

EFFECTS OF DROUGHT ON BLACK-CAPPED VIREO HABITAT SELECTION  
AND REPRODUCTION

A Dissertation

by

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## ABSTRACT

Texas experienced extreme drought conditions in 2011, followed by moderate conditions the next year. I examined the effects of these annual weather conditions on habitat selection and reproduction of a federally endangered songbird, the Black-capped Vireo (*Vireo atricapilla*; hereafter vireo), in Texas. Vegetation and topographic characteristics in vireo territories and at vireo nest-sites were similar across years. However, vireos used different nesting substrates depending on year. Vireos typically nest in deciduous substrates, but they used Ashe juniper (*Juniperus asheii*), an evergreen species, as a nest substrate more frequently in 2011. This was, perhaps, because it was one of few plant species with consistently leafy foliage. Vireos had lower pairing and fledging success in 2011 than in 2012. Clutch size and brood size did not differ by year, but vireos delayed nest initiation and, consequently, laid fewer eggs and had fewer nesting attempts in 2011. Delayed nest initiation is often associated with reduced food availability, and it may provide a mechanism whereby individuals can reduce reproductive effort and increase survival when resources are limited. However, it is not without consequence as later nests may be subject to greater predation or brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). During this study, predation and brood parasitism were higher in 2011, and year, substrate, and nest concealment best predicted nest success. Daily nest survival decreased over time in both years, but was lower in 2011. Annual variation in songbird reproduction is common and can be attributable to factors unrelated to weather. However, the responses of, and

consequences to vireos during the 2011 season are similar to those observed for birds nesting in other regions with variable rainfall that are periodically exposed to drought events. Drought is not preventable, but by understanding how at-risk species respond to it, we can better manage their populations. Common management strategies for vireos include removal of Ashe juniper and Brown-headed Cowbirds from vireo habitat. In drought-prone regions, managers should consider retaining some Ashe juniper in vireo habitat to provide refuge for foraging and nesting during dry conditions. Additionally, increased Brown-headed Cowbird removal efforts during drought years could reduce parasitism risk.

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## CHAPTER I

### INTRODUCTION

Climate is a representation of the average weather conditions in an area over an extended period (Allaby 2010), and it influences all aspects of a species' niche (i.e., the conditions under which a species can live) (Grinnell 1917; Hutchinson 1957). For example, physiological tolerances to temperature, along with water requirements, determine a species' geographic range (Andrewartha and Birch 1954; Root 1988; Parmesan 1996). Similarly, climate regulates species' abundance (e.g., Andrewartha and Birch 1954; Mehlman 1997; Veit et al. 1997), community structure (Cody 1981; Brown et al. 1997; Albright et al. 2010), and ecosystem dynamics (e.g., Pascual and Levin 1999; Post and Forchhammer 2001; Traill et al. 2010). Understanding how climate shapes evolutionary adaptation is necessary for long-term conservation and management of wildlife species. However, information on species' responses to short-term variation (e.g., months, years) in local and regional weather patterns is also important for conservation planning because the selective pressures imposed by weather can have consequences for population dynamics (Stenseth et al. 2002; Knappe and Valpine 2011; Harrison et al. 2015).

In arid and semi-arid environments, rainfall is low and unpredictable, and drought is common (e.g., in Texas) (Myoung and Nielsen-Gammon 2010). Though definitions vary (see Wilhite and Glantz 1985; McKee et al. 1993; Quiring 2009), drought is characterized by inadequate precipitation over a time sufficient to impact vegetation and deplete soil moisture (Kramer 1983). Heat waves and high temperatures

are often associated with summertime droughts as soil moisture declines and solar energy heats the air (Namias 1982). Low cloud cover during drought periods allows more of the sun's energy to reach the ground, and the release of that energy into the environment can further exacerbate drought conditions via feedback loops that increase precipitation deficits (Myoung and Nielsen-Gammon 2010; also see Clark and Arritt 1995).

Birds inhabiting arid and semi-arid environments may experience direct reproductive consequences under drought conditions. For instance, the development and function of ovaries and oviducts of water-deprived females is lower than that of non-deprived females (Cain and Lien 1985; Koerth and Guthery 1991). Water-stressed females lay fewer, smaller, less fertile eggs and have young with lower survival rates (e.g., Cain and Lien 1985; Fair and Whitaker 2008; Skagen and Yackel Adams 2012). Similarly, under drought conditions, males can have lower testicular weight or sperm production, which can limit (though rarely prevents) reproductive function (Cain and Lien 1985). Additionally, embryonic development is disrupted and egg-hatchability compromised when eggs are exposed to extreme temperatures for extended periods (Dawson 1984; Stoleson and Beissinger 2002; Gill 2007), and nestlings born during drought may have reduced immune responses (Thaxton and Siegel 1970; Fair and Whitaker 2008).

Drought can also impact birds indirectly through its effects on vegetation. Precipitation is the main driver of aboveground primary productivity (Noy-Meir 1973; Sala et al. 1988), and it influences vegetation structure (Tyree et al. 1993; Chaves et al.

2003), composition (Cody 1981; Brown et al. 1997), and mortality (Allen and Breshears 1998; Breshears et al. 2005). When precipitation is low, delayed phenological events, reduced leaf area, or altered plant chemistry can occur (Rathcke and Lacey 1985; Larsson and Ohmart 2008; Gutbrodt et al. 2011). The overall effect is reduced greenness (i.e., foliage cover) on the landscape during drought, which can affect the timing and abundance of plant and insect foods available to nesting birds (Morrison and Bolger 2002; Ogaya and Peñulas 2007; Greven et al. 2009) and increase the risk of predation (Sugden and Beyersbergen 1986; Martin 1992) and exposure to the elements (e.g., wind, rain, cold, heat) (Walsberg 1981).

Birds inhabiting drought-prone environments experience considerable variation in precipitation and adjust their behaviors accordingly during dry periods (Cody and Mooney 1978). Food limitation and predation are strong drivers of habitat selection in birds (Cody 1981; Martin 1987, 1988, 1993; Cuttriss et al. 2015), and birds may select habitat features differently depending on how weather conditions affect these factors. Individuals may relocate to wetter sites during drought (e.g., Strong et al. 1997; Gaines et al. 2000; Takekawa and Beissinger 2005) or follow shifting plant distributions after drought (e.g., Mueller et al. 2005). Alternatively, individuals that do not relocate may select territories or nest-sites that maximize their use of the limited vegetation cover (Martin 1993).

Birds may also adjust their reproductive behaviors according to weather conditions. Life history theory predicts that individuals inhabiting highly unpredictable environments will temper reproductive investment to maximize adult survival when

conditions are poor (Hirshfield and Tinkle 1975; Benton et al. 1995; Erikstad et al. 1998). For example, birds may delay (or forgo) breeding during drought (e.g., Christman 2002; Preston and Rotenberry 2006; Visser et al. 2006) when food or other resources are limited. Birds can also reduce their reproductive effort irrespective of nest initiation date by laying smaller clutches, abandoning nests, or engaging in fewer nesting attempts (Erikstad et al. 1998).

Birds that delay nesting reduce their number of effective breeding days within a season, thus limiting the number of nesting attempts possible. Additionally, birds that delay nesting have smaller clutches (e.g., Lack 1947; Daan et al. 1989; Perrins and McCleery 1989), lower nestling and fledgling survival (e.g., Harris et al. 1994; Lindholm 1994; Naef-Daenzer et al. 2001), and reduced recruitment of offspring into subsequent generations (e.g., Harris et al. 1994; Verboven and Visser 1998). Nests initiated later in the season may also have greater rates of predation (e.g., Best and Stauffer 1980; Schaub et al. 1992) or brood parasitism (Marvil and Cruz 1989; Kus 1999; Boves et al. 2014). However, despite seasonal fitness consequences, individual decisions regarding reproductive investment in any given year likely reflect trade-offs between current and future reproductive success that optimize lifetime reproductive success (Stearns 1989; Daan et al. 1990; Svensson and Nilsson 1995).

By understanding how species respond to varying weather conditions land managers are better equipped to create, restore, or maintain habitat for species of conservation concern in the long-term. Shrub-nesting birds are of particular interest because of widespread population declines (Robbins et al. 1986; Askins 1993; Brawn et

al. 2001). Many shrub-nesting species require early- and mid-successional vegetation, but fire suppression and other practices (e.g., farm abandonment) have allowed vegetation in many shrubland environments to reach seral stages that prohibit occupancy or reproduction by shrub-nesting birds (Askins et al. 1990; Droege 1998).

The Black-capped Vireo (*Vireo atricapilla*; hereafter vireo) is a federally endangered songbird that breeds in early-successional shrub-scrub vegetation in arid and semi-arid regions of Oklahoma, Texas, and Mexico (Fig. 1) (Graber 1961; Gryzbowski 1995; Wilkins et al. 2006; González-Rojas et al. 2014). Major threats to the species include habitat loss and fragmentation and reduced reproductive success resulting from brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Marshall et al. 1985; Ratzlaff 1987). Understanding these threats as well as the vireo's biological and ecological requirements may help inform conservation and management strategies necessary for the species' recovery (USFWS 1991).

Vireos typically breed in vegetation of irregular height and distribution that provides adequate cover (35–55%) for foraging and nesting (Graber 1961; Gryzbowski et al. 1994). Drought, fire, and grazing interact with topographic features (Graber 1961; McFarland et al. 2013) to maintain the vegetation configuration needed for vireo reproduction (Wilkins et al. 2006). Yet, little information exists regarding habitat selection and reproduction by vireos during periods of drought. Smith et al. (2012) detailed habitat use and nesting ecology by vireos at Devil's River State Natural Area in the drier, southwestern portion of the species' breeding range in Texas. They noted that vireo productivity is greatly influenced by precipitation, and management strategies

aimed at conserving vireo habitat in the west should be considerably different than those proposed for use in other (wetter) portions of the vireo's breeding range (Smith et al. 2012).

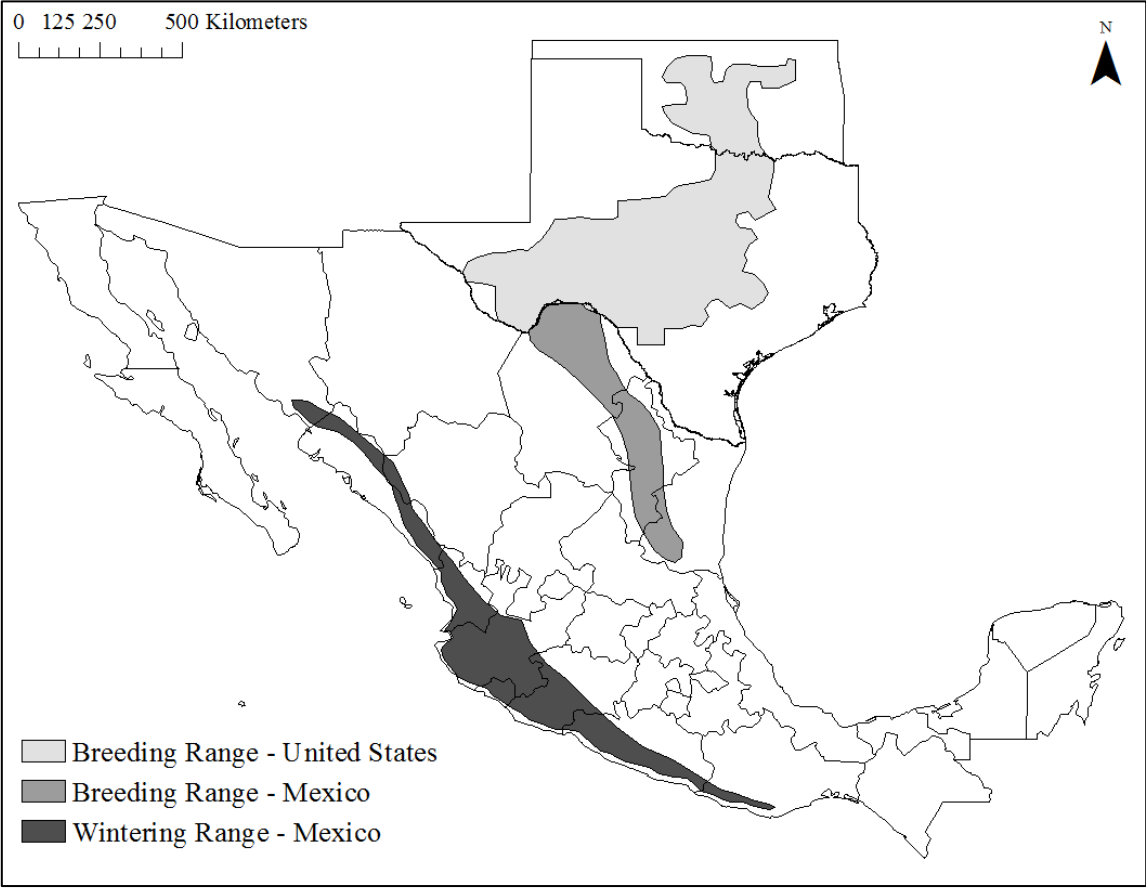


Figure 1. Known breeding and wintering ranges for the Black-capped Vireo (*Vireo atricapilla*) based on data presented in Wilkins et al. (2006).



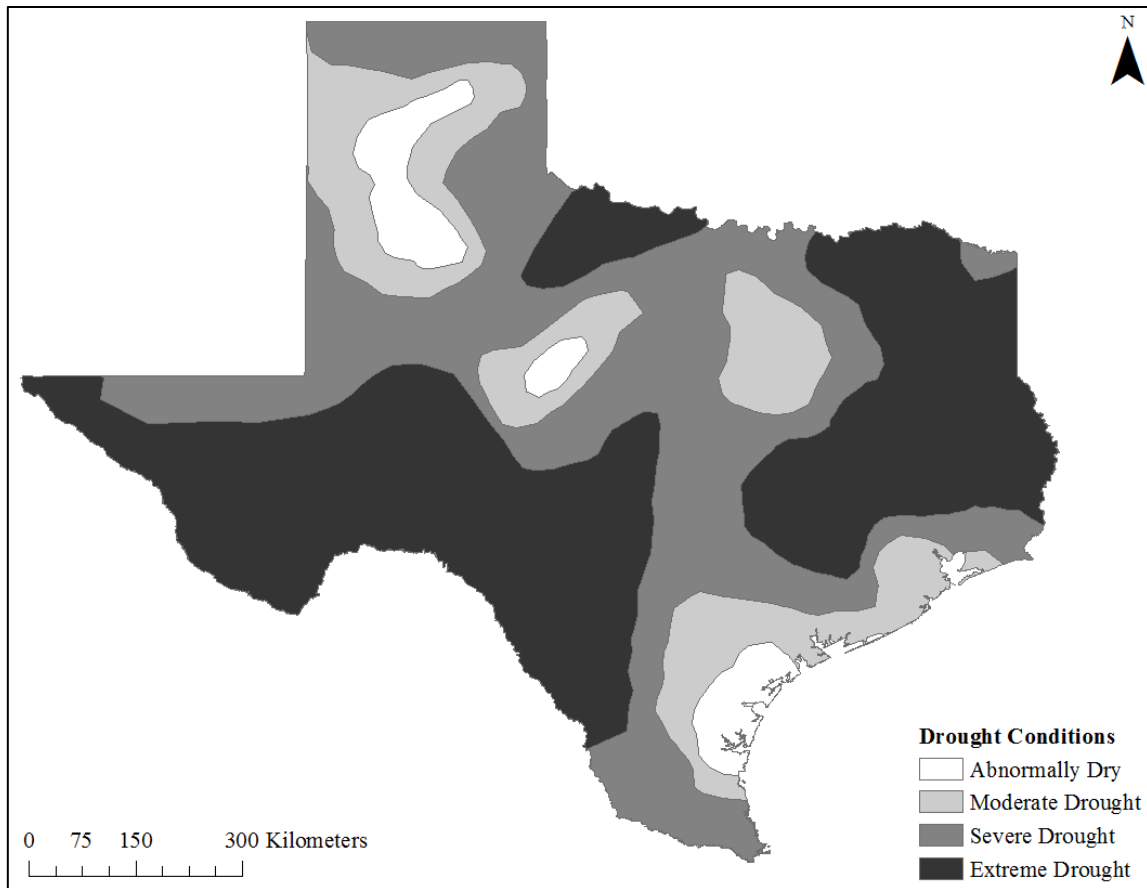


Figure 2. Drought status in Texas on 29 March 2011. Map created using ArcMap version 10.2.2 with data from the National Drought Mitigation Center, U.S. Department of Agriculture, and National Oceanic and Atmospheric Administration.

The objectives of this study were to examine habitat selection, breeding behavior, and productivity of vireos in Texas during two years of varying drought intensity. In September 2010, a large storm system, which had provided rain to much of the state, dissipated—signaling the beginning of the 2011 drought (Nielsen-Gammon 2011). Precipitation in fall and winter of 2010 and in spring 2011 were less than average (NCEI 2016), and by the end of March, more than half the state experienced severe or extreme drought conditions (USDM 2016) (Fig. 2). The period from March–May 2011 was the

driest March–May period on record in Texas (Nielsen-Gammon 2011), and below average precipitation continued statewide for the next six months (NCEI 2016). From December 2011–March 2012, Texas received average or above average rainfall. Dry conditions returned for the remainder of 2012, but not with the same intensity of the previous year (USDM 2016). Only two other years (since 1895 when people began keeping records) have experienced precipitation deficits comparable to 2011 (i.e., 1917 and 1956) (Fig. 3).

Extreme drought events are, by definition, rare or infrequent. The 2011 drought in Texas provided a unique opportunity to observe vireo responses under extreme drought conditions compared to responses under more moderate (common) conditions. Drought has been common throughout much of the vireo’s range in Texas for over 1,000 years (Toomey et al. 1993; Cleaveland et al. 2011; USDM 2016). As such, I expected vireos to exhibit behaviors during the 2011 season that minimized the impacts of the harsher conditions. I expected that differences in rainfall would result in lower vegetation greenness in 2011 than in 2012, and I predicted that, under such conditions, vireos would select larger territories because territory size is often inversely related to food availability (e.g., Seastedt and MacLean 1979; Smith and Shugart 1987), which is correlated with rainfall and vegetation greenness (e.g., Morrison and Bolger 2002; Ogaya and Peñulas 2007; Greven et al. 2009). I also predicted vireos would establish territories and nest-sites with flatter, northern-facing slopes in 2011 because precipitation and solar radiation can degrade vegetation conditions on steep, southern-facing slopes (Cottle 1932; Gallardo-Cruz et al. 2009; Sternberg and Shoshany 2011). Additionally, I

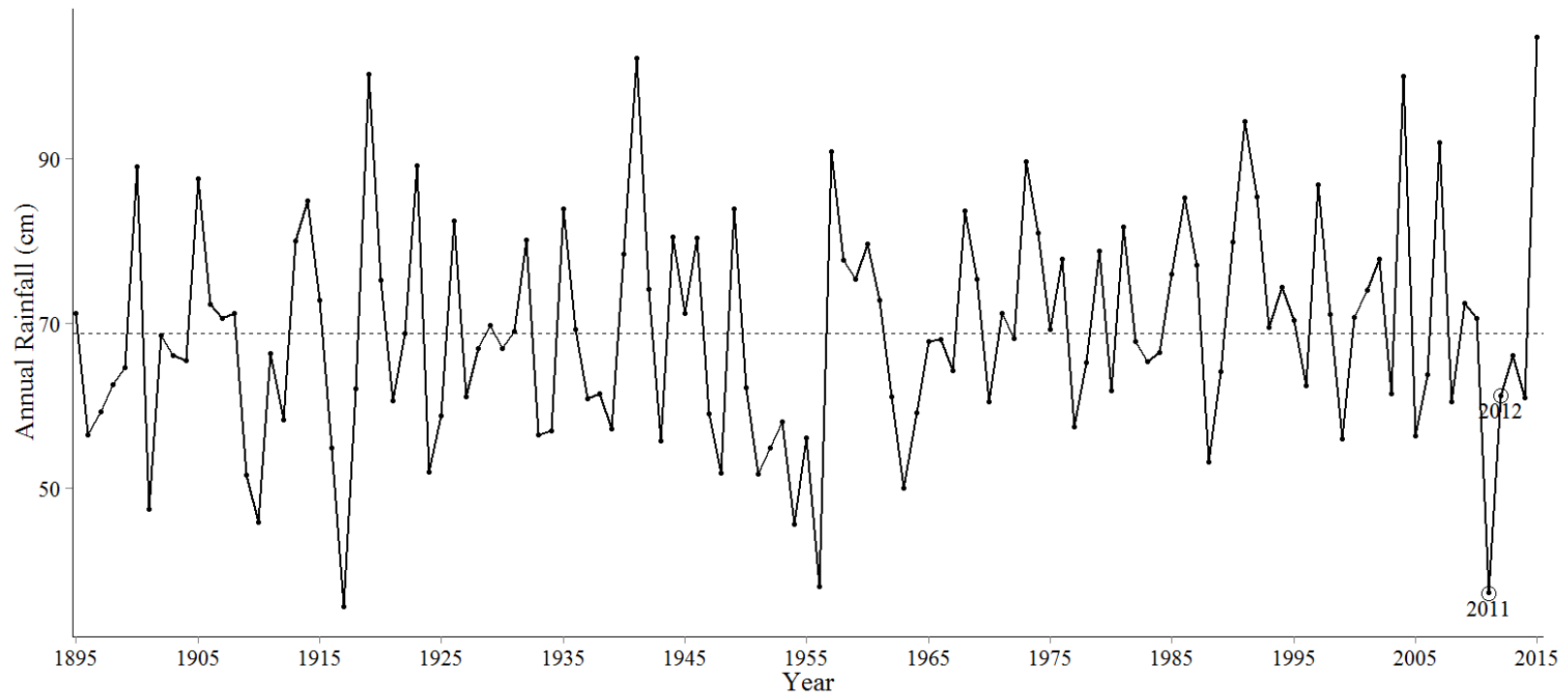


Figure 3. Annual rainfall in Texas from 1895–2014. Dashed line indicates average annual precipitation in Texas from 1901–2000 (considered baseline). Data were obtained from National Centers for Environmental Information (NCEI 2016) and graphed using the statistical program R version 3.2.2. The years corresponding to the study described herein (2011 and 2012) are circled.

expected lower precipitation and greenness in 2011 to limit nest-sites with adequate concealment, such that nest-site characteristics would vary between years (Martin 1993). With regards to breeding behaviors, I predicted that vireos would exhibit reduced reproductive investment via lower pairing success, delayed nest initiation, lower clutch size, or greater nest abandonment in 2011 compared to 2012. If birds delayed nesting, I expected they would experience greater nest failure and lower fledging success resulting from increased predation and brood parasitism. Although drought is not preventable, understanding vireo responses to variable environmental conditions and extreme weather events can inform management strategies aimed at conservation and recovery, and the information may prove useful when considering the potential effects of climate change on vireo populations.

## CHAPTER II

### EFFECTS OF DROUGHT ON HABITAT SELECTION IN BLACK-CAPPED

#### VIREOS (*VIREO ATRICAPILLA*)

#### **INTRODUCTION**

Habitat refers to the location where an animal lives (Odum 1971), and it is comprised of abiotic and biotic features that support occupancy (Hall et al. 1997). Ecologists have long been interested in the factors that influence habitat selection, which is a hierarchical (Hildén 1965; Johnson 1980) and scale-dependent (Orians and Wittenberger 1991; Wiens 1989) process based on innate and learned behaviors (Klopfer 1963; Klopfer and Hailman 1965; Partridge 1974) that allow organisms to assess habitat characteristics directly or indirectly (Hildén 1965; Cody 1981; Block and Brennan 1993:38). In birds, food limitation and nest predation are strong drivers of habitat selection (Cody 1981; Martin 1987, 1988, 1993; Cuttriss et al. 2015), and weather can act as an extrinsic pressure influencing habitat selection through its impacts on these factors. For instance, precipitation is the main driver of aboveground primary productivity (Noy-Meir 1973; Sala et al. 1988); it influences vegetation structure (Tyree et al. 1993; Chaves et al. 2003), composition (Cody 1981; Brown et al. 1997), and mortality (Allen and Breshears 1998; Breshears et al. 2005). When precipitation is low, delayed phenological events, reduced leaf area, or altered plant chemistry can occur (Rathcke and Lacey 1985; Larsson and Ohmart 2008; Gutbrodt et al. 2011). The overall effect is reduced greenness (i.e., foliage cover) on the landscape, which affects the availability (i.e., timing and abundance) of plant and insect foods (Morrison and Bolger

2002; Ogaya and Peñulas 2007; Greven et al. 2009) and reduces vegetation cover at foraging and nesting sites, increasing the risk of predation (e.g., Sugden and Beyersbergen 1986; Martin 1992, 1993) and exposure to the elements (e.g., wind, rain, cold, heat) (Walsberg 1981).

In arid and semi-arid environments, rainfall is low and unpredictable, and drought is common (e.g., in Texas) (Myoung and Nielsen-Gammon 2010). As such, birds living in these environments experience considerable annual variation in precipitation and must adjust their behaviors accordingly during dry periods. For example, they may select habitat differently during drought than they do when conditions are wetter. Individuals may relocate to wetter sites during drought (e.g., Strong et al. 1997; Gaines et al. 2000; Takekawa and Beissinger 2005) or follow shifting plant distributions after drought (e.g., Mueller et al. 2005). Those that do not relocate may select territories or nest-sites that maximize their use of limited vegetation cover (Martin 1993).

By understanding how species select habitat under varying conditions managers are better equipped to create, restore, or maintain habitat for species of conservation concern in the long-term. Shrub-nesting birds are of particular interest because of widespread population declines (Robbins et al. 1986; Askins 1993; Brawn et al. 2001). Many shrub-nesting species require early- and mid-successional vegetation, and fire-suppression and other practices (e.g., farm abandonment) have allowed vegetation in many shrubland environments to reach seral stages that prohibit occupancy or reproduction by shrub-nesting birds (Askins et al. 1990; Droege 1998).

The Black-capped Vireo (*Vireo atricapilla*; hereafter vireo) is a federally endangered songbird that breeds in early-successional shrub-scrub vegetation in arid and semi-arid regions of Oklahoma, Texas, and Mexico (Fig. 4) (Graber 1961; Gryzbowski 1995; Wilkins et al. 2006; González-Rojas et al. 2014). Major threats to the species include habitat loss and fragmentation and reduced reproductive success resulting from brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Marshall et al. 1985; Ratzlaff 1987). Understanding these threats as well as the vireo's biological and ecological requirements may help inform conservation and management strategies necessary for the species' recovery (USFWS 1991).

Vireos typically breed in vegetation of irregular height and distribution that provides adequate cover (35–55%) for foraging and nesting (Graber 1961; Gryzbowski et al. 1994). Drought, fire, and grazing interact with topographic features (Graber 1961; McFarland et al. 2013) to maintain the vegetation configuration needed for vireo reproduction (Wilkins et al. 2006). Yet, little information exists regarding habitat selection by vireos during periods of drought. Smith et al. (2012) detailed habitat use and nesting ecology by vireos at Devil's River State Natural Area in the drier, southwestern portion of the species' breeding range in Texas. They noted that management strategies aimed at conserving vireo habitat in the west should be considerably different than those proposed for use in other (wetter) portions of the vireo's breeding range (Smith et al. 2012).

