collected near feather collection sites. Shaded areas indicate regions for which the interpolation is valid. Labelled boxes indicate sites at which feathers were collected. Background lines indicate Texas counties.

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Discussion

  For both rectrices and feathers collected from the capital tract, I rejected the hypothesis that δD ratios would be sufficiently different to distinguish among collection site based on feather δD. Additionally, for both rectrices and capital tract feathers, I rejected the hypothesis that I could distinguish among recovery regions based on feather δD. Because there was not statistical difference among feather δD in collection site or recovery region, there appears to be no relationship between δD and geographic regions of the bird's breeding grounds. Though many collection sites and recovery regions share similar latitude, there is a sufficient latitudinal gradient across all sites to expect differentiation among some collection sites. No statistical differences among sites and recovery regions indicates that this species' source of hydrogen isotopes during feather growth on the breeding ground does not vary geographically in the same way that most bird's hydrogen isotope sources vary.

  Many studies have found a relationship between δD in feathers and δD in growing season rainfall across several groups of birds in North America (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Wassenaar and Hobson 2000, Hobson, et al. 2001, Lott and Smitt 2006), indicating that growing season rainfall is a primary source of hydrogen isotopes in these species' feathers. In my study, stable isotope analyses of Black-capped Vireo feathers collected from the bird's breeding range in Texas and Oklahoma indicate this species' feather isotope ratios do not follow the expected isotopic ratio pattern for North American birds based on growing season precipitation patterns. There is no significant relationship between feather δD and latitude and the

range of feather δD (-118.9‰ – 3.1‰) values are substantially different from expected

precipitation δD values (-59‰ – 21‰). While the traditional relationship among feather

δD, rainfall δD, and latitude is absent, there appears to still be some relationship between

feather isotopes and rainfall totals. I found a significant relationship between rectirces

and rainfall when I compared sites with high and low growing season 30 year rainfall

averages. This significant result indicates that rainfall may still drive some aspect of this

species' feather isotope ratio but more study is still required to understand this

relationship. Powell (2013) similarly found that Black-capped Vireo feathers δD do not

reflect the ratios expected when using a typical growing season precipitation δD map.

He suggested that precipitation, the main source of δD in most neotropical migrant

feathers, may not be the largest source of δD in Black-capped Vireo feathers. Instead of

precipitation, Powell suggested that investigation into groundwater stable isotope values

on the bird's breeding grounds might reveal more about the source of this species'

isotopic feather content across its breeding grounds.

Because of Powell's (2013) suggestion about groundwater as a source of feather

isotope content, I collected groundwater samples from seven of the feather collection

sites in Texas to determine if feather δD more closely resembled groundwater δD instead

of precipitation δD. I found that δD values were significantly different among water

collections sites and among recovery regions. However, these differences among sites

and recovery regions did not vary along a latitudinal gradient. In comparison between

feather maps (Figs. 3.11 and 3.12) and the groundwater map (Fig. 3.13), it is clear that

feather δD and groundwater δD do not vary in a similar way.

Lack of similarity between feather δD and groundwater δD indicates that groundwater is not a primary source for δD in Black-capped Vireo feathers either. With the elimination of groundwater as the hydrogen source and previous elimination of precipitation as a likely hydrogen source, there are several possibilities left that could cause the unusually depleted δD values found in this study.

First, feathers collected on the breeding grounds during my study may have been grown in different locations than those from which they were collected. Several species in the western United States perform a molt migration wherein they leave the breeding grounds prior to fall molt and, during migration, stop in the Sonoran and Chihuahan deserts where fall molt commences (Voelker 2000). Other species stop in high altitude regions in Mexico to molt and regrow feathers, taking advantage of late summer monsoon rains (Douglas et al. 1993). This migration and molt timing pattern likely evolved so western species could avoid the energetic cost of regrowing molted feathers during late summer droughts in the western US and take advantage of monsoon-like rains at the same time in the deserts or montane areas (Rohwer and Manning 1990, Voelker and Rohwer 1998). Because Black-capped Vireos breed in xeric areas that also experience seasonal droughts in late summer, I thought it was reasonable that they could partake in the same molt migration. At the inception of this study, I decided to collect inner rectrices and feathers from the capital tract with the assumption that these feathers are grown on the breeding grounds. While Pyle (1997) states that all rectrices are molted and regrown on the breeding grounds prior to fall migration, he does suggest that contour feathers, including those of the capital tract, may be continuously molted

beginning on the breeding grounds and continued throughout migration and on the wintering grounds. Pyle (1997) left room for the possibility of a molt migration in this species. However, Butler et al. (2008) has confirmed that Black-capped Vireos do molt rectrices and capital tract feathers on the breeding grounds so molt migration is not likely to be responsible for the unexpected feather δD values in the present study.