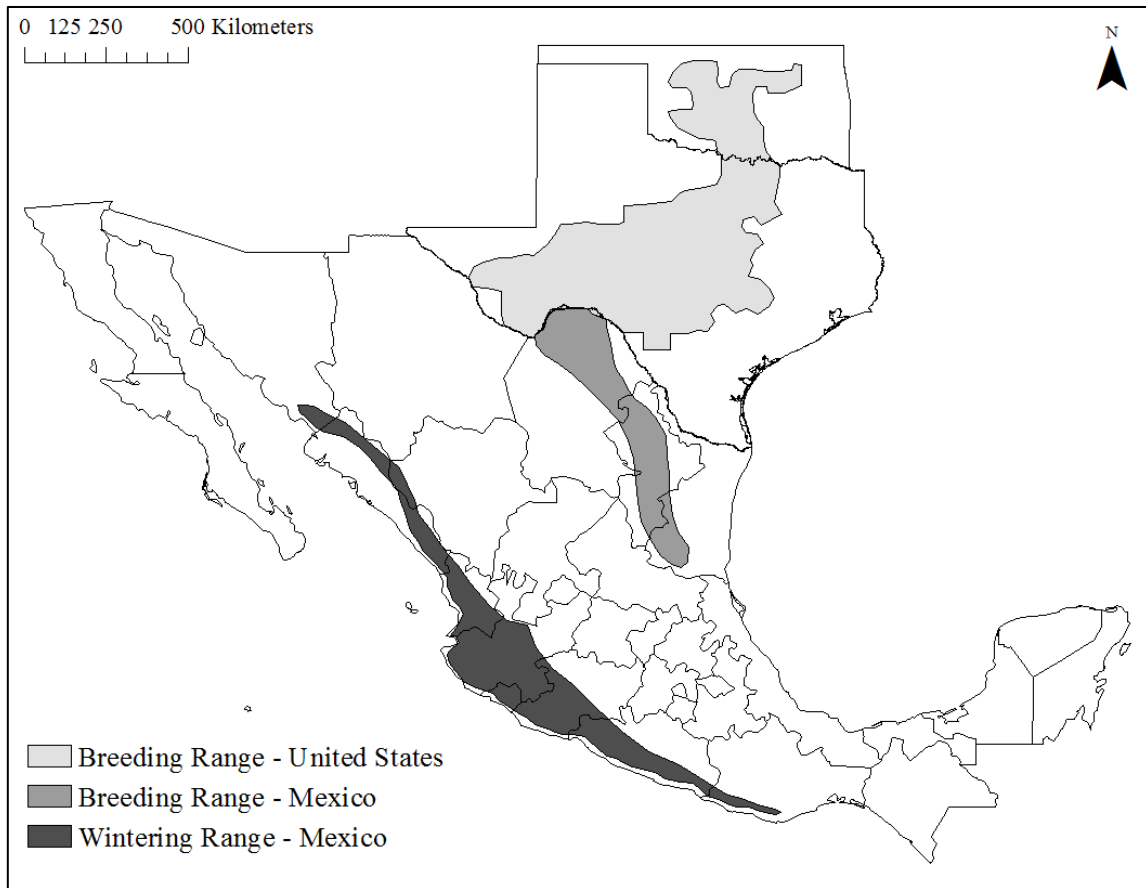


Figure 4. Map of breeding and wintering ranges for the Black-capped Vireo (*Vireo atricapilla*) based on data presented in Wilkins et al. (2006).

The objective of this study was to examine habitat selection by vireos over two years of varying drought intensity. In 2011, Texas experienced one of the most extreme droughts in its recent history (USDM 2016). Precipitation was less than half of the 30-year average, and temperatures exceeded the 30-year average (SCIPP 2016). Drought conditions persisted the following year, but not with the same intensity as in 2011 (USDM 2016). The differences in weather between 2011 and 2012 provided a unique opportunity to examine habitat selection by vireos during an extreme drought event compared to more moderate (common) conditions.



I quantified differences in precipitation and vegetation cover (greenness) associated with the 2011 and 2012 vireo breeding seasons and compared topographic and vegetation features of vireo habitat because both can affect microenvironments (Suggitt et al. 2011) and influence habitat selection (e.g., Weiss et al. 1988). I expected that the differences rainfall would result in lower vegetation greenness in 2011 compared to 2012, and I predicted that, under such conditions, vireos would select larger territories because territory size is often inversely related to food availability (e.g., Seastedt and MacLean 1979; Smith and Shugart 1987), which is correlated with rainfall and greenness (e.g., Morrison and Bolger 2002; Ogaya and Peñulas 2007; Greven et al. 2009). I also predicted vireos would establish territories and nest-sites with flatter, northern-facing slopes because precipitation and solar radiation can degrade vegetation conditions on steep, southern-facing slopes (Cottle 1932; Gallardo-Cruz et al. 2009; Sternberg and Shoshany 2011). Lastly, I predicted lower precipitation and greenness in 2011 would limit nest-sites with adequate concealment, such that nest-site characteristics would vary between years (Martin 1993). Although drought is not preventable, understanding vireo responses to variable environmental conditions and extreme weather events can inform management strategies aimed at conservation and recovery, and the information may prove useful when considering the potential effects of climate change on vireo populations.

## METHODS

### Study Area

I surveyed vireos across an 1,100 ha study site within Dobbs Run Ranch (2,030 ha; ~29° 38' 60" N, -100° 24' 36" W) (Fig. 5) from late March–late July in 2011 and 2012. Dobbs Run Ranch is a privately-owned property located in Edwards County, Texas on the southwestern edge of the Edwards Plateau ecoregion (Omernik 1995). The Edwards Plateau is a semi-arid region (Thornwaite 1948) with highly variable summer climate and a large, east-west precipitation gradient (Daly et al. 2008) that experiences notable variation in temperature and precipitation annually and seasonally. The average maximum summer (April–July) temperature is 31 °C, and the cumulative average summer precipitation is ~25 cm (NCEI 2016).

Soil in the study site is mainly limestone bedrock (99.6%) (NRCS 2013). Common woody plants in the study site include Ashe juniper (*Juniperus ashei*), live oak (*Quercus fusiformis*), piñon pine (*Pinus remota*), Texas persimmon (*Diospyros texana*), and Texas mountain laurel (*Dermatophyllum secundiflorum*). Livestock grazing, which can interfere with avian nest success by altering vegetation structure (Kreuper et al. 2003; Gill and Fuller 2007) or the distribution of harmful species (e.g., predators [reviewed in Atkinson et al. 2004] and brood parasites [e.g., Goguen and Mathews 2000]), did not occur on or near the ranch during this study. I regularly observed individuals or small groups of wild, grazing ungulates, such as blackbuck (*Antelope cervicapra*), white-tailed deer (*Odocoileus virginianus*), axis deer (*Cervus axis*), and

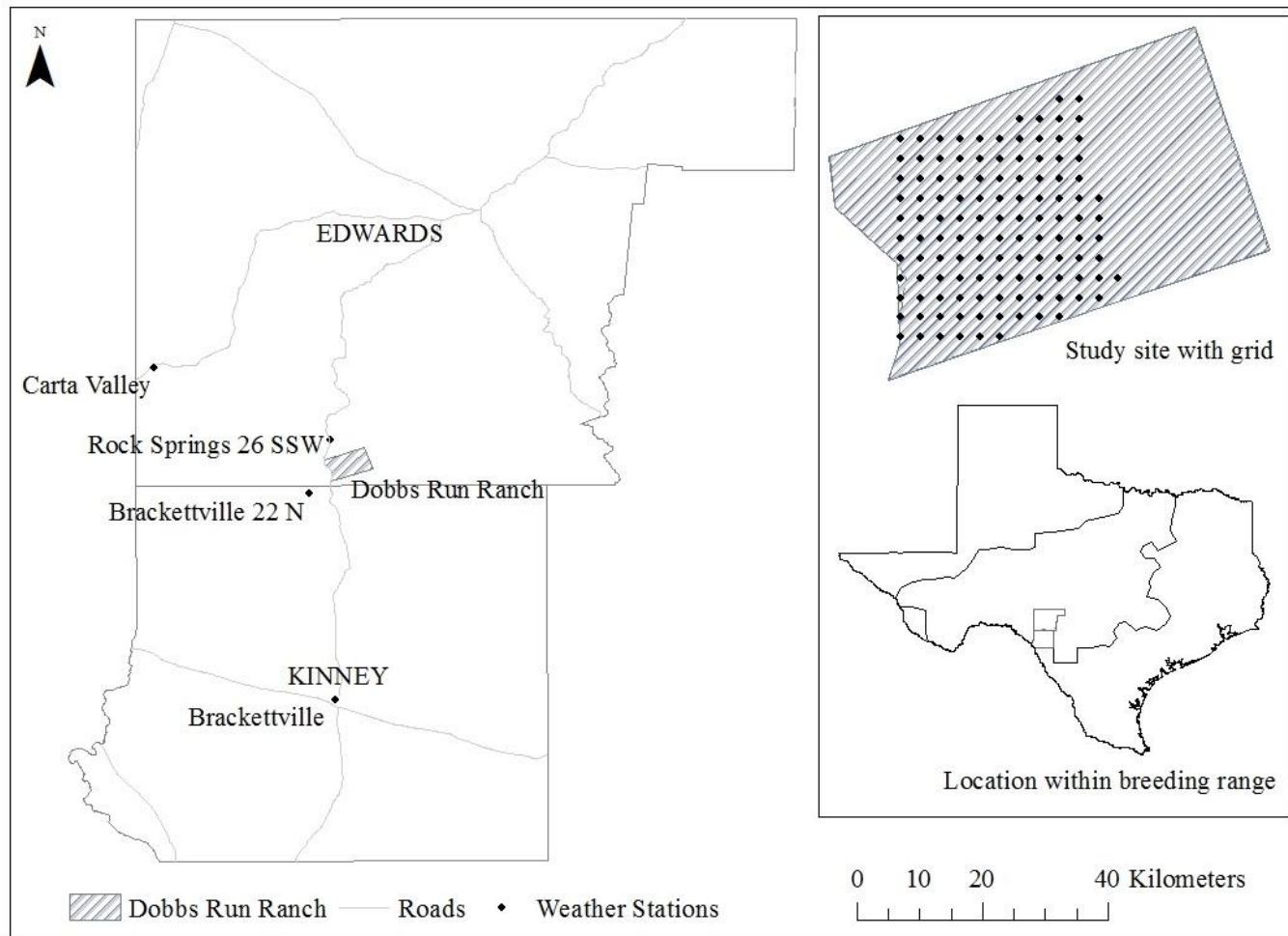


Figure 5. Location of Dobbs Run Ranch in relation to nearby weather station in Edwards and Kinney counties. Top inset shows the study site and sampling grid within Dobbs Run Ranch where I monitored Black-capped Vireos (*Vireo atricapilla*) in 2011–2012. Bottom inset shows the location within the Black-capped Vireo’s breeding range in Texas.

aoudad (*Ammotragus lervia*). However, it is unlikely that the presence of these species negatively affected vireo reproduction during my study (e.g., Locatelli et al. 2016). Additionally, hunting (of game birds and ungulates) was limited to a small area northwest of my study site and likely had no impact on the vireo population or my results. There were three active Brown-headed Cowbird traps at Dobbs Run Ranch during the years of this study, but data regarding number of Brown-headed Cowbirds trapped annually are not available.

### **Annual Variation in Weather**

To quantify differences in weather between years, I obtained daily maximum temperature and daily precipitation data for 2010–2012 from the National Centers for Environmental Information (NCEI 2016). Most data were recorded at the Brackettville 22 N station (GHCND:USC00411013) (Fig. 5) located at Kickapoo Caverns State Park (KCSP) (29° 36' 36" N, -100° 27' 07" W), which is adjacent to Dobbs Run Ranch. However, a small number of records were missing at this station during the study period. When necessary, I substituted precipitation values from the Rocksprings 26 SSW station (GHCND:USC00417717; 29° 41' 16" N, -100° 25' 18" W) (Fig. 5), which was located <15 km away. The Rocksprings 26 SSW station did not record temperature information, so when temperature records were not available from the Brackettville 22 N station, I substituted average values from the next two nearest stations, which were both located both <30 km away. These stations were Carta Valley (GHCND:USC00411492; 29° 47' 24" N, -100° 40' 26" W) (Fig. 5) and Brackettville (GHCND:USC00411007; 29° 18' 58" N, -100° 24' 50" W) (Fig. 5). Substitutions accounted for <5% of weather data.

Spring and summer precipitation influences vegetation growth during the growing season (mid-March–mid-November in Edwards County [TSHA 2016]), but so does soil moisture, which is determined by fall and winter precipitation (Pielke and Doeskin 2008). As such I examined precipitation data for the months of September to March preceding each vireo breeding season as well as precipitation during each vireo breeding season (April–July [Gryzbowski 1995]). In addition to daily weather variables, I obtained monthly Palmer Drought Severity Index (PDSI) values for the study period to further demonstrate differences in weather conditions by year. The PDSI uses precipitation, soil moisture, and temperature data to assess water availability and the intensity of drought at regional scales (Palmer 1965). PDSI values  $\leq -4$  reflect extreme drought conditions, and values  $\geq 4$  indicate extreme wet conditions (Table 1). Though it is the most commonly used drought index in the United States, PDSI has been criticized for arbitrary designations of drought intensity, sensitivities to rainfall events, and different sensitivities across regions (Alley 1984).

Table 1. Classification of weather according to the Palmer Drought Severity Index (Palmer 1965).

Value	Description
$\geq 4.00$	Extremely Wet
3.00 to 3.99	Very Wet
2.00 to 2.99	Moderately Wet
1.00 to 1.99	Slightly Wet
0.50 to 0.00	Incipient Wet Spell
-0.49 to 0.49	Near Normal
-0.99 to -0.50	Incipient Drought
-1.99 to -1.00	Mild Drought
-2.99 to -2.00	Moderate Drought
-3.99 to -3.00	Severe Drought
$\leq -4.00$	Extreme Drought

## **Annual Variation in Greenness**

I quantified vegetation greenness across the landscape because it is associated with foliage cover and may influence the availability of food for vireos (Sweet et al. 2015) or their risk of predation. I obtained 30 m resolution Landsat 5 Thematic Mapper (TM) imagery for 2011 and 30 m resolution Landsat 7 Enhanced Thematic Mapper Plus (ETM+) imagery for 2012 for the months associated with vireo breeding (April–July [Gryzbowski 1995]). I pre-processed all Landsat images available during the months of interest for both years by performing radiometric calibration to correct for sensor differences between images (reviewed in Dinguirard and Slater 1999) and dark object subtraction to correct for atmospheric scattering (e.g., Chavez 1988). I used ENVI software versions 5.1 and 5.3 (Exelis Visual Information Solutions, Boulder Colorado) for all pre-processing.

Pre-processing Landsat scenes enabled me to compare images taken during different months and years by the two satellites. However, on 31 May 2003, the Scan Line Corrector (SLC) on the ETM+ satellite failed, causing large data gaps to appear on Landsat 7 images (Fig. 6) (USGS 2016). The Landsat 7 ETM+ satellite orbits the Earth every 16 days, sometimes recording multiple images for each path and row during a given month, with images from different paths and rows often overlapping in spatial coverage. Overlapping Landsat 7 images of my study site were available from Path 29 Row 39 and Path 28 Row 40. There were 3–4 images encompassing the study site available for each month of vireo breeding. To account for the data gaps in Landsat 7 images, I first used the USGS gap phase statistic calculator (USGS 2016) to determine

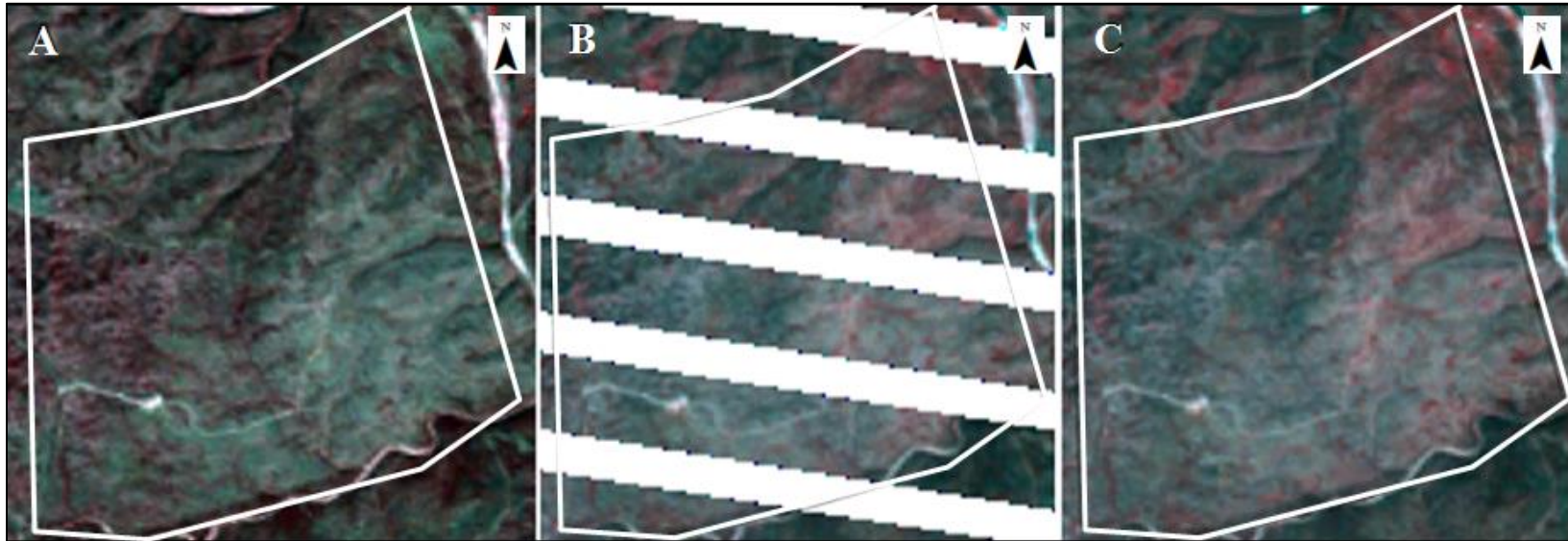


Figure 6. A. Landsat 5 TM image taken 11 April 2011; B. Landsat 7 ETM+ image taken 5 April 2012; white lines indicate missing data due to failure of the Scan-Line Corrector; C. Gap-filled image created from Landsat 7 ETM+ images taken on 5 April 2012 and 21 April 2012. All images are false-color composites that have undergone pre-processing. White polygon indicates the study site boundary within Dobbs Run Ranch.

the degree of overlap between images taken in the same month. I then selected the within-month image pairs with the greatest amount of overlap and the least amount of cloud cover. Finally, I used the landsat\_gapfill.sav extension toolbox for ENVI, which uses localized linear histogram matching to fill data gaps (Scaramuzza et al. 2004) (Fig. 6). Gap-filling was not necessary for 2011 Landsat 5 images, but I selected images from 2011 with the least cloud cover.

Low cloud cover images from June 2012 had less overlap than images from other months, and there were large areas with missing data. Similarly, July images from both years had excessive cloud cover masking significant portions of the study site. As such, I excluded images from June and July and only examined images from April and May (i.e., months of peak vireo nest initiation; Chapter 3) from each year. Specifically, I used images taken on 11 April and 29 May in 2011 and gap-filled images for 2012 that were comprised of scenes recorded on 5 April, 21 April, 23 May, and 30 May.

I used ENVI software to create Normalized Difference Vegetation Index (NDVI) maps from the finalized April and May Landsat images, and I used the Spatial Analyst extension in ArcMap version 10.2.2 (Environmental Research Systems Institute, Redlands, California) to extract NDVI values from each pixel for all periods. NDVI is a widely used vegetation index correlated with vegetation cover (Wellens 1997), leaf-area index (Law and Waring 1994), and plant productivity (Reed et al. 1994) as well as climate variables (e.g., rainfall, temperature, evapotranspiration) (Nicholson et al. 1990; Cihlar et al. 1991). NDVI is a ratio derived from differences in the reflectance of radiation in the visible (red) and near-infrared (NIR) wavelengths ( $NDVI = [NIR -$



red]/[NIR+red]) (Rouse et al. 1973). NDVI values range from -1 to 1, with higher values corresponding to increased photosynthetic activity and the presence of healthy vegetation.

### **Landscape-scale Data**

I established a 300 m grid across the study site (Fig. 5), which allowed for a reasonable detection of singing vireos with a maximum distance of sound attenuation of 150 m (e.g., Smith 2011; McFarland et al. 2013). Each year from 20 March to 15 July, I walked different routes along the grid and used auditory and visual surveys to map the locations of male vireos across the study site. When I detected a male vireo, I marked its location using a handheld Garmin RINO 120 Global Positioning System (GPS) unit with  $\leq 10$  m accuracy. I returned to marked locations every 5–10 days between the hours of sunrise and 1400. I spent  $\leq 1$  h per day with each bird, which maximized the number of territories I could visit each day while limiting disturbance to nesting vireos. I observed vireos from a distance to minimize observer effects and noted their locations. Each time a focal bird moved  $\geq 20$  m, I marked its location with a GPS. It is difficult to identify potential vireo habitat using remotely sensed images, so I used ArcMap to create a 100 m buffer around all vireo location points collected over the two years of this study and considered the area within the buffered region to represent habitat available (i.e., suitable) to vireos. This method seemed a reasonable approximation of available habitat as I regularly encountered vireos throughout the buffered region.

I then used remotely sensed data to characterize the topography within the buffered region. I used the Spatial Analyst extension in ArcMap to extract information

on the steepness and direction (i.e., aspect) of slopes within available habitat from a USGS National Elevation Dataset (NED) 1/3 arc-second digital elevation model (DEM; 10 m resolution) corresponding to my study site. I determined the mean (percent) slope per 1.7 ha block within available habitat and used this information to represent the availability of slope of varying steepness to vireos. I similarly determined aspects (i.e., slope directions) available to vireos within the 1.7 ha blocks. This size block roughly corresponded to the overall mean vireo territory size at my study site and was similar to mean territory size reported by Graber (1961 [mean 1.5 ha]). For analyses purposes, I grouped slope values into 5% increments (similar to Castiaux 1995). I similarly classified aspect values into discrete categories corresponding to compass directions (N, NE, E, SE, S, SW, W, NW) and calculated the area of slopes facing each direction in each block. I identified the aspect category that best represented each block (i.e., covered the most area) and used this information to determine the aspects available to vireos. I only included blocks if  $\geq 1$  ha fell within available habitat.

### **Territory-scale Data**

I considered male vireos territorial if I consistently detected them in the same locations for  $\geq 4$  weeks. To improve my assignment of individuals to specific territories, I used standard target mist-netting techniques (described by Johnston 1965; Keyes and Grue 1982) with playback of recorded vireo song to capture adult vireos and mark them with unique color-band combinations. I used Geospatial Modelling Environment version 0.7.3.0 (Beyer 2009) to create minimum convex polygons (MCP) for all territories with  $\geq 15$  location points, which I considered the minimum number required to adequately

represent territory boundaries (e.g., Smith 2011; Morgan 2012). I defined territory size as the area within each MCP, and I considered the area within MCPs to represent habitat selected by vireos. I extracted information regarding the steepness and direction of slopes within territories from the DEM described previously.

### **Nest-scale Data**

While mapping vireo locations, I watched for behavioral cues indicative of breeding (e.g., copulation, material or food carry) to help pinpoint nest locations. I focused on females because they tend to spend more time near nests (Gryzbowski 1995; Pope 2013a, b), but I noted male behaviors and movement patterns as well because this species shares parental duties (Gryzbowski 1995; Pope et al. 2013b). If I did not detect vireos on arrival in a territory, I searched the territory systematically for a nest—concentrating on vegetation structure common among vireo nests (e.g., Gryzbowski et al. 1994; Gryzbowski 1995). This method often proved effective in the absence of behavioral cues, especially during the egg-laying phase, when nests were most difficult to find (Martin and Geupel 1993), and also accounted for differences in detection attributed to variation in vegetation.

I extracted topographic metrics (i.e., slope steepness and direction) at nest locations from the DEM (described above). I also catalogued vegetation characteristics for each active (i.e., observed contents, tended by adults) vireo nest after it fledged, failed, or was abandoned. Specifically, I recorded the nest substrate and measured the distance to the nearest edge (i.e., nest rim to nearest leafy edge), nest height (from ground to nest rim), substrate height, and canopy height all to the nearest 0.1 m. I

defined canopy height as the height of the tallest tree or shrub immediately above the nest. When the substrate tree or shrub was the tallest tree or shrub above the nest, I recorded the same value for the substrate height as for canopy height. In addition, I positioned a 2 m coverboard marked with 0.1 m<sup>2</sup> squares immediately in front of each nest and estimated the percent of each square obscured by vegetation from 7 m away in each cardinal direction. I then averaged these values to obtain a single measurement of foliage cover. Lastly, I placed a 0.1 m<sup>2</sup> board at each nest and estimated the percent visual obstruction by vegetation from 1 m away in each cardinal direction as well as from above and below nests. I averaged these values to get a single measurement of nest concealment. All measurements were consistent with those collected during other studies of nesting vireos (e.g., Conkling et al. 2012; Smith et al. 2012; Pope et al. 2013a, b).

## **Analyses**

I conducted all tests using the statistical program R version 3.2.2 (R Core Team, Vienna, Austria). I presented all means described below with standard deviations. Because this was a two-year study at a single site, I presented weather and greenness data simply to demonstrate the differences between years but, I did not include these data in further analyses. Instead, I used temporal variables (e.g., month, year) to examine differences in vireo habitat selection in response to weather.

*Annual Variation in Weather.*—I calculated the mean maximum daily temperature for each year, and I used a Welch's two-sample *t*-test (Ruxton 2006; Crawley 2014:94–95) with Cohen's *d* (Lakens 2013) as a measure of effect size to compare means between years. I also used linear regression to examine temperature as a

function of date within seasons (Crawley 2014:114–140). Additionally, I summed daily precipitation to determine cumulative monthly precipitation totals for the seven months prior to and the four months of each breeding season and calculated the percent differences between years.

*Annual Variation in Greenness.*—I compared NDVI across the study site and mean NDVI within territories between months and years using two-way factorial analysis of variance tests (ANOVA) (Crawley 2014:170–173). If there was a significant interaction between month and year, I used Tukey’s Honest Significant Difference (HSD) test to examine pairwise differences (Crawley 2014:226) in months between (e.g., April 2011 vs. April 2012) and within (e.g., April 2011 vs. May 2011) years. If there was no significant interaction, I examined the main effects of month and year separately.

*Landscape-scale.*— I quantified the amount of habitat available to vireos within the 100 m buffered region and used Chi-square tests (Crawley 2014:101–105) to examine the distributions of slope steepness and aspect categories across the landscape.

*Territory-scale.*— I compared territory size between years using a Welch’s two-sample *t*-test (Ruxton 2006; Crawley 2014:94–95) with Cohen’s *d* as a measure of effect size (Lakens 2013). Additionally, I used Chi-square goodness-of-fit tests (Crawley 2014:104–105) to determine if the steepness or direction of slopes within territories each year differed from that expected given the slopes available on the landscape. I used Fisher’s exact tests (Crawley 2014:105–107) instead of Chi-square tests to determine if

territory-scale slopes selected differed between years because some slope categories were not well represented (i.e., sample sizes <15).

*Nest-scale.*—I used Chi-squared tests of independence (Crawley 2014:104–105) to compare slope steepness at nest-sites between years, and I used a Watson’s two-sample test of homogeneity (Lund and Agostinelli 2009:41) to compare slope direction (i.e., aspect) at nest-sites. This test is the equivalent of a one-factor ANOVA or two-sample *t*-test for circular data (Berens 2009). Additionally, I used a Chi-square test (Crawley 2014:104–105) to determine if nest substrate use differed between years.

I used a one-way, non-parametric multivariate test within the *npmv* package in program R (Burchett and Ellis 2015) to evaluate inter-annual differences in vegetation at nest-sites and differences in vegetation characteristics among the most common nest substrates (i.e., global models). The *npmv* package provides several options for multivariate tests of this type. To determine which test would be most suitable, I first examined correlations between the six vegetation variables of interest (i.e., nest height, substrate height, overstory height, distance to the nearest edge, average cover, average concealment). Because data were not normally distributed, I used a Spearman’s rank test to examine correlations (Zar 2005). A nonparametric, ANOVA-type test (Brunner et al. 1997) performs best when response values are positively correlated, and a Lawley-Hotelling-type test performs better when responses are negatively correlated (reviewed in Bathke et al. 2008).

I selected the appropriate test based on correlations and applied it to the global models and subsequently to *post hoc* univariate tests examining the differences in each

vegetation characteristic by year and substrate. I accounted for multiple comparisons in *post hoc* tests using the Bonferroni-correction and interpreted *P*-values accordingly. In addition to the global test statistics, I provided the relative effects for each test. Relative effects are measures of effect size, which reflect the probability that a particular vegetation characteristic measured at a randomly chosen nest in a given year (or substrate) had a greater value than that from a randomly chosen nest from any year (or substrate) (Burchett and Ellis 2015).

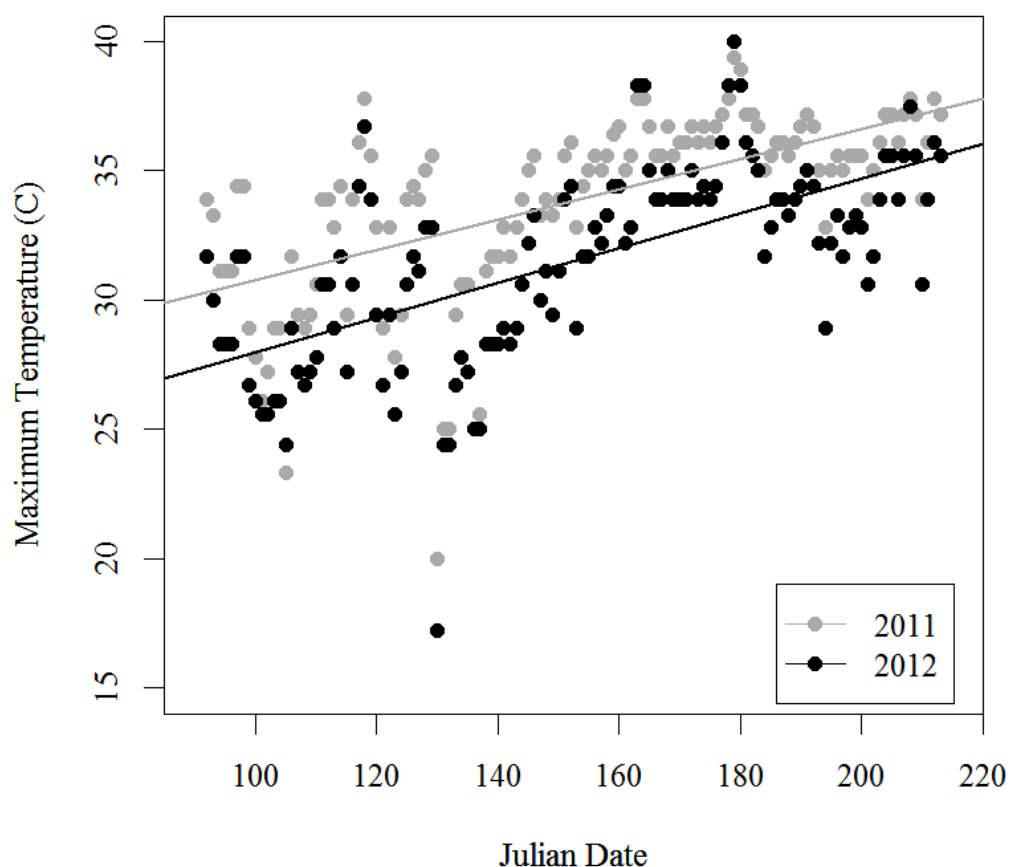


Figure 7. Maximum temperature (°C) at Dobbs Run Ranch, Edwards County, Texas from April–July in 2011 and 2012. Lines indicate linear trends of increasing temperature over time in both years.

## RESULTS

### Annual Variation in Weather

Weather varied significantly between the years of my study, with the 2011 vireo breeding season being warmer and drier than the 2012 breeding season. Maximum daily temperature varied between years ( $t_{241.4} = 4.85$ ,  $P \leq 0.01$ ,  $d = 0.62$ ). Yet, mean maximum daily temperature in either year (i.e.,  $34 \pm 4$  °C [range 20–39 °C] in 2011 and  $32 \pm 4$  °C [range 17–40 °C] in 2012) was comparable to the average maximum temperature for the region during the months of vireo breeding (NCEI 2016). Daily maximum temperature increased over time within years (2011:  $F_{1,120} = 59.66$ ,  $r^2 = 0.33$ ; 2012:  $F_{1,120} = 80.78$ ,  $r^2 = 0.40$ ) (Fig. 7). There was 54% less rainfall in the months leading up to the 2011 breeding season (13.1 cm) (Fig. 8) than during the corresponding months the following year (28.4 cm) (Fig. 8). Similarly, 56% less rain fell during the 2011 season (10.7 cm) (Fig. 9) than during the 2012 season (24.5 cm) (Fig. 9). Rainfall in 2011 was approximately half of the seasonal average for the region (NCEI 2016). However, monthly precipitation totals (Fig. 9) belied the true conditions of the 2011 breeding season during which 61% (6.48 cm) of the total rainfall occurred on a single day (May 12), and mean precipitation of other rainfall events ( $n = 7$ ) was low ( $0.61 \pm 0.44$  cm). Monthly PDSI values for the study period better captured the extreme difference in rainfall between years. PDSI ranged from -6.02 to -3.98 (extreme conditions) in 2011 and -2.65 to -2.03 (moderate conditions) in 2012 (NCEI 2016).



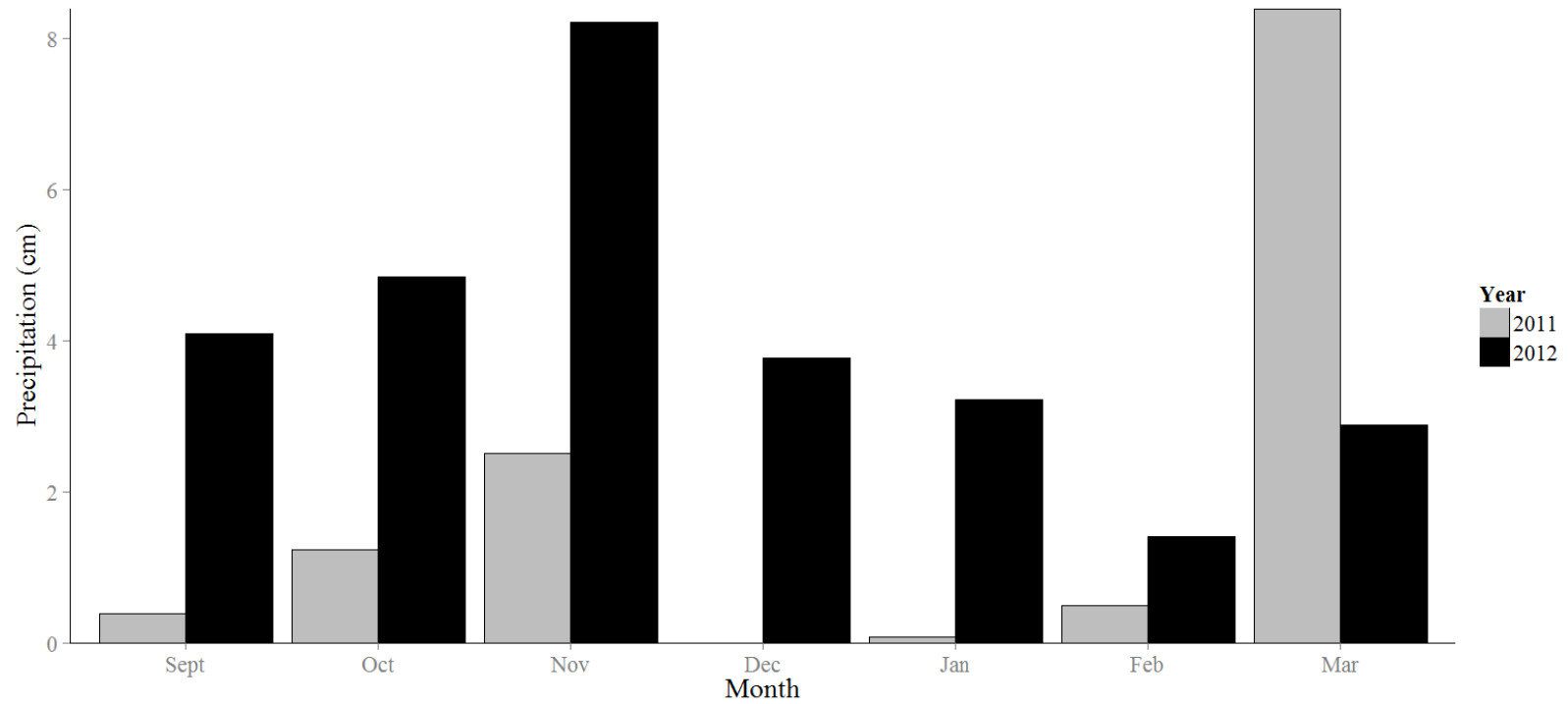


Figure 8. Cumulative monthly precipitation from Dobbs Run Ranch, Edwards County, Texas during the seven months preceding the 2011 and 2012 Black-capped Vireo (*Vireo atricapilla*) breeding seasons.

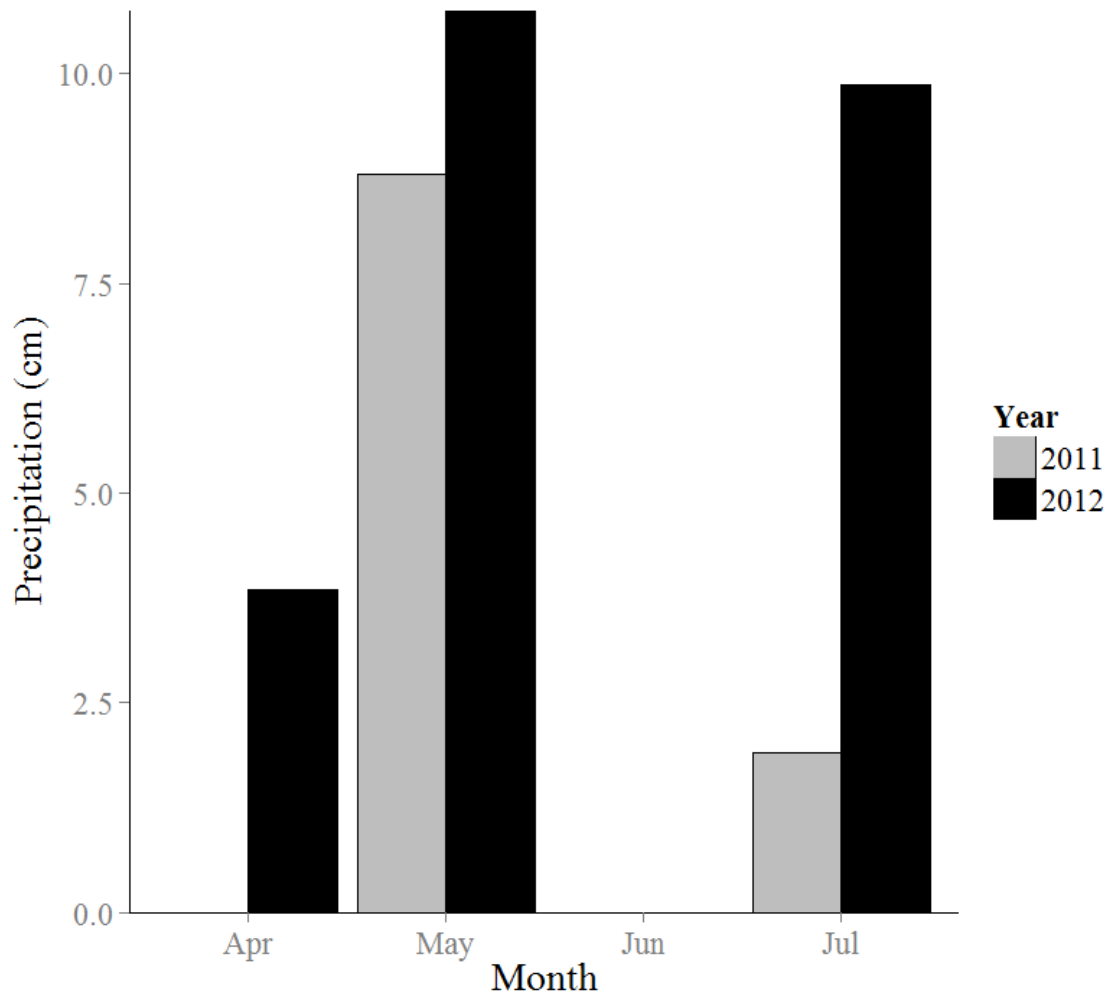


Figure 9. Cumulative monthly precipitation from Dobbs Run Ranch, Edwards County, Texas during the 2011 and 2012 Black-capped Vireo (*Vireo atricapilla*) breeding seasons.

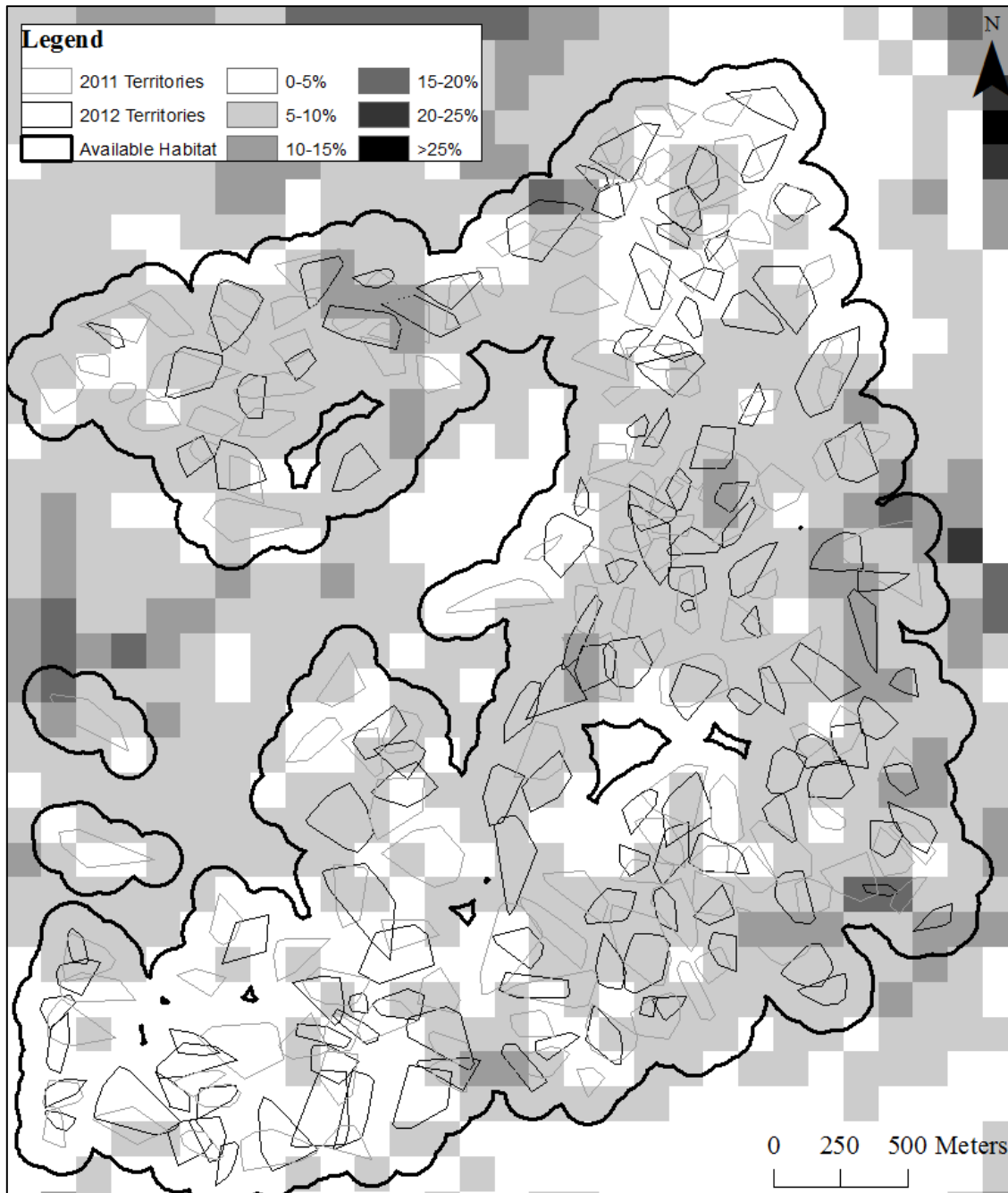


Figure 10. Slope (sampled at 1.70 ha) available to and used by Black-capped Vireos (*Vireo atricapilla*) within the study site at Dobbs Run Ranch, Edwards County, Texas in 2011–2012.

### **Annual Variation in Greenness**

There was a significant interactive effect of month and year on NDVI across the study site ( $F_{1,52184} = 7,326$ ,  $P \leq 0.01$ ). *Post hoc* Tukey's HSD tests showed that NDVI was significantly different across the study site for all combinations of months and years ( $\alpha \leq 0.01$ ). NDVI across the landscape was ~3% greater in April 2012 compared to April 2011, and ~28% greater in May 2012 compared to May 2011. Within territories, there was no significant interactive effect of month and year on mean NDVI ( $F_{1,556} = 0.70$ ,  $P = 0.70$ ). However, mean NDVI within territories varied both by month ( $F_{1,558} = 5.83$ ,  $P = 0.02$ ) and year ( $F_{1,558} = 1225.00$ ,  $P \leq 0.01$ ). Mean NDVI within territories was ~28% greater in 2012 than in 2011 and ~3% greater during May compared to April.

### **Landscape-scale**

I identified ~952 ha of available habitat within the study site with slopes ranging from ~2–18% ( $\bar{x} = 6\% \pm 3$ ) (Fig. 10). Slope steepness categories were not equally distributed across the landscape ( $X^2_3 = 274.72$ ,  $P \leq 0.01$ ). More than half (57%) of all available habitat was characterized by 5–10% slope, while only 7% was characterized by slopes >10% (Figs. 10, 11). Similarly, aspect categories were not equally distributed within available habitat ( $X^2_7 = 30.21$ ,  $P \leq 0.01$ ). Southerly-facing slopes were most common (including SE, S, SW; 44%) (Fig. 12), while western-facing slopes were uncommon (5%).

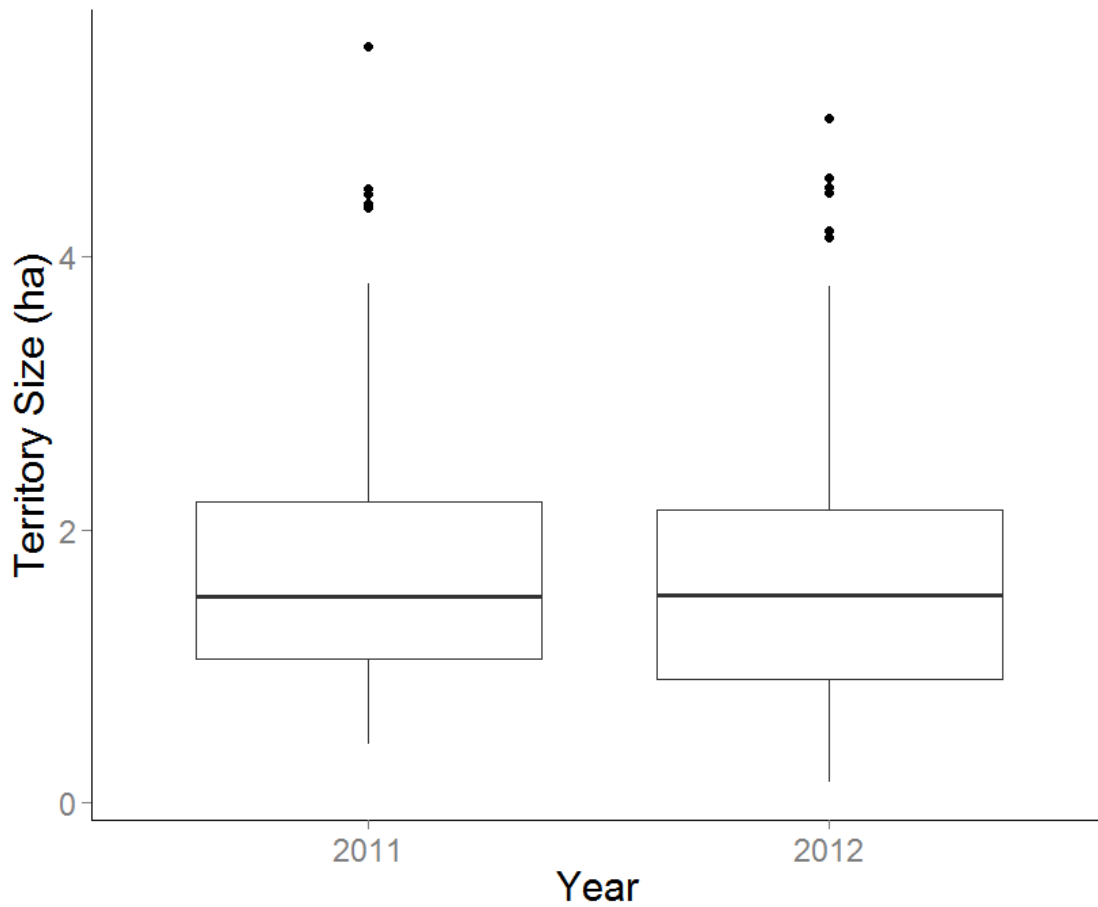


Figure 11. Distribution of Black-capped Vireo (*Vireo atricapilla*) territory sizes at Dobbs Run Ranch, Edwards County, Texas in 2011–2012.

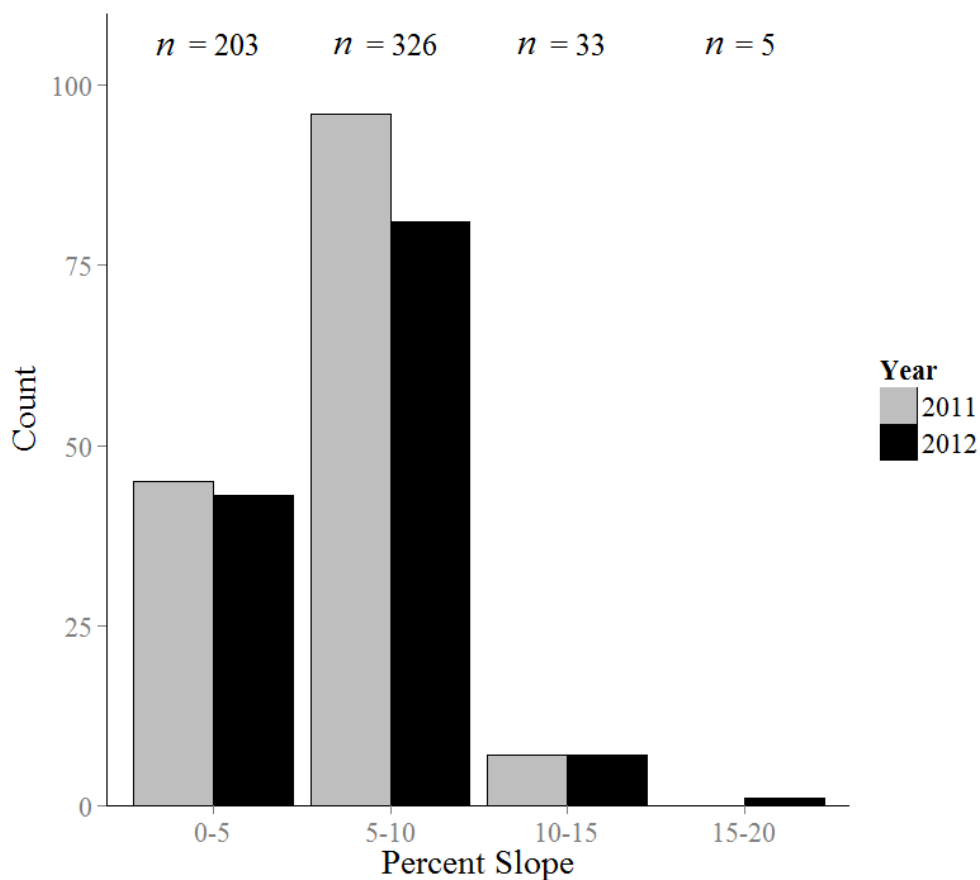


Figure 12. Count of territories by mean slope (percent) used by Black-capped Vireos (*Vireo atricapilla*) in 2011 and 2012 at Dobbs Run Ranch, Edwards County, Texas. Values at the top of the graph indicate the number of 1.70 ha blocks by mean slope available to Black-capped Vireos within the study site.