Instrument failure could also explain the unexpectedly wide range of δD values found in feathers in this study. However, instrument failure is unlikely in this case as the technicians at CPSIL, the laboratory where the analyses were performed, processed all feather samples after first testing their instrumentation on standards of known isotopic content. Only after results from analyses of standards fell within an acceptable range, indicating the instruments were performing properly, did the feather samples get analyzed. The assistant director (M. Caron) of the lab verified that all instrumentation was functioning properly at the time of the feather analyses.

A third possibility is that unusual rainfall patterns in late summer during the years of collection influenced δD values in analyzed feathers. Indeed, certain aspects of my results do suggest that year-specific rainfall may affect Black-capped Vireo feather δD values. For example, rectrices from Devil's River State Natural Area were not significantly different but did show some clear separation from other sites (Fig. 3.5). This site is much father west than all other sites and its landscape is much more arid than other sites. Longitude and aridity may play a role in the regional variation of this species' feather δD values. While rainfall is the most common source of δD in neotropical migrants' feathers, systems that experience infrequent and large amounts of

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rainfall are commonly considered to be poor candidates for SIA (K. Hobson, personal communication). During the late summer months, the Black-capped Vireo's breeding range in Texas and Oklahoma does commonly experience pulses of precipitation that vary from one year to the next. These pulses of rainfall generally coincide with a depletion of δD values (Ziegler 1989) and could contribute to feather δD values being more depleted than expected.

Because I suspected that these pulses of rainfall might influence δD values in this study, I looked at the 30 year averages of rainfall during the vireo's molting season (June, July, August) in each of the counties where I collected feathers and compared those with monthly rainfall totals of the same three months of each collection year. I found that several feather collection sites received large pulses of rainfall during various months but there were many months where rainfall was substantially lower than 30 year averages. In 2010, July rainfall totals were higher (as much as three times higher at some sites) than 30 year averages for the same month at all collection sites except Kerr Wildlife Management Area. By contrast, rainfall totals in 2009 and 2011 were much lower than 30 year averages at all sites except Taylor County in 2009 (NCDC.NOAA.gov 2015). This variation in rainfall totals across the years should produce variation in δD values of feathers grown during those molting seasons.

Because rainfall totals in 2010 were much higher than those of 2009 and 2011, I investigated the δD values among the years affected by these rainfall totals. Rainfall totals in 2010 would affect stable isotope values of feathers collected in 2011 as those feathers were initially grown in 2010. I found that in rectrices, 2011 δD values

($\bar{x}$ = -59.38, SD = 18.74) were higher than 2010 ($\bar{x}$ =-37.62, SD = 17.80) and 2012

($\bar{x}$ = -47.26, SD = 26.11) δD values. In capital tract feathers, δD values were also

higher in 2011 ($\bar{x}$ = -55.63, SD = 16.67) than in 2012 ($\bar{x}$ = -51.64, SD = 30.97).

Because rectrix and capital tract feather δD values in 2011 were both higher than other

years, I think that rainfall during the molting season is a major driver in the stable

isotope content of Black-capped Vireo. While rainfall effects on δD values in migratory

bird feathers was not a focus of my study, these preliminary results suggest that seasonal

rainfall's relationship with feather isotopes in this species warrants further investigation.

 In addition to long-term rainfall amounts driving molt patterns and, by extension,

deuterium isotope ratios in Black-capped Vireo, it is possible that individual rainfall

events may be the proximate factor in vireo molt inception. Molt and breeding are

ultimately timed to coincide with periods of maximum rainfall and resources (Snow

1974). Climatological trends are almost certainly the ultimate cause of molt inception in

most species. However, if individual rainfall events are also the proximate cause of molt

inception in Black-capped Vireo from one year to the next as others have found in

species in arid areas (Keast 1968), this would explain much of the unexpected results I

got in this study when comparing feather deuterium ratios to expected precipitation

deuterium ratios. As a region experiences a heavy rainfall event, birds may initiate molt.

Therefore, if birds grow feathers during or immediately after the rainfall event, those

feathers will have an isotope signature more similar to the recent rain and less similar to

the ratios expected using long-term datasets. Much more research is needed to

determine how much proximate rainfall events affect Black-capped Vireo molt initiation.

Conclusions

Black-capped Vireo δD values in rectrices and capital tract feathers conform to neither patterns generated from growing season rainfall δD values nor patterns generated from groundwater δD values. Because these two sources of hydrogen stable isotopes are the only ones that are predictable on a long-term basis, this species appears to be a poor candidate for stable isotope studies using naturally occurring stable hydrogen isotopes and the conventional methods of comparing feather isotopes to growing season rainfall isotope maps. However, year-specific rainfall during this species' molting season is a likely contributor to feather hydrogen isotope values. Because annual rainfall variation appears to play a role in establishment of this species' feather δD values, any future studies that attempt to discern the Black-capped Vireo's migratory connectivity should focus on two unconventional aspects of this species' feather stable isotopes.