### Territory-scale

I mapped and monitored 148 vireo territories in 2011 and 132 vireo territories in 2012. Monitored territories covered ~249 ha of the available habitat in 2011 and ~234 ha in 2012. Vireos utilized other areas, but data were insufficient to include these in analyses (e.g., I observed individuals for <4 weeks or I collected <15 location points

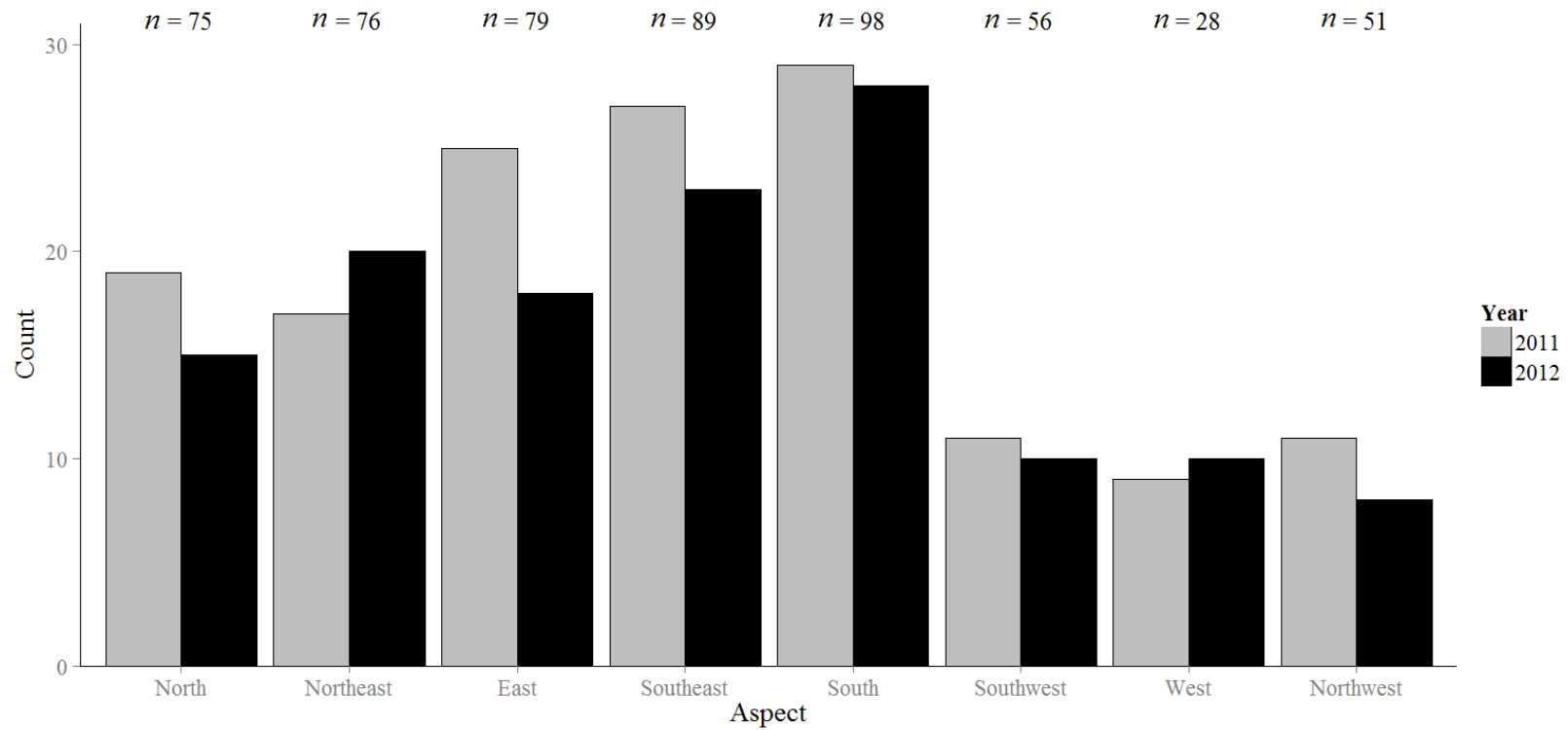


Figure 13. Count of territories by slope direction (aspect) used by Black-capped Vireos (*Vireo atricapilla*) in 2011 and 2012 at Dobbs Run Ranch, Edwards County, Texas. Values at the top of the graph indicate the number of 1.70 ha blocks by slope direction (aspect) available to Black-capped Vireos within the study site.

over the course of the breeding season). Overall mean territory size was  $1.69 \text{ ha} \pm 0.95$ , with annual means of  $1.68 \text{ ha} \pm 0.09$  in 2011 and  $1.70 \text{ ha} \pm 1.00$  in 2012 (Fig. 11). There was no significant difference in territory size between years ( $t_{265.24} = -0.09$ ,  $P = 0.93$ ,  $d = 0.01$ ).

In 2011, mean slope steepness within territories ranged from ~2–14% ( $\bar{x} = 6\% \pm 2$ ) (Fig. 12); slope steepness within vireo territories did not differ from what was expected given its availability across the landscape ( $X^2_3 = 1.66$ ,  $P = 0.65$ ). In 2012, mean slope steepness within territories ranged from ~2–16% ( $\bar{x} = 6\% \pm 3$ ) (Fig. 12); again, the slope steepness within territories was not different than expected ( $X^2_3 = 3.55$ ,  $P = 0.31$ ). Similarly, there was no difference in selection of slopes between years (Fisher's exact  $P = 0.41$ ). Aspect within vireo territories was also as expected in both years given the distribution of aspects within available habitat (2011:  $X^2_7 = 3.90$ ,  $P = 0.79$ ; 2012:  $X^2_7 = 5.67$ ,  $P = 0.58$ ), and there was no difference in aspects selected between years (Fisher's exact  $P = 0.97$ ). Southerly (16%) and southeasterly (18%) slopes were most common within territories (Fig. 13), while western facing slopes were least common (5%) (Fig. 13).

### **Nest-scale**

I monitored and collected vegetation and topographic data for 186 active nests (i.e., observed with eggs or nestlings) in 2011 ( $n = 74$ ) and 2012 ( $n = 112$ ). Mean steepness of slopes at vireo nests was  $\sim 6\% \pm 3$  in 2011 and  $\sim 7\% \pm 4$  in 2012 (Fig. 14); there was no difference in the steepness of slopes at vireo nest-sites between years ( $X^2_3 = 7.41$ ,  $P = 0.06$ ). The majority of nests ( $\sim 45\%$ ) were on southerly-facing slopes (i.e., S,



SE, SW) in both years (Fig. 15) with no difference in the distribution between years ( $F_{1,185} = 0.09, P > 0.05$ ).

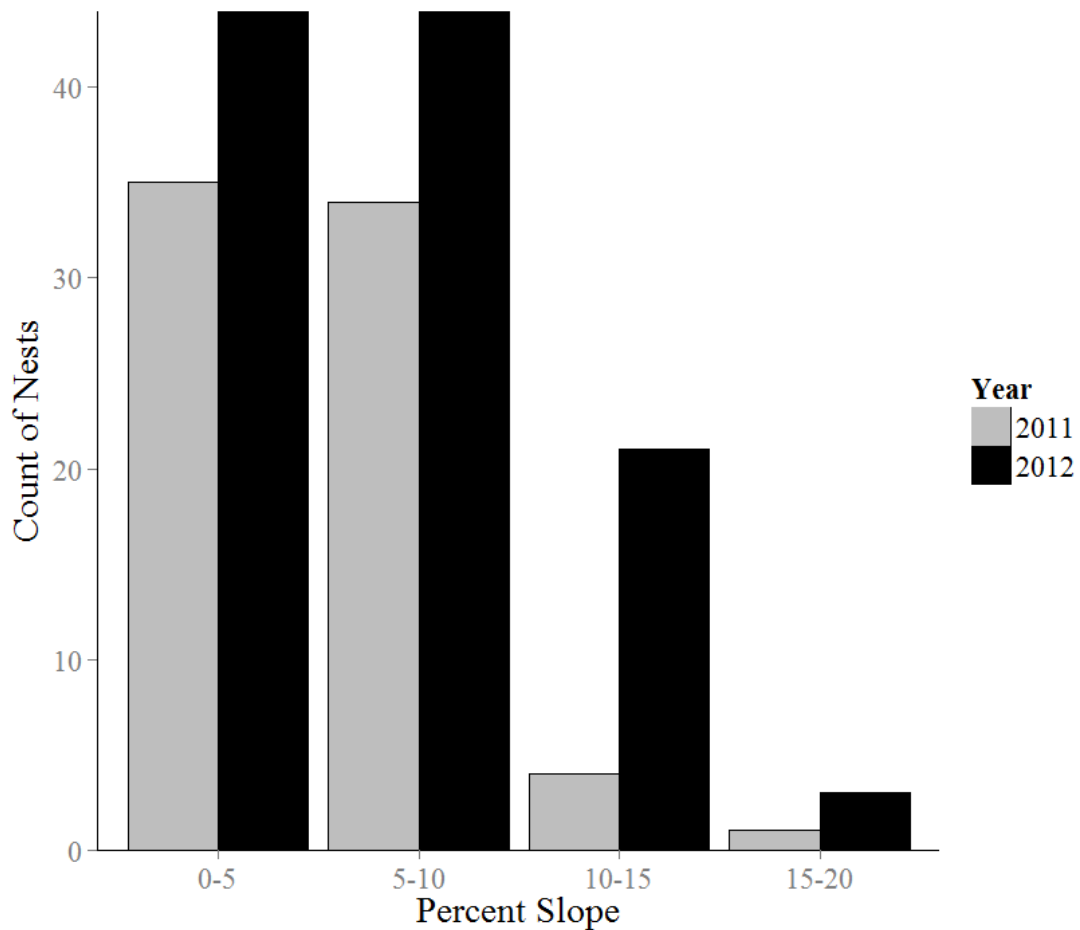


Figure 14. Distribution of slopes observed at Black-capped Vireo (*Vireo atricapilla*) nests within the study site at Dobbs Run Ranch, Edwards County, Texas in 2011 and 2012.

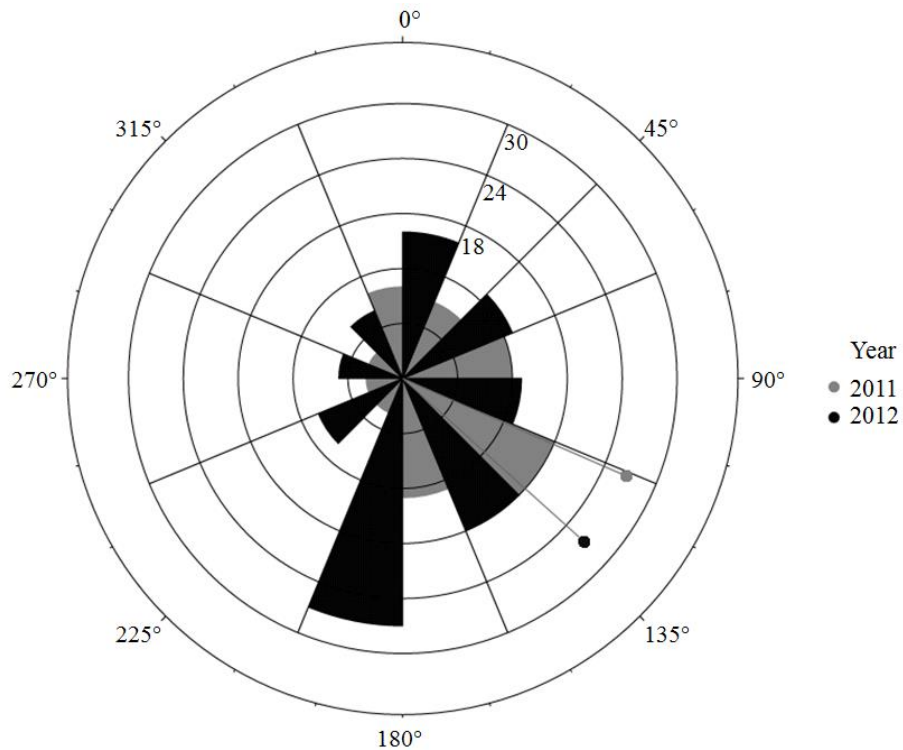


Figure 15. Distribution of slope direction (aspect) observed at Black-capped Vireo (*Vireo atricapilla*) nests within study site at Dobbs Run Ranch, Edwards County, Texas in 2011 and 2012.

Vireos placed nests in eight different plant substrates (Fig. 16), and there was a significant difference in nesting substrate use between years ( $\chi^2_7 = 75.41, P \leq 0.01$ ). In 2011, vireos placed 64% ( $n = 47$ ) nests in Ashe juniper compared with only 15% ( $n = 16$ ) of nests in Ashe juniper in 2012 (Fig. 16). Texas persimmon was the most common nest substrate in 2012, accounting for 58% ( $n = 65$ ) of nests compared to only 5% ( $n = 4$ ) of nests in 2011 (Fig. 16). Vireos did not place nests net-leaf forestiera (*Forestiera reticulata*) in 2011 or coyotillo (*Karwinskia humboldtiana*) or shin oak (*Quercus sinuata*) in 2012; they placed nests in all other substrates similarly across years (Fig. 16).

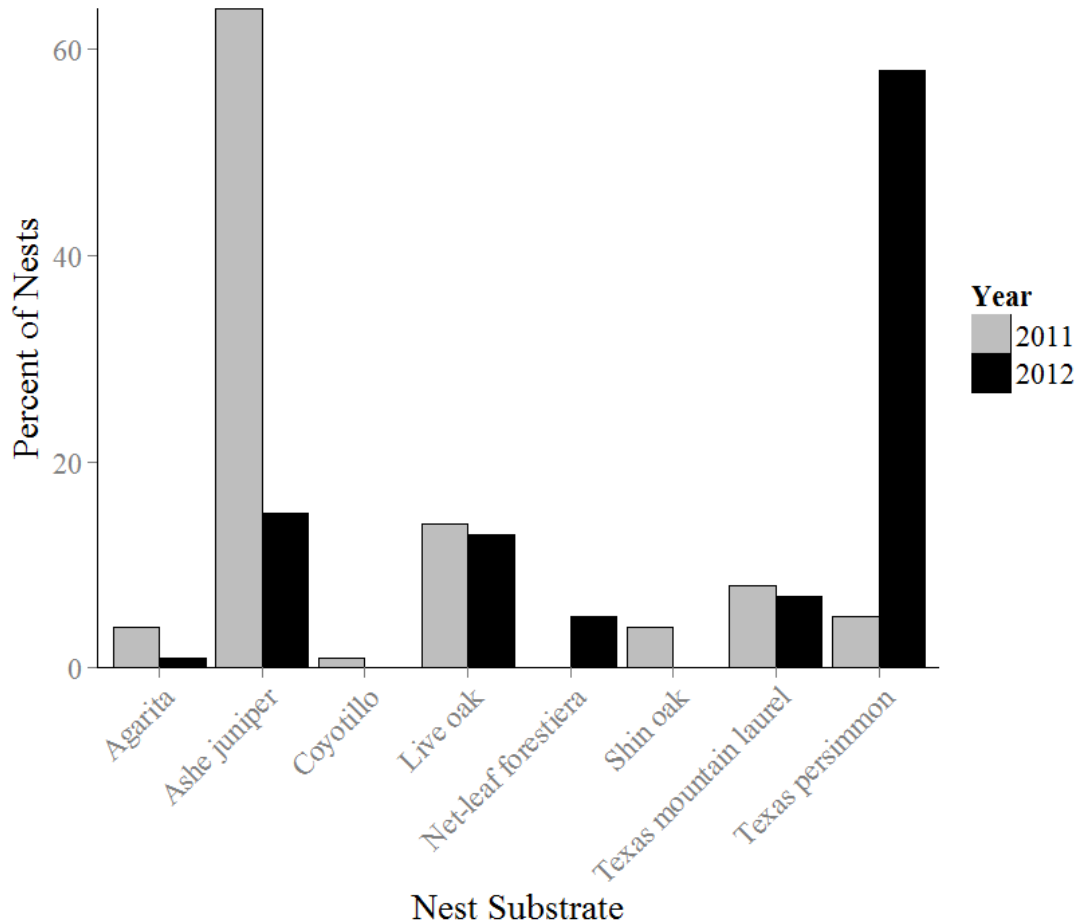


Figure 16. Percent of nest substrates used in 2011 and 2012 by Black-capped Vireos (*Vireo atricapilla*) within study site at Dobbs Run Ranch, Edwards County, Texas. Agarita = *Mahonia trifoliolata*; Ashe juniper = *Juniperus asheii*; Coyotillo = *Karwinskia humboldtiana*; Live oak = *Quercus fusiformis*; Net-leaf forestiera = *Forestiera reticulata*; Shin oak = *Quercus sinuate*; Texas mountain laurel = *Dermatophyllum secundiflorum*; Texas persimmon = *Diospyros texana*.

Several of the vegetation measurements taken at nest-sites significantly correlated with one another (Table 2). Most correlations were positive, though all were relatively weak ( $r \leq 0.31$ ). Because most correlations were positive (Table 2), I used the non-parametric ANOVA-type test (Brunner et al. 1997) to examine differences in nest

Table 2. Spearman rank correlation matrix of vegetation and topographic variables at nest-sites used by Black-capped Vireos (*Vireo atricapilla*) within the study site at Dobbs Run Ranch, Edwards County, Texas in 2011 and 2012. Top value indicates Kendall's tau, and bottom value indicates *P*-value.

	Substrate Height	Overstory Height	Average Cover	Average Concealment	Distance to Edge
Nest Height	<b>0.39</b> <b>0.00</b>	<b>0.22</b> <b>0.00</b>	-0.06 0.45	-0.08 0.30	<b>0.15</b> <b>0.04</b>
Substrate Height		<b>0.17</b> <b>0.02</b>	-0.06 0.42	<b>-0.16</b> <b>0.03</b>	0.01 0.89
Overstory Height			-0.02 0.75	<b>-0.30</b> <b>0.00</b>	<b>0.43</b> <b>0.00</b>
Average Cover				0.10 0.19	<b>0.18</b> <b>0.02</b>
Average Concealment					<b>-0.22</b> <b>0.00</b>

Table 3. Relative effects of vegetation characteristics at Black-capped Vireo (*Vireo atricapilla*) nests within the study site at Dobbs Run Ranch, Edwards County, Texas in 2011 and 2012. Relative effects are descriptive measures of effect size that reflect the probability that a particular vegetation characteristic measured at a randomly chosen nest in a given year had a greater value than that from a randomly chosen nest from any year (Burchett and Ellis 2015).

Nest Characteristic	2011	2012
Nest Height	50%	50%
Substrate Height	50%	50%
Overstory Height	39%	61%
Distance to Edge	42%	58%
Average Cover	48%	52%
Average Concealment	43%	57%

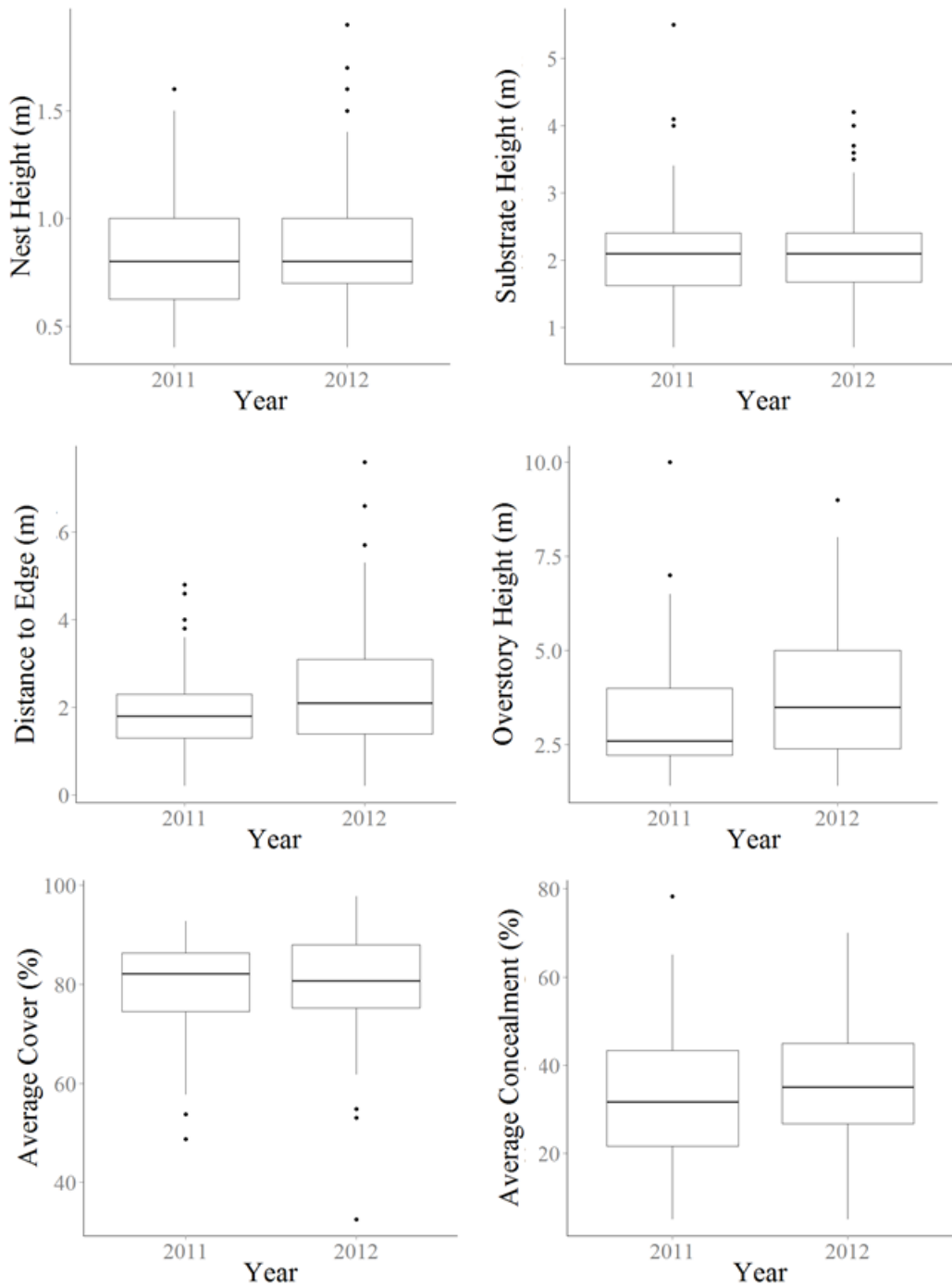


Figure 17. Boxplots comparing Black-capped Vireo (*Vireo atricapilla*) nest vegetation characteristics between years at Dobbs Run Ranch, Edwards County, Texas.

vegetation between years. The global test was not significant indicating little overall difference in vegetation characteristics at nest-sites between years ( $F_{4.97,875.27} = 1.96$ ,  $P = 0.08$ ). The relative effects indicated a >50% probability that overstory height, distance to edge, average cover, or average concealment were higher at nests in 2012 compared with randomly selected nests (Table 3). However, univariate *post hoc* tests showed no annual differences in these or other characteristics (Fig. 17).

Because there was not a significant difference in vegetation characteristics between years, I pooled vegetation data across years to examine differences in the vegetation characteristics at nests placed in the most common substrates. Again, I reported results associated with the ANOVA-type test (Brunner et al. 1997). The global model suggested there were significant differences in overall nest vegetation characteristics depending on the nest substrate ( $F_{15.54,555.71} = 4.20$ ,  $P = 0.00$ ). The relative effects indicated a >50% probability that certain metrics were greater in some substrates compared to randomly selected substrates (Table 4). However, univariate *post hoc* tests suggested the only significant difference between substrates was in substrate height ( $F_{3.00,107.26} = 15.37$ ,  $P = 0.00$ ) (Fig. 18), wherein there was a 65% probability that substrate height measured at a randomly chosen nest placed in Ashe juniper would have a greater value than that from a randomly chosen nest from all possible nest substrates.

Table 4. Relative effects of vegetation characteristics at Black-capped Vireo (*Vireo atricapilla*) nests placed within different nesting substrates within the study site at Dobbs Run Ranch, Edwards County, Texas in 2011 and 2012. Relative effects are descriptive measures of effect size that reflect the probability that a particular vegetation characteristic measured at a randomly chosen nest in a given substrate had a greater value than that from a randomly chosen nest from any substrate (Burchett and Ellis 2015). Only the most commonly used substrates were included in analyses: Ashe juniper (*Juniperus ashei*), live oak (*Quercus fusiformis*), mountain laurel (*Dermatophyllum secundiflorum*), and Texas persimmon (*Diospyros texana*).

Nest Characteristic	Ashe Juniper	Live Oak	Mountain Laurel	Texas Persimmon
Nest Height	53%	33%	50%	53%
Substrate Height	67%	19%	34%	51%
Overstory Height	49%	51%	41%	53%
Distance to Edge	47%	61%	47%	50%
Average Cover	54%	63%	38%	44%
Average Concealment	48%	53%	45%	51%

## DISCUSSION

My results suggest that the extreme drought conditions experienced during 2011 did not affect most aspects of vireo habitat selection. In both years, vireos used slopes of varying steepness and directions according to their availability. Additionally, vegetation at nest-sites was similar between years. However, vireos placed their nests in Ashe juniper more often in 2011 and in Texas persimmon more often in 2012.

It is interesting that I did not see differences in most metrics given the extreme nature of the drought conditions in 2011. Food availability is an important component of habitat selection for birds (e.g., Cody 1981), particularly for species that rely on insects as a primary food source during the breeding season. Vireos are foliage-gleaning

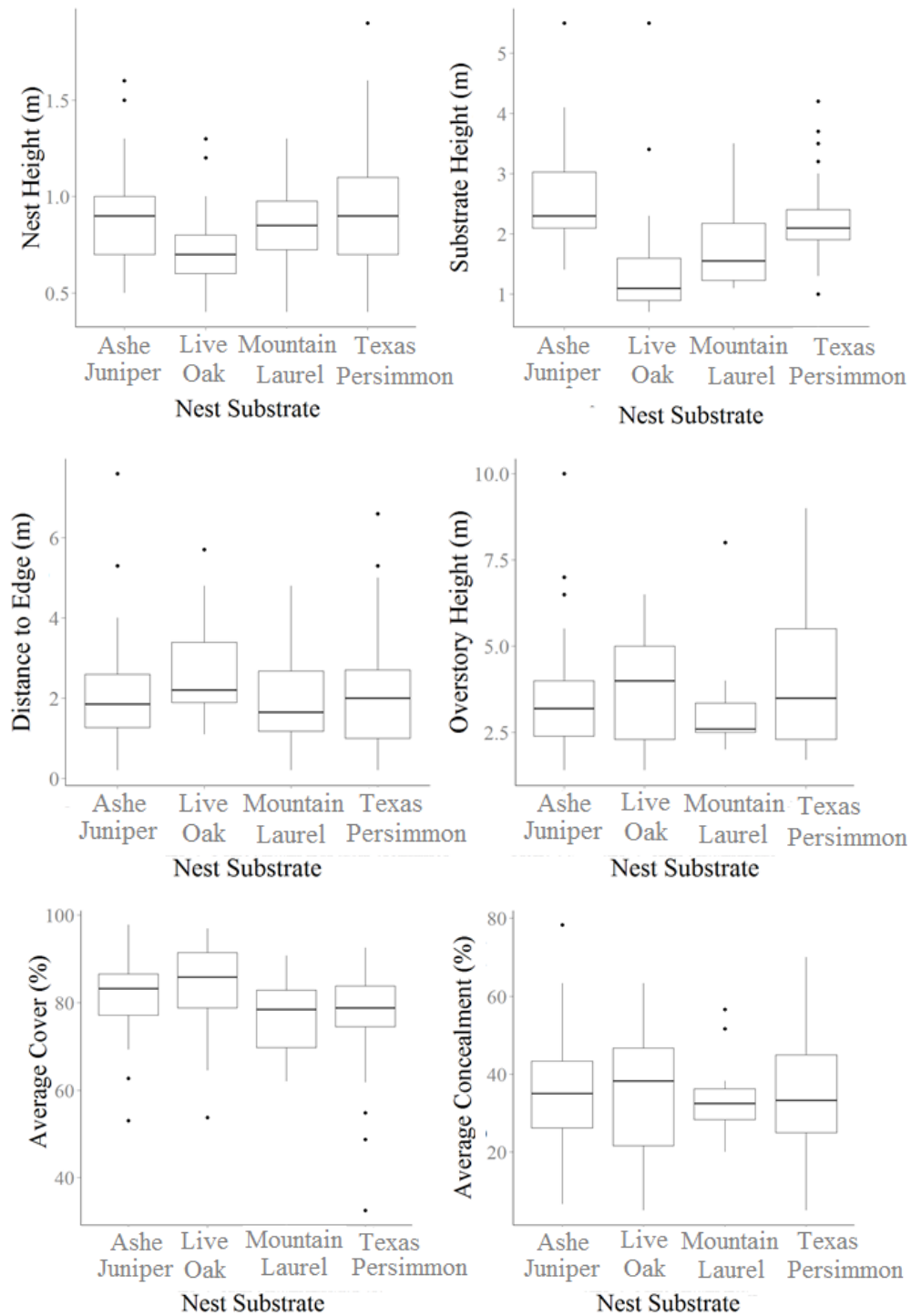


Figure 18. Boxplots comparing Black-capped Vireo (*Vireo atricapilla*) nest vegetation characteristics by nesting substrates at Dobbs Run Ranch, Edwards County, Texas. Ashe juniper = *Juniperus ashei*, live oak = *Quercus fusiformis*, mountain laurel = *Dermatophyllum secundiflorum*, Texas persimmon = *Diospyros texana*.



insectivores (Gryzbowski 1995; Houston 2008; Morgan 2012) whose prey base is dependent on leafy, green vegetation. I expected that as drought lowered overall greenness in 2011, food availability would be reduced. Although I did not measure food availability, this assumption was not without merit because NDVI can be used to predict arthropod biomass (e.g., Sweet et al. 2015), and NDVI was lower in my study site in 2011. Moreover, Cody (1981) described lower insect density in Arizona during a drought year compared with years of greater rainfall, and Morgan (2012) recorded lower mean diversity and biomass of arthropods within vireo habitat during the drought of 2011 compared to 2010—a significantly wetter year. Thus, it is plausible that food resources were limited within my study site in 2011. Individuals may use foliage density at the time of territory selection as a cue for future food availability (e.g., Marshall and Cooper 2004), and territory size and food availability are often inversely related (e.g., Orians 1961, 1966; Pitelka et al. 1993). As such, I predicted that vireos would maintain larger territories in 2011 when NDVI was lower. However, my data did not support this prediction, and I must conclude that if food was limited, vireos compensated in other ways (e.g., reduced reproductive effort; see Chapter 3).

Graber (1961) often found vireos on steep slopes, which tend to have less soil due to rainfall runoff and other factors (McCool et al. 1997). She suggested that soil conditions on slopes facilitate microclimates and edaphic conditions conducive to the clumpy vegetation preferred by vireos. I expected that flatter areas would present similar conditions during dry years to those found on slopes in wet years. As such, I predicted vireos would select flatter areas more often in 2011 than they did in 2012. Contrary to

this prediction, however, vireos selected slopes as expected given their availability in both years. There are several reasons why this might be so. Most notably, slope was fairly uniform across the study site; 93% of slopes had inclines <10%. Alternatively, soil type may be more important than slope incline in creating the vegetation conditions preferred by vireos. More than 95% of my study site was characterized by two ecosites, which differ in slope but have similar soils (i.e., Low Stony Hill and Steep Rocky) (NRCS 2013).

The direction of slopes may also be important to nesting vireos. Vireos prefer early successional shrub habitat with open spaces and short vegetation (Graber 1961; Gryzbowski et al. 1994), and they are commonly found on southern-facing slopes in other parts of their range (e.g., Shaw 1989; LCRA 2007; Benson and Benson 1990, 1991)—perhaps because vegetation on northern-facing slopes is more dense than is ideal for nesting vireos (Graber 1961). In fact, in the Northern Hemisphere, northern-facing slopes receive less solar radiation than southern-facing slopes and, as a result, have cooler and wetter climates that promote vegetation growth (Cottle 1932; Gallardo-Cruz et al. 2009; Sternberg and Shoshany 2011). At some locations, extreme temperatures, winds, or exposure on southern-facing slopes can erode potential nesting and foraging vegetation, and northern-facing slopes may be preferred (e.g., Cummings 2006; Smith 2011). As such, I predicted a switch in aspect use between years, such that reduced vegetation greenness during drought would render northern-facing slopes more amenable to nesting vireos during the 2011 season. However, vireos selected slopes of all directions as expected given availability with no difference between years. Southerly-

facing slopes were most common within my study site, and vireos may have settled there over other locations (landscape scale) because the slope direction promoted the vegetation characteristics necessary for nesting, but at smaller scales aspect did not appear to be a major component in settlement decisions. Alternatively, the assumed impact of drought on the vegetation on northern-facing slopes may not have been sufficient enough to promote increased use by vireos.

Finally, I expected to see differences in nest-site characteristics between years. I assumed that lower greenness would limit the availability of nest-sites with adequate foliage cover to conceal nests. Predation is the primary cause of nest failure in birds (Ricklefs 1969); though vireo nests are also vulnerable to brood parasitism (Graber 1961; Gryzbowski 1995). The most common predators (and brood parasites) at vireo nests are snakes and birds (e.g., cowbirds, jays [Corvidae]) (Stake and Cimprich 2003; Conkling et al. 2012), both of which use visual cues to locate nests (Clotfelter 1998; Mullin and Cooper 1998; Robinson and Robinson 2001). The risk of nest predation and brood parasitism may be lower with greater nest concealment (Martin and Roper 1988; Martin 1993; Larison et al. 1998). However, I found no differences between years in average cover or average concealment (i.e., measures of nest concealment at 7 m and 1 m, respectively), suggesting that vireos were able to identify sites with similar nest concealment in both years despite differences in vegetation greenness across the landscape. Conkling et al. (2012) found that nest concealment varied by site according to plant species composition and that other characteristics were better predictors of predation at vireo nest-sites. Similarly, Barber and Martin (1997) found no difference in

vegetation characteristics of parasitized and unparasitized vireo nests and suggested that the genus may be vulnerable to parasitism irrespective of vegetation at nest-sites.

I did observe one difference in nest-site characteristics between years. In 2011, vireos at my study site overwhelmingly selected Ashe juniper as a nest substrate, then switched to Texas persimmon in 2012. This response is similar to that observed for MacGillivray's Warblers (*Geothlypis tolmiei*) when drought affected leaf-out in their preferred nesting substrate (Martin 1993). Ashe juniper and live oak are drought-tolerant species (Gilman and Watson 1993) that can access deep water sources when surface soils are dry (Jackson et al. 1999). In late March–early April 2011 when vireos arrived at my study site, Ashe juniper and live oak were among the few woody species that consistently had green foliage; though many of the small and medium sized live oaks were leafless (pers. obs.). This was a stark contrast to the same period the following year, when nearly all vegetation was green and leafy (pers. obs.).

Bailey and Thompson (2007) indicated that vireos were 283% more likely to nest in deciduous substrates compared to Ashe juniper. As such, I expected that Ashe junipers were likely to exhibit characteristics that made them less desirable as nest substrates than other tree species. However, I found no difference between vegetation characteristics among nest substrates, except for a slightly greater probability that Ashe junipers selected were slightly taller, which likely had little effect on nest-site selection. The use of Ashe juniper at my study site in 2011 suggests that adequate nest-sites in preferred substrates were limited, but that vireos were able to find similar conditions within Ashe junipers. That vireos typically place nests in deciduous species suggests

there may be differences among substrates that contribute to reproductive success that the variables I measured failed to capture.

In systems with highly variable weather, breeding habitat preferences likely represent the conditions best suited for reproductive success in the long-term, rather than immediate considerations (Clark and Shutler 1999; McLoughlin et al. 2006). Drought is a recurring and common phenomenon in the Edwards Plateau and other parts of the vireo's range (Toomey et al. 1993; Cleaveland et al. 2011; USDM 2016), and it represents a source of periodic disturbance that maintains the early successional vegetation preferred by vireos (Wilkins et al. 2006). Evidence suggests that vireos prefer areas with lower Ashe juniper density throughout much of their range (Gryzbowski et al. 1994). However, Gryzbowski et al. (1994) noted that habitat varies regionally, and in drier portions of the species range, Ashe juniper may provide necessary cover. In this study, the use of Ashe juniper as a nest substrate during drought suggests that it may provide a necessary alternative for vireos when suitable deciduous substrates are limited. Campbell (1995) recommends cool season burns and the selective removal of Ashe juniper within vireo habitat to help maintain the early successional vegetation preferred by vireos. However, this practice may not be necessary or beneficial to vireos in drier portions of their range. Morgan (2012) indicated that Ashe juniper was an important foraging substrate for vireos in the eastern portion of their range, but research is still needed to determine the extent to which vireos rely on Ashe juniper in other parts of its range under drought conditions.

## CHAPTER III

### EXTREME VARIATION IN RAINFALL AND ITS EFFECTS ON REPRODUCTION IN BLACK-CAPPED VIREOS (*VIREO ATRICAPILLA*)

#### INTRODUCTION

Climate is a representation of the average weather conditions in an area over an extended period (Allaby 2010), and it influences all aspects of a species' niche (i.e., the conditions under which a species can live) (Grinnell 1917; Hutchinson 1957). For example, physiological tolerances to temperature, along with water requirements, determine a species' geographic range (Andrewartha and Birch 1954; Root 1988, Parmesan 1996). Similarly, climate regulates species' abundance (e.g., Andrewartha and Birch 1954; Mehlman 1997; Veit et al. 1997), community structure (Cody 1981; Brown et al. 1997; Albright et al. 2010), and ecosystem dynamics (e.g., Pascual and Levin 1999; Post and Forchhammer 2001; Traill et al. 2010). Understanding the ways climate shapes evolutionary adaptation in species is necessary for long-term conservation and management. However, information on species' responses to short-term variation (e.g., months, years) in local and regional weather patterns is also important for conservation planning because the selective pressures imposed by weather can have consequences for population dynamics (Stenseth et al. 2002; Knape and Valpine 2011; Harrison et al. 2015).

In arid and semi-arid environments, rainfall is low and unpredictable, and drought is common (e.g., in Texas) (Myoung and Nielsen-Gammon 2010). Though

definitions vary (see Wilhite and Glantz 1985; McKee et al. 1993; Quiring 2009), drought is characterized by inadequate precipitation over a time sufficient to impact vegetation and deplete soil moisture (Kramer 1983). Heat waves and high temperatures are often associated with summertime droughts as soil moisture declines and solar energy heats the air (Namias 1982). Low cloud cover during periods of drought allows more of the sun's energy to reach the ground, and the release of that energy into the environment can further exacerbate drought conditions via feedback loops that increase precipitation deficits (Myoung and Nielsen-Gammon 2010; also see Clark and Arritt 1995).

Birds inhabiting arid and semi-arid environments may experience direct impacts to reproduction under drought conditions. For instance, the development and function of ovaries and oviducts of water-deprived females is lower than that of non-deprived females (Cain and Lien 1985; Koerth and Guthery 1991). Water-stressed females lay fewer, smaller, less fertile eggs and have young with lower survival rates (e.g., Cain and Lien 1985; Fair and Whitaker 2008; Skagen and Yackel Adams 2012). Similarly, under drought conditions, males can have lower testicular weight or sperm production, which can limit (though rarely prevents) reproductive function (Cain and Lien 1985). Additionally, embryonic development is disrupted and egg-hatchability compromised when eggs are exposed to extreme temperatures for extended periods (Dawson 1984; Stoleson and Beissinger 2002; Gill 2007), and nestlings born during drought may have reduced immune responses (Thaxton and Siegel 1970; Fair and Whitaker 2008).

Drought can also impact birds indirectly through its effects on vegetation. Precipitation is the main driver of aboveground primary productivity (Noy-Meir 1973; Sala et al. 1988), and it influences vegetation structure (Tyree et al. 1993; Chaves et al. 2003), composition (Cody 1981; Brown et al. 1997), and mortality (Allen and Breshears 1998; Breshears et al. 2005). When precipitation is low, delayed phenological events, reduced leaf area, or altered plant chemistry can occur (Rathcke and Lacey 1985; Larsson and Ohmart 2008; Gutbrodt et al. 2011). The overall effect is reduced greenness (i.e., foliage cover) on the landscape during drought, which can affect the timing and abundance of plant and insect foods available to nesting birds (Morrison and Bolger 2002; Ogaya and Peñulas 2007; Greven et al. 2009) and reduce vegetation cover at foraging and nesting sites, increasing the risk of predation (Sugden and Beyersbergen 1986; Martin 1992) and exposure to the elements (e.g., wind, rain, cold, heat) (Walsberg 1981).

Birds inhabiting drought-prone environments experience wide variation in precipitation and adjust their behaviors accordingly (Cody and Mooney 1978). Life history theory predicts that individuals inhabiting highly unpredictable environments will temper reproductive investment to maximize adult survival when conditions are poor (Hirshfield and Tinkle 1975; Benton et al. 1995; Erikstad et al. 1998). For example, birds may delay (or forgo) breeding during drought (e.g., Christman 2002; Preston and Rotenberry 2006; Visser et al. 2006) when food or other resources are limited. Birds can also reduce their reproductive effort irrespective of nest initiation date by laying smaller clutches, abandoning nests, or engaging in fewer nesting attempts (Erikstad et al. 1998).



Birds that delay nesting reduce their number of effective breeding days within a season, thus limiting the number of nesting attempts possible. Additionally, birds that delay nesting have smaller clutches (e.g., Lack 1947; Daan et al. 1989; Perrins and McCleery 1989), lower nestling and fledgling survival (e.g., Harris et al. 1994; Lindholm 1994; Naef-Daenzer et al. 2001), and reduced recruitment of offspring into subsequent generations (e.g., Harris et al. 1994; Verboven and Visser 1998). Nests initiated later in the season may also have greater rates of predation (e.g., Best and Stauffer 1980; Schaub et al. 1992) or brood parasitism (Marvil and Cruz 1989; Kus 1999; Boves et al. 2014). However, despite seasonal fitness consequences, individual decisions regarding reproductive investment during drought likely reflect trade-offs between current and future reproductive success that optimize lifetime reproductive success (Stearns 1989; Daan et al. 1990; Svensson and Nilsson 1995).

By understanding how species respond to varying weather conditions, managers may be able to identify long-term conservation actions that benefit species of conservation concern. Shrub-nesting species are of particular interest because of widespread population declines (Robbins et al. 1986; Askins 1993; Brawn et al. 2001). Many of these species require early- and mid-successional vegetation, but fire-suppression and other practices (e.g., farm abandonment) have allowed vegetation in many areas to reach seral stages that prohibit occupancy or reproduction by shrub-nesting birds (Askins et al. 1990; Droege 1998).

The Black-capped Vireo (*Vireo atricapilla*; hereafter vireo) is a federally endangered songbird that breeds in early-successional shrub-scrub vegetation in arid and semi-arid

regions of Oklahoma, Texas, and Mexico (Fig. 19) (Graber 1961; Gryzbowski 1995; Wilkins et al. 2006; González-Rojas et al. 2014). Major threats to the species include habitat loss and fragmentation and reduced reproductive success resulting from brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Marshall et al. 1985; Ratzlaff 1987). Understanding these threats as well as the vireo's biological and ecological

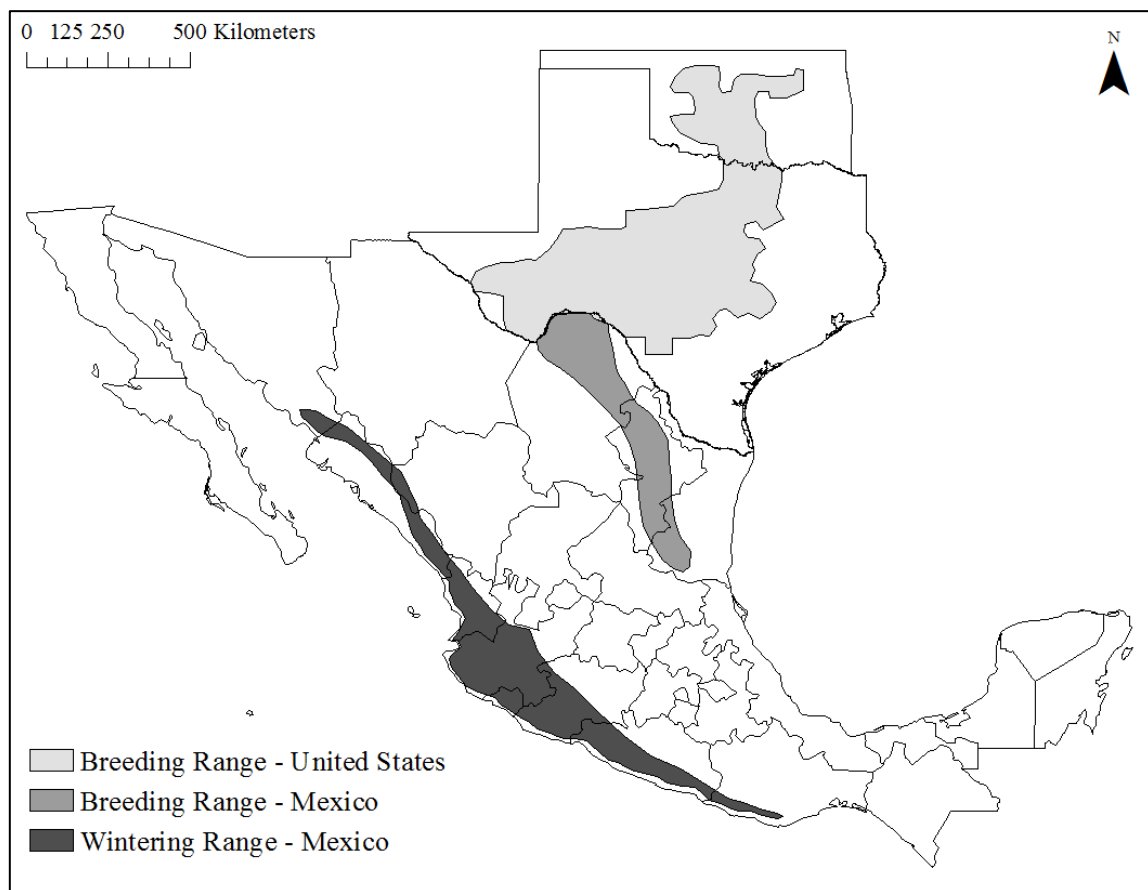


Figure 19. Black-capped Vireo (*Vireo atricapilla*) range map based on data presented in Wilkins et al. (2006).

requirements may help inform conservation and management strategies necessary for the species' recovery (USFWS 1991).

Vireos typically breed in vegetation of irregular height and distribution that provides adequate cover (35–55%) for foraging and nesting (Graber 1961; Gryzbowski et al. 1994). Drought, fire, and grazing interact with local features (e.g., topography) (Graber 1961; McFarland et al. 2013) to maintain the vegetation configuration needed for vireo reproduction (Wilkins et al. 2006). Yet, little information exists regarding reproduction by vireos during periods of drought. Smith et al. (2012) detailed the reproductive ecology of vireos at Devil's River State Natural Area in the drier, southwestern portion of the species' breeding range in Texas. They noted that vireo productivity is greatly influenced by precipitation, and management strategies aimed at conserving vireo habitat in the west should be considerably different than those proposed for use in other (wetter) portions of the vireo's breeding range (Smith et al. 2012).

In this study, my objectives were to examine breeding behavior and productivity of vireos in Texas during two years of varying drought intensity. In September 2010, a large storm system, which had provided rain to much of Texas, dissipated—signaling the beginning of what became the 2011 drought (Nielsen-Gammon 2011). Fall and winter precipitation in 2010 and spring precipitation in 2011 were less than average (NCEI 2016), and by the end of March, more than half of the state experienced severe or extreme drought conditions (USDM 2016) (Fig. 20). The period from March–May 2011 was the driest March–May period on record in Texas (Nielsen-Gammon 2011), and below average precipitation continued statewide for the next six months (NCEI 2016).

From December 2011–March 2012, Texas received average or above average rainfall.

Dry conditions returned for the remainder of 2012 but not with the same intensity as the previous year (USDM 2016).

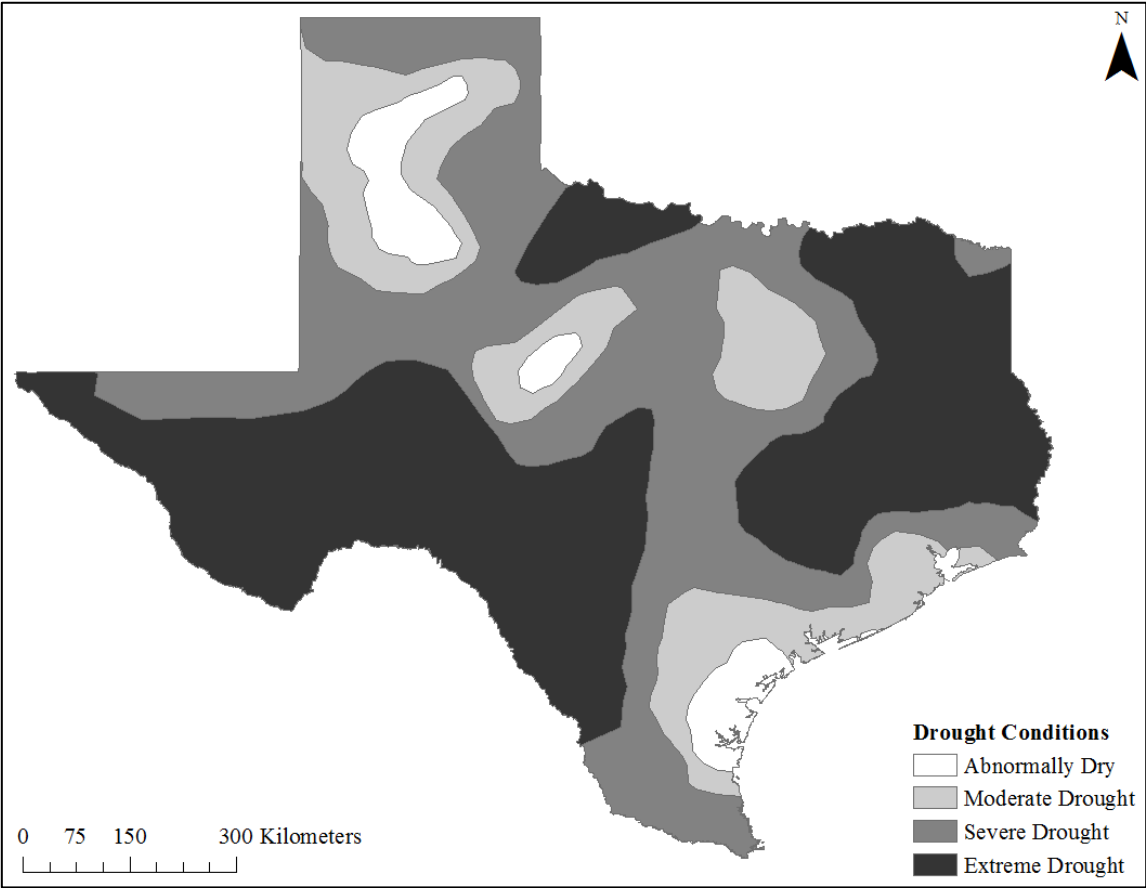


Figure 20. Status of drought in Texas on 29 March 2011. Data were made available by the National Drought Mitigation Center, U.S. Department of Agriculture, and the National Oceanic and Atmospheric Administration and mapped using ArcMap version 10.2.2.

Extreme weather events are, by definition, rare or infrequent. The 2011 drought in Texas provided a unique opportunity to observe the responses of vireos under extreme conditions compared to responses under more moderate conditions. I examined the reproductive ecology of vireos inhabiting a semi-arid region in the Edwards Plateau in Texas during the 2011 drought as well as the wetter 2012 season. Drought has been common in the Edwards Plateau for over 1,000 years (Toomey et al. 1993; Cleaveland et al. 2011; USDM 2016), and, as such, I expected vireos in this region to exhibit reduced reproductive effort and experience lower reproductive success during the drought but be resilient when conditions improved the following year.

Specifically, I compared pairing and fledging success at the territory scale and examined nest initiation dates, clutch and brood size, and frequency of nest abandonment, parasitism, and failure. Vireos in other parts of their range show varied nest success and daily nest survival as a consequence of nest-scale vegetation as well as temporal factors (e.g., Noa et al. 2007; Conkling et al. 2012; Smith et al. 2012). As such, I also measured vegetation at each nest and created models of nest success and daily nest survival that incorporated vegetation characteristics and temporal components. I expected differences in rainfall between years (and associated differences in vegetation; Chapter 2) to correspond to one or more of the following responses in 2011 compared to 2012: lower pairing success, lower fledging success, later mean initiation date, lower clutch size, reduced egg hatchability, or higher overall nest failure via increased abandonment, brood parasitism, or predation. Although drought is not preventable, by understanding species' responses to drought, managers can inform long-term

management and conservation plans. In addition, information on drought-response may prove useful when considering the potential effects of climate change on species of conservation concern.

## **METHODS**

### **Study Area**

I surveyed breeding vireos across an open (i.e., not enclosed) 1,100 ha study site within Dobbs Run Ranch (2,030 ha; ~29° 38' 60" N, -100° 24' 36" W) (Fig. 21) from late March–late July in 2011 and 2012. Dobbs Run Ranch is on the southwestern edge of the Edwards Plateau ecoregion (Omernik 1995) in the southwestern portion of the vireo's breeding range in Texas (Fig. 21). The Edwards Plateau is a semi-arid region (Thornwaite 1948) with highly variable summer climate and a large, east-west precipitation gradient (Daly et al. 2008) that experiences notable variation in temperature and precipitation annually and seasonally. The average maximum summer (April–July) temperature is 31 °C, and the cumulative average summer precipitation is ~25 cm (NCEI 2016).