First, any studies should incorporate a comprehensive study of rainfall stable isotopes during the molting season. Researchers should collect rainfall samples on the breeding grounds while also collecting feathers grown during the same season. Ideally, feathers would be collected while growing to ensure knowledge of the location at which the feathers were grown. Then, δD values of feathers grown could be directly compared to another likely source (rainwater) of the isotopes found in those feathers to determine if seasonal rainfall is, indeed, a source of feather δD values.

Second, any research on this species' migratory connectivity should focus on collecting feathers from the breeding grounds and wintering grounds during the same season. This will ensure that annual variation in rainfall on the breeding ground during

molting season is captured in maps of the breeding season δD values. Likewise, feathers collected on the wintering grounds will have been subjected to the same annual rainfall variation and will, therefore, be directly comparable to maps of δD values on the breeding grounds.

In addition to the stable isotope approaches I and others have attempted, other methods may contribute to a more complete understanding of Black-capped Vireo's migratory connectivity. Hydrogen stable isotopes are consistently the most informative isotopes used in migratory bird studies but other elemental isotopes have been used in coordination with hydrogen isotopes to determine migratory connectivity (Marra et al. 1998; Norris et al. 2005; Norris et al. 2006). Powell (2013) attempted to use isotopes of carbon and nitrogen in addition to hydrogen isotopes to establish migratory connectivity. Results for carbon and nitrogen isotope distributions were uninformative for his study in a similar fashion that hydrogen was uninformative to my study and using any combination of these stable isotopes is unlikely to improve results. As previously mentioned, stable isotope studies, regardless of which elemental isotopes are used, do not appear to be an effective method for discerning migratory connectivity of Black-capped Vireo.

While stable isotope analyses do not appear to be a viable method for establishing migratory connectivity in Black-capped Vireo, other more traditional methods may still prove useful though difficult. Individual mark-recapture techniques, typically reserved for large birds with easily visible tags or game birds that are routinely hunted, may prove useful if we could establish a program to intensively band birds with

a unique color combination across all portions of their breeding range. Though band returns from deceased birds or resights from living birds on the wintering ground would likely be limited in amount (Clark, et al. 2000; Stolt et al. 2000), an intensive program like this could provide the information necessary to establish migratory connectivity.

While banding individual birds, researchers could easily collect data for another technique that has been used to determine migratory connectivity. Genetic markers could be used to determine migratory connectivity. Fazio III et al. (2004) and Barr et al. (2008) both found that genetic markers vary sufficiently among populations that one could reliably assign an individual bird collected on the wintering ground to a genetically distinct region of the breeding ground. Of course, this technique would require an intensive banding regimen in all regions of the breeding grounds as well as all regions of the wintering grounds for comparison of genetic markers to be informative. However, if used in conjunction with mark-recapture techniques, genetic markers are a viable way to accomplish the task of more thoroughly understanding this bird's migratory connectivity.

To gain a full picture of this organism's annual cycle, we must more completely understand how this species' ecology on the wintering grounds and breeding grounds mutually affect each other. One aspect of that understanding is migratory connectivity. I, as well as other researchers (Powell 2013), have attempted to establish the migratory connectivity of the Black-capped Vireo using stable isotope analyses. Neither of our studies has succeeded in doing so. However, in this study I have eliminated one

potential source of δD values in vireo feathers and suggested another source for future study.

CHAPTER IV

SUMMARY OF CONCLUSIONS AND MANAGEMENT IMPLICATIONS

During the post-breeding season, Golden-cheeked Warblers use breeding

vegetation in the low stony hill ecosite most consistently. When found during surveys,

groups were most commonly composed of lone males or family groups that were

foraging in ashe juniper or Texas oak. This result indicates that there is not any reason

to expand the definition of protected habitat to include non-breeding vegetation used

during the post-breeding period. Further, managers of Golden-cheeked Warblers have

traditionally focused on identification of high quality habitat based on canopy cover.

However, this study suggests that, during the post-breeding period, high quality habitat

is more clearly indicated by ecosite type. Protection of habitat for breeding and post-

breeding purposes should focus on oak-juniper woodlands found in the low stony hill

ecosite and maintenance of these locations should include allowing young ashe junipers

to grow for use as foraging substrates.

In my attempt to futher the knowledge of the migratory connectivity of Black-

capped Vireos, I found that the traditional stable isotope analysis approach of comparing

feather hydrogen isotopes to long-term rainfall isotope patterns is not a viable option for

this species. I also found that feather isotope patterns do not match local groundwater

isotope patterns. I have eliminated groundwater as a likely source of the hydrogen

isotopes in Black-capped Vireo feathers and suggested other approaches to establish the

migratory connectivity of this species.

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