Soil at the study site is predominantly limestone bedrock (99.6%) (NRCS 2013), and common woody plants include Ashe juniper (*Juniperus ashei*), live oak (*Quercus fusiformis*), piñon pine (*Pinus remota*), Texas persimmon (*Diospyros texana*), and Texas mountain laurel (*Dermatophyllum secundiflorum*). Livestock grazing, which can interfere with avian nest success by altering vegetation structure (Kreuper et al. 2003; Gill and Fuller 2007) or the distribution of harmful species (e.g., predators [reviewed in Atkinson et al. 2004], brood parasites [e.g., Goguen and Mathews 2000]), did not occur

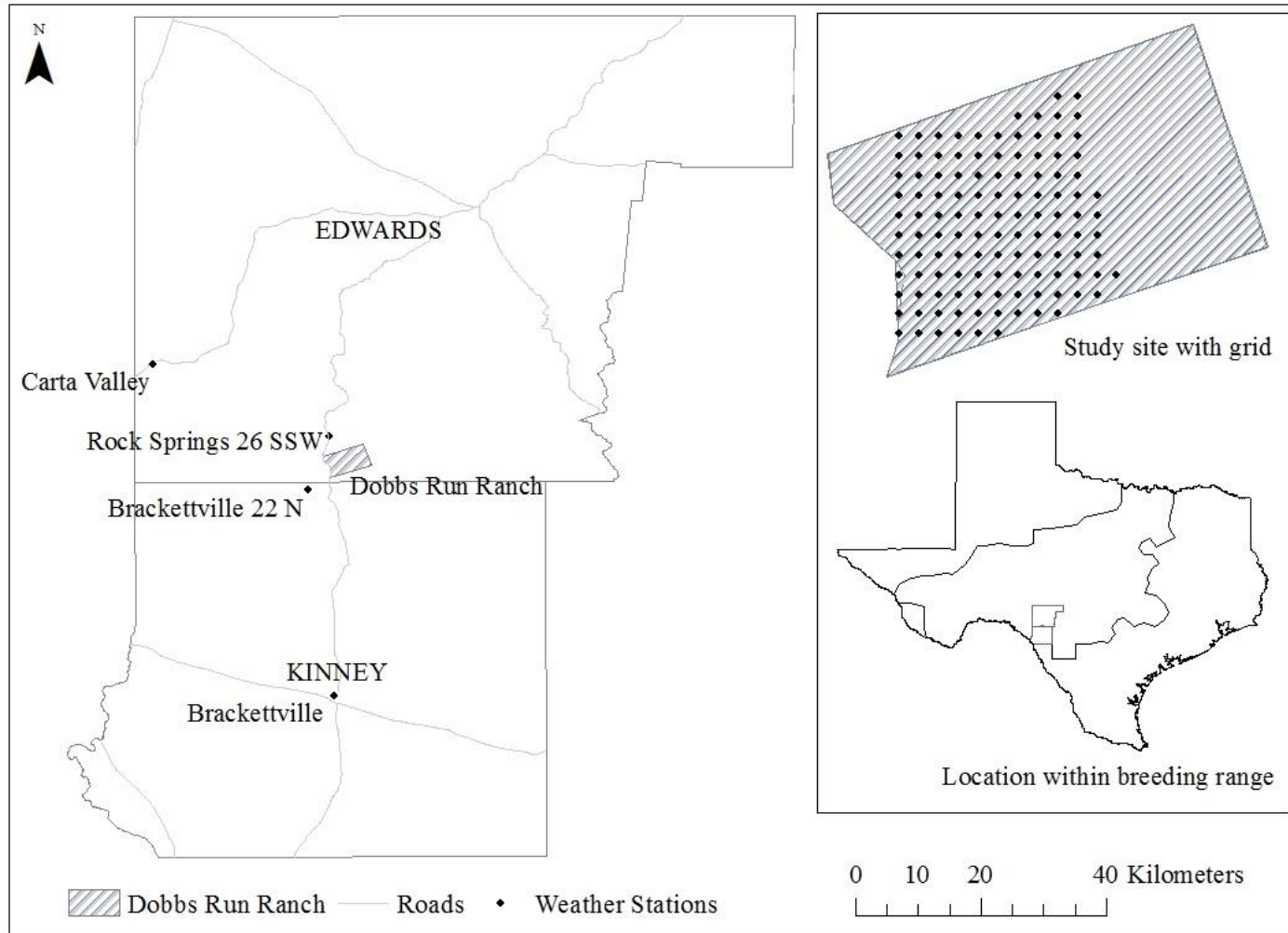


Figure 21. Dobbs Run Ranch and nearby weather station locations, located in Edwards and Kinney counties, Texas. Top inset shows the study site and sampling grid within Dobbs Run Ranch where I monitored Black-capped Vireos (*Vireo atricapilla*) in 2011–2012. Bottom inset shows the location within the Black-capped Vireo’s range in Texas.

on or near the ranch. I regularly observed individuals or small groups of wild, grazing ungulates, such as blackbuck (*Antelope cervicapra*), white-tailed deer (*Odocoileus virginianus*), axis deer (*Cervus axis*), and aoudad (*Ammotragus lervia*). However, it is unlikely that the presence of these species negatively affected vireo reproduction during my study (e.g., Locatelli et al. 2016). Hunting (of game birds and ungulates) was limited to a small area northwest of my study site and likely had no impact on the vireo population or my results. There were three active Brown-headed Cowbird traps at Dobbs Run Ranch during the years of this study, but data regarding number of Brown-headed Cowbirds trapped are not available.

### **Annual Variation in Weather**

To quantify differences in weather between years, I obtained daily maximum temperature and precipitation data for 2010–2012 from the National Centers for Environmental Information (NCEI 2016). Most data were recorded at the Brackettville 22 N station (GHCND:USC00411013) (Fig. 21) located at Kickapoo Caverns State Park (KCSP) (29° 36' 36" N, -100° 27' 07" W), which is adjacent to Dobbs Run Ranch. However, a small number of records were missing at this station during the study period. When necessary, I substituted precipitation values from the Rocksprings 26 SSW station (GHCND:USC00417717; 29° 41' 16" N, 100° 25' 18" W) (Fig. 21), which was <15 km away. The Rocksprings 26 SSW station did not record temperature information during my study, so when temperature records were not available from the Brackettville 22 N station, I substituted average values from the next two nearest stations, which were both <30 km away. These stations were Carta Valley (GHCND:USC00411492; 29° 47' 24"



N, 100° 40' 26" W) (Fig. 21) and Brackettville (GHCND:USC00411007; 29° 18' 58" N, 100° 24' 50" W) (Fig. 21). Substitutions accounted for <5% of weather data.

Spring and summer precipitation influences vegetation growth during the growing season (mid-March–mid-November in Edwards County [TSHA 2016]), but so does soil moisture, which is determined by fall and winter precipitation (Pielke and Doeskin 2008). As such I examined precipitation data for the months of September to March preceding each vireo breeding season as well as precipitation during each vireo breeding season (April–July [Gryzbowski 1995]).

In addition to daily weather variables, I obtained monthly Palmer Drought Severity Index (PDSI) values for the study period to further demonstrate differences in weather conditions by year. The PDSI uses precipitation, soil moisture, and temperature data to assess water availability and the intensity of drought at regional scales (Palmer 1965). PDSI values  $\leq -4$  reflect extreme drought conditions and values  $\geq 4$  indicate extreme wet conditions (Table 5). Though it is the most commonly used drought index in the United States, PDSI has been criticized for arbitrary designations of drought intensity, sensitivities to rainfall events, and different sensitivities across regions (Alley 1984).

Table 5. Classification of drought according to the Palmer Drought Severity Index (Palmer 1965).

Value	Description
$\geq 4.00$	Extremely Wet
3.00 to 3.99	Very Wet
2.00 to 2.99	Moderately Wet
1.00 to 1.99	Slightly Wet
0.50 to 0.00	Incipient Wet Spell
-0.49 to 0.49	Near Normal
-0.99 to -0.50	Incipient Drought
-1.99 to -1.00	Mild Drought
-2.99 to -2.00	Moderate Drought
-3.99 to -3.00	Severe Drought
$\leq -4.00$	Extreme Drought

### Vireo Surveys

I established a 300 m grid across the study site (Fig. 21), which allowed for a reasonable detection of singing vireos with a maximum distance of sound attenuation of 150 m (e.g., Smith 2011 and McFarland et al. 2013). Each year from 20 March to 15 July, I walked different routes along the grid and used auditory and visual surveys to map the locations of male vireos across the study site. When I detected a male vireo, I marked its location using a handheld Garmin RINO 120 Global Positioning System (GPS) unit with  $\leq 10$  meter accuracy. I returned to marked locations every 5–10 days between the hours of sunrise and 1400 to define territory boundaries and determine mating (i.e., paired or unpaired) and reproductive (e.g., nesting behavior, presence of fledglings) status. I spent no longer than one hour per day in each territory, which maximized the number of territories I could visit each day, while limiting disturbance to nesting vireos. When I detected vireos during territory visits, I observed them from a

distance to minimize observer effects and noted their locations. Each time a focal bird moved  $\geq 20$  m, I marked its location with a GPS. To improve my assignment of individuals to specific territories, I used standard target mist-netting techniques (described by Johnston 1965 and Keyes and Grue 1982) with playback of recorded vireo song to capture and band adult vireos with unique color-band combinations. I considered male vireos territorial if I consistently detected them in the same locations for  $\geq 4$  weeks.

To locate nests, I identified behaviors indicative of breeding (e.g., copulation, material carry, food carry, presence of fledglings) and observed the movements of vireos engaged in those behaviors. While nest-searching, I focused on females because they tend to spend more time near nests (Gryzbowski 1995; Pope et al. 2013b), but I noted male behaviors and movement patterns as well because this species shares parental duties (Gryzbowski 1995; Pope et al. 2013b). If I did not detect vireos on arrival in a territory, I searched the territory systematically—concentrating on vegetation structure common among vireo nests (e.g., Gryzbowski et al. 1994; Gryzbowski 1995). This method often proved effective in the absence of behavioral cues, especially during the egg-laying phase, when nests were most difficult to find (Martin and Geupel 1993), and also accounted for differences in detection attributed to variation in vegetation.

I checked vireo nests every 2–3 days until they fledged young, failed, or were abandoned (i.e., no longer active). On each visit, I recorded adult behaviors and nest contents. I defined active nests as those attended by vireo adults and containing at least one egg or nestling (vireo, Brown-headed Cowbird, or both). I did not remove Brown-headed Cowbird eggs from parasitized nests as their presence may deter future

parasitism (Ortega et al. 1994), but I did dispatch and remove all Brown-headed Cowbird young on discovery. Parasitized vireo nests rarely fledge host young (Tazik 1991; Gryzbowski 1995; Boves et al. 2014). By dispatching Brown-headed Cowbird young before they fledged, vireos did not engage in post-fledging care of non-host young and had greater opportunities to re-nest. Additionally, removing newly hatched Brown-headed Cowbird young enabled me to observe nests for longer periods, thereby improving opportunities to observe predation events, vireo fledgling movements, and other activities important in concurrent research projects.

I banded vireo nestlings aged 6–8 days with unique color-band combinations, which aided in assessments of nest success. Occasionally, I found nests with vireo young  $\geq 9$  days of age. I did not band these older nestlings because banding at this age can cause premature fledging. I considered a nest successful if it fledged  $\geq 1$  vireo young provided there were no Brown-headed Cowbird eggs present or the cowbird eggs failed to hatch. It is not always possible to visit nests on the day of fledging, but young vireos remain with the adults for two or more weeks before gaining independence (Gryzbowski 1995). So, I surveyed all territories in which I suspected fledging for a minimum of two weeks after the expected fledging date. If I detected a fledgling ( $\leq 2$  weeks of age) within the territory, I recorded the nest as successful. I also considered a nest successful if two or more observers independently identified the unique color-band combination of a hatch-year (HY) bird banded in the nest regardless of fledgling age or location within the study site.

I randomly deployed nest cameras on a subset of nests, which further improved my nest fate assignments. The camera system consisted of a weatherproof bullet camera (Rainbow, Costa Mesa, CA) connected to a digital video recorder (Detection Dynamics, Austin, TX) and powered by a 12v26ah battery (Batteries Plus, Hartland, WI) and 20-watt solar panel (Suntech, San Francisco, CA). I placed cameras no closer than 1 m to active nests, and I placed all other components under vegetation within 15 m of nests, which reduced disturbance to nesting vireos during subsequent equipment checks. I observed adult behavior for 30 min after camera installation, and I removed cameras if adults had not returned to normal behaviors during this period. I installed cameras as early as possible during the nesting cycle, but only after the egg-laying stage was completed (Stake and Cimprich 2003).

### **Nest Vegetation**

I catalogued vegetation characteristics for each active (i.e., observed contents, tended by adults) vireo nest after it fledged, failed, or was abandoned. Specifically, I recorded the nest substrate and measured the distance to the nearest edge (i.e., nest rim to nearest leafy edge), nest height (from ground to nest rim), substrate height, and canopy height all to the nearest 0.1 m. I defined canopy height as the height of the tallest tree or shrub immediately above the nest. When the substrate tree or shrub was the tallest tree or shrub above the nest, I recorded the same value for the substrate height as for canopy height. In addition, I positioned a 2 m coverboard marked with 0.1 m<sup>2</sup> squares immediately in front of each nest and estimated the percent of each square obscured by vegetation from 7 m away in each cardinal direction. I then averaged these values to

obtain a single measurement of foliage cover. Lastly, I placed a 0.1 m<sup>2</sup> board at each nest and estimated the percent visual obstruction by vegetation from 1 m away from nests in each cardinal direction as well as from above and below. I averaged these values to get a single measurement of nest concealment. All measurements were consistent with those collected during other studies of nesting vireos (e.g., Conkling et al. 2012; Smith et al. 2012; Pope et al. 2013a, b).

### **Analyses**

I conducted all tests using the statistical program R version 3.2.2 (R Core Team, Vienna, Austria). I presented all means described below with standard deviations. Because this was a two-year study at a single site, I presented weather data simply to demonstrate the differences between years but, I did not include these data in further analyses. Instead, I used temporal variables (e.g., day, year) to examine differences in vireo reproduction in response to weather.

*Annual Variation in Weather.*— I calculated the mean maximum daily temperature for each year, and I used a Welch's two-sample *t*-test (Ruxton 2006; Crawley 2014:94–95) with Cohen's *d* (Lakens 2013) as a measure of effect size to compare means between years. I also used linear regression to examine temperature as a function of date within seasons (Crawley 2014:114–140). I summed daily precipitation to determine cumulative monthly precipitation totals for the seven months prior to and the four months of each breeding season and calculated the percent differences between years.

*Territory Pairing and Fledging Success.*—I considered male vireos paired if they were consistently observed with females ( $\geq 4$  weeks) or had active nests. I calculated pairing success as the number of paired males consistently observed with females (or active nests) relative to the total number of territorial males (e.g., Stewart et al. 2014; Long et al. 2015). Similarly, I considered territories successful if I observed dependent host fledglings. I calculated fledging success as the number of paired males in territories with one or more host fledglings relative to the total number of paired males (e.g., Stewart et al. 2014; Long et al. 2015). I examined inter-annual differences in pairing and fledging success using Fisher's exact tests (Crawley 2014:105–107) and calculated the odds ratio (OR) as a measure of effect size (McHugh 2009).

*Nesting Phenology, Clutch Size, and Brood Size.*—I estimated the laying date of the first egg (i.e., initiation date) of each nest by backdating observations from nest checks with known nesting intervals. After excluding nests for which nest initiation dates could not be determined (e.g., a nest found with four eggs that failed before the next nest check), I calculated the mean initiation date for each year and examined annual differences using a Welch's two-sample *t*-test (Welch 1938, 1947; Ruxton 2006) and Cohen's *d* as a measure of effect size (Lakens 2013). I then subtracted the mean initiation date of the earliest 20% of nests from the mean initiation date of the latest 20% of nests to characterize the length of each breeding season (e.g., Weatherhead 2005).

I calculated mean clutch and brood sizes of nests from each year, excluding from analyses nests for which clutch or brood size could not be determined (e.g., nests found in the nestling stage with less than full a complement of nestlings). I used a one-way

analysis of covariance (ANCOVA) (Tabachnick and Fidel 2006:20) to examine the effect of year on clutch size while controlling for nest initiation date because clutch size in many passerines decreases over the season (Klomp 1970; Drent and Daan 1980; Martin 1987), and this pattern is present in Black-capped Vireos (Graber 1961; Gryzbowski 1995; Campomizzi et al. 2013; Locatelli et al. 2016). I used a Chi-square test (Crawley 2014:101–105) with phi ( $\phi$ ) as a measure of effect size (Hojat and Zu 2004) to compare hatching success between years. I then used ANCOVA (Tabachnick and Fidel 2006:20) to examine the effect of year on brood size, while controlling for clutch size. I excluded parasitized nests from analyses of clutch and brood size because Brown-headed Cowbirds may remove eggs or young from nests (Sealy 1992; Conkling et al. 2012; Peer and Bollinger 2012). I calculated eta-squared ( $\eta^2$ ) (Maher et al. 2013) as a measure of effect size for all ANCOVA tests.

*Nest Fate.*—I used Fisher’s exact tests (Crawley 2014:105–107) with odds ratios (OR; McHugh 2009) to examine inter-annual differences in the frequency of nest abandonment, brood parasitism, and nest failure. In addition, I developed *a priori* models that included year and nest vegetation characteristics (i.e., nest height, distance to edge, average cover, average concealment, overstory height, nest substrate) to examine their effects on nest success. I coded nest substrate as a binary variable with 1 = dominant substrate (i.e., Ashe juniper in 2011 or Texas persimmon in 2012; Chapter 2) and 0 = other substrate (i.e., all other year-substrate combinations).

I used a generalized linear model approach to determine which models best predicted nest success. Models included a null model, main effects models for year and



each of the vegetation characteristics, and additive models with year and each vegetation characteristic. I also examined additive models with nest substrate and each of the other vegetation characteristics with year as a covariate. Nest substrate was correlated with distance to edge ( $r = -0.16$ ,  $P = 0.03$ ) and substrate height ( $r = 0.23$ ,  $P \leq 0.01$ ). As such I excluded additive models that included substrate and these metrics from the final model set. I ranked models of nest success using Akaike's Information Criterion adjusted for small samples sizes ( $AIC_c$ ) (Burnham and Anderson 2002:49–97). I considered models with  $\Delta AIC_c < 2.0$  to be equally possible and used Akaike weight ( $w_i$ ) to determine the most plausible model from among the possible models.

In addition to looking at nest success, I also examined at daily nest survival. I developed *a priori* models that included year, parasitism, nest stage (i.e., egg or nestling), and linear and quadratic terms representing day of season because these are known to impact daily nest survival in vireos and other species (e.g., Conkling et al. 2012; Skagen and Yackel Adams 2012). To account for differences in season length between years, I considered the first day of each season to coincide with the earliest nest initiation date in that year. I used the logistic exposure method described by Shaffer (2004) to estimate daily nest survival. This method examines survival during the intervals between nest checks and accounts for varying interval lengths (i.e., exposure). I excluded all nests with unknown fates ( $n = 4$ ) from analyses, but I included abandoned nests, which I considered as failed during the interval that I first suspected abandonment. I also included nests parasitized by Brown-headed Cowbirds, but because I dispatched all cowbird young on discovery, it was impossible to know with certainty how much

longer parasitized nests would have survived with cowbird young. That said, Brown-headed Cowbird nestlings often outcompete nestlings of their hosts (e.g., Dearborn 1998), and host nestlings that are small relative to cowbird nestlings have higher mortality (Kilner 2003). Vireos are markedly smaller than Brown-headed Cowbirds, and it is rare that vireos successfully fledge host young from parasitized nests (Tazik 1991; Gryzbowski 1995; Boves et al. 2014). As such, I considered parasitized nests as failed during the interval in which Brown-headed Cowbird eggs hatched.

Models included a null model, main effects models for all variables, and additive models with combinations of these variables. Again I ranked models of daily nest survival using Akaike's Information Criterion adjusted for small samples sizes ( $AIC_c$ ) (Burnham and Anderson 2002:49–97) and considered models with  $\Delta AIC_c < 2.0$  to be equally possible. I used Akaike weight ( $w_i$ ) to determine the most plausible model from among the possible models. Using the best fit model, I then calculated the mean predicted daily survival rates for each year and their associated 95% confidence intervals.

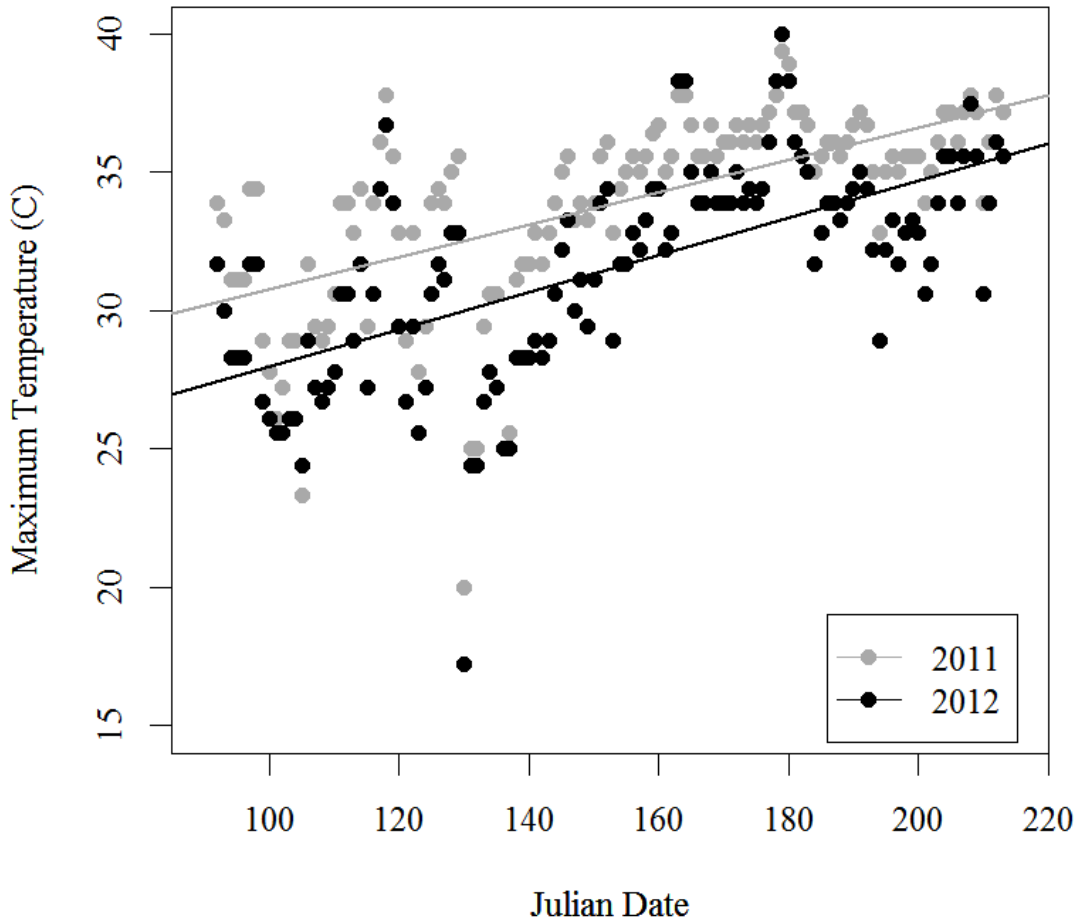


Figure 22. Seasonal trends in maximum daily temperature (°C) at Dobbs Run Ranch, Edwards County, Texas from April–July in 2011 and 2012. Lines show linear models of increasing temperature over time in both years.

## RESULTS

### Annual Variation in Weather

Weather varied significantly between the years of my study, with the 2011 vireo breeding season being warmer and drier than the 2012 breeding season. Maximum daily temperature varied statistically among years ( $t_{241,4} = 4.85, P \leq 0.01, d = 0.62$ ). Yet, mean

maximum daily temperature in either year (i.e.,  $34 \pm 4$  °C [range 20–39 °C] in 2011 and  $32 \pm 4$  °C [range 17–40 °C] in 2012) was comparable to the average maximum temperature for the region during the months of vireo breeding (NCEI 2016). Daily maximum temperature increased over time within years (2011:  $F_{1,120} = 59.66$ ,  $r^2 = 0.33$ ; 2012:  $F_{1,120} = 80.78$ ,  $r^2 = 0.40$ ) (Fig. 22). There was 54% less rainfall in the months leading up to the 2011 breeding season (13.1 cm) (Fig. 23) than during the corresponding months the following year (28.4 cm) (Fig. 23). Similarly, 56% less rain fell during the 2011 season (10.7 cm) (Fig. 24) than during the 2012 season (24.5 cm) (Fig. 24). Rainfall in 2011 was approximately half of the seasonal average for the region (NCEI 2016). However, monthly precipitation totals (Fig. 24) belied the true conditions of the 2011 breeding season during which 61% (6.48 cm) of the total rainfall occurred on a single day (May 12), and mean precipitation of other rainfall events ( $n = 7$ ) was low ( $0.61 \pm 0.44$  cm). Monthly PDSI values for the study period better captured the extreme difference in rainfall between years. PDSI ranged from -6.02 to -3.98 (extreme conditions) in 2011 and -2.65 to -2.03 (moderate conditions) in 2012 (NCEI 2016).

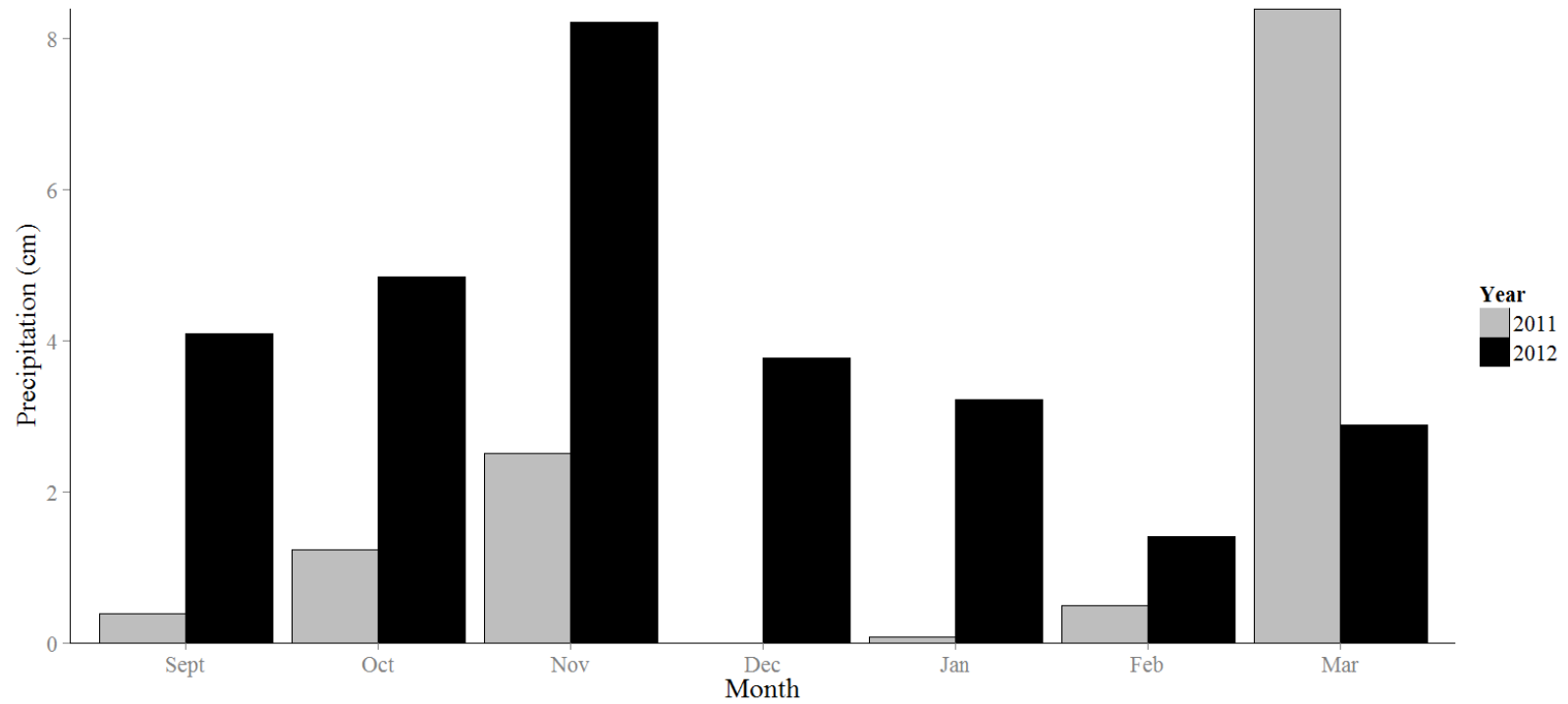


Figure 23. Total monthly precipitation at Dobbs Run Ranch, Edwards County, Texas during the seven months preceding the 2011 and 2012 Black-capped Vireo (*Vireo atricapilla*) breeding seasons.

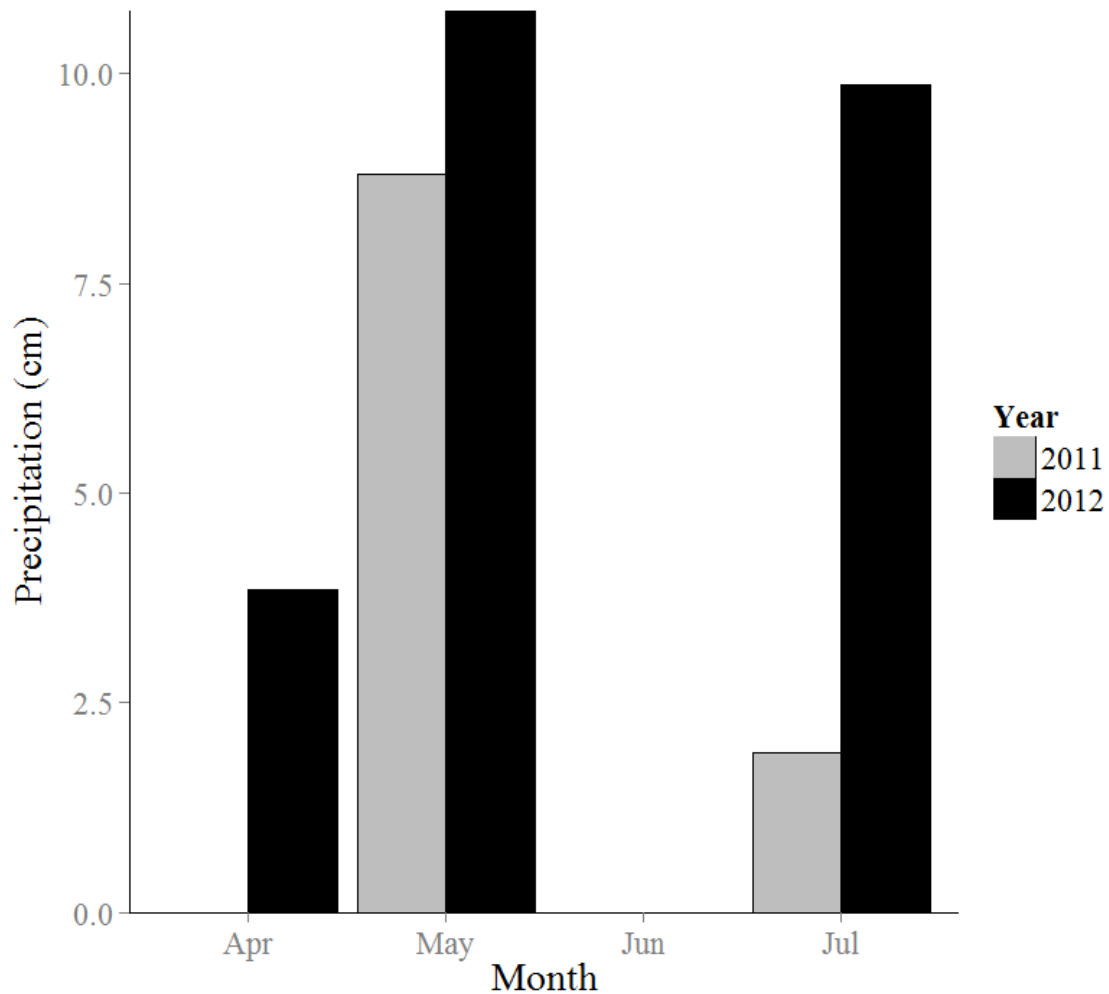


Figure 24. Total monthly precipitation at Dobbs Run Ranch, Edwards County, Texas during the 2011 and 2012 Black-capped Vireo (*Vireo atricapilla*) breeding seasons.

### **Territory Pairing and Fledging Success**

I mapped and monitored 148 vireo territories in 2011 and 132 vireo territories in 2012. The percentage of males within these territories that successfully paired was 82% ( $n = 121$ ) in 2011 and 99% ( $n = 130$ ) in 2012. The number of paired males differed significantly between years (Fisher's exact test  $P \leq 0.01$ , OR = 14.40). Twelve percent ( $n$

= 15) of paired males successfully fledged host young in 2011, and 78% ( $n = 102$ ) of paired males successfully fledged host young in 2012. Brown-headed Cowbirds parasitized nests in two of territories that successfully fledged vireo young in 2011. Because I interfered with Brown-headed Cowbird young at nests in both territories, it is unclear what fate these territories may have otherwise experienced. Excluding these territories reduced the percentage of paired males that successfully fledged young in 2011 to 11% ( $n = 13$ ). The number of paired males that fledged young varied significantly between years (Fisher's exact test  $P \leq 0.01$ , OR = 29.66).

### **Nesting Phenology, Clutch Size, and Brood Size**

I located and monitored 186 active nests in 2011 ( $n = 74$ ) and 2012 ( $n = 112$ ). Through backdating, I determined the earliest initiation dates were 18 April in 2011 and 1 April in 2012. There were nests each year for which I was unable to determine initiation dates; however, based on nest observations and the known nesting phenology of vireos (described in Gryzbowski 1995), it is unlikely that nest initiation of monitored nests did not occur prior to these dates in either year. Mean nest initiation date overall was 9–10 May  $\pm$  19 days, but variation in the timing of breeding was significantly different among years ( $t_{153.96} = 3.45$ ,  $P < 0.01$ ,  $d = 0.56$ ). On average, vireos laid their clutches 11 days later in 2011 than they did in 2012 (2011:  $\bar{x} = 16$  May  $\pm$  14 d, 2012:  $\bar{x} = 5$  May  $\pm$  23 d). Note, however, that later breeding in 2011 was not a function of later arrival on the breeding grounds as vireos arrived in similar numbers in both years starting in late March (pers. obs.). The mean initiation dates of the earliest 20% of nests

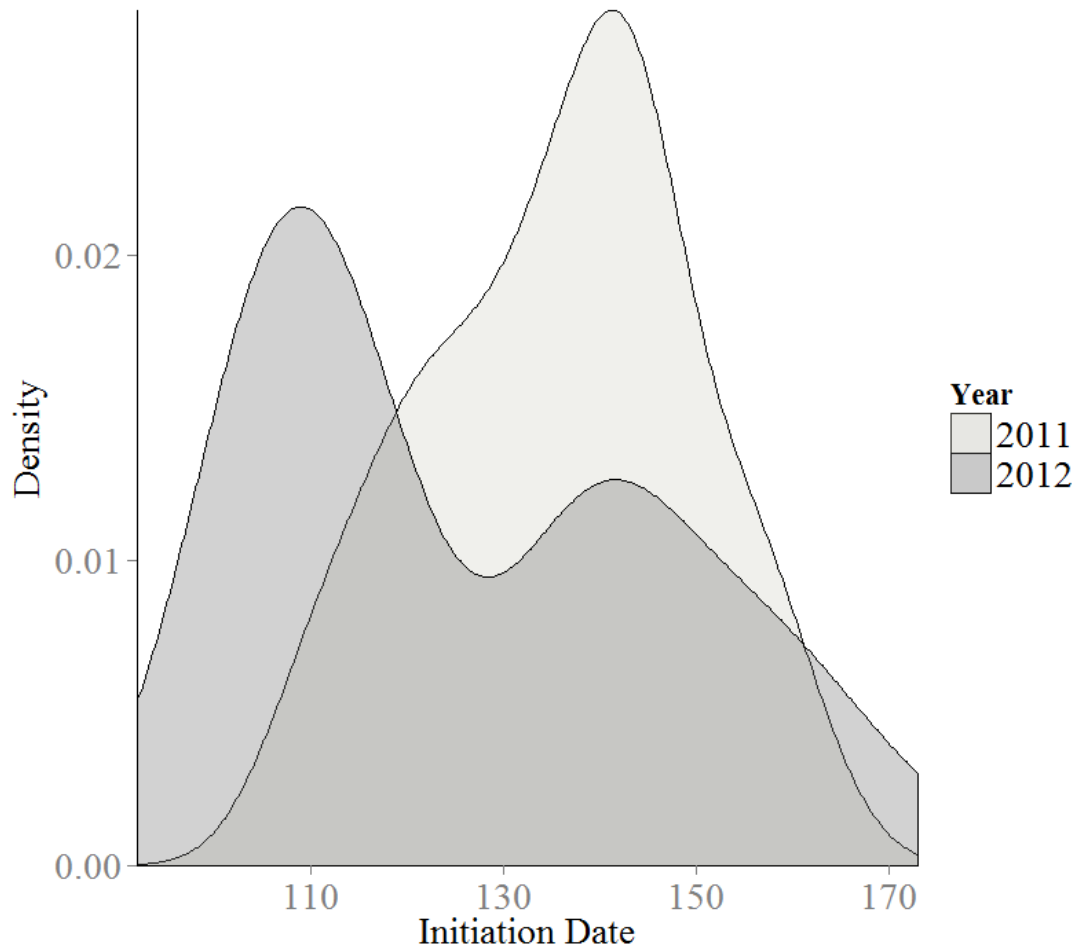


Figure 25. Density plot showing initiation dates (Julian) of Black-capped Vireo (*Vireo atricapilla*) nests within the study site at Dobbs Run Ranch, Edwards County, Texas in 2011 and 2012.

were 25 April and 11 April in 2011 and 2012, respectively. The mean initiation dates of the latest 20% of nests were 4 June 2011 and 6 June 2012. Based on these values, season length was 39 days in 2011 and 56 days in 2012, a difference of 17 days.

Because vireos often re-nest after failed nesting attempts or lay a second clutch after successful attempts (Gryzbowski 1995), mean nest initiation dates alone may not accurately reflect the difference in the timing of breeding between years. To better



demonstrate inter-annual differences, I graphed nest initiation dates by year (Fig. 25). In 2012, nest initiation dates had a bimodal distribution, with the second peak likely corresponding with re-nesting or second brood attempts. It is difficult, however, to limit analyses only to first nesting attempts because many failed attempts go unfound (Mayfield 1975), and observed nests may unknowingly be re-nesting attempts. That said, three nests in 2011 and 19 nests in 2012 were known re-nesting attempts following a prior nest failure, and seven nests in 2012 were attempts to produce a second brood after an earlier nest fledged; only one pair successfully double brooded in 2012.

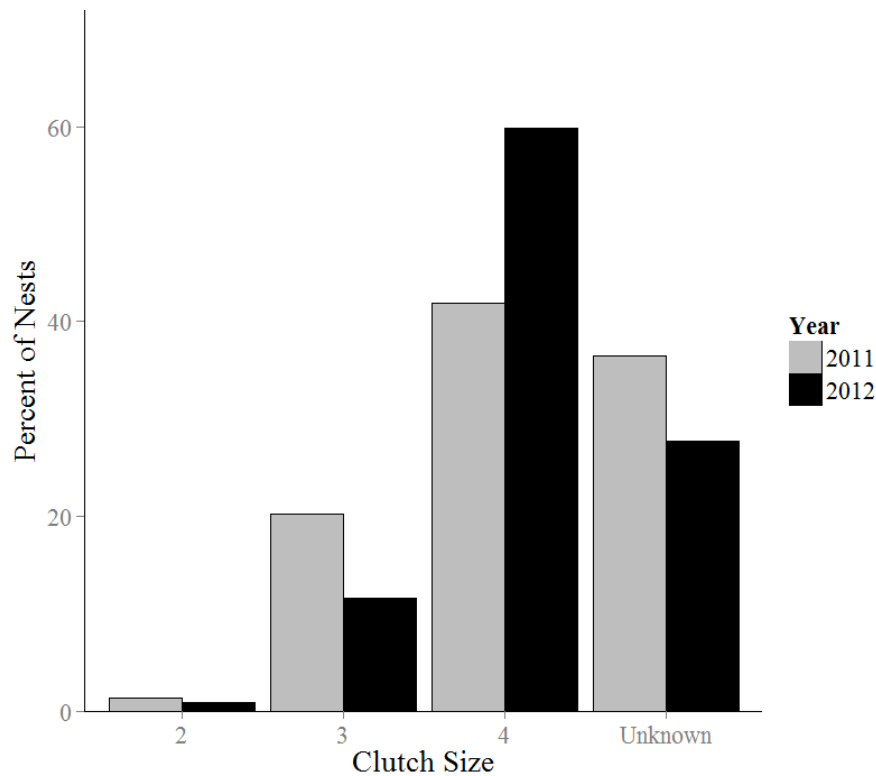


Figure 26. Clutch size by year for Black-capped Vireos (*Vireo atricapilla*) nesting within the study site at Dobbs Run Ranch, Edwards County, Texas (2011–2012).

Overall clutch size ranged from 2–4 eggs with a mean of  $3.75 \pm 0.47$  eggs ( $n = 128$  nests). Annual means were  $3.64 \pm 0.53$  eggs in 2011 and  $3.81 \pm 0.42$  eggs in 2012. Proportionally, there were more 3-egg clutches in 2011 than in 2012 ( $F_{1,110} = 5.62$ ,  $P = 0.02$ ) (Fig. 26), but there was no effect of year on the clutch size of nests after controlling for nest initiation date ( $F_{1,109} = 2.57$ ,  $P = 0.11$ ,  $\eta^2 = 0.02$ ). Fifty-one percent ( $n = 30$ ) and 67% ( $n = 70$ ) of non-parasitized vireo nests survived to hatching in 2011 and 2012, respectively ( $X^2_1 = 3.14$ ,  $P = 0.08$ ,  $\phi = 0.14$ ). Overall brood size ranged from 1–4 young (Fig. 27) with a mean of  $3.48 \pm 0.79$  young. The annual mean was  $3.18 \pm 0.91$  in 2011 and  $3.61 \pm 0.70$  in 2012. After for controlling for clutch size, there was no effect of year on brood size ( $F_{1,68} = 1.27$ ,  $P = 0.26$ ,  $\eta^2 = 0.01$ ) suggesting no differences in egg hatchability.

### **Nest Fate**

Vireos abandoned 9% ( $n = 7$ ) of nests in 2011 and 6% ( $n = 7$ ) in 2012 (Fisher's exact test  $P = 0.57$ , OR = 1.56). Brown-headed Cowbirds parasitized 20% ( $n = 15$ ) and 7% ( $n = 8$ ) of nests in 2011 and 2012, respectively (Fisher's exact test  $P = 0.01$ , OR = 3.28). It was rarely possible to determine the exact dates that Brown-headed Cowbirds parasitized nests, but I only found two parasitized nests before mid to late May. Nest failure (including abandonment and parasitism) occurred in 85% ( $n = 60$ ) of nests in 2011 and 56% ( $n = 65$ ) of nests in 2012 (Fisher's exact test  $P < 0.01$ , OR = 3.83). I placed cameras at 12 nests in 2011 and captured six predation events (i.e., ants [2], gray fox [1; *Urocyon cinereoargenteus*], Western Scrub-jay [2; *Aphelocoma californica*],

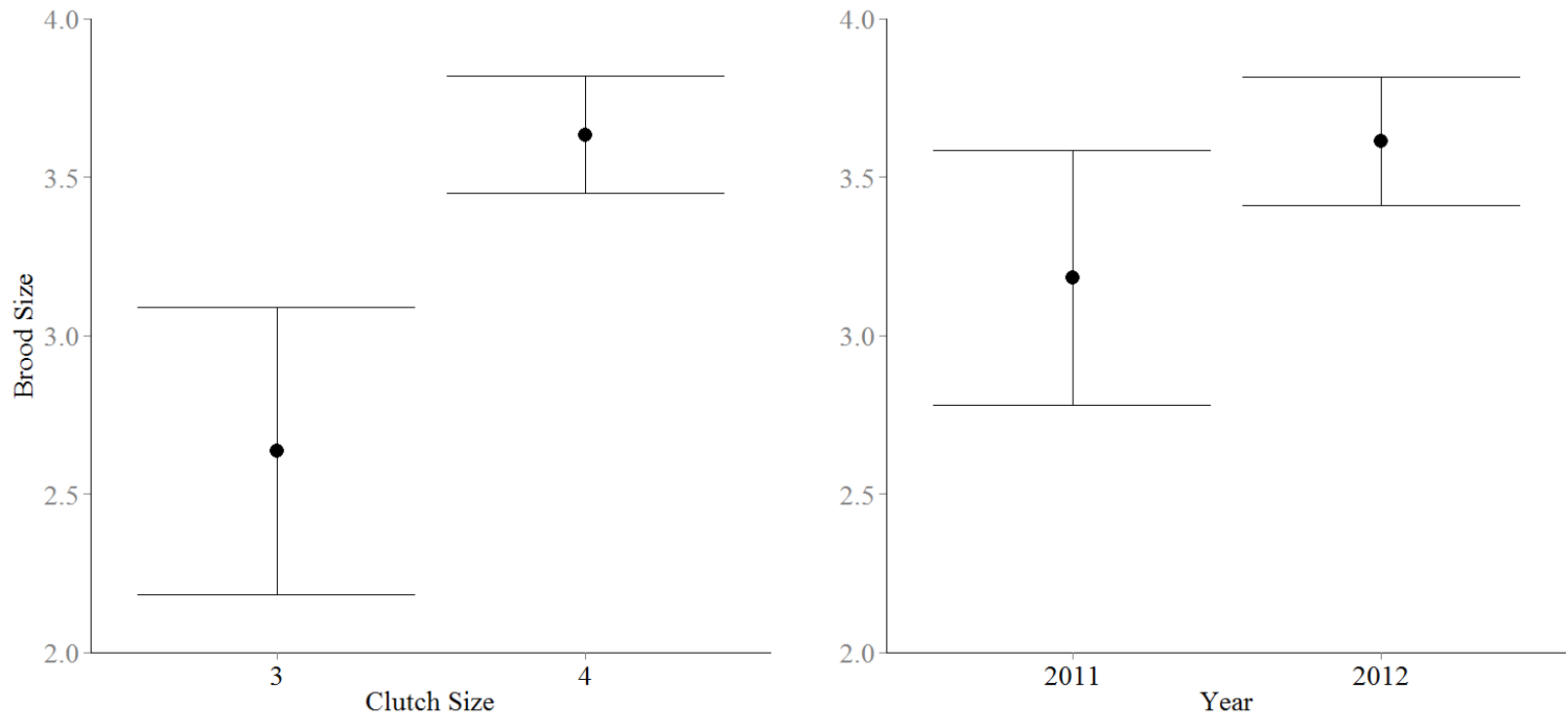


Figure 27. Brood size (i.e., number of eggs hatched) as a function of clutch size and year for Black-capped Vireo (*Vireo atricapilla*) nests in 2011 and 2012 within the study site at Dobbs Run Ranch, Edwards County, Texas.

Table 6. Models of nest success of Black-capped Vireos (*Vireo atricapilla*) monitored at Dobbs Run Ranch, Edwards County, Texas in 2011 and 2012.

Model	$K^a$	Log likelihood	$AIC_c^b$	$\Delta AIC_c^c$	$w_i^d$
Year + Nest Substrate + Average Concealment	4	-98.44	205.61	0.00	0.60
Year + Nest Substrate + Overstory Height	4	-99.49	207.71	2.10	0.21
Year + Nest Substrate	3	-101.50	209.42	3.81	0.09
Year + Nest Substrate + Nest Height	4	-101.02	210.77	5.16	0.05
Year + Nest Substrate + Average Cover	4	-101.41	211.55	5.94	0.03
Year + Average Concealment	3	-103.51	213.44	7.83	0.01
Year + Overstory Height	3	-103.57	213.57	7.96	0.01
Year	2	-106.08	216.38	10.77	0.00
Year + Substrate Height	3	-105.21	216.86	11.25	0.00
Year + Nest Height	3	-105.34	217.11	11.50	0.00
Nest Substrate	2	-108.67	221.56	15.95	0.00
Average Concealment	2	-110.18	224.57	18.96	0.00
Overstory Height	2	-112.36	228.94	23.33	0.00
Null	1	-113.51	229.09	23.48	0.00
Substrate Height	2	-112.61	229.43	23.82	0.00
Nest Height	2	-112.91	230.04	24.43	0.00
Average Cover	2	-113.02	230.25	24.64	0.00
Distance to Edge	2	-113.33	230.88	25.27	0.00
Year + Average Cover	3	-112.56	231.55	25.94	0.00
Year + Distance to Edge	3	-112.81	232.04	26.43	0.00

<sup>a</sup> Number of parameters in the model

<sup>b</sup> Akaike's Information Criteria corrected for small sample size

<sup>c</sup> AICc relative to best fit model

<sup>d</sup> Model weight

Brown-headed Cowbird [1]). In 2012, I placed 19 cameras and captured three predation events (Brown-headed Cowbird [1], greater arid-land katydid [2; *Neobarrettia spinosa*]). Apparent nest success was 15% in 2011 compared to 41% in 2012. The additive effects of year, nest substrate, and average concealment best predicted overall nest success (Table 6). The predicted probability of nest success increased with increasing nest concealment in 2012 but was lower with use of the most common nesting substrate (i.e., Texas persimmon; Chapter 2) that year (Fig. 28). The same pattern was also evident, but not significant, in 2011 due to widely overlapping confidence intervals (Fig. 28). I did not consider nest initiation date in models of nest success because this information was missing for a number of nests, especially from 2011. However, nest initiation date was most likely a factor influencing nest success. After graphing only those nests with known nest initiation dates (Fig. 29), I found that nests initiated during the first six weeks of 2012 fledged young more often than nests initiated after the sixth week (May 6–12). That same week corresponded to the greatest percentage of nest success in 2011; however, nesting earlier in 2011 did not confer the same benefit it did in 2012.

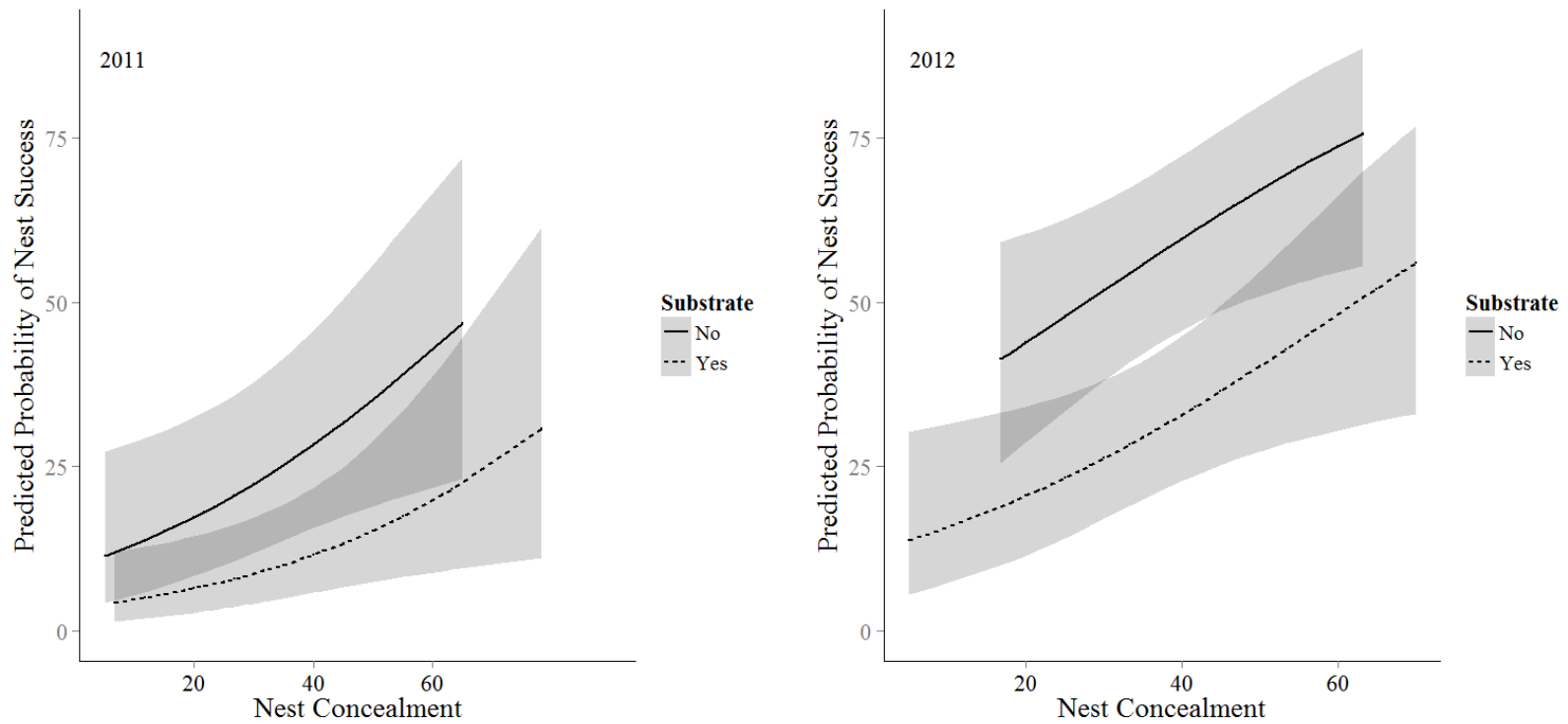


Figure 28. Predicted probability of Black-capped Vireo (*Vireo atricapilla*) nest success (with 95% confidence intervals) as a function of nest concealment and use of common nesting substrate at Dobbs Run Ranch, Edwards County, Texas in 2011 and 2012. Vireos that nested in Ashe juniper (*Juniperus asheii*) in 2011 are coded yes as are those that nested in Texas persimmon (*Diospyros texana*) in 2012. Vireos using other substrates in either year are coded no.

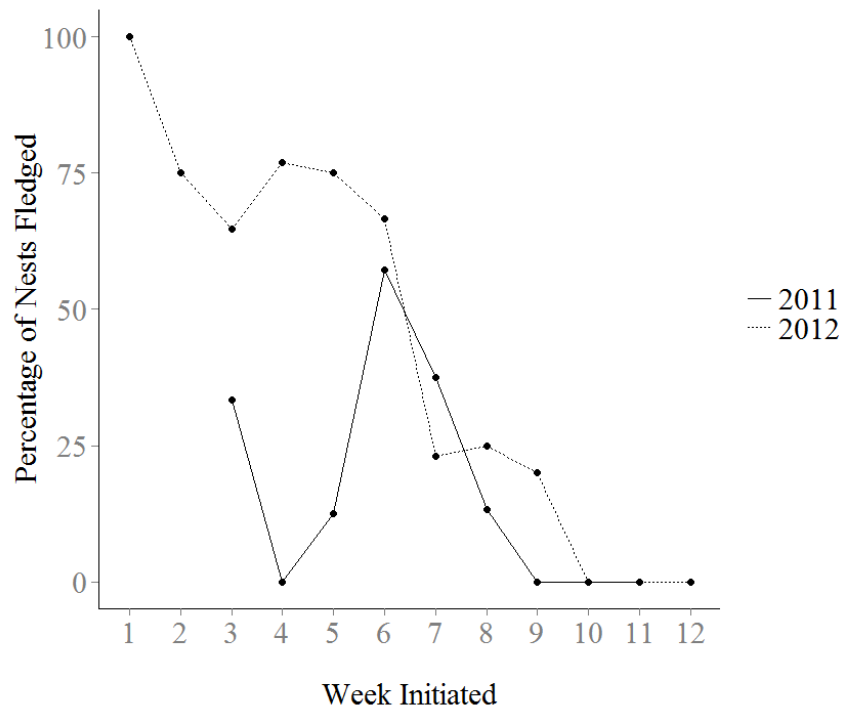


Figure 29. Percentage of Black-capped Vireo (*Vireo atricapilla*) nests that fledged by initiation date across the breeding seasons of 2011 and 2012 at Dobbs Run Ranch, Edwards County, Texas. Week 1= April 1–7, Week 6 = May 6–12, Week 12 = June 17–23.

Table 7. Models of daily nest survival of Black-capped Vireo (*Vireo atricapilla*) nests monitored at Dobbs Run Ranch, Edwards County, Texas in 2011 and 2012.

Model <sup>a</sup>	K <sup>b</sup>	Log likelihood	AIC <sub>c</sub> <sup>c</sup>	ΔAIC <sub>c</sub> <sup>d</sup>	w <sub>i</sub> <sup>e</sup>
Year + Day <sup>2</sup> + Nest Stage	4	-349.72	708.18	0.00	0.46
Year + Day <sup>2</sup>	3	-351.83	710.09	1.92	0.18
Year + Day + Nest Stage	4	-350.86	710.46	2.28	0.15
Year + Day	3	-352.33	711.09	2.92	0.11
Year + Day <sup>2</sup> + Parasitism	4	-351.58	711.89	3.71	0.07
Year + Day + Parasitism	4	-352.16	713.04	4.87	0.04
Day	2	-358.76	721.72	13.55	0.00
Day <sup>2</sup>	2	-359.18	722.57	14.39	0.00
Year + Parasitism + Nest Stage	4	-367.18	743.09	34.91	0.00
Year + Nest Stage	3	-368.44	743.31	35.13	0.00
Nest Stage	2	-371.10	746.41	38.23	0.00
Year + Parasitism	3	-371.10	746.63	38.45	0.00
Year	2	-371.29	746.80	38.62	0.00
Parasitism	2	-371.44	747.09	38.92	0.00
Null	1	-373.22	748.51	40.33	0.00

<sup>a</sup> Abbreviations for explanatory variables as follows: Day = day of season, Parasitism = nests parasitized by Brown-headed Cowbird (*Molothrus ater*)

<sup>b</sup> Number of parameters in the model

<sup>c</sup> Akaike's Information Criteria corrected for small sample size

<sup>d</sup> AIC<sub>c</sub> relative to best fit model

<sup>e</sup> Model weight

Daily nest survival was best predicted by year, quadratic day trends, and nest stage (Table 7). Daily nest survival was lower in 2011 and decreased over time within seasons (Fig. 30). Survival was also lower during the nestling stage than during egg-laying or incubation (e.g., egg stage). Mean predicted daily nest survival was 93% ( $\pm 3$ ) in 2011 and 95% ( $\pm 4$ ) in 2012.



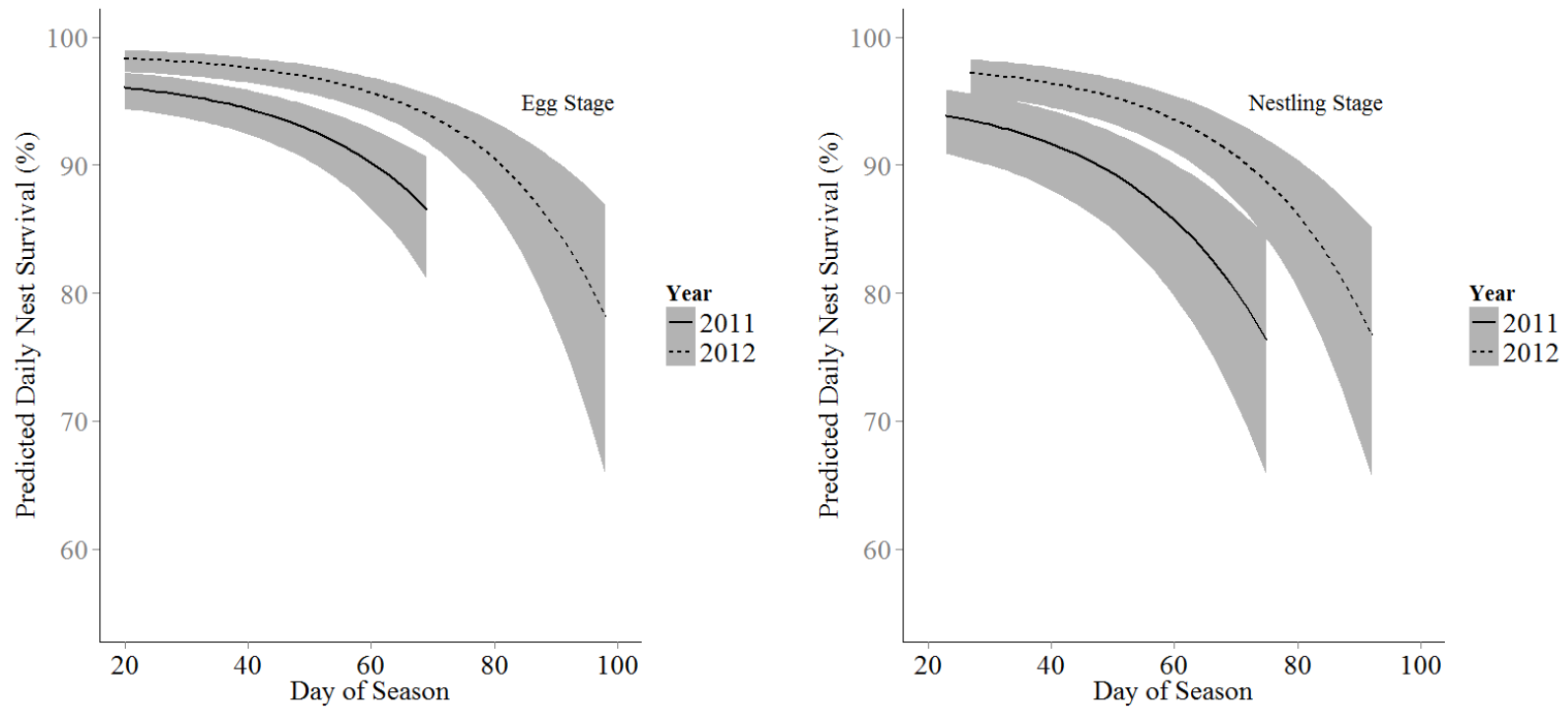


Figure 30. Predicted daily nest survival of Black-capped Vireo (*Vireo atricapilla*) nests as a function of quadratic day trend and year within the study site at Dobbs Run Ranch Edwards County, Texas in 2011 and 2012.

## **DISCUSSION**

I identified significant differences in several measures of reproductive behavior and productivity in vireos during two years of varying drought intensity. Specifically, vireos had reduced pairing and fledging success and later nest initiation during the dry 2011 season compared to the wetter 2012 season. Additionally, they experienced greater nest parasitism, lower overall nesting success, and lower daily nest survival in 2011 than in 2012. I attributed the observed variation to differences in cumulative rainfall both before and during the breeding seasons because the differences between years were substantial and because others have observed similar reproductive behaviors and consequences for this (Smith et al. 2012) and other species (e.g., Grant and Boag 1980; Boag and Grant 1984; Morrison and Bolger 2002) during dry periods. However, I recognize that differences between years could have resulted from annual variation in other factors (e.g., carry-over effects [Harrison et al. 2010], sex or age composition [Oro et al. 2010]).

Morrison and Bolger (2002) suggested that reproductive success was food-mediated in dry years and predator-mediated in wet years. Food availability can influence many of the metrics I measured in this study, each of which contributes to overall productivity. For example, pairing success is low when food resources are limited (e.g., Probst and Hayes 1987; Burke and Nol 1988; Gibbs and Faaborg 1990). Though I did not measure food abundance during this study, there is evidence to support the hypothesis that arthropod availability was lower in 2011 than in 2012—especially at the start of the season. Arthropod biomass is positively correlated with primary

productivity (e.g., Bell 1985), which is driven by rainfall (Noy-Meir 1973; Sala et al. 1988), and many researchers have reported reduced arthropod biomass during drought (e.g., Bell 1985; Morgan 2012). The density of arthropods, particularly of Lepidopteran larvae—an important component of the vireo's diet (Graber 1961)—is typically greatest on oak species in April and on Ashe juniper in May (Quinn 2000; Morgan 2012; Marshall et al. 2013). Vireos arrive on the breeding grounds in late March and usually begin nesting in April (Gryzbowski 1995), but no rain fell at my study site in March or April of 2011, and most deciduous oak species, and many live oaks, were leafless during this period (pers. obs.). It is plausible that the lack of foliage on oak species early in the 2011 season resulted in reduced food availability, which contributed to the differences I observed between years.

For birds, as with most animals, the timing of breeding activities has important consequences for reproductive success (Clutton-Brock 1988; Nilsson 1999). To maximize fitness, birds must engage in reproductive activities on a schedule that coincides with the environmental conditions best suited for each stage of breeding. For example, pairs must anticipate when adequate food resources will be available to meet nestling demands and then initiate nest-building and egg-laying accordingly. Thus, they must use environmental cues, such as photoperiod (light), rainfall, temperature, vegetation phenology, or current food availability to predict future conditions (Farner and Follett 1979; Marshall and Cooper 2004; Bourgault et al. 2010). Timing reproductive activities with rainfall is a common behavioral strategy for birds inhabiting arid regions (e.g., Ohmart 1969; Zann et al. 1995; Lloyd 1999). Immelmann (1963,

1965), for instance, observed Zebra Finches (*Taeniopygia guttata*) copulating within the first few hours of a rainfall event following months of drought, and Lloyd (1999) noted that rainfall stimulates breeding activities in several South African arid-zone species. Vireos at my study site initiated clutches considerably later in 2011 than in 2012. The mean nest initiation date in 2011 (May 16) was within a few days of the single greatest day of rainfall that season (May 12), suggesting that, as with other species, rainfall stimulated breeding in vireos.

Though delayed nest initiation may be adaptive when food resources are limited, but there are still consequences for annual fecundity in birds. For example, clutch size declines seasonally in many bird species (Klomp 1970; Drent and Daan 1980; Martin 1987). In this study, I found no difference in clutch size after accounting for nest initiation date. However, birds that nested later in the season did lay fewer eggs than those that nested earlier. Similarly, fecundity may be determined by the number of nesting attempts, which is a function of season length. Later nest initiation at my study site in 2011 corresponded to a shortened breeding season that year, and I observed fewer re-nesting attempts and lower overall fledging success within territories.

Predation is the leading cause of nest failure in birds (Ricklefs 1969; Martin 1993; Schmidt and Whelan 1999), and, in many systems, predation increases over time within seasons putting nests initiated later at greater risk (Best and Stauffer 1980; Marvil and Cruz 1989; Schaub et al. 1992). Predation accounted for the majority of nest failure at my study site, and daily nest survival decreased with season day in both years. Snakes and birds are among the most frequent predators of vireo nests (Stake and Cimprich

2003; Conkling et al. 2012). Snakes are more active later in the summer in Texas (Sperry et al. 2008), and Brown-headed Cowbirds were more active at my study site beginning in May. Later nest initiation in 2011 likely exposed a higher proportion of nests that year to snakes and Brown-headed Cowbirds leading to the differences in apparent nest success between years.

Vegetation at nest-sites is an important component of habitat for breeding breeds that can reduce their likelihood of being depredated or parasitized (Martin 1993), and at my study site, nests with greater concealment had a greater probability of success than less concealed nests. Average concealment at the nest, however, did not differ among years (Chapter 2), so this feature is not likely responsible for the inter-annual difference in nest success that I observed. Parasitism was low at my site in 2012 ( $n = 8$ ), and I did not have an adequate sample size to examine the incidence of parasitism in relation to characteristics of nest vegetation. I did, however, identify a significant difference in the rate of parasitism between years, with greater parasitism during 2011.

Nest substrate was also important in predicting nest success in 2012, but not in the way I had expected. In 2011, vireos overwhelmingly placed their nests in Ashe juniper. Texas persimmon was the most commonly selected nest substrate the following year. I assumed vireos selected these species because they offered the greatest likelihood of success under the conditions of each year. However, in 2012, vireos nesting in Texas persimmon actually had a lower probability of nest success than those nesting in other substrates. Selection of Ashe juniper as a nest substrate is uncommon within vireo habitat (Bailey and Thompson 2007). Under drought conditions it may have offered

greater cover than deciduous species that were leafless, while still being of lower quality than deciduous nest substrates. Martin (1993) observed a similar pattern with McGillivray's Warblers (*Geothlypis tolmiei*) which had lower nest success in evergreen fir trees following drought. Vireos may have selected Texas persimmon more frequently in 2012 because it was the most common deciduous species available rather than for any characteristics associated with the species that offered an advantage as a nest substrate over other species. I did not measure species composition, however, so I can only speculate.

Though it is not possible to control abiotic weather events, wildlife managers can plan for their inevitability by understanding the responses of species of conservation concern and identifying ways to minimize reproductive consequences. In this study, vireos had lower overall productivity under drought but showed resilience the following year with increasing rainfall. Historically, low rainfall and extreme drought events have persisted for more than one year, and global climate models predict drought will become more frequent and intense (e.g., Watson et al. 1998; Seager et al. 2007). Jiang and Yang (2012) predict that temperatures will steadily increase in Texas through the 21<sup>st</sup> century, with warmer weather corresponding to drier conditions. My study provides only a snapshot of the consequences of drought to nesting vireos, and longer term studies are needed to understand how population persistence (or species recovery) might be affected if climate predictions are realized and the frequency and severity of drought increases.

Food supplementation could help to maintain populations of species of conservation concern during dry conditions. Studies suggest that provisioned birds nest

earlier and have greater nesting success (reviewed in Martin 1987). However, this is not a realistic solution for managing wild, insectivorous birds, like vireos. Current management recommendations include the selective removal of Ashe juniper within vireo habitat to help maintain the vegetation structure preferred by vireos (Campbell 1995). However, this practice may not be necessary or beneficial to vireos in drier portions of the range. Morgan (2012) indicated that Ashe juniper was an important foraging substrate for vireos, and I showed that vireos depend on Ashe juniper as a nest substrate under drought conditions. As such, retaining an appropriate level of Ashe juniper within vireo habitat may provide vireos with necessary resources when conditions are dry. Morgan (2012) suggested that Ashe juniper cover between 10–25% is sufficient to meet the foraging needs of vireos, but research is still needed to determine what levels might be most beneficial for vireos nesting in dry areas.

The total number of vireo nests parasitized by Brown-headed Cowbirds at my site was low. However, in 2011, parasitism accounted for 20% of nests found. Managers typically try to limit parasitism to <10% of vireo nests annually (e.g., USFWS 2000; Kostecke et al. 2005). During drought years, however, greater Brown-headed Cowbird removal efforts (e.g., shooting, trapping) may be warranted. However, it is important to plan activities so as to be most effective. March and April are most effective months to run cowbird traps that remove locally-breeding individuals from the population before they become reproductively active (Summers et al. 2006). Cowbird trapping is less effective in May—when most nest parasitism takes place (Smith 2011, Summers et al. 2006)—and shooting is recommended (Summers et al. 2006). It is possible that locally-

breeding Brown-headed Cowbirds are no longer attracted to grain-baited traps in May, because they switch to an insectivorous diet once they become reproductively active (Ankney and Scott 1980). If insect abundance is lower during drought years, continued trapping during May might be beneficial alone or in addition to shooting.



## CHAPTER IV

### CONCLUSIONS

My results suggest that habitat selection by Black-capped Vireos (*Vireo atricapilla*; hereafter vireo) is similar under moderate and extreme drought conditions. Vireos prefer early successional shrub habitat with open spaces and short vegetation (Graber 1961; Gryzbowski et al. 1994). Within vireo habitat, these conditions are common on steep (Graber 1961), southern facing slopes (Shaw 1989; LCRA 2007; Benson and Benson 1990, 1991), as these slopes tend to have less soil due to rainfall runoff and other factors (McCool et al. 1997) and may facilitate microclimates and edaphic conditions conducive to the vegetation structure preferred by vireos. At a landscape scale, vireos may have selected my study site because the topography present (i.e., southerly-facing slopes with  $\leq 10\%$  steepness) enabled suitable vegetation growth. Weather conditions can erode potential nesting and foraging vegetation on slopes in some locations (e.g., Cummings 2006; Smith 2011); however, vireos at my study site selected slopes as they were available both years, suggesting that differences in vegetation across slope-types and years did not influence selection decisions at smaller scales.

In both years, vireos selected nest-sites with similar vegetation characteristics that were consistent with nest-sites across the vireo's breeding range (Smith 2011; Conkling et al. 2012; Pope et al. 2013a, b). However, vireos at my study site overwhelmingly placed nests in Ashe juniper (*Juniperus asheii*) under the extreme

drought conditions of 2011. Others have indicated that vireos are considerably less likely to place nests in Ashe juniper (Bailey and Thompson 2007). However, Ashe juniper is a drought-tolerant, evergreen species (Gilman and Watson 1993) that can access deep water sources when surface soils are dry (Jackson et al. 1999), and at my study site, Ashe juniper was one of the few species with consistently leafy, green foliage in 2011. Vireos may prefer deciduous nest substrates (Bailey and Thompson 2007), but my research suggests that Ashe juniper can offer potential nest-sites with characteristics similar to those found in deciduous substrates, thus increasing opportunities for nesting when conditions are dry.

Though vireos were able to locate nest-sites in Ashe juniper during drought, they still experienced lower reproductive success in 2011 some of which may have resulted from different reproductive investment between years. Fewer vireos paired during the dry conditions in 2011 compared to the wetter 2012 season. Those that did pair in 2011 delayed nesting until mid-May. Birds often use environmental cues to predict future conditions (Farner and Follett 1979; Marshall and Cooper 2004; Bourgault et al. 2010), and timing reproductive activities with rainfall is a common behavioral strategy for birds inhabiting arid regions (e.g., Ohmart, 1969; Zann et al., 1995; Lloyd 1999). The mean nest initiation date for vireos at my study site in 2011 (May 16) was within a few days of the single greatest day of rainfall that season (May 12), suggesting that, as with other species, rainfall stimulated breeding in vireos.

Delayed nest initiation may be adaptive when food resources are limited, however, there are still consequences for annual fecundity in birds. For example, clutch

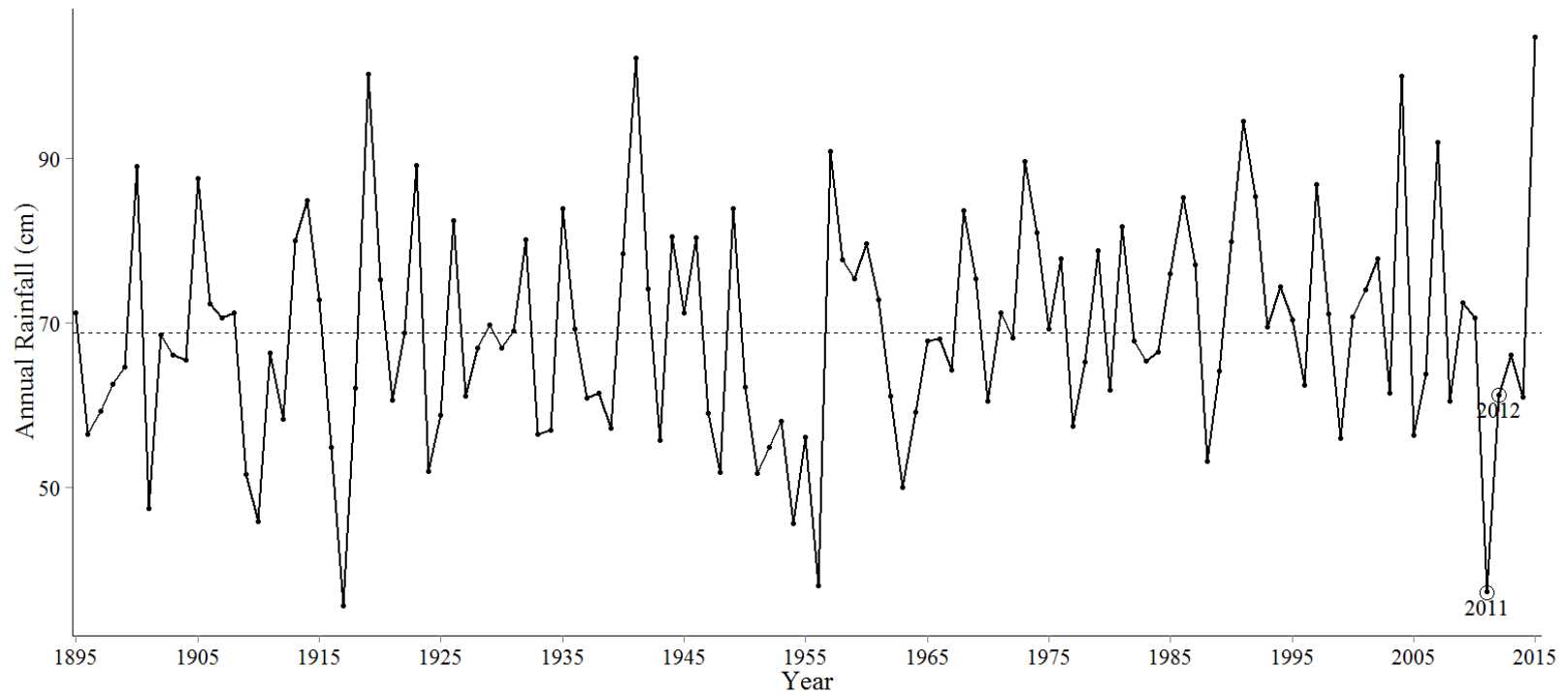


Figure 31. Annual precipitation in Texas from 1895–2014. Dashed line indicates average annual precipitation in Texas from 1901–2000 (considered baseline). Data were obtained from National Centers for Environmental Information (NCEI 2016) at graphed using the statistical program R version 3.2.2. The years corresponding to the study described herein (2011 and 2012) are circled.

size declines seasonally in many bird species (Klomp 1970; Drent and Daan 1980; Martin 1987). In this study, I found no difference in clutch size after accounting for nest initiation date, but birds that nested later in the season did lay fewer eggs than those that nested earlier. Similarly, fecundity may be determined by the number of nesting attempts, which is a function of season length. Later nest initiation at my site in 2011 corresponded to a shortened breeding season that year, and I observed fewer re-nesting attempts and lower overall fledging success within territories. Additionally, nests initiated later may experience higher predation or brood parasitism (Best and Stauffer 1980; Marvil and Cruz 1989; Schaub et al. 1992). Vireo nests in 2011 were less successful and depredated and parasitized more frequently than nests in 2012. Snakes and Brown-headed Cowbirds are among the most frequent predators and brood parasites at vireo nests (Stake and Cimprich 2003; Conkling et al. 2012), and both tend to be more active later in the season (e.g., Sperry et al. 2008; pers. obs.) increasing the risks for birds who delay nesting.

Though it is not possible to control abiotic weather events, wildlife managers can plan for their inevitability by understanding the responses of species of conservation concern and identifying ways to minimize the consequences. In this study, vireos had lower overall productivity under drought but showed resilience the following year with increasing rainfall. Historically, low rainfall and extreme drought events have persisted for multiple years (Fig. 31), and global climate models predict drought will become more frequent and intense (e.g., Watson et al. 1998; Seager et al. 2007). Jiang and Yang (2012) predict that temperatures will steadily increase in Texas through the 21<sup>st</sup> century,

with warmer weather corresponding to drier conditions. My study provides only a snapshot of the consequences of drought to nesting vireos, and longer term studies are needed to understand how population persistence (or species recovery) might be affected if climate predictions are realized and the frequency and severity of drought increases.

Food supplementation can help maintain populations of some species of conservation concern during dry conditions. Studies suggest that food provisioned birds nest earlier and have greater nesting success (reviewed in Martin 1987). However, this is not a realistic solution for managing wild, insectivorous birds, like vireos. Current management recommendations for vireos include the selective removal of Ashe juniper within vireo habitat to help maintain the vegetation structure preferred by vireos (Campbell 1995). However, this practice may not be necessary or beneficial to vireos in drier portions of their range. Morgan (2012) indicated that Ashe juniper was an important foraging substrate for vireos, and I showed that vireos depend on Ashe juniper as a nest substrate under drought conditions. As such, retaining an appropriate level of Ashe juniper within vireo habitat may provide vireos with necessary resources when conditions are dry. Morgan (2012) suggested that Ashe juniper cover between 10–25% is sufficient to meet the foraging needs of vireos, but research is still needed to determine what levels might be most beneficial for vireos nesting in dry areas.

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removal efforts (e.g., shooting, trapping) may be warranted. However, it is important to plan activities so as to be most effective. March and April are most effective months to run cowbird traps that remove locally-breeding individuals from the population before they become reproductively active (Summers et al. 2006). Cowbird trapping is less effective in May—when most nest parasitism takes place (Smith 2011, Summers et al. 2006)—and shooting is recommended (Summers et al. 2006). It is possible that locally-breeding Brown-headed Cowbirds are no longer attracted to grain-baited traps in May, because they switch to an insectivorous diet once they become reproductively active (Ankney and Scott 1980). If insect abundance is lower during drought years, continued trapping during May might be beneficial alone or in addition to shooting.

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